



ELSEVIER

Palaeogeography, Palaeoclimatology, Palaeoecology 149 (1999) 1–14

PALAEO

A mechanism to explain the preservation of leaf litter lenses in coals derived from raised mires

Robert A. Gastaldo^{a,*}, James R. Staub^b

^a Department of Geology, Auburn University, Auburn, AL 36849-5305, USA

^b Department of Geology, Southern Illinois University at Carbondale, Carbondale, IL 62901, USA

Received 20 November 1996; revised version received 22 May 1997; accepted 8 June 1998

Abstract

Leaves and other non-woody canopy parts are rarely preserved in coals. Although the pH of pore waters within peat swamps is usually relatively low (≤ 3.5), providing geochemical conditions that would promote preservation after burial, shed canopy parts may remain at the air–soil interface for periods of up to several months prior to burial by additional organic detritus. Leaf half-life in tropical forests has been reported to range from several weeks to months, depending upon species histology. During this time of exposure on the forest floor, catabolic (internal enzymatic), fungal, bacterial and root degradation, as well as saprophagous scavenging, act upon the least resistant parts to promote decay into hemic and sapric macerals. It is unusual, then, to find well-preserved leaves in peats or coals. When such accumulations are encountered, either permineralized in coal balls or duripartically preserved in lignites, the bedded leaves generally are spatially isolated. Several explanations have been proposed to account for such fossil Lagerstätten that require temporal changes in accumulation or degradation rates. Neither of these mechanisms is required to account for such accumulations. Bedded leaves, showing minimal evidence of subaerial exposure and degradation, have been recovered at depth from a vibracore taken 1 km into the interior of a peat swamp in the Rajang River delta, Sarawak, East Malaysia. Evidence is provided to indicate that such accumulations form within peat substrate depressions resulting from the displacement of rootstocks as trees either die and fall over, or are blown down in severe storms. These localized, acidic water-filled pools act as a natural buffer to the degradation of fallen canopy parts that accumulate therein. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: taphonomy; plant taphonomy; leaf litter; coal geology; peat mires

1. Introduction

The occurrence of well-preserved leaves of various systematic affinities and a variety of histological architectures begins in coals of Carboniferous age. The anatomical and morphological details of

such permineralized and duripartic leaves have provided paleontologists with a wealth of information about major peat-forming vegetation through time (e.g., lycopsids — Chaloner and Meyer-Berthaud, 1983; ferns — Lesnikowska and Gaultier, 1991; cordaites — Rothwell and Warner, 1984; Costanza, 1985; pteridosperms — Reihman and Schabillon, 1976a,b, 1978; gymnosperms — Pigg and Taylor, 1990; Basinger, 1991; angiosperms — Riegel and

* Corresponding author. Tel.: +1 334 844 4282; Fax: +1 334 844 4486; E-mail: gastara@mail.auburn.edu

Blickwede, 1996). Speculation has arisen as to the possible mechanism(s) by which such preservation could occur. Cohen and Spackman (1977), with reference to topogenous peats such as those found in the Florida Everglades, stated that peats with a high frequency of leaves could be preserved only in the presence of standing water. In raised mires, where standing water is generally absent, increased rates of biomass production, inhibited rates of degradation, or the absence of a well-developed detritovore community have been invoked to explain the preservation of these ancient leaf litters (e.g., Robinson, 1990; Raymond and Cutlip, 1996). Even early diagenetic permineralization, before any decay processes had begun, has been proposed to explain the presence of permineralized tissues showing exceptional details (Scott and Rex, 1985).

Vibracores extracted from ombrogenous peat swamps in the Rajang River delta, Sarawak, East Malaysia, provide evidence for a mechanism responsible for the preservation of delicate tissues in these

peat accumulations. Based upon a comparison of characteristics of forest floor litter and leaves recovered from the subsurface, in conjunction with reported litter fall, decay rates, and pore-water chemistry, a mechanism is proposed to account for leaf-litter Lagerstätten in peats throughout the stratigraphic record.

2. Locality and methods

The Rajang River delta is located in the East Malaysian state of Sarawak on the island of Borneo (Fig. 1). It is a tropical, peat-dominated coastal plain system that occurs in an embayment formed by the folded Mesozoic and Cenozoic strata of the Central Borneo Massif (Staub and Esterle, 1993). The massif consists of a limited amount of Tertiary igneous rocks and is dominated by Cretaceous to Eocene-age folded, fine-grained siliciclastic sedimentary rocks and limestones, some of which have

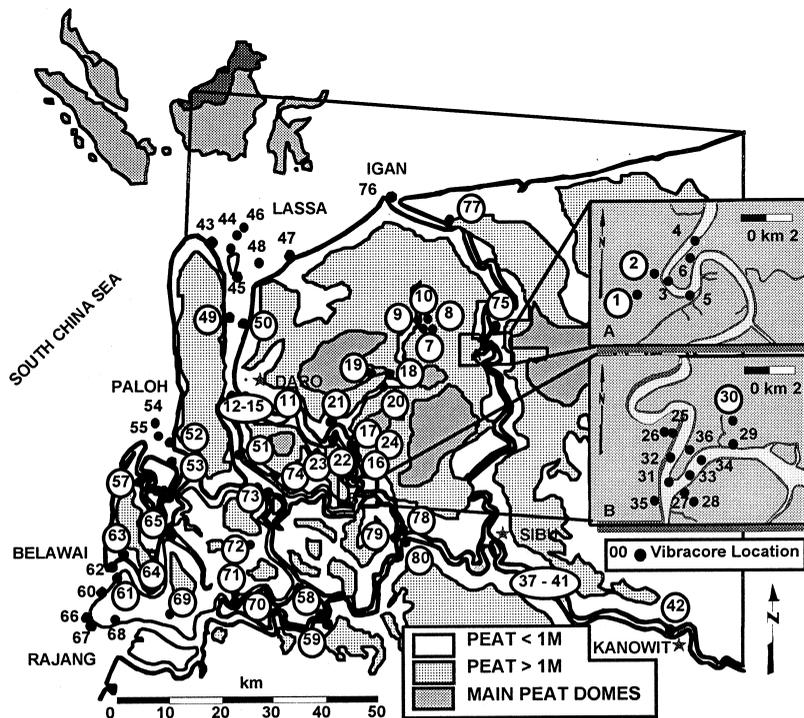


Fig. 1. Locality map of the Rajang River delta, Sarawak, East Malaysia, on which the distribution of peat accumulations are mapped. Vibracore locations are numbered. Peat water chemistry (Table 1) was analyzed at sites 1 and 2 (insert A); bedded leaf litter was recovered from site 30 (insert B; Figs. 3 and 4).

experienced low grade metamorphism (Lam, 1988). The delta plain and river valley upstream cover an area of approximately 6900 km² and include three physiographic regions, an alluvial valley floodplain (approximately 400 km²), an ‘abandoned’ tidally flushed and actively accreting rectilinear delta plain (combined area approximately 6500 km²). The main trunk of the Rajang River cuts a relatively straight path through the Central Borneo Massif but begins to bifurcate in a rectilinear pattern at the approximate position of the town of Sibuluan. The resultant main rivers are, from the southwest to north, the Rajang, Belawai, Paloh, Lassa, and Igan. Chemical analyses of tributary waters were taken during the 1992 and 1993 field seasons.

Tropical vegetation covers all available sites of colonization and provides biomass to accumulating sediments. Riparian vegetation in the distal reaches of the delta is composed of marine to brackish water-fed mangroves (*Rhizophora*, *Avicennia*, *Sonneratia*) and *Nipa*; the proximal areas are fringed by dipterocarp forests and cultivated lands (Scott, 1985). Peat swamp forests occur adjacent to riparian vegetation and are dominated by dipterocarps (Anderson and Müller, 1975), in which several ecological catenas have been identified (Anderson, 1961, 1983), each of which is related to the thickness of underlying peat. Peats greater than 1 m thick cover about 50% of the delta plain surface, 80% of the adjacent coastal plain, and 75% of the alluvial valley. Maximum peat thickness exceeds 20 m, and all peats have accumulated within the past 7000 to 7500 years (Staub and Esterle, 1994). Chemical analyses of near-surface peat pore-waters were undertaken in 1992.

Eighty vibracores, ranging from less than 3 m to greater than 7 m in length, were recovered throughout the delta. Vibracores were extracted from a variety of barforms in fluvial- and tidal-dominated river channels (including black-water channels), ombrogenous peat swamps and their underlying soils, tributary mouth bars, and beaches. Fourteen vibracores were extracted from peat swamps, recovering not only the histosol but also the subjacent clastic soils (Fig. 1). Field descriptions of peat followed that of Esterle (1989). Subsurface peat samples were taken for palynological (Gastaldo et al., 1994), palynofacies (Gastaldo et al., 1996; Pedentchouk, 1997), macrofloral (Gastaldo and Staub, 1996) and ¹⁴C investigations;

subjacent soils were sampled and analyzed for grain-size (conducted at Southern Illinois University at Carbondale). Observations on the quality of surficial leaf litters were made at all sampling sites.

Leaf samples were isolated from subsurface bedded litters and prepared for histological sections in the Department of Botany and Microbiology, Auburn University. Sections were stained with periodic acid-Schiff’s (PAS; a stain specific for carbohydrates including starch, cellulose, and complex polysaccharides found in extracellular ground substances), PAS-aniline (naphthol) blue black (ABB; specific for carbohydrates and proteins), and acid fuchsin (AF)-toluidine blue O (TBO; specific for RNA, DNA, etc.), and mercuric bromophenol blue (MBPB; specific for proteins).

3. Results

3.1. Empirical observations on forest floor litters

Peat-swamp forest-floor litters reflect the heterogeneous nature of the dense canopy and subcanopy jungle vegetation. Canopy and subcanopy trees and understory plants adjacent to each coring site provide litter to the forest floor. The peat surface is characterized by a mixture of semi-decomposed bark, twig, leaf, root, and fruit components, held together by a dense mass of woody material. Forest floor litters accumulate above this surface to an average thickness of 3–5 leaves. The maximum number of leaves observed in any litter mat was 8. The ‘freshest’, least degraded leaves are found at the surface, whereas the most degraded and skeletonized leaves occur near the bottom of the mat (Fig. 2). Completely degraded and unrecognizable litter occurs beneath the thin leaf mat. In most instances, all but the uppermost leaves in any leaf mat are sewn together by intergrown fungal hyphae. These fungal hyphae not only proliferate along leaf surfaces but also penetrate the leaves, promoting and accelerating biotic degradation of leaf tissues. Leaves at the bottom of the leaf mat accumulation may be affected by fine, horizontally growing roots that originate from the rooting zone.

Leaves and other canopy detritus generally lie on top of the rooted horizon, above degraded peat and the water table. The water table within these raised



Fig. 2. Leaves taken from forest floor litter illustrating stages of half-life deterioration. Leaf on far left shows areas of pre-depositional insect damage with accompanying decay. Note that areas outside of the insect damage show no signs of deterioration, characterizing the appearance of 'freshest' leaves encountered. Leaf on near left illustrates progressive deterioration of parenchymatous tissues in the lower and upper areas. Note that deterioration is unevenly distributed in the leaf. Specimen on near right is translucent with the loss of most internal cellular structure and the presence of fungal infestation (darkened areas). Leaf on far right is partially skeletonized; only the resistant lignified vascular tissue remains in the lower part. Leaves photographed under transmitted light. (Scale in mm.)

mires fluctuates within 10 cm of the peat surface and, because the rate of organic accumulation is high, a stilted water table is found (Staub and Esterle, 1994). It is within and just above this vadose zone that there are numerous, dense rooting structures. In most areas, the surface of the peat and overlying leaf mat is generally moist due to high humidity and meteoric waters (ever-wet conditions), rather than due to perched ground water. During the wet season, though, the surface of the peat may be covered by shallow (< dm) standing waters. The pH of near-surface ground waters is acidic, ranging from 4.1 in a peat adjacent to a channel margin setting (vibracore 2) to 3.6 approximately 1 km inland (vibracore 1; Table 1). CO₂ values are significantly higher than distributary channel waters, whereas O₂ values vary in our limited sample suite.

3.2. Empirical observations on a subsurface peat and leaf mat

Peat textures range from sapric to fibric, with the latter texture the most commonly encountered.

Sapric peats are comprised of a matrix of dark yellowish-brown (10 YR 4/2 Munsell color) to reddish (10 R 3/4) and grayish brown (5 YR 3/2) amorphous degradational products in which there is little to no visual evidence of fibrous plant remains. Pendentchouk (1997), though, has found that the matrix of sapric peat has a statistically higher proportion of structured organic matter (SOM) than the matrix of hemic peats from these mires. Fibric peat, similar in coloration, is distinguished by the presence of dispersed or concentrated fibric, macroscopic plant remains. Rarely, though, are large woody canopy detritus or bedded leaf litters encountered in the subsurface. In our vibracore sample suite, all of the vibracored peat bodies contained woody and/or non-woody root remains.

Subsurface, bedded leaf litter was recovered from only one vibracore (core 30; Figs. 1 and 3). Vibracore 30 is composed of almost 5 m of muck, clayey peat, and peat that overlie an olive gray (5Y 4/1), mottled, rooted silt (5.76 Φ; sorting coefficient 1.16; skewness 0.25; $N = 3$). The peat is dark reddish brown (10 R 3/4) to moderate brown (5 YR 4/4–3/4) in color, and

Table 1

Field measurements of water chemistry in the Rajang River delta

	Near-surface peat waters			Igan distributary		Lassa distributary		Paloh distributary	
	Core Site 30	≥1 km inland (N = 6)	100 m inland (N = 8)	surface waters (N = 1)	–17 m depth (N = 1)	surface waters (N = 3)	–11 m depth average (N = 3)	surface waters (N = 1)	–8 m depth (N = 1)
pH	4.0	4.1	5.6	6.2	6.7	6.7	6.7	6.5	6.7
Fe (mg/l)	<1	2.2	2.9	<1	<1	<1	<1	<1	<1
Sulfite (mg/l)	10	23.2	11.3	30	18	15.3	13.3	16	14
Acidity (CaCO ₃) (mg/l)	90	76.7	47.1	40	25	35	24.8	10	8
CO ₂ (mg/l)	69	60.2	34.6	17	19	8.3	11.3	7	7
O ₂ (mg/l)	0.9	1.3	2.04	6.5	5.5	4.9	5.3	5	4.6



Fig. 3. Vibracore 30 illustrating the transition from poorly sorted, rooted silt to muck, clayey peat, and hemic peat. Note the position of a woody vertical root and interval from which bedded leaf litter was recovered. (Scale is in cm, with each decimeter marked on the meter stick.)

coarse hemic with vertical rooting structures present. Rooting structures range from large woody to fine parenchymatous. The leaves occur in the uppermost part of the core in a 15 cm interval that was more than 0.5 m below the forest floor (some peat was removed from the mire's surface before vibracoring). The leaves are laminated one atop another and, when disaggregated from the peat, the leaves show no signs of catabolic degradation or skeletonization (Fig. 4). There were no fungal hyphae found penetrating these leaves, although fungal hyphae are present in the peat matrix.

There are two preservational grades to leaves recovered from this interval, and these represent the degradational extremes. Three leaves have been recovered during disaggregation of the interval that could only be recognized as such because of the presence of a 'cuticular bag'. In these conditions, the leaves are amorphous due to the degradation of all internal cellular components. All other leaves recovered from the peat matrix are well-preserved. Structural rigidity is found throughout the lamina. In transverse section (Fig. 4B), all cellular components are preserved including thick-walled upper and lower epidermis, multi-storied and thick-walled palisade parenchyma, and thin-walled mesophyll parenchyma. Lacunae in the mesophyll reflect original architecture (there is some distortion due to sectioning) and do not appear to have formed by lysis. Xylem elements and sclerenchymatous cells are well preserved. Cell walls are intact and there is no evidence for fungal penetration in all leaf sections examined.

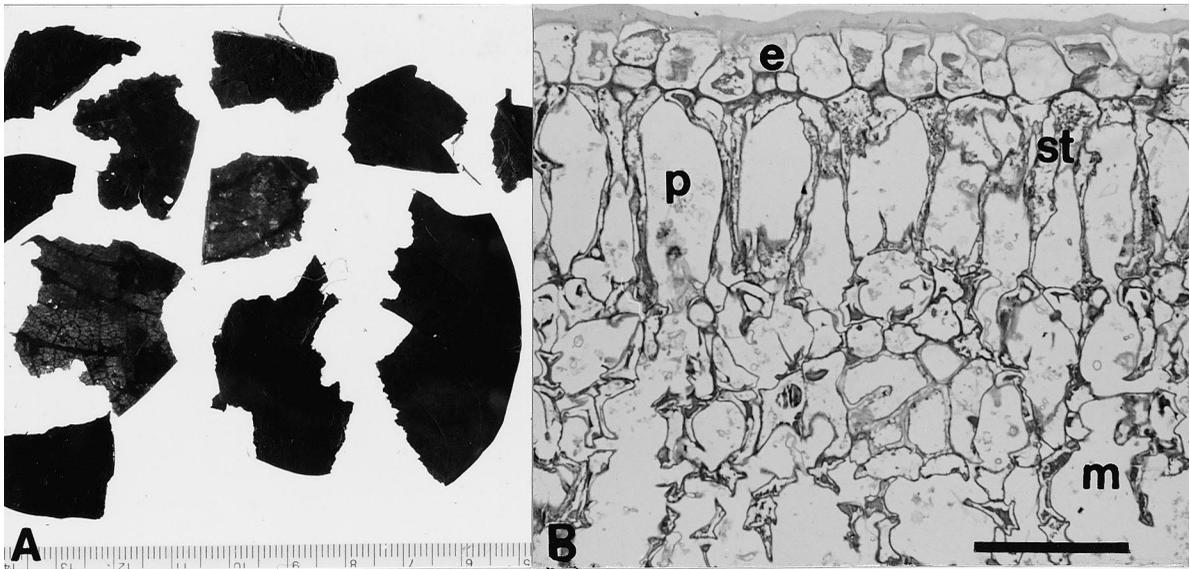


Fig. 4. (A) Leaf fragments recovered from interval of bedded leaf litter. Note that several pieces display pre-depositional insect damage and slight deterioration of internal cell structure (as indicated by transparency), but most leaves are opaque and comparable to the 'fresh' leaves of Fig. 2. (Leaves photographed under transmitted light; scale in mm.) (B) Photomicrograph of leaf transverse section showing structurally intact cuticle, epidermis (*e*), palisade parenchyma (*p*) with residual starch (*st*), and aerenchymatous mesophyll (*m*). Note that several mesophyll cell walls are broken as a result of sectioning. (Scale bar is 50 μm .)

Stained leaf sections reveal that carbohydrates are still present in the form of cellulose (cell walls) and residual starch in some palisade parenchyma (Fig. 4B). Lignin was identified in xylem elements when sections were stained with TBO (lignin and some polyphenols stain green). Proteins were found to be present in several leaf sections that were stained with MBPB.

4. Discussion

Decomposition of leaves in tropical forest floor litters may be influenced by a number of factors including macroclimate, microclimate, soil bacteria, soil nutrients, substrate piece size and quality (Trofymow et al., 1995). Although measurements of leaf area loss provide a more graphical display of degradation (Stout, 1980) and can be correlated to actual weight loss, standardization of decomposition rates has been based around the calculation of the decay constant (k ; Perry, 1994). This decay constant assesses the actual weight loss over time (usually derived from litter bag experiments), and is

expressed as the amount of decay per year. Therefore, a leaf with a decay constant of $k = 1$ will be completely degraded in one year's time. Leaf skeletonization generally accompanies the initial phases of decomposition, when volatiles and less resistant cells and tissues are lost, leaving the more structurally resistant lignin and cuticular components. For the purposes of this discussion, leaf skeletonization (Fig. 2) is assumed to occur during the first half-life.

In tropical forest litters, the decay rates and leaf half lives are highly variable and dependent upon the leaf histology and biochemistry of individual taxa (Table 2). In humid tropical forests, k -values have been reported that vary between 1 and 4 (Olson, 1963; Cuevas and Medina, 1988), although k -values as high as 7.5 have been reported for isolated species (Bernhard-Reversat, 1972). Other researchers, though, have reported very low decomposition rates on the order of $k = 0.4$ – 0.5 (Fösler and De las Salas, 1976; Irmiler and Furch, 1980; Cuevas and Medina, 1988). These decomposition rates are believed to be the result of low nutritional value of the decomposing litter (Edwards, 1977; Klinge, 1978). In equatorial southeast Asian alluvial

Table 2
Leaf half-life and decay constants from humid tropical forests

Citation	Locality	Vegetation	Depositional setting \pm soil type	Ecoregion and climate ^a	Leaf half-life ^b and decay constant (where available)
Tanner, 1981	Jamaica	Montane rain forest	montane	Humid-tropical	58 weeks
Frangi and Lugo, 1985	Puerto Rico	Montane palm flood plain forest	montane; flood plain	Humid-subtropical	27–44 weeks
La Caro and Rudd, 1985	Puerto Rico	Lower montane evergreen rain forest	montane; 400–600 m elevation	Humid-tropical	4–<32 weeks
Ewel, 1976	Guatemala	Broadleaf forests	alluvial and lacustrine lowlands	Humid-tropical	10 weeks
Nadkarni and Matelson, 1992	Costa Rica	Neotropical montane forest	montane; typic dystandept	Humid-tropical; cool tropics	38 weeks ($k = 0.69$)
Stout, 1980	Costa Rica	Atlantic rain forest	lowland streams and forest floor	Humid-tropical; seasonal tropics	2–>37 weeks
Cornejo et al., 1994	Panama	Tropical moist forest	montane	Humid-tropical; seasonal tropics	12–36 weeks
Cuevas and Medina, 1988	Venezuela	Mixed tropical forest; Tierra Firme	hills of 100 m; oxisols and ultisols	Humid-tropical	20 weeks ($k = 0.58 - -0.50$)
Cuevas and Medina, 1988	Venezuela	Tall Amazon Caatinga	floodplain; spodosols at 100 m	Humid-tropical	34 weeks ($k = 2.3 - -3.8$)
Cuevas and Medina, 1988	Venezuela	Low Bana woodlands	floodplain; spodosols at 100 m	Humid-tropical	52 weeks ($k = 0.22 - -0.44$)
Egunjobi, 1974	Nigeria	Teak forest	dry forest	Humid-tropical	2–32 weeks (season dependent)
Okeke and Omaliko, 1992	Nigeria	Bush fallows, savannah	savannah; ultisol	Humid-tropical	18 weeks ($k = 1.45$)
Burghouts et al., 1992	Sabah	Dipterocarp forest	coastal lowland; ultisol	Humid-tropical	<6 weeks
Anderson et al., 1983	Sarawak	Tropical alluvial forest	podozol	Humid-tropical	7.4–37.5 weeks ($k = 3.50 - -0.69$)
Anderson et al., 1983	Sarawak	Dipterocarp forest	montane	Humid-tropical	15 weeks ($k = 1.7$)
Anderson and Swift, 1983	New Guinea	Tropical forest	continental	Humid-tropical	17 weeks ($k = 1.5$)
Bullock and Khoo, 1969	Malaysia	Dipterocarp forest	hill forest	Humid-tropical	3.1–19 weeks
Gong and Ong, 1983	Malaysia	Dipterocarp forest	coastal lowlands	Humid-tropical	2.5 weeks
Gong and Ong, 1983	Malaysia	Dipterocarp forest	hill forest	Humid-tropical	23.5 weeks ($k = 1.1$)
Edwards, 1977	New Guinea	Rainforest	montane	Humid-tropical	21 weeks
Lu and Lin, 1990	Hainan Island, China	Mangrove	estuarine; inceptisol	Humid-tropical	2–8 weeks

^a Generalized ecoregion and climate after Bailey (1996).

^b Half-life is often determined based upon weight-loss and, hence, it may not reflect directly the state of physical deterioration that can be observed. Some of the half-lives have been calculated from the decomposition rate constants (k) derived from litter bag experiments. As has been demonstrated by Stout (1980), leaf skeletonization accompanies decomposition. By the time biomass half-life is reached, many different leaf types are already skeletonized.

and dipterocarp forests, half-lives have been reported to be as little as a few weeks (Bullock and Khoo, 1969; Burghouts et al., 1992; Lavelle et al., 1993) to more than half a year (Anderson et al., 1983).

Leaf litter fall in the tropics occurs throughout the year (Gong and Ong, 1983; Burghouts et al., 1992), as leaves become non-functional and are physiologically lost. Equatorial forests have been reported to produce total litter fall (including branches) between 9.3 and 10.9 t ha⁻¹ year⁻¹, whereas leaf litter fall has been reported to average 6.7 t ha⁻¹ year⁻¹ (Bray and Gorham, 1964; O'Neill and DeAngelis, 1980). Total fine litter and leaf litter productivity in lowland dipterocarp forests of Peninsular Malaysia range from 7.5 and 5.4 t ha⁻¹ year⁻¹ (Gong and Ong, 1983) to 10.6 and 6.3 t ha⁻¹ year⁻¹ (Ogawa, 1978), whereas Proctor et al. (1983) report values of 8.8 and 5.4 t ha⁻¹ year⁻¹ for lowland dipterocarp forests in Sarawak. There may be a pronounced peak in litter fall when either dry (Gong and Ong, 1983; Madge, 1965), wet (Ogawa, 1978; Proctor et al., 1983), or very windy conditions prevail (Proctor et al., 1983). But, in contrast, Lim (1978) has reported that there is no correlation between rainfall pattern and litter fall in Pasoh, Peninsular Malaysia. This wide variability in plant response or non-response to rainfall patterns is probably related to the systematic heterogeneity and soil characters of the forests investigated. It has been shown in other climatic belts that decomposition rates are dramatically retarded during drought with an accompanying reduction in the number of saprophagous animals (e.g., Williams and Gray, 1974). The effects in the wet tropics are not as well documented.

Canopy litter may also be introduced to the forest floor by trauma (Gastaldo, 1992). Traumatic events in the tropics include rainy-season/monsoonal storms and accompanying high winds, insect infestation, and canopy-dwelling fauna. Although the timing of input to the forest floor as the result of trauma is unpredictable, these events add additional biomass to what is normally contributed through physiological processes.

The residency time of leaves on tropical forest floors is generally short (on the order of weeks) due to bacterial, fungal, and saprophagous (e.g., oribatid mites — Labandiera, 1997; termites — Matsumoto and Abe, 1979) interactions, as well as the adherence

of, and degradation by, fine roots of the underlying superficial root mat (Cuevas and Medina, 1988). This combination results in rapid cellular deterioration and destruction of internal anatomy, the interlocking of leaves via fungal growth, and leaf skeletonization. The superficial root mat captures or extracts (via mycorrhizal associations) nutrients from decomposing litter (Stark and Jordan, 1978). The organic residuum is incorporated into the peat matrix. Biomass and nutrient loss rates in tropical forests have been explained either by an exponential (see: Olson, 1963) or a linear model (Edwards, 1977), depending upon a multitude of interrelated factors. As with leaf litter fall, there appears to be no simple model to account for the observed weight loss in various tropical forests.

Leaf fall patterns in tropical forests are varied. Tropical forests generally do not have one large pulse of leaves entering the system (Stout, 1980), although there have been reports of leaf flushing that correlate with either the wet or dry season (Fogden, 1972; Whitmore, 1983; Leigh and Windsor, 1996). Because there is no temporal change in temperature that may alter the rate of microbial decay (Stout, 1980), the near constant addition of canopy detritus replenishes the leaf litter mat, maintaining its relatively constant thickness of 3–5 leaves throughout the year. In addition, as decay rates are also constant due to prevailing climatic conditions, degraded organic detritus is continually contributed to the peat, accounting for the high accumulation rates as noted in the literature (Anderson, 1983). Therefore, the mechanism(s) responsible for the preservation of pristine leaves (those without signs of cellular catabolism, skeletonization, or fungal penetration) in peat substrates must provide for a bypass of the day-to-day degradation processes operating on the forest floor. In this respect, Cohen and Spackman (1977) were correct when they stated that modern peat with high leaf frequencies and low matrix must have accumulated in standing peat (acidic) water.

Ancient peats (coals) in which high leaf-frequencies have been encountered also must have accumulated in standing water. It is generally accepted, though, that many of these ancient peats that are now economic coals were not rheotropic mires. Rather, many of these peats were either planar or raised mires (McCabe, 1984; Hazeldine, 1989; Cohen and

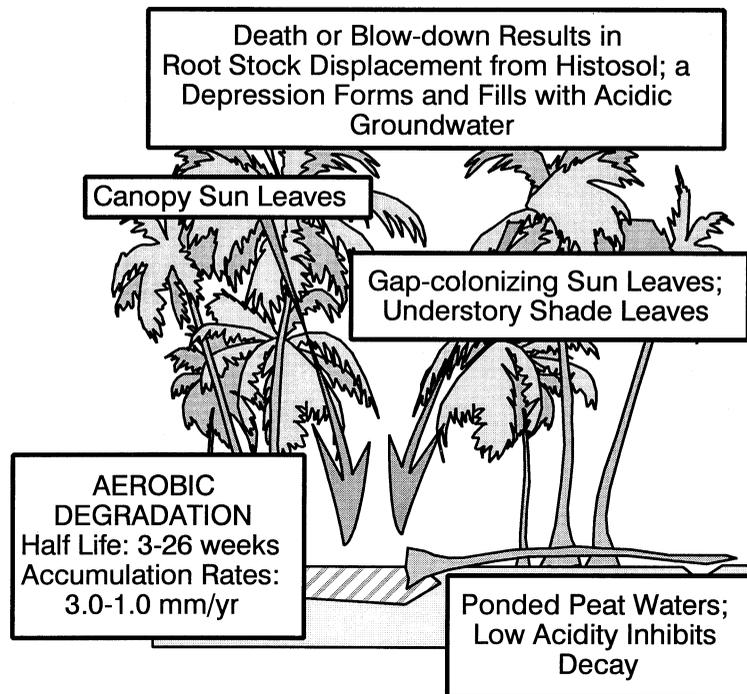


Fig. 5. Illustration of mechanism proposed for preservation of structurally preserved leaves in peat accumulations in raised mires throughout the Phanerozoic.

Stack, 1996), similar to those now forming in south-east Asia and other parts of the globe. Then, in raised mires where the water table rarely is perched above the surface of the peat for extended periods of time (when rainfall exceeds drainage), how is it possible to account for the appearance of such bedded litters in the subsurface?

The accumulation site in which canopy leaves amass as pristine or near-pristine organs in raised or planar mires needs to arrest or retard degradation, inhibit fungal and bacterial growth, and protect the organic matter against saprophagous attack. Ideally, this site requires the same highly acidic waters as noted by Cohen and Spackman (1977) for leaf mats found in the Florida Everglades and Okefenokee Swamp (Cohen, 1973). In raised or planar mires, these waters are only found throughout the year beginning at shallow depth (± 10 cm) beneath the forest floor. Therefore, in order to expose such a site, the densely entwined peat substrate must be naturally excavated to create an acid-water filled depression.

Excavation of a soil substrate naturally occurs when there is tree fall, either as the result of death or

blow-down, and the root bole is displaced (Gastaldo, 1990; Brokaw, 1996; Fig. 5). Seasonal tree fall has been documented in some areas to be correlated with wet-season rainfall patterns (i.e., monthly rainfall and mean monthly percent soil moisture; Oldeman, 1972; Brokaw, 1996). The primary and secondary roots and intertwined soil matrix are ripped from the substrate, leaving a light gap in the canopy and a depression in the soil that may be as deep as 1 meter. In non-histosols, this depression may be temporarily filled with meteoric waters following a rainfall and rise in the water table. In histosols, though, where the water table is already high, the depression fills with acidic pore-waters and provides a small, localized pool in which canopy detritus can not only accumulate but also evade the decay processes operating on the forest floor. Depending upon the depth of the depression and subsequent fluctuations in water table, the canopy parts may remain intact or may be penetrated by rooting structures of subsequent colonizers. Hence, it is not necessary to invoke changes in either the temporary production of biomass (although forest rhythms of leaf flushing will contribute

large quantities of leaves in a short period of time) or changes in decay rates through time to account for the presence of what appear to be forest floor litters in ancient tropical peat swamps.

4.1. Ecological implications

Localized ecosystem disturbance in tropical forests is caused by natural gap formation in the canopy, resulting in temporal alteration of local vegetation and aerial contribution to the forest floor. When canopy gaps form, the number of light-demanding pioneer species increases while the number of shade-tolerant taxa decreases (Brown and Whitmore, 1992; Kennedy and Swaine, 1992). Light-demanding, pioneering plants generally are fast developing taxa that overgrow the disturbed area. In light gaps, the greatest number of seedlings emerge after the first heavy rains with surviving individuals characterized by larger leaf areas and higher growth rates (Garwood, 1996). Chemical and physical leaf characteristics of these taxa are very different from those of the emergent forest trees. The leaves of pioneering taxa are generally more robust (possessing a greater leaf thickness that has been referred to as toughness), have higher tannin and lignin concentrations while, at the same time, have lower nutrient concentrations and C/N quotients (Ewel, 1976; Dantas and Phillipson, 1989). Pioneering tree species also differ in leaf fall and reproductive patterns (Whitmore, 1983). With all of these parameters in mind, it is easy to understand neontological results indicating that mesofaunal degradation is less efficient on the forest floor where pioneering species dominate. It may also be possible that this set of biological conditions may help to explain the hypothesis of Raymond and Cutlip (1996) concerning detritivore guild structure and decomposition efficiency based upon preserved leaf mats in peats through the Phanerozoic.

Reihman and Schabillion (1976a,b) noted that the foliage of several Carboniferous pteridosperm taxa recovered from permineralized peat (coal balls) exhibit xeromorphic features while others exhibit no pronounced xeromorphy. For example, pinnules of two alethopterid taxa (*A. sullivantii* and *A. lesquereuxi*) and one neuropterid taxon (*Macroneuropteris scheuchzeri* — Schabillion and Reihman,

1985; Cleal et al., 1990) are characterized by thick cuticles, a prominent hypodermal layer, sclerotic bundle sheath extensions, sunken stomata, and abaxial multicellular hairs. In addition, stomata are further protected by strongly enrolled pinnule margins. In contrast, xeromorphic characters are absent in pinnules of *Reticulopteris muensteri* and *Laveineopteris rarinerivis* (Reihman and Schabillion, 1978). Cleal and Zодrow (1989) and other authors also have noted the presence of variable cuticular and stomatal features in neuropterid taxa recovered from similar clastic wetland sites. Reihman and Schabillion (1978) concluded that although the aforementioned taxa were components of peat mires, the peats must have accumulated in completely different terrestrial settings. Reihman and Schabillion (1978) believed that those plants exhibiting xeromorphic traits must have grown in brackish coastal regions or in drier upland areas; whereas plants that did not possess these features must have grown in moist environments characterized by high humidity. It must be noted that this apparent disparity in the interpretation for the growth site is related to the idea prevailing at the time that peat accumulated in topogenous low-lying areas and not in planar or raised (ombrogenous) mires. With these taxa occurring in coal ball localities that are interpreted as representing some type of raised mire, the concept of brackish-versus-freshwater and lowland-versus-upland must be discounted to explain the presence and absence of xeromorphic characters in coeval taxa.

Similar anatomical differences have been reported in permineralized *Glossopteris* from a Permian peat at Skaar Ridge, Antarctica (Pigg and Taylor, 1990). Leaves with affinities to *G. angustifolia* are characterized by a narrow-meshed venation pattern, a mesophyll that is aerenchymatous, and a hypostomatic apparatus with undifferentiated subsidiary cells. In contrast, leaves that resemble *G. retifera* possess a coarse venation pattern, a thickened hypodermal layer, and a sunken hypostomatic apparatus in which the guard cells are thickened.

Recently, Arens (1997) has evaluated leaf anatomy in the modern tree fern taxon *Cyathea caracasana*. She demonstrated that epidermal and hypodermal thickness and the palisade:spongy mesophyll ratio were plastic characters, varying developmentally in response to light incidence. Arens (1997)

presents a set of criteria from which to evaluate the potential influence that light incidence may have played in the ontogeny of sun and shade leaves. In general, taxa that possess well-developed, vertically elongate palisade parenchyma are found in sunny sites. They may be components of the canopy or grow as canopy emergents. Taxa that grow in shaded sites generally have greater leaf-surface area, thinner epidermal and hypodermal layers, and an overall decrease in leaf thickness. Arens (1997) compared her finding to the Carboniferous examples noted above and concluded that several of these taxa (i.e., *A. sullivanti*, *A. lesauereuzi*, and *M. scheuchzeri*) preferred growth under sunny conditions, while other taxa preferred shady conditions (e.g., *A. schneideri*) or may have responded plastically to light intensity (i.e., *L. rarinervis*).

By combining the results of Arens (1997) with the preservational mechanism herein proposed, it may be possible to identify the ecological relationships of peat-forming vegetation when leaf taxa co-occur in permineralized or duripartially preserved peat. Leaves that co-occur in a stratigraphically-restricted assemblage (single coal ball, silicified peat horizon, or lenticular bed in lignite), some of which display sun and shade leaf characters, may represent one of two ecological scenarios. These assemblages may represent either the local canopy and understory tier(s) or the canopy/gap-colonizing taxa and understory tier(s). It would be very difficult to differentiate whether or not sun leaves originated from the canopy or gap-forming plants. On the other hand, if an assemblage was found in which only sun leaves of a single taxon were found, this collection would most probably reflect contribution from gap-colonizing plants. Where sun leaves of more than two taxa are encountered in the same leaf mat, these plants may either represent contribution from only gap-colonizing plants or a combination of contemporaneous gap-colonizing and canopy vegetation. Again, differentiating between the two growth strategies would be difficult.

5. Conclusions

The presence of plants with leaves that reflect xeromorphic adaptations in tropical or subtropical/tem-

perate peats, ancient or Recent, is a reflection of their ecological response to light intensity. Their presence in a peat body can be the result of preservation in acidic-water pools that may be generated by canopy-gap formation as a result of root bole displacement. Leaves that enter these isolated, lenticular depressions are sheltered from normal degradational processes operating in the litter mat on the forest floor. The presence of thick, leathery and robust leaves in these assemblages appears to be a reflection of internal (autogenic) spatio-temporal disturbance within the swamp rather than any external (allogenic) change in atmospheric climate. The presence of such taxa may, in many instances, reflect short-term community replacement due to changes in light incidence and intensity rather than long-term community turnover in response to regional or global climate perturbations. It is not necessary to invoke changes in biomass production or accumulation rates or changes in detritivore community structure to explain the presence of leaf mats in ancient peat bodies. Additionally, it is not necessary to believe that early diagenetic mineralization is responsible for the exquisite details found in many permineralized leaves found in ancient peats. Buried leaves that are more than 300 years old (calculated using an average yearly accumulation rate of 2.5 mm/yr) retain all histological features as well as some biochemical markers. By examining leaf histologies of taxa preserved in contemporaneous assemblages, it may be possible to differentiate between the ecological habits of canopy and/or gap-colonizing, gap-colonizing, and understory taxa in ancient peat mires.

Acknowledgements

The authors are indebted to the personnel of the Geological Survey of Malaysia, Sarawak, and the Soils Division, Department of Agriculture, Sarawak, without whom this research would have been impossible. H. Among, H. Rosli bin Sahari, and J. Ward are thanked for field assistance in Sarawak. C.M. Peterson, Department of Botany and Microbiology, Auburn, is thanked for preparation of leaf thin-sections. Financial support was provided by the National Science Foundation (EAR-9111842 to RAG and EAR 9104945 to JRS).

References

- Anderson, J.A.R., 1961. The ecology and forest types of peat swamp forests of Sarawak and Brunei in relation to their silviculture. Unpubl. Ph.D. thesis, University of Edinburgh, Scotland, 117 pp.
- Anderson, J.A.R., 1983. The tropical swamps of western Malaysia. In: Gore, A.P.J. (Ed.), *Mires: Swamp Bog, Fen, and Moor. Ecosystems of the World, Regional Studies 4B*. Elsevier, Amsterdam, pp. 181–200.
- Anderson, J.A.R., Müller, J., 1975. Palynological study of a Holocene peat deposit and a Miocene coal deposit from NW Borneo. *Rev. Palaeobot. Palynol.* 19, 291–351.
- Anderson, J.M., Swift, M.J., 1983. Decomposition in tropical forest. In: Sutton, S.L., Chadwick, A.C., Whitmore, T.C. (Eds.), *The Tropical Rain Forest: Ecology and Management*. Blackwell, Oxford, pp. 287–309.
- Anderson, J.M., Proctor, J., Vallack, H.W., 1983. Ecological studies in four contrasting lowland rainforests in Gunung Mulu National Park, Sarawak. 3. Decomposition processes and nutrient losses from leaf litter. *J. Ecol.* 71, 503–527.
- Arens, N.C., 1997. Plastic response of leaf anatomy to light environment in the tree fern *Cyathea caracasana* (Cyatheaceae) and its application to some ancient seed ferns. *Palaios* 12, 84–94.
- Bailey, R.G., 1996. *Ecosystem Geography*. Springer, New York, 204 pp.
- Basinger, J.F., 1991. The fossil forests of the Buchanan Lake Formation (early Tertiary), Axel Heiberg Island, Canadian Arctic Archipelago: Preliminary floristics and paleoclimate. *Geol. Surv. Can. Bull.* 403, 39–65.
- Bernhard-Reversat, F., 1972. Décomposition de la litière de feuilles en forêt ombrophile de basse Côte-d'Ivoire. *Oecol. Plant.* 7, 279–300.
- Bray, J.R., Gorham, E., 1964. Litter production in forests of the world. In: Cragg, J.B. (Ed.), *Advances in Ecological Research*, Vol. 2. Academic Press, New York, pp. 101–157.
- Brokaw, N.V.L., 1996. Treefalls: frequency, timing and consequences. In: Leigh, E.G., Jr., Rand, A.S., Windsor, D.M. (Eds.), *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*, 2nd ed. Smithsonian Institution, Washington, D.C., pp. 101–108.
- Brown, N.D., Whitmore, T.C., 1992. Do dipterocarp seedlings really partition tropical rain forest gaps? *Philos. Trans. R. Soc. London B* 335, 369–378.
- Bullock, J.A., Khoo, B.K., 1969. The litter layer. *Malay. Nat. J.* 22, 136–143.
- Burghouts, T., Ernsting, G., Korthals, G., Devries, T., 1992. Litterfall, leaf litter decomposition and litter invertebrates in primary and selectively logged Dipterocarp forest in Sabah, Malaysia. *Philos. Trans. R. Soc. London B* 335, 407–416.
- Chaloner, W.G., Meyer-Berthaud, B., 1983. Leaf and stem growth in the Lepidodendrales. *Bot. J. Linnean Soc.* 86, 135–148.
- Cleal, C.J., Zodrow, E.L., 1989. Epidermal structure of some medullosan *Neuropteris* foliage from the Middle and Upper Carboniferous of Canada and Germany. *Palaeontology* 32, 837–882.
- Cleal, C.J., Shute, C.H., Zodrow, E.L., 1990. A revised taxonomy for Palaeozoic neuropterid foliage. *Taxon* 39, 486–492.
- Cohen, A.D., 1973. Petrology of some Holocene peat sediments from the Okefenokee swamp-marsh complex of southern Georgia. *Geol. Soc. Am. Bull.* 84, 3867–3878.
- Cohen, A.D., Spackman, W., 1977. Phytogenic organic sedimentary environments in the Everglades-mangrove complex. *Palaeontogr. Abt. B* 162, 71–114.
- Cohen, A.D., Stack, E.M., 1996. Some observations regarding the potential effects of doming on tropical peat deposits on the composition of coal beds. *Int. J. Coal Geol.* 29, 39–65.
- Cornejo, F.H., Varela, A., Wright, S.J., 1994. Tropical forest litter decomposition under seasonal drought — Nutrient release, fungi and bacteria. *Oikos* 70, 183–190.
- Costanza, S.H., 1985. *Pennsylvanioxylon* of Middle and Upper Pennsylvanian coals from the Illinois Basin and its comparison with *Mesoxylon*. *Palaeontogr. Abt. B* 197, 81–121.
- Cuevas, E., Medina, E., 1988. Nutrient dynamics within Amazonian forests. II. Fine root growth, nutrient availability and leaf litter decomposition. *Oecologia* 76, 263–273.
- Dantas, M., Phillipson, J., 1989. Litterfall and litter nutrient content in primary and secondary Amazonian 'terre firme' rainforest. *J. Trop. Ecol.* 5, 27–36.
- Edwards, P.J., 1977. Studies of mineral cycling in a montane rain forest in New Guinea. *J. Ecol.* 65, 971–992.
- Egunjobi, J.K., 1974. Litter fall and mineralization in a teak (*Tectona grandis*) stand. *Oikos* 25, 222–226.
- Esterle, J.S., 1989. Trends in petrographic and chemical characteristics of tropical domed peats in Indonesia and Malaysia as analogues for coal formation. Ph.D. thesis, University of Kentucky, Lexington, KY.
- Ewel, J.J., 1976. Litterfall and leaf decomposition in a tropical rain forest succession in eastern Guatemala. *J. Ecol.* 64, 293–308.
- Fogden, M.P.L., 1972. The seasonality and population of equatorial forest birds in Sarawak. *Ibis* 114, 307–342.
- Fösler, H., De las Salas, G., 1976. Litter fall and mineralization in three tropical evergreen forest sands, Colombia. *Acta Cientias Venez.* 21, 196–202.
- Frangi, J.L., Lugo, A.E., 1985. Ecosystem dynamics of a subtropical floodplain forest. *Ecol. Monogr.* 55, 351–369.
- Garwood, N.C., 1996. Seasonal rhythm of seed germination in a semideciduous tropical forest. In: Leigh, E.G., Jr., Rand, A.S., Windsor, D.M. (Eds.), *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*, 2nd ed. Smithsonian Institution, Washington, D.C., pp. 173–185.
- Gastaldo, R.A., 1990. The paleobotanical character of log assemblages necessary to differentiate blow-downs resulting from cyclonic winds. *Palaios* 5, 472–478.
- Gastaldo, R.A., 1992. Taphonomic considerations for plant evolutionary investigations. *Palaeobotanist* 41, 211–223.
- Gastaldo, R.A., Staub, J.R., 1996. Macrofloral remains in the Rajang River delta, Sarawak, East Malaysia: A peat accumulating analog for ancient coastal-deltaic regimes. *I.O.P.C. Abstr.* V, 33.

- Gastaldo, R.A., Bartram, K., Staub, J.R., 1994. Contemporaneous palynoscapes from tidally-influenced fluvial settings in the Holocene Rajang River delta, Sarawak, East Malaysia. *Palynology* 18, 245.
- Gastaldo, R.A., Feng, W., Staub, J.R., 1996. Palynofacies patterns in channel deposits of the Rajang River and delta, Sarawak, East Malaysia. *Palaios* 11, 266–279.
- Gong, W.K., Ong, J.E., 1983. Litter production and decomposition in a coastal hill dipterocarp forest. In: Sutton, S.L., Whitmore, T.C., Chadwick, A.C. (Eds.), *Tropical Rain Forest: Ecology and Management*. Blackwell, Oxford, pp. 275–285.
- Hazeldine, R.S., 1989. Coal reviewed: depositional controls, modern analogues and ancient climates. In: Whateley, M.K.G., Pickering, K.T. (Eds.), *Deltas: Sites and Traps for Fossil Fuels*. Geol. Soc. Spec. Publ. 41, 289–308.
- Irmiler, U., Furch, K., 1980. Weight, energy and nutrient changes during decomposition of leaves in the emersion phase of Central Amazonian inundation forests. *Pedobiologia* 20, 118–130.
- Kennedy, D.N., Swaine, M.D., 1992. Germination and growth of colonizing species in artificial gaps of different sizes in dipterocarp rain forest. *Philos. Trans. R. Soc. London B* 335, 357–366.
- Klinge, H., 1978. Litter production in tropical ecosystems. *Malay. Nat. J.* 30, 415–422.
- Labandiera, C., 1997. Oribatid mites, decomposition in Paleozoic coal-swamp forests, and the history of plant-borers. *Palaios* 12, 317–351.
- La Caro, F., Rudd, R.L., 1985. Litter disappearance rates in a Puerto Rican montane rain forest. *Biotropica* 17, 465–515.
- Lam, K.S., 1988. Sibuan Area, Central Sarawak Malaysia, Explanation Sheet 2/111/12. Geol. Surv. Rep., Geol. Surv. Malaysia, 151 pp.
- Lavelle, P., Blanchart, E., Martin, A., Martin, S., 1993. A hierarchical model for decomposition in terrestrial ecosystems: Applications to soils of humid tropics. *Biotropica* 25, 130–150.
- Leigh, E.G., Jr., Windsor, D.M., 1996. Forest production and regulation of primary consumers in Barro Colorado Island. In: Leigh, E.G., Jr., Rand, A.S., Windsor, D.M. (Eds.), *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*, 2nd ed. Smithsonian Institution, Washington, D.C., pp. 111–122.
- Lesnikowska, A.D., Gaultier, J., 1991. A reconsideration of four genera of permineralized Marattiales from the Stephanian and Autunian of France. *Rev. Palaeobot. Palynol.* 67, 141–152.
- Lim, M.T., 1978. Litterfall and mineral nutrient content of litter in Pasoh Forest Reserve. *Malay. Nat. J.* 30, 375–380.
- Lu, C.Y., Lin, P., 1990. Studies on litter fall and decomposition of *Bruguiera-Sexangula* (Lour) Poir, Community on Hainan Island, China. *Bull. Mar. Sci.* 47, 139–148.
- Madge, D.S., 1965. Litterfall and litter disappearance in a tropical forest. *Pedobiologia* 5, 273–288.
- Matsumoto, T., Abe, T., 1979. The role of termites in an equatorial rain forest ecosystem of West Malaysia. II. Leaf litter consumption on the forest floor. *Oecologia* 38, 261–274.
- McCabe, P., 1984. Depositional environments of coal and coal-bearing strata. In: Rahmani, R.A., Flores, R.M. (Eds.), *Sedimentology of Coal and Coal-bearing Sequences*. Spec. Publ. Int. Assoc. Sedimentol. 7, 13–42.
- Nadkarni, N.M., Matelson, T.J., 1992. Biomass and nutrient dynamics of fine litter of terrestrially rooted material in a neotropical montane forest, Costa-Rica. *Biotropica* 24, 113–120.
- Ogawa, H., 1978. Litter production and carbon cycling in Pasoh Forest, Malaysia. *Malay. Nat. J.* 30, 367–373.
- Okeke, A.I., Omaliko, C.P.E., 1992. Leaf litter decomposition and carbon-dioxide evolution of some agroforestry fallow species in southern Nigeria. *Forest Ecol. Manage.* 50, 103–116.
- Oldeman, R.A.A., 1972. L'architecture de la végétation ripicole forestière de fleuves des crikues guyanais. *Adansonia* 12, 253–265.
- Olson, J., 1963. Energy storage and balance of producers and decomposers in ecological systems. *Ecology* 44, 322–351.
- O'Neill, R.V., DeAngelis, D.L., 1980. Comparative productivity and biomass relations of forest ecosystems. In: Reichle, D.E. (Ed.), *Dynamic Properties of Forest Ecosystems*. Cambridge University Press, Malta, pp. 411–449.
- Pedentchouk, N., 1997. Palynofacies analysis of Holocene sediments in the Rajang River delta, Sarawak, East Malaysia. M.Sc. thesis, Auburn University, Auburn, AL.
- Perry, D.A., 1994. *Forest Ecosystems*. The Johns Hopkins University Press, Baltimore, 649 pp.
- Pigg, K.B., Taylor, T.N., 1990. Permineralized *Glossopteris* and *Dicroidium* from Antarctica. In: Taylor, T.N., Taylor, E.L. (Eds.), *Antarctic Paleobiology*. Springer, New York, pp. 164–172.
- Proctor, J., Anderson, J.M., Fogden, S.C.L., Vailack, H.W., 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. II. Litter fall, litter standing crop and preliminary observations on herbivory. *J. Ecol.* 71, 261–283.
- Raymond, A., Cutlip, P.G., 1996. Evolutionary ecology of terrestrial invertebrate detritivores: Implications for nutrient cycling and primary productivity. *Geol. Soc. Am. Abstr. Progr.* 27, 363.
- Reihman, M.A., Schabillion, J.T., 1976a. Two species of *Alethopteris* from Iowa coal balls. *Proc. Iowa Acad. Sci.* 83, 10–19.
- Reihman, M.A., Schabillion, J.T., 1976b. Cuticles of two species of *Alethopteris*. *Am. J. Bot.* 63, 1039–1046.
- Reihman, M.A., Schabillion, J.T., 1978. Petrified neuropterid foliage from a Middle Pennsylvanian coal ball. *Am. J. Bot.* 65, 834–844.
- Riegel, W., Blickwede, H., 1996. A Middle Eocene leaf coal from Helmstedt, Germany. *I.O.P.C. Abstr.* 5, 85.
- Robinson, J.M., 1990. Lignin, land plants, and fungi: Biological evolution affecting Phanerozoic oxygen balance. *Geology* 18, 607–610.
- Rothwell, G., Warner, S., 1984. *Cordaioxyton dumusum* n. sp., (Cordaitales). I. Vegetative structures. *Bot. Gaz.* 145, 275–291.
- Schabillion, J.T., Reihman, M.A., 1985. Anatomy of petrified *Neuropteris scheuchzeri* pinnules from the Middle Pennsylvanian.

- nian of Iowa: A paleoecological interpretation. In: Dutton, J.T., Jr., Pfefferkorn, H.W. (Eds.), *Neuvième Congr. Int. Stratigraphie et Géologie Carbonifère*, Vol. 5, 3–12.
- Scott, I.M., 1985. The soils of Central Sarawak Lowlands, East Malaysia. *Dep. Agric. Sarawak, East Malaysia. Soil Mem.* 2, 293 pp.
- Scott, A.C., Rex, G., 1985. The formation and significance of Carboniferous coal balls. *Philos. Trans. R. Soc. London B* 311, 123–137.
- Stark, N., Jordan, C.F., 1978. Nutrient retention by the root mat of an Amazonian rain forest. *Ecology* 59, 434–437.
- Staub, J.R., Esterle, J.S., 1993. Provenance and sediment dispersal in the Rajang River delta/coastal plain system, Sarawak, East Malaysia. *Sediment. Geol.* 85, 191–201.
- Staub, J.R., Esterle, J.S., 1994. Peat accumulating depositional systems of Sarawak, East Malaysia. *Sediment. Geol.* 89, 91–106.
- Stout, J., 1980. Leaf decomposition rates in Costa Rican lowland tropical rainforest streams. *Biotropica* 12, 264–272.
- Tanner, E.V.J., 1981. The decomposition of leaf litter in Jamaican montane rain forest. *J. Ecol.* 69, 263–275.
- Trofymow, J.A., Preston, C.M., Prescott, C.E., 1995. Litter quality and its potential effect on decay-rates of materials from Canadian forests. *Water Air Soil Pollut.* 82, 215–226.
- Whitmore, T.C., 1983. *Tropical Rain Forests of the Far East*. Oxford University Press, Oxford, 352 pp.
- Williams, S.T., Gray, T.R.G., 1974. Decomposition of litter on the soil surface. In: Dickinson, C.Y., Pugh, G.J.F. (Eds.), *Biology of Plant Litter Decomposition*, Vol. II. Academic Press, London, pp. 633–658.