Journal of Tropical Forest Science 22(1): 21–35 (2010)

HETEROGENEITY OF SOIL MORPHOLOGY AND HYDROLOGY ON THE 50 HA LONG-TERM ECOLOGICAL RESEARCH PLOT AT PASOH, PENINSULAR MALAYSIA

Y Adzmi[1], WC Suhaimi[2], MS Amir Husni[3], H Mohd Ghazali[2], SK Amir[2] & I Baillie[4]

[1]*Faculty of Applied Sciences, University Technology Mara, 40450 Shah Alam, Selangor Darul Ehsan, Malaysia. E-mail: adzmiy@salam.uitm.edu.my*
[2]*Forest Research Institute Malaysia, 52109 Kepong, Selangor Darul Ehsan, Malaysia*
[3]*1 Jalan Bidara 2/1, Taman Bidara, 68100 Batu Caves, Selangor Darul Ehsan, Malaysia*
[4]*Harvard Forest, Petersham & Arnold Arboretum–CTFS Asia Project, Harvard University, 22 Divinity Avenue, Cambridge, MA 02138, USA*

Received December 2008

ADZMI Y, SUHAIMI WC, AMIR HUSNI MS, MOHD GHAZALI H, AMIR SK & BAILLIE I. 2010. Heterogeneity of soil morphology and hydrology on the 50 ha long-term ecological research plot at Pasoh, Peninsular Malaysia. The soils of the 50 ha long-term Centre for Tropical Forest Science (CTFS) research plot at Pasoh, Peninsular Malaysia were surveyed in detail in 1994–1996 and briefly re-examined in 2005–2006. Pasoh is rain shadowed by mountains to both east and west, and the aseasonal 1800 mm annual rainfall is marginal for an evergreen forest. There is a low ridge of Triassic shale in the north-eastern corner but two thirds of the plot consists of alluvial flats. The ridge is capped by remnants of a laterite (ferricrete) sheet, and the well-drained, brown fine loam over clay soils range from < 50 cm over a sheet of dense gravel laterite on the crest, through moderately dense gravels on midslopes, to deep clays with few gravels on lower slopes. The alluvial sediments are derived from variable mixtures of granite, sandstone and shale. Drainage varies from moderately free on a low (1–3 m) terrace to perennially saturated in low parts of a floodplain. Many of the poorly drained soils are stagnogleys, with mucky surfaces, and very wet, mottled grey upper mineral horizons, overlying moist and less mottled brown subsoils. The ridge soils are moderately dystrophic, and soil depth and available moisture reserves for dry spells appear to be major edaphic constraints. The alluvial soils are also moderately dystrophic, and vary substantially with respect to aeration of root zones. Stagnogleying imposes a particular combination of aeration stresses on young plants, as young seedlings have to cope initially with the saturated upper horizons, but encounter better aerated lower subsoils if they survive and grow. Nutrients are also important, but it is the extent and type of drainage constraints that make Pasoh unusual among CTFS plots.

Keywords: Soil survey, drainage, stagnogley, laterite, lowland dipterocarp forest

ADZMI Y, SUHAIMI WC, AMIR HUSNI MS, MOHD GHAZALI H, AMIR SK & BAILLIE I. 2010. Keheterogenan morfologi tanah dan hidrologi tanah di plot 50 ha kajian jangka panjang di Pasoh, Semenanjung Malaysia. Tanah di plot kajian jangka panjang 50 ha Pusat Sains Hutan Tropika (CTFS) di Pasoh, Semenanjung Malaysia dikaji dengan terperinci pada tahun 1994–1996 dan diperiksa semula pada 2005–2006. Pasoh terletak di kawasan lindungan hujan di antara banjaran gunung di timur dan barat dengan hujan tak bermusim sebanyak 1800 mm setahun, jumlah yang agak sedikit untuk hutan malar hijau. Terdapat satu banjaran syal rendah berusia Trias di timur laut plot kajian tetapi dua pertiga plot terdiri daripada dataran aluvium. Banjaran dilitupi tinggalan lapisan laterit (ferikret) dan tanah lom halus berwarna perang yang sangat salir di atas lempung. Ia berada < 50 cm dari lapisan padat kelikir laterit di puncak, diikuti kelikir yang sederhana padat di pertengahan banjaran, seterusnya lempung dalam dan sedikit kelikir di kaki banjaran. Enapan aluvium dibentuk daripada campuran batuan granit, batu pasir dan syal. Saliran tanah berubah dari sederhana di teres rendah (1–3 m) hingga agak tepu sepanjang tahun di bahagian rendah dataran banjir. Kebanyakan tanah tidak mempunyai saliran yang baik terbentuk daripada glei genang yang berlumpur dengan horizon mineral sangat berair dan berarau kelabu berada di atas subtanah perang yang lembab dan kurang arau. Tanah banjaran mempunyai distrofi sederhana. Kedalaman tanah dan kandungan simpanan lembapan tersedia semasa musim kering berkemungkinan menjadi halangan edafik yang utama. Tanah aluvium juga mempunyai distrofi sederhana dan pengudaraan zon akarnya berubah-ubah dengan ketara. Glei genang menyebabkan berlakunya tegasan pengudaraan ke atas tumbuhan muda kerana anak-anak pokok terpaksa menghadapi horizon atas yang tepu air tetapi subtanah yang lebih baik pengudaraannya. Walaupun pengaruh nutrien juga penting, taburan dan jenis kekangan saliran dipercayai menjadikan Pasoh agak berbeza daripada plot CTFS yang lain.

INTRODUCTION

The extent to which tree species richness can be explained by niche specialisation for heterogeneous soil environments appears to vary considerably between tropical forests. Due to the generally high rainfall and intensive leaching, soil nutrient deficiencies and imbalances are the most extensive edaphic constraints on tropical forests with aseasonal and perhumid rainfall regimes. Significant associations of forest composition, structure and dynamics with soil nutrient fertility gradients have been reported in lowland forests in Malaysia and elsewhere in Asia (Ashton & Hall 1992, Webb & Peart 2000, Wan Juliana 2001, Palmiotto *et al.* 2004, Potts *et al.* 2004, Baltzer *et al.* 2005, Davies *et al.* 2005, Russo *et al.* 2005, Gunatilleke *et al.* 2006) but appear to be patchier in neotropical forests (Duivenvoorden & Lips 1995, Clark *et al.* 1999, Duivenvoorden *et al.* 2002, Phillips *et al.* 2003, Tuomisto *et al.* 2003, Valencia *et al.* 2004). There are other potentially severe edaphic constraints, such as moisture stress, impeded drainage and site instability, and these are significant in some forests (Baillie 1996).

Pasoh Forest Reserve in Negeri Sembilan, Peninsular Malaysia is an important site for the investigation of soil associations in tropical forests. There are conflicting early findings on the importance of edaphic influences on the floristic composition and diversity of its lowland dipterocarp forest. Wong and Whitmore (1970) concluded that edaphic effects were slight, and that biotic processes were the main determinants of forest composition. Ashton's (1976) re-examination showed that some of the floristic variation was associated with topography and related soil differences, especially drainage. Neither of these studies had chemical data and could not evaluate the effects of nutrients. This was remedied by Wan Juliana (2001), who found that the floristically significant division between alluvial and residual/colluvial sites relates to differences in nutrients as well as soil hydrature.

The Reserve has been the venue for ecological research programmes run by the Forest Research Institute of Malaysia (FRIM) and also for several of its international programmes, run bilaterally with Japanese and British institutions, and multilaterally with the International Biological Program and the Center for Tropical Forest Studies (CTFS) (Ashton *et al.* 2003). FRIM established a 50 ha long-term ecological research plot at Pasoh as part of the pantropical network of plots co-ordinated by CTFS and for Asia, the Arnold Arboretum of Harvard University. Pasoh was the first CTFS plot in Asia and the second in the world (Manokaran *et al.* 1990, Ashton *et al.* 2003)

The soils of the Pasoh reserve being characterised and mapped in several surveys, including a regional soils reconnaissance (Dumanski & Ooi 1969) and a semi-detailed survey of the 650 ha core research area (Allbrook 1973). The latter identified four main groups of soils, separated mainly on parent material lithology, with granitic soils in the east, shale soils in the west and mixed sandstone/shale and alluvial soils in the central belt, which includes the 50 ha plot. There have been more recent detailed soil surveys of individual research sites within the reserve. The soils of several areas, each of 2 ha, in the western part of the 50 ha plot were characterised during studies of the relationships between soil nutrient fertility and the distributions and foliar nutrients of canopy tree species (Amir Husni & Mona 1990, Amir Husni *et al.* 1991, Amir Husni & Miller 1992). The soils of the whole 50 ha were surveyed in 1994–1996 (Adzmi & Suhaimi 1996). The resultant soil map appeared in Yamashita *et al.* (2003) and their findings had been cited and interpreted in other studies (Wan Juliana 2001, Yamashita & Takeda 2003, Okuda *et al.* 2004).

We re-examined some of the soils at the plot in 2005–2006 and incorporated the resultant interpretations in this synthesis, which aims at providing accessible background on the soils on the plot. We concentrated on topography, soil morphology and pedo-hydrology, and only limited chemical data. Soil nutrient–forest relationships on the plot have been examined by Wan Juliana (2001), and the nutrient status of the soils will be further characterised in the on-going pantropical comparison of Mehlich 3 extractable topsoil nutrients in CTFS plots, including Pasoh.

MATERIALS AND METHODS

Survey area

The 50 ha CTFS plot is located in the 24 km^2 Pasoh Forest Reserve (2° 58' N, 102° 20' E) in the Jelebu district of the state of Negeri Sembilan, West Malaysia, and is about 5 km north-north-east of Simpang Pertang. The Reserve has good road access and the 50 ha plot in the centre of the reserve is accessible by a good path. The rectangular plot is aligned 1 km E–W × 0.5 km N–S. It is pegged out as 1250 quadrats of 20 × 20 m. Mapped paths, quadrat pegs, tree number tags and well-flagged FRIM/Universiti Putra Malaysia/University of Georgia seed traps facilitated intra-plot navigation in 2005.

The reserve lies in an undulating intermontane basin between low mountains to east and west (Okuda *et al.* 2003a). It is, therefore, in rain shadow from both the south-west and north-east monsoons, and is one of the driest parts of the peninsula. Annual rainfall averages about 1800 mm, ranging from under 1200 to over 2400 mm (Noguchi *et al.* 2003). Although the mean annual total is low to marginal for evergreen forest, there is no regular prolonged dry season, and the weakly bimodally distributed rainfall just about satisfies forest evapotranspirative demand in non-El Nino Southern Oscillation (ENSO) years (Tani *et al.* 2003). The highest mean monthly rainfall (> 200 mm) is in November at the start of the north-east monsoon, with some individual November totals > 400 mm. There are also occasional high totals in May, at the start of the south-west monsoon. The drier times of the year are January–February and June–August but, even then, monthly means are still almost 100 mm (Tani *et al.* 2003). Inter-annual variations result in occasionally severe dry spells, and some months with < 10 mm have been recorded in ENSO years. Much of the rain is convectional and falls in the afternoons and evenings. Most falls last less than three hours and intensities are moderate to high, with brief bursts exceeding 70 mm hour^{-1} in the heaviest storms (Noguchi *et al.* 2003). This is sufficient to generate surface runoff, even under high forest (Leigh 1992, Elsenbeer & Verstessy 2000). Overall, strong winds are low but brief and narrow-fronted pre-rain squalls are strong enough to cause localised windthrow and are significant in the dynamics of the forest (Manokaran & LaFrankie 1990).

The 50 ha plot lies on the eastern side of the intermontane basin and includes the lower end of a spur from an outlier of the Main Range of the peninsula. Mesozoic granite underlies the upslopes of the Main Range to the east, but there are no granite outcrops on the plot. However, the alluvia contain variable amounts of granitic materials. The lower end of the spur forms a low ridge in the north-east of the plot, and is underlain by non-calcareous sandstone and shale of the Triassic Gemas formation. Shales are locally predominant and give mainly argillaceous residual and colluvial regoliths. Most of the plot is underlain by recent and subrecent alluvia, some of which depositional layering is discernible. Alluvial textures range from loamy sand to clay, and sand sizes vary from coarse (> 1 mm) angular and subangular quartz to fine (< 0.25 mm) and smooth.

The alluvial part of the plot is fairly flat at about 110 m asl, but the north-eastern ridge rises to about 140 m and gives intraplot relief of slightly less than 30 m. The topography is, therefore, muted compared with that on most other Asian CTFS plots.

The ridge crest consists of three low and flat-topped knolls and two gentle cols. The knolls are capped with substantial sheets of relict laterite (ferricrete) and appear to be remnants of the relict older pene-pediplain of Dapper *et al.* (1988). The convexo-concave connecting slopes from the laterite-capped knolls down to the alluvial flats have gradients of 6–16°.

The alluvia were deposited by Sungai Marong Kanan, a tributary of Sungai Pertang that drains the inter-montane basin northwards towards Batang Pahang. There is a substantial floodplain in the north-west of the plot, which is under water during wet periods. The alluvium in the south and east of the plot mostly consists of a dissected low terrace, 1–3 m above normal flood levels. The floodplain and terrace are intricately inter-digitated in places, with hollows and channels on the terrace, and slightly better drained hummocks on the floodplain (Kemper & Bell 1985).

The reserve is surrounded on three sides by agricultural land (Okuda *et al.* 2003a). It is one of the largest remnants of lowland dipterocarp forest in the peninsula. Wyatt-Smith (1961) characterised the Pasoh forest as mixed red meranti–keruing while Salleh (1968), as mixed red meranti (Appanah & Weinland 1993). Logging has disturbed parts of the reserve (Okuda *et al.* 2003b), but the central research area, including the 50 ha plot, is more or less intact.

The 50 ha plot was established in 1988, and all free standing stems with diameter $\geq$ 1 cm at reference height (1.3 m above ground or 0.6 m above the highest buttress junction) were measured and identified to species level, according to standard CTFS procedures (Condit 1998, Manokaran *et al.* 1990), with re-censuses in

1995, 2000 and 2005. There are over one third of a million stems in the diverse, slim-boled high canopy dipterocarp forest on the plot. The 1995 census identified 818 species in 81 families (Davies *et al.* 2003). With 85 species, the Euphorbiaceae is the most species-rich family, and also accounts for the highest number of stems, although most are small. The larger size classes, basal area, biomass and composition of the canopy are dominated by 30 species of dipterocarps. Almost 60% of the total dipterocarp basal area consists of light red merantis (*Mutica* section of the genus *Shorea*), and a little less than 20% are keruings (*Dipterocarpus* spp.) (Davies *et al.* 2003). Canopy height ranges from 11 m in young gaps to 40 m in old growth, with some emergents reaching 60 m. The mean basal area is about 31 m^2 ha^{-1}, and the aboveground biomass ranges from 200 to 400 Mg ha^{-1}, averaging about 350 Mg ha^{-1} (Manokaran *et al.* 2001).

Soil survey

During the main survey in 1994–1996, we examined the soils with 10 cm diameter Jarrett augers down to 1.2 m, hard rock or standing water. Over 300 soils were examined on a 40 × 40 m grid. The observation density of > 6 ha^{-1} qualifies the survey as very intensive (FAO 1979, Anonymous 1987, Landon 1991, Soil Survey Staff 1993). Matrix and mottle colours, hand texture, stones and wetness were described by natural horizons. The better-drained soils were examined in more detail in five pit profiles, but it was not feasible to dig profiles in inundated soils on the floodplain. The profiles were described by natural horizons for matrix Munsell colours; proportions, colours and clarity of mottles; hand texture; strength, size and type of soil structures; strength, colour and continuity of argillans; density and size of visible pores; moisture condition and consistence; density and size of roots; and the density, size, type and degree of weathering of clasts. In 2005 and 2006, we augered at a further 30+ sites, concentrating on distinctions between groundwater and perched water-tables and hence between deep (endogleying) and stagnogleying (epigleying) in the alluvial soils, and also on the possibility of granitic soils, as reported in the north-eastern corner of the plot (Thomas 2003).

Disturbed samples were taken from the main horizons of the pit profiles and analysed in the soil laboratory at FRIM by the following methods: pH by pH meter in a 1:2.5 soil: water suspension; organic C by Walkley-Black rapid titration (Walkley 1947); total N by dry combustion with a LECO FP-528 nitrogen analyser; available P by Bray & Kurtz No. 2 extraction and calorimetric determination by Denige's method; exchangeable cations were extracted with 1 M NH_4OOCH_3 buffered to pH 7 and assayed by inductively coupled plasma, cation exchange capacity (CEC) by leaching of the NH_4-saturated soil with KCl, distilling off the ammonia using MgO, collection in boric acid solution and titration against 0.01 M HCl (Black 1965).

RESULTS AND DISCUSSION

Soil classification and morphology

The soil mapping units (Figure 1 and Table 1) are based on series and phases of the West Malaysian soil classification (Anonymous 1987, Paramananthan 1987). The correlations with the World Reference Base (WRB) of the FAO (2006) and Soil Taxonomy (ST) of the US Department of Agriculture (Soil Survey Staff 1999, 2006) are for the soils seen on the plot, rather than for the official type descriptions for the series.

There are three distinct pedo-physiographic zones on the plot: ridge, terrace and floodplain. Within the ridge group, some researchers have further distinguished between soils on the crests and those on the slope (e.g. Wan Juliana 2001, Yamashita *et al.* 2003).

The ridge soils have dark brown, friable, crumb structured topsoils that are only a few centimetres deep. Topsoil textures are medium to fine, varying between sandy clay loam and clay loam according to the proportion of sandstone in the predominantly shale-derived parent material. The yellowish or strong brown subsoils are heavier textured, with moderate blocky and slightly firm clay loam or sandy clay. Three series are differentiated on the depth and form of subsoil laterite (ferricrete) (Figure 2). Indurated slabs or dense gravel layers of this rocklike material occur at < 50 cm in the Gajah Mati series on the crests of the knolls. On the upper slopes, the laterite occurs as moderately dense gravel and stones at depths of 50–100 cm in the colluvial yellowish-strong brown sandy clay subsoils of Terap series. In Bungor series on the lower slopes there are few laterite gravels and they are at least 1 m deep, so that most of the subsoil consists of gravel-free yellowish-strong

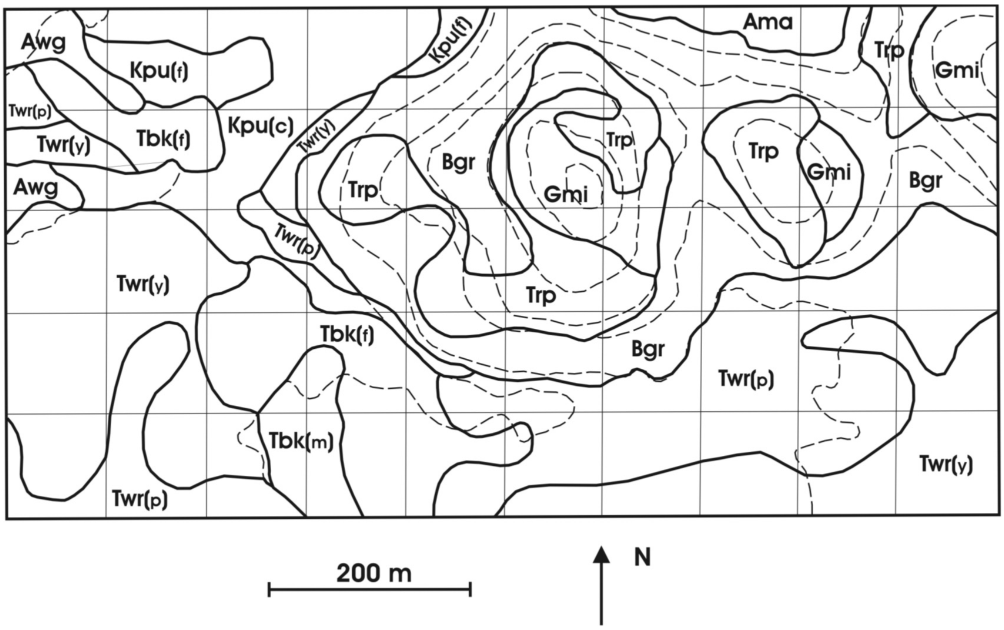

Figure 1 Soil series and phases on the 50 ha plot, Pasoh FR. 100 m grid = thin line, 5 m contours = dashed line. Alluvial soils: Ama = Alma, Awg = Awang, Kpu(c) = Kampong Pusu coarse sand phase, Kpu(f) = Kampong Pusu fine sand phase; Twr(p) = Tawar pale phase, Twr(y) = Tawar yellow phase, Tbk(f) = Tebuk fine sand phase, Tbk(m) = Tebuk, medium sand phase. Ridge soils: Bgr = Bungor, Gmi = Gajah Mati, Trp = Terap.

brown sandy clay to clay with subangular blocky structures with weak to moderate clayskins. All of the ridge soils drain freely and qualify for class 7 (well drained) of the West Malaysian drainage classification (Anonymous 1987).

We found granitic soils on the Main Range outlier in the east of the Reserve, similar to that observed by Allbrook (1973). A population of *Pentace strychoidea* has been interpreted as indicating granitic influence on a small area of soils in the north-eastern corner of the plot (Thomas 2003). However, when we specifically re-examined the soils where the ridge crosses the north-eastern boundary of the plot in 2006, we found that the ridge soils in and near the plot appear to be wholly derived from clastic sedimentary parent materials and include no visible granite fragments or coarse angular quartz sand. Clear granitic influences are seen only in some of the alluvial soils.

The soils of the extensive alluvial terrace were originally designated as wet alluvial soils (Adzmi & Suhaimi 1996). They have thin, friable, crumb-structured topsoils, which tend to be less dark than those on the ridge or floodplain. The subsoils are mostly yellowish brown, with few or no mottles in the upper metre. Grey and rust-coloured mottles increase in frequency and contrast below 1 m and the matrix tends to become paler, often pale brown or pale yellow. The coloration indicates imperfect drainage in classes 4–5 in the West Malaysian classification (Anonymous 1987). The subsoils have moderate subangular blocky structures, some of which have discontinuous and weak or moderate clayskins. Clay contents generally increase with depth, but there are also some inherited coarse textured layers in the subsoil. The general textural profile is from sandy loam or sandy clay loam topsoil over sand clay loam or sandy clay subsoil.

In the Tebuk series, which predominates on the western part of the terrace, the sand is predominantly fine grained, and the alluvium appears to be derived from sandstones and shales, but there is also a medium sand phase. The more extensive Tawar series predominates in the south and east of the plot. Its sand is mainly coarse grained, much of it very coarse and gritty (< 1 mm) angular quartz that is apparently derived from granite. There is a pale phase of Tawar, which has matrix colours lighter than pale brown (Munsell 10YR 6/3) but no mottles in the upper metre. It does not look substantially worse drained than the brighter subsoils of the main series, and these soils may form in patches of hypo-ferriferous alluvium.

Table 1 Main features, West Malaysian soil classification and international correlations of soils of 50 ha plot, Pasoh FR

Physiography		Soil features		West Malaysian soil classification (Anonymous 1986, Paramanathan 1989)			Map code (Fig. 1)	Main international correlations	
Group	Subgroup	Shared	Distinguishing	Soil series	Phase	Drainage class		World reference base (FAO 2006)	Soil Taxonomy (Soil Survey Staff 1999, 2006)
Ridge - residual and colluvial	Crest	Thin dark brown fine loam topsoil over strong brown fine loam or clay subsoil	Massive laterite or dense gravel within 50 cm	*Gajah Mati*	–	7–8 (Good)	Gmi	Acric Plinthosol	Typic Plinthudult or Plinthic Kanhapludult
	Slopes		Many laterite gravel at 50-100 cm	*Terap*	–		Trp	Plinthic Acrisol	Plinthic Kanhapludult
			Few laterite gravel below 100 cm	*Bungor*	–		Bgr	Haplic Acrisol	Typic (or Plinthic) Kanhapludult (& Kanhaplaquult)
Alluvial	Low terrace	Thin dark brown topsoil over unmottled yellowish/ brownish loam to 1m+ , mottled below	Sand predominantly medium or fine	*Tebuk*	Fine sand	5–6 (Good–imperfect)	Tbk(f)	Haplic Acrisol	Typic (or Oxyaquic) Kanhapludult (& Kanhaplaquult)
					Medium sand		Tbk(m)		
			Sand predominantly coarse	*Tawar*	Yellow		Twr(y)		
					Pale		Twr(p)		
Alluvial	Floodplain	Thin muck, over mottled pale brown wet layered, over moist brownish less mottled	Sandy clay subsoil	*Awang*	–	3–4 (Imperfect – poor)	Awg	Umbric Acric Stagnosol	Umbric & Humic Epiaquept (& Kanhaplaquult)
			Sandy clay loam subsoil	*Alma*	–	–	Ama		
		Thick muck, over mottled grey wet layered loam, over moist brownish mottled		*Kampong Pusu*	Fine & medium sand	1–2 (Poor)	Kpu(f)	Umbric Acric Gleysol (& Stagnosol)	Humic Endoaquept (& Epiaquept)
					Coarse sand		Kpu(c)		

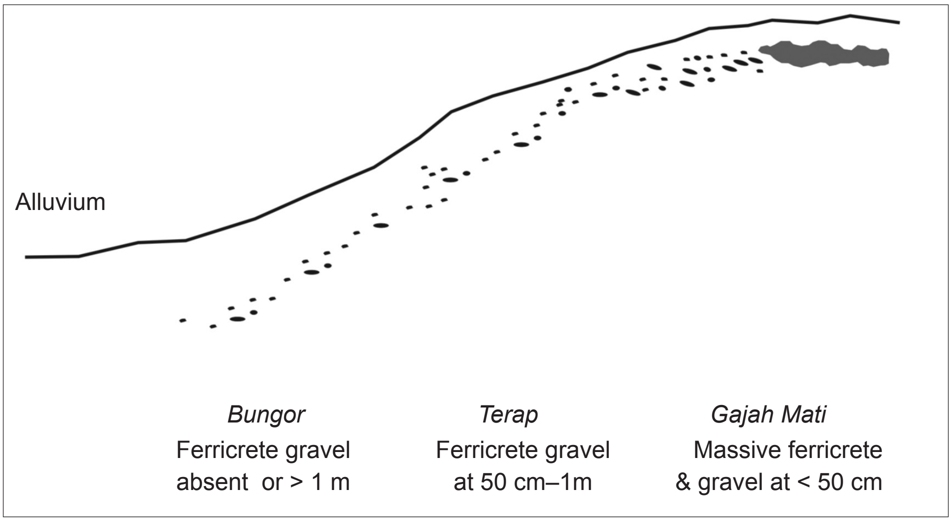

Figure 2 Laterite form, frequency and depth in soils on the NE ridge, 50 ha plot, Pasoh FR

The soils of the floodplain were designated as wet alluvial soils (Adzmi & Suhaimi 1996). The soils of Kampong Pusu series are the worst drained. They have moderately thick (< 20 cm) dark topsoils with substantial contents of organic matter, but these are mucks, rather than true peats (Figure 3). The upper subsoil is wet for most of the year and augering hits water at < 1 m, usually < 50 cm. Matrix colours are light grey or very pale yellow, and there are many prominent rusty brown or reddish mottles. The consistency is very firm and compact, and this horizon is only slowly permeable. The wetness and colours indicate poor drainage, in classes 1–2 (Anonymous 1987). Textures range from sandy clay loam to clay, predominantly sandy clay. There are variations with depth, and the subsoils tend to have higher clay contents than the surface horizons. The coarse sand phase on mainly granitic alluvium predominates on the plot. The fine sand phase derived from clastic sedimentary parent material is less extensive and is confined to areas close to the ridge.

Alma and Awang series are associated with slightly elevated areas on the floodplain. Their drainage is imperfect (classes 3–4 in Anonymous 1987). In both series a mucky grey topsoil of 5–15 cm depth overlies yellowish or pale brown upper subsoil (Figure 3). This becomes more mottled with depth and has profuse grey mottles within 50 cm. The lower subsoil becomes wet, mottled light grey or pale brown, and very firm–compact within the top metre. In Alma series, the predominant subsoil texture is sandy clay, whereas Awang series is coarser with sandy clay loam predominant. Alma and Awang series are not subdivided into phases on sand size.

Initially the drainage for the floodplain soils was assessed and the series were characterised on the basis of colour, mottling and wetness of the upper metre. Really wet soils are difficult and messy to auger, and examination usually stops once standing water is encountered. However, later deep augering showed that, beneath the grey saturated upper subsoils, the deeper subsoils of many floodplain soils on the plot are moist, rather than wet, and become browner and less mottled. Once the auger is through the compact aquiclude gleyed horizon, the standing water in the hole drains away. The lower layers therefore appear to be better drained and more permeable than those above, and many of the water tables in these soils are therefore perched, rather than vertically continuous. These perched watertable soils are stagnogleys (epigleyic) (Table 1) rather than deep endogleys.

The stagnogleying is attributed to limited permeability in the upper subsoil due to high compaction and low porosity, possibly abetted by increases in clay content with depth. Awang and Alma series appear to be mainly stagnogleyic. Some Kampong Pusu soils are also stagnogleyic and have better drained deep subsoils, even where there is standing surface water and the topsoils are really grey and wet. However, Kampong Pusu soils adjacent to streams and pools appear to be wet throughout and endogleyic.

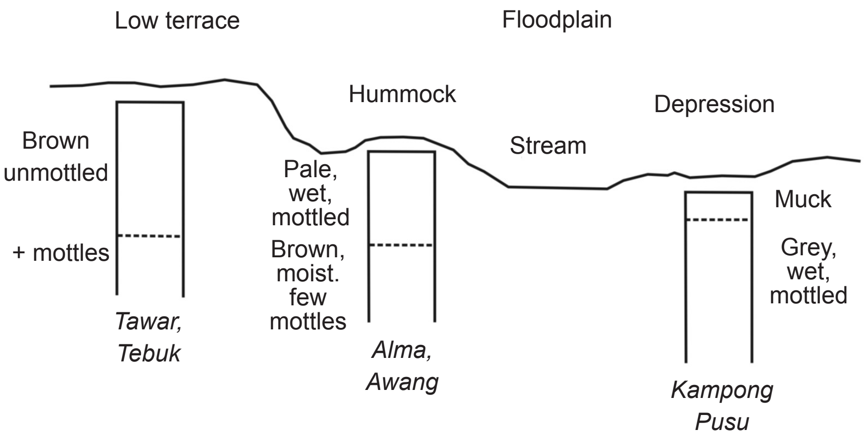

Figure 3 Drainage in alluvial soils on 50 ha plot, Pasoh FR. Moderately well-drained Tawar and Tebuk on low terrace; imperfectly drained stagnogley Alma and Awang on floodplain hummocks; poorly drained deep gley Kampong Pusu on floodplain depressions.

Soil chemical properties

Our chemical data are limited and readers are referred to Wan Juliana (2001) and Yamashita *et al.* (2003) for details. Our data showed no clear chemical differences between the soils on the plot. They are all very acid by global standards (Landon 1991) although not exceptional for tropical forests (Baillie 1996). Values for pH in 1:2.5 soil:water suspension are mostly 4.2–4.7. The soils are highly leached, with low contents of the individual exchangeable cations and total exchangeable bases (TEB). Although cation exchange capacities are low (< 10 $\text{cmol}^+ \text{kg}^{-1}$), the very low TEBs mean that base saturations are mostly very low (< 10%). The slight elevation of exchangeable base status in the topsoils is attributed to nutrient cycling. Exchangeable Ca levels are especially low (Yamashita & Takeda 2003).

General agricultural experience with tree crops in Peninsular Malaysia suggests that the ridge soils are moderately endowed with K and Mg, because of their shale origins and micaceous mineralogy, but K levels are likely to be low in the terrace soils (Guha & Pushparajah 1966, Guha & Yeow 1966a, b, Thigalingam & Grimme 1976). However, the data of Wan Juliana (2001) did not confirm these expectations and showed that levels of all exchangeable cations were slightly but significantly higher in the alluvial than ridge soils. She also found that available P and pH were slightly higher, and exchangeable Al correspondingly lower, in the alluvial soils.

Surface litter is patchy and thin on the ridge soils, and there are no accumulations of raw humus. Organic matter contents are moderate for the top few centimetres, with organic C at 1.5–2%, and then decreases rapidly with depth. Total N and available P has similar depth profiles. C:N ratios are 10–20 in the topsoils and drop to about 6 in the subsoils, indicating that the organic matter is not recalcitrant and likely to have overall decomposition half lives < 1 year (Rasidah 2001). C:P ratios are high, suggesting that decomposition processes significantly affect soil P dynamics (Nor 1981). Visual impressions are that organic matter contents are higher and penetrate deeper in the floodplain soils than in the ridge soils. However, even Kampong Pusu does not have true peat topsoils (Leamy 1966). Wan Juliana (2001) found higher organic matter contents in ridge than alluvial soils, possibly because the alluvial group combined ochric (weakly darkened) terrace topsoils with umbric or humic (darker) floodplain topsoils

DISCUSSION

Pedology and international soil correlations

Triassic non-calcareous sandstones and shales outcrop extensively in the lowlands of Peninsular Malaysia. They give rise to a range of leached and acid soils, including Gajah Mati, Terap and Bungor series (Law & Leamy 1966, Paramananthan 1987). The leaching of clay from topsoils and its deposition as thin shiny clayskins on pore walls and structural faces in subsoils, i.e. argilluviation, is an important pedogenetic process in these soils (Eswaran & Noordin 1980). The clay increases with depth seen in Bungor series on the plot are attributed to moderate argilluviation, which is important for their international correlations. The subsoils of Bungor series appear to qualify as argic in the FAO World Reference Base (WRB), and argillic in the USDA Soil Taxonomy (ST). The cation exchange capacities of the Bungor soils on the plot are low enough to qualify as kandic, so these soils correlate as Acrisols in WRB and Kandiudults in ST. Morphologically similar shale soils in Malaysia with more active illitic clays and higher CEC values qualify as Alisols in WRB and non-kandic Udults in ST (Andriesse 1975, Eswaran & Noordin 1980, Anonymous 1987, Dapper *et al.* 1988). The shallow laterite qualifies the plot's Gajah Mati soils for a separate taxon — Plinthosol — in WRB, while Terap and Bungor are Plinthic and Haplic Acrisols respectively. In ST, all of the ridge soils are Kandiudults, with Gajah Mati in the Plinthic subgroup, Bungor in the Typic, and Terap intermediate.

Laterite, Gajah Mati and Terap series are widespread on shales in the lowlands of Peninsular Malaysia. The most extensive laterites occur as continuous massive porous sheets on interfluves. The laterites on connecting slopes down to the valleys are mostly discrete gravels and look like wash of comminuted fragments from upslope (Law & Leamy 1966). Limited areas of laterite are forming in current conditions on some toeslopes and floodplains (Eyles 1970). These neoformations often incorporate colluvial gravel from upslope (Panton 1956) and are comprised of material of mixed ages. The massive relict sheets, thus, contribute to laterite in all parts of the landscape, not only on the interfluves.

The formation of the interfluve laterites is attributed to seasonally fluctuating high water tables in a formerly undissected pedi-peneplain. Repeated oscillations between wet and dry moisture conditions within solum depth fostered alternating valencies, lability states and mobilisation/precipitation cycles in iron, manganese and other transition elements. This led to segregation of these elements, especially iron, and its concentration, initially as mottles, then as concretions, and eventually to their coalescence, cementation and induration as massive laterite. The full induration process is slow and needs repeated wet–dry cycles within a limited depth range. Massive laterite develops only during long periods of topographic and base level stability. When water-table levels fluctuate, as in tecto-geomorphologically dynamic landscapes, the concentration processes are not prolonged within any depth range and do not progress beyond the formation of mottles or discrete concretions. There were earlier suggestions that all types of laterite are currently forming in the lowlands of Peninsular Malaysia (Scrivenor 1909). However, the later consensus is that the interfluve sheet laterites formed on the relict pedi-peneplain of Dapper *et al.* (1988) during phases in the Quaternary that predated the most recent topographic dissection cycle and also had wet but more seasonal palaeoclimates (Panton 1956, Law & Leamy 1966, Eyles 1970, Allbrook 1973).

The distribution of laterite on the plot is typical, with Gajah Mati soils over relict massive laterite on the crests, Terap soils containing substantial shallow colluvial laterite gravels on upper slopes, and Bungor soils with fewer and more deeply buried gravels on the lower slopes (Figure 2). No neoformations of re-cemented gravels or fresh laterite were seen on the lower slopes or alluvial flats on the plot.

Although organic matter contents in the ridge soils are moderate (Wan Juliana 2001), the surfaces of these soils are not capped with thick layers of unincorporated litter or humus. This parallels the absence of thick surface necromass on shale soils on the CTFS plot at Lambir in Sarawak, and contrasts with the humus blanketing the sandstone soils there. At Lambir, the contrast was attributed to better litter quality and less dystrophic nutrient conditions on the shale soils (Baillie *et al.* 2006). The absence of humus suggests that the Pasoh ridge soils are only moderately dystrophic.

The development of stagnogleying in the floodplain soils is attributed to low permeability in the upper and middle subsoils. Argilluviation may contribute to this, although these are young soils and argilluviation does not seem very advanced. Moreover, some of the increases in clay content with depth appear to be inherited from alluvial deposition. Stagnogleying is seen in profiles with medium textured subsoils, so high clay contents are not essential and texture may not be the main driver of this process. All of the upper subsoils in the stagnogleys are compact and were difficult to auger. It appears to be dense physical packing that causes the low porosity and permeability, rather than cementation, as the peds crumble and slake *ex situ*. The packing appears to be pedogenic rather than inherited, as it occurs consistently in the same upper subsoil position in the soil profile, and the lower subsoils are usually less compact as well as browner and less mottled than the stagnogleyic horizons above, irrespective of texture.

The stagnogleyic floodplain soils correlate with Umbric Acric Stagnosols in WRB and Umbric and Humic Epiaquepts in ST. The deeply gleyed soils in Kampong Pusu are Humic Gleysols (WRB) and Humic Endoaquepts (ST) (Table 1). Many of the terrace soils are well enough drained and showed sufficient argilluviation to qualify as Typic or Plinthic Acrisols in WRB, and Typic and Oxyaquic Kanhapludults in ST, with Kanhaplaquults in wetter areas. The less argic/argillic soils are Cambisols (WRB) and Inceptisols (ST).

Although contents of organic matter are quite high in some of the alluvial soils, none of them develop thick, wet surface peats, such as that occurring on many poorly drained soils on inland terraces and floodplains in Malaysia and elsewhere in South-East Asia (Tie & Kueh 1979, Andriesse 1988, Wuest *et al.* 2003).

Edaphecological aspects

Abiotic edaphic factors that can mediate biotic processes and act as interspecific filters in tropical forests include water supply, root aeration, mechanical stability and especially nutrients (Baillie 1996).

The topography of the Pasoh plot, with relief < 30 m, is considerable less rugged than in the CTFS plots at Lambir in Sarawak, Sinharaja in Sri Lanka and Khao Chong in Southern Thailand, all of which with considerable relief exceeding 100 m. However, the Pasoh plot actually encompasses the greater topographic heterogeneity, especially with respect to soil hydrature. The other plots are on steep rugged terrain and virtually all of their soils are well drained, whereas soil hydrology at Pasoh ranges from poor drainage and aeration in the alluvial soils to variable droughtiness on the ridge. This apparent anomaly confirms strictures (Hall *et al.* 2004) against the uncritical use of altitude and relief as independent variables in analyses of edaphecological effects at small and medium scales.

Despite its relatively low rainfall, Pasoh has a greater hydrological range and a higher proportion of soils with aeration constraints than other plots in the CTFS network (Kemper & Bell 1985, Rogstad 1990). Limited aeration is unimportant in the ridge soils, and it is only one of several constraints, together with nutrient stress and drought spells, in the terrace soils. However, it appears to be the main constraint in the floodplain soils. Directly deleterious effects of poor drainage include oxygen deficits, suppression of root respiration and metabolic activity and elevated soil solution concentrations of transition elements, especially Fe and Mn. These can be directly toxic if labile and very concentrated but this may be partly offset by ferrimanganiferous mottles acting as sinks for more toxic heavy metals (Vodyanitskii 2006). Even at subtoxic concentrations, Fe and Al can hamper forest nutrition by blanking sorption sites sufficiently to inhibit cationic nutrient uptake, and by immobilising P in co-precipitates of insoluble Al- and Fe-phosphates. The supplies of the other anionic macronutrients, N and S, are also affected by poor aeration, as they are concentrated in organic matter and their release depend on decomposition, which is mainly aerobic (Rasidah 2001, Rasidah *et al.* 2001). Wet soils also facilitate infection by pathogenic fungi such as damping-off in seedlings and root, collar and butt rots in larger stems. Some tree species cope with wet anaerobic subsoils by remaining predominantly shallow-rooted throughout their lives. When combined with the low shear strength of wet soils, this renders them vulnerable to windthrow.

On the plot, the full syndrome of anaerobic constraints appears to operate in the Gleysols (Endoaquepts) of Kampong Pusu series on the lower parts of the floodplain. The situation is more complex in the Stagnosols (Epiaquepts), in which the lower subsoil is better aerated than the horizon above. Caution is needed in assuming that the warmer colours in the lower subsoil indicate better aeration, as the reduction of ferric iron in gleying is an endothermic process and its absence may be partly due to a shortage of organic matter and microbial energy (Stemmler & Berthelin 2003). However, the characterisation of these horizons as freely drained is not based on colour alone, as they are also less compact and water drains freely from auger holes. If their aeration is indeed better, gas exchange with the atmosphere is assumed to bypass the low porosity gleyed horizon above through old root and other biogenic channels. Tip-up treefalls in Awang and Alma series on the plot show that woody roots penetrate the stagnogleyic horizon and into the browner soil beneath.

Stagnogleying is, therefore, likely to impose varying aeration constraints at different tree growth stages. Germination and young seedlings have to cope with the multiple hazards associated with the anoxia in the saturated upper horizons. The compaction of the upper subsoil may physically hinder downward growth of seedling roots. However, stems that survive these conditions and become saplings may eventually root through into the better-aerated and more friable lower subsoil, and enjoy an edaphic environment with less oxygen stress and mechanical impedance. However, even stems that root through to the moderately drained subsoils are likely to be affected by the wet surface layers, especially with respect to collar and butt rot infections.

Moisture stress is important for forests in climates with severe dry seasons but tends to be less significant in aseasonal regimes. Although generally aseasonal, the total rainfall at Pasoh is low enough to mean that ENSO events can involve long dry spells and impose significant moisture stress. The terrace soils appear slightly droughty but their moderate drainage, potential for deep rooting and medium-fine textures suggest substantial reserves of plant available water. Moisture stress is likely to be more intense in the ridge soils (Guha 1969). The droughtiest series is Gajah Mati on convex shedding sites and with rooting depth restricted by dense laterite (Hashim 2003). In contrast, Bungor soils occur on concave receptor sites and has no mechanical barriers to deep rooting (Chan *et al.* 1972). There may be occasional moisture stress in some trees on the Kampong Pusu Gleysols if water-tables fall significantly and leave shallow root systems stranded.

The soils of the plot are quite dystrophic. Although ranges are narrow, nutrient variation may push levels below critical thresholds so that nutrients are effective edaphic differentiae. Comparisons with Tekam Forest Reserve showed that soil nutrients are related to dipterocarp distributions and leaf chemistry at Pasoh (Amir & Miller 1989, 1990, 1992, Amir & Mona 1990). The associations are as or more obvious with less labile forms of soil nutrients than for easily extractable availables (Amir *et al.* 1991). This parallels findings for agricultural tree crops in Peninsular Malaysia (Edgar 1958, Lau *et al.* 1972) and dipterocarp forests on similar soils in Sarawak (Baillie *et al.* 1987, Ashton & Hall 1992, Potts *et al.* 2002, Russo *et al.* 2005, Baillie *et al.* 2006).

The Pasoh landscape appears to be geomorphologically quiescent at present, and the soils and forest are not subject to drastic disturbances. Nonetheless, tree size class distributions indicate that disturbance is significant in the dynamics of the forest (Manokaran & LaFrankie 1990). Windthrow is a major cause of gap formation and some species on floodplains may be particularly vulnerable because of their shallow rooting in wet upper horizons (Gale & Hall 2001, Davies *et al.* 2003). Some soils on the plot are also disturbed by wild pigs, which are abundant at Pasoh (Ickes 2001). The pigs severely disturb the topsoils at their nest sites and when foraging (Ickes *et al.* 2005). These activities mainly affect the upper few decimetres and they do not disrupt subsoils to the same extent as treefall. Nonetheless, the soils are sufficiently affected to be potentially favourable germination and seedling sites for some tree species (Ashton 1976, Plotkin *et al.* 2002).

Most tests of spatial associations of tree species distribution and floristic variation with habitats on the Pasoh plot have used simple topographic attributes as edaphic indicators (He *et al.* 1996, Potts *et al.* 2004), sometimes combined with generalised soil textures (Davies *et al.* 2003) or soil classes (Debski *et al.* 2002, Okuda *et al.* 2004, Nur Supardi *et al.* 2005). About 40% of the 578 commonest tree species on the plot and 44% of 32 palm species (Nur Supardi *et al.* 2005) appear to be edaphic specialists to some extent. Some species distributions clearly correspond closely with the soil pattern (Thomas 2003), but distribution maps (Appanah & Weinland 1993) and torus analyses (Nur Supardi *et al.* 2005) suggest that many of the common dipterocarps are edaphic generalists or only moderately discriminant. There are exceptions, such as the concentration of *Shorea maxwelliana* on terrace soils. Edaphic specialisation may be greater than that appearing at present due to insufficient taxonomic differentiation. *Aporosa falcifera* was initially mapped throughout the plot and appeared to be an edaphic generalist. When taxonomically subdivided, the distributions of the two new species showed some edaphic discrimination (Thomas 2003).

There is less edaphic influence on species distributions reported at Pasoh than in some other dipterocarp forests. Compared with 30–40% at Pasoh, about 85% of the commoner tree species on the Lambir CTFS plot show some degree of edaphic specialisation (Davies *et al.* 2005). Furthermore, no congeneric pairs at Pasoh show the striking edaphic segregation seen between the distributions of *Dryobalanops aromatica* and *D. lanceolata* at Lambir (Hirai *et al.* 1997, Iwasaki *et al.* 1997), and *Mesua ferruginea* and *M. nagassarium* on the Sinharaja CTFS plot in Sri Lanka (Gunatilleke *et al.* 2004, Ashton *et al.* 2006, Gunatilleke *et al.* 2006). The relatively muted edaphic effects at Pasoh were confirmed by Potts *et al.* (2004), who compared environmental niche associations for hundreds of tree species at Pasoh and Lambir. Since they used altitude as the main criterion to define abiotic niche, heterogeneity appeared greater on the rugged Lambir plot than in the subdued topography of Pasoh. However, altitude differences below 500 m asl are unlikely to be ecologically significant per se, and altitude acts as an indicator of other edaphic differentiae (Hall *et al.* 2004). Altitude surrogates different factors in different landscapes, such as soil hydrature at Pasoh, and nutrients and site stability at Lambir.

Interplot comparisons of edaphic effects are more plausible if related taxa are used. Several species of *Scaphium* (Sterculiaceae) occur on both the Pasoh and Lambir plots. The distributions of the two most common species on the Pasoh plot are associated with topography, and both are significantly more frequent on the ridge than elsewhere. However, no intra-generic differences in the distributions were apparent (Yamada *et al.* 2000, 2003). In contrast, *Scaphium* at Lambir shows clear intra-generic differences in edaphic specialisation (Yamada *et al.* 1997). *Aporosa* (Euphorbiaceae) is another genus with multiple species at both Pasoh and Lambir. Inter-specific soil specialisation differences partly account for their clustered distributions on both plots. The effect is clearer at Lambir, and this is attributed to greater intra-plot nutrient variability (Debski *et al.* 2002).

The relatively muted edaphic effects at Pasoh may indicate that restricted aeration is less effective as an interspecific filter than nutrient deficiencies, moisture stress or site instability, and that many species in dipterocarp forests can cope with some variations in soil drainage. Alternatively, variations in soil aeration at Pasoh floodplain soils may be less important than first apparent because of the extensive stagnogleying, as this means that larger stems can root through the saturated horizon into the relatively well aerated lower subsoils.

Pasoh is well suited to further investigation of responses and adaptations of tropical forests to variations in soil drainage and aeration, and also of soil mediation of moisture supply in an aseasonal but marginal climate.

ACKNOWLEDGEMENTS

We thank S Ahmad, Shamizam and H Zairul for participating in the field work, FRIM colleagues for facilitation of the field work and soil analyses. The plot at Pasoh was established and is maintained by FRIM with assistance from the Forest Department of the State of Negri Sembilan, with contributions from the National Science Foundation (USA) grant INT-89-12201, National Institute for the Environment (Japan), the Harvard University (USA) Arnold Arboretum–CTFS Asia Programme, the Smithsonian Tropical Research Institute (USA and Panama), several Man and Biosphere Programme and ROSTEA grants, (UNESCO) grants, and the Conservation Food Health Foundation Inc. IC Ballie received a travel grant from the Arnold Arboretum of Harvard University for his 2005 fieldwork. We are grateful to Wan Juliana for provision of unpublished materials, and to PS Ashton for detailed and constructive comments on an earlier draft.

REFERENCES

Adzmi Y & Suhaimi WC. 1996. Details on soil survey of the 50 ha plot of Pasoh Forest Reserve. Unpublished report.

Allbrook RF. 1973. The soils of the Pasoh Forest Reserve, Negeri Sembilan. *Malaysian Forester* 36: 22–33.

Amir Husni MS & Miller HG. 1989. Influence of soil chemical properties on site carrying capacity of two Malaysian lowland dipterocarp forests. Paper presented at the 4th Dipterocarp Round Table Conference. 12–15 December 1989, Bogor.

Amir Husni MS & Miller HG. 1990. *Shorea leprosula* as an indicator species for site fertility evaluation in dipterocarp forests of Peninsular Malaysia. *Journal of Tropical Forest Science* 3: 101–110.

Amir Husni MS & Miller HG. 1992. Soil fertility and its influence on the stocking of dipterocarp seedlings in the tropical rainforest of Peninsular Malaysia. *Journal of Tropical Forest Science* 4: 189–201.

Amir Husni MS, Miller HG & Appanah S. 1991. Soil fertility and tree species diversity in two Malaysian forests. *Journal of Tropical Forest Science* 3: 318–331.

Amir Husni MS & Mona Z. 1990. Soil and foliar nutrient relationships in selected *Shorea* and *Koompassia* species in two forest reserves, Peninsular Malaysia. *Journal of Tropical Forest Science* 2: 320–330.

Andriesse JP. 1975. *Characteristics and Formation of So-Called Red-Yellow Podzolic Soils in the Humid Tropics (Sarawak, Malaysia)*. Communication 66. Royal Tropical Institute, Amsterdam.

Andriesse JP. 1988. *Nature and Management of Tropical Peat Soils*. Soils Bulletin 59. Food and Agriculture Organisation of United Nations, Rome.

Anonymous. 1987. *Panduan Penyiasatan Tanah*. Jabatan Pertanian Semenanjung Malaysia, Kuala Lumpur.

Appanah S & Weinland G. 1993. *A Preliminary Analysis of the 50-Hectare Pasoh Demography Plot: I Dipterocarpaceae*. Research Pamphlet 112. Forest Research Institute Malaysia, Kepong.

Ashton PS. 1976. Mixed dipterocarp forest and its variation with habitat in the Malayan lowlands: a re-evaluation at Pasoh. *Malayan Forester* 39: 56–72.

Ashton PS & Hall P. 1992. Comparisons of structure among dipterocarp forest of northwestern Borneo. *Journal of Ecology* 80: 459–481.

Ashton PS, Okuda T & Manokaran N. 2003. Pasoh research, past and present. Pp. 1–14 in Okuda T *et al.* (Eds.) *Pasoh. Ecology of a Lowland Rain Forest in Southeast Asia*. Springer, Tokyo.

Ashton MS, Singhakumara BMP & Gamage HK. 2006. Interaction between light and drought affects performance of Asian tropical tree species that have different topographic affinities. *Forest Ecology and Management* 221: 42–51.

Baillie IC. 1996. Soils of the humid tropics. Pp. 256–286 in Richards PW (Ed.) *The Tropical Rain Forest* . Second edition. Cambridge University Press, Cambridge.

Baillie IC, Ashton PS, Court MN, Anderson JAR, Fitzpatrick EA & Tinsley J. 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forest on tertiary sediments in central Sarawak, Malaysia. *Journal of Tropical Ecology* 3: 201–220.

Baillie IC, Ashton PS, Chin SP, Davies SJ, Palmiotto PA, Russo SE & Tan S. 2006. Spatial associations of humus, nutrients and soils in mixed dipterocarp forest at Lambir, Sarawak, Malaysian Borneo. *Journal of Tropical Ecology* 22: 543–553.

Baltzer JL, Thomas SC, Nilus R & Burslem DFRP. 2005. Edaphic specialisation in tropical rain forest trees: physiological correlates and responses to reciprocal transplantation. *Ecology* 86: 3063–3077.

Black CA (Ed.). 1965. *Methods of Soil Analysis. Part 2: Chemical and Microbiological Properties*. American Society of Agronomy, Madison.

Chan HY, Pushparajah E & Sivanadyan K. 1972. A preliminary assessment of the influence of soil morphology and physiography on the performance of *Hevea*. Paper presented at the Second ASEAN Soils Conference. 18–21 July 1972, Jakarta.

Clark DB, Palmer WM & Clark DA. 1999. Edaphic factors and the landscape distribution of tropical rain forest trees. *Ecology* 80: 2662–2675.

Condit R. 1998. *Tropical Forest Census Plots: Methods and Results From Barro Colorado Island, Panama and a Comparison With Other Plots*. Springer-Verlag, Berlin.

Dapper M, De Biot Y, Boukaert W & Debaveye J. 1988. Geomorphology for soil survey: a case study from the humid tropics. *Zeitschrift fur Geomorphologie* (Supplementenband) 68: 21–56.

Davies SJ, Nur Supardi MN, LaFrankie JV & Ashton PS. 2003. The trees of Pasoh forest: stand structure and floristic composition of a 50 ha forest research plot. Pp. 35–50 in Okuda T *et al* (Eds.) *Pasoh. Ecology of a Lowland Rain Forest in Southeast Asia*. Springer, Tokyo.

Davies SJ, Tan S, LaFrankie JV & Potts MD. 2005. Soil-related floristic variation in the hyperdiverse dipterocarp forest in Lambir Ridges, Sarawak. Pp. 22–37 in Roubik DW, Sakai S & Hamid A (Eds.) *Pollination Ecology and Rain Forest Diversity, Sarawak Studies*. Springer-Verlag, New York.

Debski I, Burslem DRFP, Palmiotto PA, LaFrankie JV, Lee HS & Manokaran N. 2002. Habitat preferences of *Aporosa* in two Malaysian forests: implications for abundance and coexistence. *Ecology* 83: 2005–2018.

Duivenvoorden JF & Lips JH. 1995. *A Land–Ecological Study of Soils, Vegetation and Plant Diversity in Colombian Amazonia*. Tropenbos Foundation Series, Wageningen.

Duivenvoorden JF, Svenning JC & Wright SJ. 2002. Beta diversity in tropical forests. *Science* 295: 636–637.

Dumanski J & Ooi CH. 1969.*The Reconnaissance Survey of the Temerloh—Gemas Region, Malaya*. Department of Agriculture, Kuala Lumpur.

Edgar AT. 1958. *Manual of Rubber Planting (Malaya)*. Incorporated Society of Planters, Kuala Lumpur.

Elsenbeer H & Verstessy RA. 2000. Stormflow generation and flowpath characteristics in an Amazonian rainforest catchment. *Hydrological Processes* 14: 2367–2381.

Eswaran H & Noordin MWD. 1980. A scanning electron microscope evaluation of the fabric and mineralogy of some soils from Malaysia. *Soil Science Society of America Journal* 44: 855–861.

Eyles RJ. 1970. *Physiographic Implications of Laterite in West Malaysia*. Bulletin 3. Geological Society of Malaysia, Kuala Lumpur.

FAO. 1998. *World Reference Base for Soils*. World Soil Resources Report 84. Food and Agriculture Organisation of United Nations, Rome.

FAO. 2006. *World Reference Base for Soils: A Framework for International Classification, Correlation and Communication*. World Soil Resources No. 103. Food and Agriculture Organisation of United Nations, Rome.

Gale N & Hall P. 2001. Factors influencing the modes of tree death three Bornean rain forests. *Journal of Vegetation Science* 12: 337–346.

Guha MM. 1969. A preliminary assessment of moisture and nutrients in soils as factors for production of vegetation in West Malaysia. *Malaysian Forester* 32: 423–433.

Guha MM & Pushparajah E.1966. Response to fertilisers in relation to soil type. *Rubber Research Institute of Malaysia Planters Bulletin* 87: 178–183.

Guha MM & Yeow KH. 1966a. Contents of major nutrients in rubber-growing soils of Malaya. Pp. 171–183 in *Proceedings of Second Malaysian Soils Conference.* 12 February 1966, Kuala Lumpur.

Guha MM & Yeow KH. 1966b. Soil and leaf nutrient status in relation to soil type. *Rubber Research Institute of Malaysia Planters Bulletin* 87: 170–177.

Gunatilleke CVS, Gunatilleke IAUN, Esufali S, Ashton PMS, Burslem DFRP & Ashton PS. 2006. Species–habitat associations in a Sri Lankan dipterocarp forest. *Journal of Tropical Ecology* 22: 371–384.

Gunatilleke CVS, Gunatilleke IUAN, Ethugala AUK & Esufar S. 2004. *Ecology of Sinharaja Rain Forest and Forest Dynamics Plot in Sri Lanka's World Natural Heritage Site.* WHT Publishers, University of Peradeniya, Peradeniya.

Hall JS, Gregoire TS, Ashton MS & Mcjenna J. 2004. Habitat characterisation underestimates the role of edaphic factors controlling the distribution of *Entandrophragma. Ecology* 85: 2171–2183.

Hashim MN. 2003. Growth of teak (*Tectona grandis*) on lateritic soil at Mata Ayer Forest Reserve, Perlis. *Journal of Tropical Forest Science* 15: 190–198.

He FL, Legendre P & LaFrankie JV. 1996. Spatial patterns of diversity in a tropical rain forest in Malaysia. *Journal of Biogeography* 23: 57–74.

Hirai H, Matsumura H, Hirotani H, Sakurai K, Ogino K & Lee HS. 1997. Soils and distribution of *Dryobalanops aromatica* and *D. lanceolata* in mixed dipterocarp forest—a case study at Lambir Ridges National Park, Sarawak, Malaysia. *Tropics* 7: 21–33.

Ickes K. 2001. Hyper-abundance of native wild pigs (*Sus scrofa*) in lowland dipterocarp rain forest of Peninsular Malaysia. *Biotropica* 33: 682–690.

Ickes K, Paciotek CJ & Thomas SC. 2005. Impacts of nest construction by native pigs (*Sus scrofa*) on lowland Malaysian rain forest saplings. *Ecology* 86: 1540–1547.

Iwasaki A, Takahashi S, Yamakura T, Kanzaki M, Ogino K, Chai EOK, Lee HS & Ashton PS. 1997. Fractal dimensions of the distribution of *Dryobalanops lanceolata* in a tropical rain forest at Lambir, Sarawak. *Tropics* 7: 1–8.

Kemper C & Bell DT. 1985. Small mammals and habitat structure in a lowland rain forest of Peninsular Malaysia. *Journal of Tropical Ecology* 1: 5–22.

Landon RJ. (Ed.) 1991. *Booker Tropical Soil Manual.* Second edition. Longman, Harlow.

Lau CH, Pushparajah E & Yap WC. 1972. Evaluation of various soil-K indices in relation to nutrition, growth and yield of *Hevea brasiliensis.* Paper presented at the Second ASEAN Soils Conference. 18–21 July 1972, Jakarta.

Law WM & Leamy ML. 1966. Factors involved in the genesis of some shale-derived soils in Malaya. Pp. 105–114 in *Proceedings of Second Malaysian Soils Conference.* 12 February 1966, Kuala Lumpur.

Leamy ML. 1966. Soil classification in Malaya. *Proceedings of Second Malaysian Soils Conference.* Kuching.

Leigh EG Jr. 1992. *Tropical Forest Ecology. A View from Barro Colorado Island.* Oxford University Press, New York.

Manokaran N & LaFrankie JV. 1990. Stand structure of Pasoh Forest Reserve, a lowland rainforest in Peninsular Malaysia. *Journal of Tropical Forest Science* 3: 14–24.

Manokaran N, LaFrankie JV, Kochummen KM, Quah ES, Klahn JE, Ashton PS & Hubbell SP. 1990. *Methodology for Fifty Hectares Research Plot at Pasoh Forest Reserve.* Research Pamphlet 104. Forest Research Institute Malaysia, Kepong.

Manokaran N, Nur Supardi MN, Awang M, Okuda T, Suzuki M, Adachi N & Niiyama K. 2001. Estimation of above-ground biomass in a lowland dipterocarp forest by 3D photogrammetric analysis. Pp. 17–28 in Okuda T (Ed.) *Research Report* of the NIES/FRIM/UPM Joint Research Project 2000. National Institute for Environmental Studies, Tsukuba.

Noguchi S, Nik AR & Tani M. 2003. Rainfall characteristics of tropical rainforest at Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia. Pp. 51–58 in Okuda T *et al.* (Eds.) *Pasoh. Ecology of a Lowland Rain Forest in Southeast Asia.* Springer, Tokyo.

Nor YM. 1981. The effect of soil depth on biological activity and nitrogen changes in soils under different vegetation. *Malaysian Applied Biology* 10: 41–48.

Nur Supardi MN, Suzuki R, Kachi N, Numata S & Okuda T. 2005. Spatial pattern and habitat associations of dipterocarp species in a Malaysian tropical rain forest. Pp. 38–43 in Okuda T (Ed.) *Research Report* of the NIES/FRIM/UPM Joint Research Project 2004. National Institute for Environmental Studies, Tsukuba.

Okuda T, Manokaran N, Matsumoto Y, Niiyama K, Thomas SC & Ashton PS (Eds.). 2003a. *Pasoh. Ecology of a Lowland Rain Forest in Southeast Asia.* Springer, Tokyo.

Okuda T, Suzuki S, Adachi N, Yoshida K, Niiyama K, Supardi MN, Azman NH, Manokaran N, Mazlan H. 2003b. Logging history and its impact on forest structure and species composition in the Pasoh forest reserve —implications for the sustainable management of natural resources and landscapes. Pp. 15–34 in Okuda T *et al.* (Eds.) *Pasoh. Ecology of a Lowland Rain Forest in Southeast Asia.* Springer, Tokyo.

Okuda T, Azman NH, Manokaran N, Saw LG, Amir HMS & Ashton PS. 2004. Local variation of canopy structure in relation to soils and topography and implications for species diversity in a rain forest of Peninsular Malaysia. Pp. 221–241 in Losos EC & Leigh EG Jr (Eds.) *Forest Diversity and Dynamism.* Chicago University Press, Chicago.

Palmiotto PA, Davies SJ, Vogt KA, Ashton MS, Vogt DJ & Ashton PS. 2004. Soils-related habitat specialisation in dipterocarp forest tree species in Borneo. *Journal of Ecology* 92: 609–623.

Panton WP. 1956. Types of Malayan laterites and factors affecting their distribution. *Proceedings of Sixth International Congress of Soil Science* (*Commission V*) 69: 419–423.

Paramananthan S. 1987. *Field Legend for Soil Surveys in Malaysia.* Penerbit Universiti Pertanian Malaysia, Serdang.

Phillips OL, Vargas PN, Montegado AL, Cruz AP, Churpe-Zans ME, Sanchez WG, Yli-Halla MM & Rose S. 2003. Habitat association among Amazonian tree species: a landscape scale approach. *Journal of Ecology* 91: 757–775.

Plotkin JB, Chave JB & Sahton PS. 2002. Cluster analysis of spatial patterns in Malaysian tree species. *American Naturalist* 160: 629–644.

Potts MD, Ashton PS, Kaufman LS & Plotkin JB. 2002. Habitat patterns in tropical rain forests: a comparison of 105 plots in northwest Borneo. *Ecology* 83: 2782–2797.

Potts MD, Davies SJ, Bossert WH, Tan S & Nur Supardi MN. 2004. Habitat heterogeneity and niche structure of trees in two tropical rain forests. *Oecologia* 139: 446–453.

Rasidah WAK. 2001. Organic matter decomposition rate in a natural forest of Pasoh Forest Reserve. Pp. 1–9 in Okuda T (Ed.) *Research Report* of the NIES/FRIM/UPM Joint Research Project 2000. National Institute for Environmental Studies, Tsukuba.

Rasidah WAK, Bekku Y, Adachi M, Okuda T & Koizumi H. 2001. Spatial variations in soil respiration rate in a tropical primary forest, secondary forest and oil palm plantation. Pp. 10–16 in Okuda T (Ed.) *Research Report* of the NIES/Joint Research Project 2000. National Institute for Environmental Studies, Tsukuba.

Rogstad SH. 1990. The biosystematics and evolution of the *Polyalthia hypoleuca* complex (Annonaceae) of Malesia. II Comparative distributional ecology. *Journal of Tropical Ecology* 6: 387–408.

Russo SE, Davies SJ, King DA & Tan S. 2005. Soil-related performance variation and distributions of tree species in a Bornean rain forest. *Journal of Ecology* 93: 879–889.

Salleh MN. 1968. *Forest Resources Reconnaissance Survey of Malaysia: Jelubu District, Negri Sembilan.* Forest Research Institute, Kepong.

Scrivenor JB. 1909. The use of the word laterite. *Geographical Magazine* 6: 574–575.

Soil Survey Staff. 1993. *Soil survey manual.* Handbook 18. National Resources Conservation Service, US Department of Agriculture, Washington, DC

Soil Survey Staff. 1999. *Soil Taxonomy.* Second edition. Agricultural Handbook 436. United States Department of Agriculture, Washington DC.

Soil Survey Staff. 2006. *Keys to Soil Taxonomy.* 10th edition. United States Department of Agriculture, Washington DC.

Stemmler SJ & Berthelin J. 2003. Microbial activity as a major factor in the mobilization of iron in the humid tropics. *European Journal of Soil Science* 54: 725–733.

Tani M, Abdul Rahim N, Ohtani Y, Yasuda Y, Sahat MM, Baharuddin K, Takanashi S, Noguchi S, Zulkifli Y & Watanabe T. 2003. Characteristics of energy exchange and surface conductance of a tropical rain forest in Peninsular Malaysia. Pp. 73–86 in Okuda T *et al.* (Eds.) *Pasoh. Ecology of a Lowland Rain Forest in Southeast Asia.* Springer, Tokyo.

Thigalingam K & Grimme H. 1976. The evaluation of K status of some Malaysian soils by means of ultra-filtration. *The Planter* 52: 83–89.

Thomas SC. 2003. Comparative biology of tropical trees: a perspective from Pasoh. Pp. 171–194 in Okuda T *et al.* (Eds.) *Pasoh. Ecology of a Lowland Rain Forest in Southeast Asia.* Springer, Tokyo.

Tie YL & Kueh HS. 1979. *A Review of Lowland Organic Soils of Sarawak.* Technical Paper 4. Department of Agriculture, Kuching.

Tuomisto H, Ruoloainen K & Yli-Halla M. 2003. Dispersal, environment and floristic variation of Western Amazonian forests. *Science* 299: 241–244.

Valencia R, Foster RB, Villa G, Condit R, Svenning JC, Hernandez C, Losos E, Margaard E & Balsev H. 2004. Trees species distribution and local habitat variation in the Amazon. Large forest plot in eastern Ecuador. *Journal of Ecology* 92: 214–229.

Vodyanitskii YN. 2006. The composition of Fe–Mn nodules as determined by synchrotron X-ray analysis. *Eurasian Soil Science* 39: 147–156.

Walkley A. 1947. A critical examination of a rapid method for determining organic carbon in soils: effect of variations in digestion conditions and of inorganic soil constituents. *Soil Science* 63: 251–263.

Wan Juliana WA. 2001. Habitat specialisation of tree species in a Malaysian rain forest. PhD thesis, University of Aberdeen, Scotland.

Webb CO & Peart DR. 2000. Habitat association of trees and seedlings in a Bornean rain forest. *Journal of Ecology* 88: 464–478.

Wong YK & Whitmore TC. 1970. On the influence of soil properties on species distribution in a Malayan lowland dipterocarp forest. *Malayan Forester* 33: 42–54.

Wuest RAJ, Bustin RM & Lavkulich LM. 2003. New classification systems for tropical organic-rich deposits based on studies of the Tasek Bera basin, Malaysia. *Catena* 53: 133–164.

Wyatt-Smith J. 1961. A note on the freshwater swamp, lowland and ridge forest types of Malaya. *Malayan Forester* 33: 42–54.

Yamada T, Yamakura T, Kanzaki M, Itoh A, Okhubo T, Ogino K, Chai EOK, Lee HS & Ashton PS. 1997. Topography dependent spatial pattern and habitat segregation of sympatric *Scaphium* species in a tropical rain forest at Lambir, Sarawak. *Tropics* 7: 57–66.

Yamada T, Itoh A, Kanzaki M, Yamakura T, Suzuki E & Ashton PS. 2000. Local and geographical distribution for a tropical tree genus, *Scaphium* (Stereculiaceae), in the Far East. *Plant Ecology* 148: 23–30.

Yamada T, Okuda T & Manokaran N. 2003. Microhabitat preference of two sympatric *Scaphium* species in a 50 ha plot in Pasoh. Pp. 137–147 in Okuda T *et al.* (Eds.) *Pasoh. Ecology of a Lowland Rain Forest in Southeast Asia.* Springer, Tokyo.

Yamashita T, Kasuya N, Rasidah WK, Suhaimi WC, Quah ES & Okuda T. 2003. Soils and below ground characteristics of Pasoh Forest Reserve. Pp. 89–109 in Okuda T *et al.* (Eds.) *Pasoh. Ecology of a Lowland Rain Forest in Southeast Asia.* Springer, Tokyo.

Yamashita T & Takeda T. 2003. Soil nutrient flux in relation to trenching effects under two dipterocarp forest sites. Pp. 59–72 in Okuda T *et al.* (Eds.) *Pasoh. Ecology of a Lowland Rain Forest in Southeast Asia.* Springer, Tokyo.