Spatial associations of humus, nutrients and soils in mixed dipterocarp forest at Lambir, Sarawak, Malaysian Borneo

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Abstract: Discrete humus layers are common on podzols under temperate coniferous and tropical heath forests, and patchy layers also occur under some temperate broadleaved forests on non-podzolic soils. We used multiple data sets to test the reported association of humus with oligotrophic but non-podzolic soils under non-heath dipterocarp forest at Lambir, Sarawak. We examined the distribution, morphology and nutrient dynamics of necromass on soils derived from sandstone and shale. Concentrations of the main mineral nutrients were lower in fresh litter on the very oligotrophic sandstone soils than on shale. The rates of litterfall were similar, so that annual litterfall fluxes of all nutrients were lower on sandstone. The lower nutrient concentrations and fluxes in the litter on sandstone resulted in slower decomposition, longer residence times and larger standing crops of forest-floor necromass, with lower concentrations of nutrients. The necromass on sandstone sequestered significantly more N, K and Mg but less Ca and Mn than on shale, with no significant difference for P. The variations in necromass nutrient dynamics were associated with morphological differences. There were mats of densely rooted humus under the litter on sandstone, whereas litter lay directly over the mineral topsoil on shale. Spatial associations with soil nutrients were weak for necromass thickness, but clear for humus. The proportions of nutrients in the litterfall and necromass reflected the stoichiometric profiles of the soils. We attribute the differences in necromass nutrient dynamics and their association with soil reserve nutrients to lower rates of nutrient replenishment from the weathering of sandstone than from shale. Necromass characteristics are robust field indicators of multivariate edaphic differences in these and other tropical forests on Acrisols/Ultisols derived from Tertiary clastic sediments.

**Key Words:** Borneo, dipterocarp forest, humus, litter, reserve nutrients, stoichiometry, weathering

INTRODUCTION

Many tropical forests grow in soils with low contents of available nutrients (Baillie 1996). A number of forest processes and features appear to be advantageous in these oligotrophic conditions. Nutrient conservation mechanisms operating at single plant level include intensive acquisition (Comerford 2005), efficient internal use (Paoli *et al.* 2005) and substantial resorption from senescent tissues (Kobe *et al.* 2005). Long leaf life, slow growth and low mortality rates (Russo *et al.* 2005)

also appear to be parsimonious of nutrients. There are also community-level processes and features that tend to protect against site losses of nutrients to particulate erosion or ionic leaching. Thick, continuous, and persistent layers of litter and humus on the forest floor dissipate the kinetic energy and erosive potential of throughfall. Dense nets of near-surface roots bind upper soil horizons, and are able to absorb ionic nutrients soon after they are mineralized.

The attribution of nutrient conservation benefits to thick necromass and surface root mats is more plausible if they are significantly associated with sites of low nutrient status. The long-term ecological research (LTER) plot at Lambir in northern Sarawak, Malaysian Borneo (Figure 1) is a good place to test for such associations, as
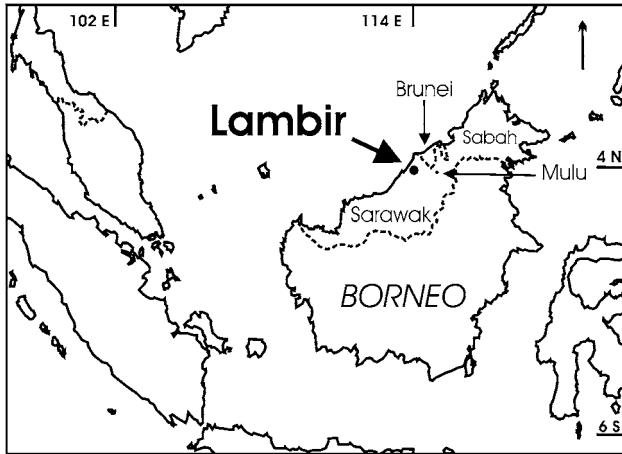
Figure 1. Location of Lambir National Park and LTER plot, and tropical forest ecological research sites in Brunei and at Mulu (northern Sarawak).

it was purposely sited to encompass wide differences in forest and soils. The intentional heterogeneity, combined with its location in the Bornean heartland of dipterocarp diversity (Ashton 1989, 1995), makes the mixed dipterocarp forest (MDF) on the plot extremely diverse, and it has the highest tree species richness documented in the palaeotropics (Lee *et al.* 2002a, Palmiotto *et al.* 2004).

Much of the variation in forest floristics, structure and dynamics on the plot is associated with a gradient from very oligotrophic soils on sandstone to less oligotrophic shale soils (Davies 2001, Debski *et al.* 2002, Hirai *et al.* 1997, Lee *et al.* 2002a, Nagamasu & Momose 1997, Palmiotto 1998, Palmiotto *et al.* 2004, Potts *et al.* 2004, Yamada *et al.* 1997, Yamakura *et al.* 1996). Davies *et al.* (2005) concluded that a substantial proportion of the plot's tree flora consists of edaphic specialists, and Russo *et al.* (2005) showed that the forests on various soil types differ considerably in their demographic dynamics, with lower mortality and slower growth in sandstone-specialist species.

Several studies have noted that there are rooted humus mats on the surfaces of sandstone soils but not on shale. The difference was sufficiently striking for the designation of the sandstone soils as Humults and the shale soils as Udults (Nagamasu & Momose 1997, Palmiotto *et al.* 2004, Potts *et al.* 2004). Even where thin, surface organic layers can have substantial effects on edaphic conditions, such as sequestration of nutrients, physical protection of the sequestered nutrients and the underlying mineral soils against erosion, and mediation of gas exchanges between soils and the atmosphere (Dyke 1996). Organic surfaces also differ from bare mineral topsoils as environments for seed germination and seedling development with respect to hydrature, mechanical penetrability, shading, acidity

and nutrient availability, organic toxins and stimulants, and the potential for inoculation by mutualist or pathogenic microbes (Itoh 1995, Molofsky & Augspurger 1992, Palmiotto 1998).

As ecological and pedological terminologies for surface organic materials vary somewhat, we define our terms as follows: necromass includes all discrete and unmixed, non-saturated organic matter on the surface of well-drained soils; litter is the upper, loose or slightly compacted part of the necromass with still discernible tissue structures; humus is the lower amorphous or fibrous compacted part; soil organic matter is material mixed into the underlying mineral soil; soil fertility includes all aspects of the capacity to provide for edaphically unimpeded forest growth; hydrature encompasses all water supply and root aeration factors in soil fertility. We were mainly concerned with nutrient fertility, which is the soil's capacity to supply nutrients in sufficient quantities, non-antagonistic proportions, and forms assimilable by root systems. Available nutrients were those removed from soils by mild extractants; reserve nutrients were those extracted by digestion with concentrated HCl.

Earlier studies characterized edaphic conditions on the plot in terms of altitude, topography, and available nutrients in the topsoils. The data were recently extended to include nutrients in subsoils and in less labile forms. This study integrated multiple data sets from the plot to test: (1) Whether and how fresh litter and litterfall nutrient fluxes differ on sandstone and shale soils; (2) How differences in litterfall relate to the morphology and nutrient dynamics of necromass; and (3) How the spatial distributions of necromass components and their nutrient dynamics relate to soil types and attributes.

METHODS

Study site

The LTER plot at Lambir, Sarawak, Malaysian Borneo, is part of the pantropical network coordinated by the Center of Tropical Forest Science (CTFS). It was established in 1991, and its vegetation was inventoried in 1992–3 and re-censused in 1997 and 2002–3, using standard CTFS methods (Condit 1998). Structurally the forest is typical of Bornean MDF, with tall, slim-boled and high-buttressed trees, a dense irregular canopy at 35–50 m, and emergents occasionally over 60 m. Basal areas are moderate, at 35–45 m^2 ha^{-1}, but above-ground biomass is estimated to average over 500 t ha^{-1} (Ashton 1978, Lee *et al.* 2002a, Yamakura *et al.* 1986). The plot contains about 1200 species of trees and saplings > 1 cm diameter at reference height (Potts *et al.* 2004). Dipterocarps of eight genera and 87 species dominate the larger size classes (Lee *et al.* 2002b).
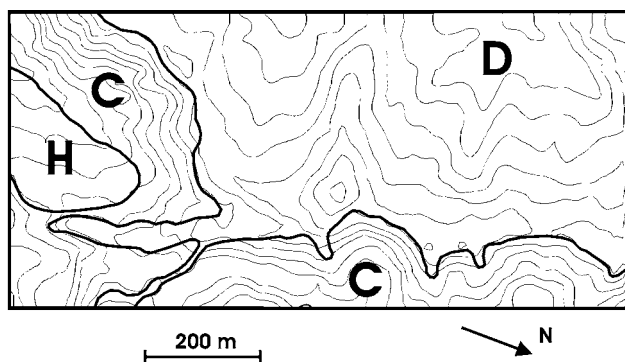
Figure 2. Generalized topography and soils of Lambir LTER plot. Contours are at 10-m intervals from 110 to 250 m above sea level. H = clays on shale dipslope; D = loams on sandstone dipslope; C = shallow and immature soils on scarp complex.

The plot is located at 4°11′N, 114° 01′E in Taman Negara Bukit Lambir (Lambir Hills National Park), Miri District, Sarawak, Malaysia, about 10 km from the north-west-facing coast of Borneo (Figure 1). It covers 52 ha and measures 1.04 × 0.5 km, corrected for slope, and is pegged out as 1300 20-m permanent quadrats (Yamakura *et al.* 1995). The mean annual rainfall is 2500–2800 mm, which is distributed more or less aseasonally, but is heavier in November–March (Kumagai *et al.* 2005). Shales and quartzitic–feldspathic sandstones of the Miocene–Pliocene Lambir Formation underlie the plot. The plot is located on the upper part of a low (< 250 m) dissected cuesta spur in a pericoastal range of low hills. The terrain is rugged, with internal relief of about 140 m and many slopes steeper than 50%. The main topographic elements on the plot are: an extensive elevated dipslope on sandstone in the north and west; a lower and less extensive dipslope on shale in the south; and an intervening complex of steep and unstable scarp slopes and streambeds on mixed lithology in the east and south. This study used data only from relatively stable dipslope sites (D and H, Figure 2).

Soils

In 2001 we sampled 501 mineral topsoils, at 5–15 cm, on 433 quadrats. The samples were analysed at the Sarawak Agricultural Research Centre, Semongok, for: pH; total organic C by dry combustion at 600 °C with a LECO RC-412 carbon determinator; total N by dry combustion with a LECO FP-528 nitrogen analyser; exchangeable cations by leaching with neutral 1M ammonium acetate and assay by inductively coupled plasma (ICP) spectrophotometry; available P by Bray 2 extraction and ICP; and total P by digestion with concentrated HNO_3 and $HClO_4$ and assay by ICP (Chin 2002). This study used data from 231 quadrats on dipslopes.

In 2003 we sampled the topsoils (0–10 cm) and subsoils (45–55 cm) on 60 quadrats. The samples were analysed at Semongok by the same methods as above, except for the omission of total P and the addition of reserve P, K, Ca, Mg, Fe, Mn, Cu, Zn and B, which were extracted by digestion with concentrated HCl and assayed by ICP. This study used data from 46 dipslope quadrats. The soil map and morphological data were derived from the descriptions of 60 dipslope soil profiles in 1971, and from 189 augerings to 1.2 m depth in dipslope quadrats in 2003.

Necromass

We measured the thickness of undifferentiated necromass on 1295 quadrats in 1994–5. We sampled litterfall in 3–6 traps (0.5 × 0.5 m) per site on each of four sites on each of the two soil types at 2-wk intervals for 21 mo. We took four necromass samples at the same sites on four occasions over 12 mo. Single values for necromass residence times for each soil were estimated from the mass ratios of mean necromass to mean litterfall. We set out 36 litterbags (15 × 15 cm, 1-mm mesh) at each of three sites on each soil type, and collected 11, 10, 10 and 5 bags per site at 0, 4, 8 and 12 mo respectively. Nutrient analyses of the samples from three randomly selected bags at month zero from each site were taken to characterize the nutrient concentrations and contents of fresh litter. The litterfall, litterbag and necromass samples were analysed for nutrients at Yale University, USA, by dry ashing or oxidation with acidified dichromate, extraction with concentrated mineral acids, and assay by ICP (Palmiotto 1998).

In 2003 we assessed the proportions of surface with necromass cover and measured the necromass strata on 189 dipslope quadrats. Because of variable compaction and leaf curl (Molofsky & Augspurger 1992), we quantified litter as the number of layers of overlapping leaves within each of the following strata: dry, intact, separate and often curled leaves; dark, moist, flat, and more or less intact leaves weakly bonded by moisture and mucilage; and greyish laminar fragments and venal skeletons densely matted by hyphae. We quantified the underlying reddish brown, densely rooted humus by depth.

Statistical analyses

We assessed the statistical significances of differences between means with t-tests, and between proportions with chi-squared. Interrelationships among all of the necromass and soil chemical variables, including the micronutrients, in the 2003 data were examined with unrotated Principal Components Analysis (PCA), after the omission of linearly dependent variables and a scree plot

to determine the number of components. All tests used SPSS, Version 12.0.

RESULTS

The soils on the sandstone and shale dipslopes (D and H, Figure 2) were pedologically well developed, with clear horizonation and systematic increases in clay, blocky structures, clayskins and firmness with depth. The soils were moderately weathered, and most had soft stones within 1 m and *in situ* weathered rock (saprolite) within 2 m. The mainly brownish or reddish yellow subsoil colours indicated that the soils were well drained. The topsoils were slightly darkened to only a few centimetres and few mineral particles were seen in the necromass, indicating limited pedoturbation. Textures ranged from loamy sand over sandy loam on sandstone to silty clay over clay on shale. Intercalation of the shale and sandstone beds gave some regoliths of mixed lithology and a textural continuum between the extremes. The coarse- and medium-textured soil series on the sandstone dipslope do not differ significantly with respect to most nutrients (S. Tan, unpubl. data), and were treated in this study as a single group. The sandstone soils were deeper, with saprolite at 80–220 cm, compared with 50–150 cm in shale soils. Even in the coarsest-textured soils there were no visible traces of incipient podzolization, such as: greyish E horizons in the lower topsoil, from which iron has been eluviated; dark mid-profile B_h horizons, into which humus has been illuviated; or bright rust-coloured lower subsoil B_s horizons, which have been enriched with illuvial iron and/or aluminium.

The necromass on the shale soils consisted of thin litter directly overlying the mineral topsoil, sometimes with a thin, non-humic surface root mat. The necromass on the sandstone soils was deeper and more stratified, with thicker and more layered litter and a discrete humus layer densely matted by reddish, horizontal fine and medium roots. There were few vertical sinker roots into the underlying mineral soil, and the whole necromass layer could be lifted off the surface like a carpet in places. Many fungal hyphae but few arthropods were seen in the necromass. Although there were common small termitaria, termites were seen only in already rotten coarse woody debris.

The increases in clay content and redness with depth qualified the soils as Red Yellow Podzolic (RYP) in the Sarawak soil classification (Teng 1996). The sandstone soils were Arenic and Ferralic Acrisols and the shale soils were Haplic Acrisols in FAO (1998). The mature RYP on the plot were Paleudults or Kandiudults in Soil Taxonomy (Soil Survey Staff 1999), with the sandstone soils in the Psammic and Hapludoxic and the shale soils in the Typic subgroups.

Contents of organic matter in the topsoils were moderate, with organic carbon at less than 2% (Table 1), decreasing to less than 1% within 20 cm (I. C. Baillie, unpubl. data). The soils were acidic, and all available nutrients were low to very low, except for exchangeable Mg in the shale soils (Landon 1991).

Although the sandstone topsoils had lower contents of all available nutrients, the differences were consistently significant only for exchangeable Mg and, in the 2001 samples only, for exchangeable K and Ca. The reserve contents of Ca and P were low, but those of Mg and K were moderate. The contents of all reserve nutrients were lower in the sandstone soils than on shale, and many of the differences were significant, especially in the subsoils. The fertility contrast between the soils was clearer for reserve than available nutrients.

The concentrations in fresh litter were generally low for P and N, high for Mg and K (Table 2), and low for Ca on sandstone, but moderate on shale. Litter concentrations of all nutrients were significantly higher on shale than on sandstone, with several-fold differences for P, Ca and Mn, but less than double for N, Mg and K.

The rates of litterfall on the two soil types were virtually equal, at just over $8 \, \text{t ha}^{-1} \, \text{y}^{-1}$. The combination of equal litterfalls and marked differences in concentrations meant that the rates of flux in litterfall were significantly lower on sandstone for all nutrients (Table 2).

The standing forest-floor necromass on sandstone soils was more than threefold larger than on shale, due to slower decomposition and longer residence times (Table 3), as confirmed by litterbag monitoring (Palmiotto 1998). The necromass concentrations of all nutrients on sandstone were lower than on shale. As in the fresh litter and litterfall, the differences in necromass concentrations were especially marked for Ca and Mn, and outweighed the greater mass so that the necromass stocks of these nutrients were significantly smaller on sandstone, whereas the larger necromass outweighed the lower concentrations for N, K and Mg, and necromass on sandstone sequestered significantly larger stocks of these nutrients than on shale (Table 3). The mass and dilution effects balanced out for P, and necromass P stocks on the two soils were not significantly different.

Total necromass and litter were thicker on sandstone than on shale, but the differences were not striking. For humus, however, the contrast between the thick and extensive cover on sandstone and the thinner and patchier layers on shale was obvious and significant (Table 4).

The PCA scree plot indicated that four components were sufficient. These gave an interpretable structure, in which the upper litter variables were only weakly associated with the edaphic axes (Table 5). Humus thickness loaded negatively on the main nutrient fertility component, which was defined mainly by the reserve forms of

Table 1. Exchangeable (Exch) and reserve (Res) nutrients, total exchangeable bases (TEB), cation exchange capacity (CEC), and base saturation (BS) in sandstone and shale soils on the Lambir LTER plot. Differences between soil means were tested with t-tests and are reported as associated probabilities (ns = not significant, *P < 0.05, **P < 0.01).

| | 2001 | | | 2003 | | | | | |
| | Topsoil (5 – 15 cm) | | | Topsoil (0–10 cm) | | | Subsoil (45 – 55 cm) | | |
	Sandstone	Shale	Significance of difference	Sandstone	Shale	Significance of difference	Sandstone	Shale	Significance of difference
n	180	51		38	8		38	8	
Organic C (%)	1.02	0.97	ns	1.91	1.21	*		no data	
Total N (%)	0.10	0.10	ns	0.14	0.12	ns		no data	
C:N	10.5	9.7	ns	13.6	9.6	**		no data	
pH (H_2O)	4.6	4.4	**	4.5	4.5	ns	4.7	4.7	ns
Exch Ca ($cmol^+ kg^{-1}$)	0.22	0.36	**	0.44	0.60	ns	0.21	0.27	ns
Exch Mg ($cmol^+ kg^{-1}$)	0.13	0.26	**	0.23	0.62	**	0.15	0.71	**
Exch K ($cmol^+ kg^{-1}$)	0.12	0.14	*	0.15	0.19	ns	0.10	0.16	*
Exch Na ($cmol^+ kg^{-1}$)	0.06	0.08	ns	0.10	0.15	*	0.10	0.18	*
TEB ($cmol^+ kg^{-1}$)	0.53	0.85	**	0.92	1.56	*	0.56	1.33	**
CEC ($cmol^+ kg^{-1}$)	7.61	7.21	ns		no data				
BS (%)	7.0	11.8	**		no data				
Avail. P ($mg kg^{-1}$)	1.4	1.4	ns	4	4	ns	3	3	ns
Total P ($mg kg^{-1}$)	49	108	**		no data				
Res. P ($mg kg^{-1}$)		No data		90	129	**	78	123	**
Res Ca ($mg kg^{-1}$)				133	170	ns	133	127	ns
Res Mg ($mg kg^{-1}$)				733	1421	**	869	1667	**
Res K ($mg kg^{-1}$)				2356	4231	**	2746	4630	**
Res Fe ($mg kg^{-1}$)				7808	14564	**	9853	16021	**
Res Mn ($mg kg^{-1}$)				5	89	**	3	68	**
Res Cu ($mg kg^{-1}$)				2	3	*	2	3	ns
Res Zn ($mg kg^{-1}$)				10	23	**	11	25	**
Res B ($mg kg^{-1}$)				18	33	**	22	38	**

Table 2. Nutrient concentrations in fresh litter, litterfall and annual litterfall nutrient fluxes (mean ± SE) on sandstone and shale soils, Lambir LTER plot. Differences between soil means were tested with t-tests, and are reported as associated probabilities (ns = not significant, *P < 0.05, **P < 0.01).

	Sandstone	Shale	Significance of differences
Nutrient concentration in fresh litter (n = 9)			
N (%)	0.9 ± 0.03	1.20 ± 0.02	**
P ($mg kg^{-1}$)	119 ± 6	296 ± 16	**
Ca ($mg kg^{-1}$)	2106 ± 100	7419 ± 479	**
Mg ($mg kg^{-1}$)	1738 ± 59	2451 ± 107	**
K ($mg kg^{-1}$)	2847 ± 163	3899 ± 252	**
Mn ($mg kg^{-1}$)	163 ± 14	697 ± 51	**
Annual litterfall (n = 4)			
($t ha^{-1} y^{-1}$)	8.20 ± 2.1	8.29 ± 0.2	ns
Annual nutrient flux in litterfall (n = 9)			
N ($kg ha^{-1} y^{-1}$)	72.5 ± 10.5	91.9 ± 1.6	*
P ($kg ha^{-1} y^{-1}$)	1.2 ± 0.1	2.4 ± 0.2	*
Ca ($kg ha^{-1} y^{-1}$)	21.5 ± 3.3	65.9 ± 0.3	*
Mg ($kg ha^{-1} y^{-1}$)	13.9 ± 1.9	16.0 ± 0.3	*
K ($kg ha^{-1} y^{-1}$)	16.2 ± 2.1	21.3 ± 0.6	*
Mn ($kg ha^{-1} y^{-1}$)	1.3 ± 0.2	3.2 ± 0.1	*

Table 3. Mass, residence times and sequestered nutrient contents (mean ± SE) of total standing necromass, Lambir LTER plot. Differences between soil means were tested with t-tests, and are reported as associated probability levels (ns = not significant, *P < 0.05).

	Sandstone	Shale	Significance of differences
Standing crop of total necromass ($t ha^{-1}$)	12.3	3.9	
Residence time of necromass (y)	1.53	0.48	
Sequestered nutrient contents of standing crop of necromass (n = 4)			
N ($kg ha^{-1}$)	90.9 ± 13.8	38.0 ± 3.1	*
P ($kg ha^{-1}$)	2.25 ± 0.3	1.62 ± 0.5	ns
Ca ($kg ha^{-1}$)	14.7 ± 2.4	32.4 ± 6.4	*
Mg ($kg ha^{-1}$)	10.6 ± 1.2	5.7 ± 0.7	*
K ($kg ha^{-1}$)	7.93 ± 2.83	2.83 ± 0.4	*
Mn ($kg ha^{-1}$)	0.83 ± 0.08	1.92 ± 0.30	*

Standing crops are single values. Residence times are quotients of standing crops/rates of litterfall (Palmiotto 1998).

DISCUSSION

Casual observation can exaggerate contrasts in necromass between tropical forests (Wieder & Wright 1995), but our results confirmed earlier observations of thicker, more continuous and more layered necromass on the forest floor of sandstone soils than on shale at Lambir. The visible differences were corroborated by measurably

the mineral nutrients, including the micronutrients but excluding Ca. The available forms of the nutrients generally had lower communalities than their reserves, and loaded on minor components.

Table 4. Total necromass, litter and humus cover and thickness on sandstone and shale soils, Lambir LTER plot. Differences between means are tested with t-tests and between proportions with χ^2; and reported as associated probability levels (ns, not significant, *P < 0.05, **P < 0.01).

	Sandstone	Shale	Significance of difference
1994–5 Total necromass	(n = 180)	(n = 51)	
Mean thickness (cm)	4.9	3.5	**
2003 Litter & humus	(n = 150)	(n = 39)	
Separate intact leaves (mean number of layers)	2.3	2.3	ns
Bonded intact leaves (mean number of layers)	1.8	1.7	ns
Laminar/skeletal remnants (mean number of layers)	1.6	1.4	ns
Sites with humus (%)	73	51	*
Mean humus thickness, where present (mm)	11.8	1.6	**

larger standing necromass on the sandstone soils, and associated with longer residence times and slower decomposition rates. The contrast was pronounced, and the differences in residence times and decomposition rates were greater than those between MDF and heath forest at Mulu in northern Sarawak (Anderson *et al.* 1983). The differences at Lambir related to the nutrient quality of the litter, with the concentrations of all of the main nutrients lower in the fresh leaf litter on sandstone than on shale. As the rates of litterfall were similar, the rates of nutrient flux through litter were also lower on sandstone. The differences in litter quality were associated with soil nutrient status, and the sandstone soils had lower concentrations of all of the main mineral nutrients. The differences between the soil types were more marked for the reserve than for the available forms of the nutrients, and in subsoils rather than topsoils. This

Table 5. Highest component loadings on first four principal components (accounting for 32%, 11%, 9% and 6% of the total variance respectively) of combined soil nutrient and necromass variables in 2003 data, Lambir LTER plot. Lesser loadings are omitted to highlight the structure. (n = 46, T = topsoil, S = subsoil).

Variable	Depth	Communality (= fraction of variance incorporated)	Principal component 1	2	3	4
Separate leaf litter	Surface	0.20		−0.29		
Bonded leaf litter		0.10	−0.21			
Skeletal debris litter		0.42				−0.55
Humus thickness		0.34	−0.44			
Organic C	T only	0.89			0.75	
C:N		0.74			0.62	
pH	T	0.62		0.64		
	S	0.61		0.55		
Exchangeable Ca	T	0.38		0.43		
	S	0.17	0.39			
Exchangeable Mg	T	0.75	0.66			
	S	0.79	0.77			
Exchangeable K	T	0.58			0.51	
	S	0.45				0.38
Exchangeable Na	T	0.59				0.64
	S	0.26				0.45
Available P	T	0.68			0.69	
	S	0.39	0.37			
Reserve P	T	0.83	0.80			
	S	0.80	0.84			
Reserve K	T	0.81	0.84			
	S	0.84	0.86			
Reserve Ca	T	0.41		0.46		
	S	0.08		0.21		
Reserve Mg	T	0.87	0.92			
	S	0.92	0.93			
Reserve Fe	T	0.71	0.78			
	S	0.62	0.73			
Reserve Mn	T	0.75	0.66			
	S	0.64	0.63			
Reserve Cu	T	0.47	0.48			
	S	0.57	0.61			
Reserve Zn	T	0.78	0.86			
	S	0.73	0.81			
Reserve B	T	0.67	0.77			
	S	0.67	0.78			

suggests that the differences in necromass characteristics and dynamics are associated with the reserve rather than available nutrient status of the soils. This accorded with the PCA, which loaded the necromass attributes on the same component as the soil reserve nutrients and separate from the available forms of the nutrients.

Organic materials accumulate on soil surfaces where decomposition is slow and there is little pedoturbation. Such accumulations can occur in sites with impeded drainage and poorly aerated soils, such as peats and gleyic mucks (Schuur & Matson 2002, Silver *et al.* 1999). However, the Lambir soils are well-drained, especially on sandstone, and waterlogging does not appear to be a significant factor in the accumulation of humus on the plot. Moisture deficiencies can also retard decomposition, but this is often matched by decreases in litter production, and xerogenic humus is rare. At Lambir moisture contents are consistently lower in the sandstone soils than on shale (S.E. Russo, unpubl. data), but moisture tensions do not appear to exceed 1.5 MPa in most years (Hirai *et al.* 1997). Differences in moisture stress are thought to have a minor role in the distribution of humus in the plot.

Our results indicate that the distribution of humus on the plot is mainly related to the poorer phytochemical quality and slower decomposition of litter on the more oligotrophic sandstone soils. Slow decomposition of litter has been correlated with low soil nutrient fertility and low litter nutrient quality in many tropical and temperate forests (Hobbie 2005, Hobbie & Vitousek 2000, Santiago *et al.* 2005). Thick necromass and discrete humus layers have been associated with low soil nutrient fertility in temperate forests, and humus-rich necromass is widespread under conifers on podzols and similar soils. Thinner and patchier humus also occurs under some temperate broadleaved woodlands (Dimbleby & Gill 1955). In well-drained sites in the lowland tropics well-drained humic necromass is thickest and most continuous under heath forests on podzols (Bruenig 1974, Dubroueq & Volkoff 1998, Miyamoto *et al.* 2003). As in temperate areas, thin humus also occurs on some non-podzolic soils under non-heath tropical forests (Kingsbury & Kellman 1997). In lowland non-heath and transitional tropical forests in Colombian Amazonia, Duivenvoorden & Lips (1995) found that humus thickness increases with decreasing contents of available and total soil nutrients. However, some specialized tropical forests counter this trend, as in the humus accumulations under *Pisonia grandis* stands on coral atoll soils with very high P and Ca contents (Woodroffe & Morrison 2001), and in lowland forest on shallow limestone soils in Jamaica (Kelly *et al.* 1988).

The Lambir plot straddles the soil nutrient fertility ecotone for humus accumulation, with humus on the sandstone soils but little on the shale soils. However, some of the shale soils do have thin root mats under the litter.

Non-humic root mats appear to have somewhat higher nutrient thresholds than humus layers and to develop on slightly less infertile soils.

The soils of the Lambir plot are similar in their high acidity and low contents of available nutrients to other tropical forest soils with humus and root mats, but have larger than usual reserves of Mg and K. The balance between multiple nutrients at varying levels of availability can be depicted with Alvim-type (1978) stoichiometric roses (Figure 3). The distinctively shaped mineral nutrient roses of the Lambir soils are congruent with those for other Bornean MDF soils on clastic sediments (Figure 3a–c), but differ from those for morphologically similar soils on crystalline rocks (Figure 3d). The stoichiometric similarity means that the Lambir and the Central Sarawak soils can be arrayed on a single gradient of nutrient fertility, with more fertile soils having larger but similarly shaped roses. Soils with incongruent roses cannot be thus arrayed and need to be compared for each nutrient and ratio separately.

Litter concentrations at Lambir were low for P and N and high for Mg and K, relative to many tropical forests (Anderson *et al.* 1983, Lips & Duivenvoorden 1996). These proportions paralleled the relative sizes of the reserves in the Lambir soils. Similar stoichiometry prevailed in the litterfall, which had higher Mg:Ca and K:Ca ratios than in most tropical forests. The necromass on the Lambir sandstone soil also had higher Mg:Ca ratios than in many other tropical forests, although similar to those in other Bornean MDF soils on Tertiary clastic sediments (Burghouts *et al.* 1998, Proctor *et al.* 1983). However, because of its great lability and copious leaching from forest canopies, necromass concentrations of K vary widely in tropical forests, and the Lambir values are not particularly high (Lips & Duivenvoorden 1996). Overall, the distinctive lithogenic nutrient stoichiometry of the Lambir soils persists in the fresh litter and necromass, but with diminishing clarity at each stage.

The PCA showed that humus was more closely associated with reserve than available nutrients. This was not unexpected, as previous studies have indicated the importance of reserve nutrients in the ecology of Bornean MDF. For example reserve nutrients, particularly P, were associated with floristic variation in MDF on Tertiary clastic sediments in Brunei (Austin *et al.* 1972). Similarly, reserve P and Mg were correlated with the floristic composition, structure and growth rates in 105 plots in Sarawak MDF on a range of lithologies and soils (Ashton 1989, Ashton & Hall 1992, Potts *et al.* 2002). The distributions of edaphically aggregated tree species were more closely associated with reserve than available nutrients in the MDF of Central Sarawak (Baillie *et al.* 1987). Fertilizer responses in perennial crops correlate better with soil nutrient reserves than with availables (Bailey 1967), which accounts for the inclusion of
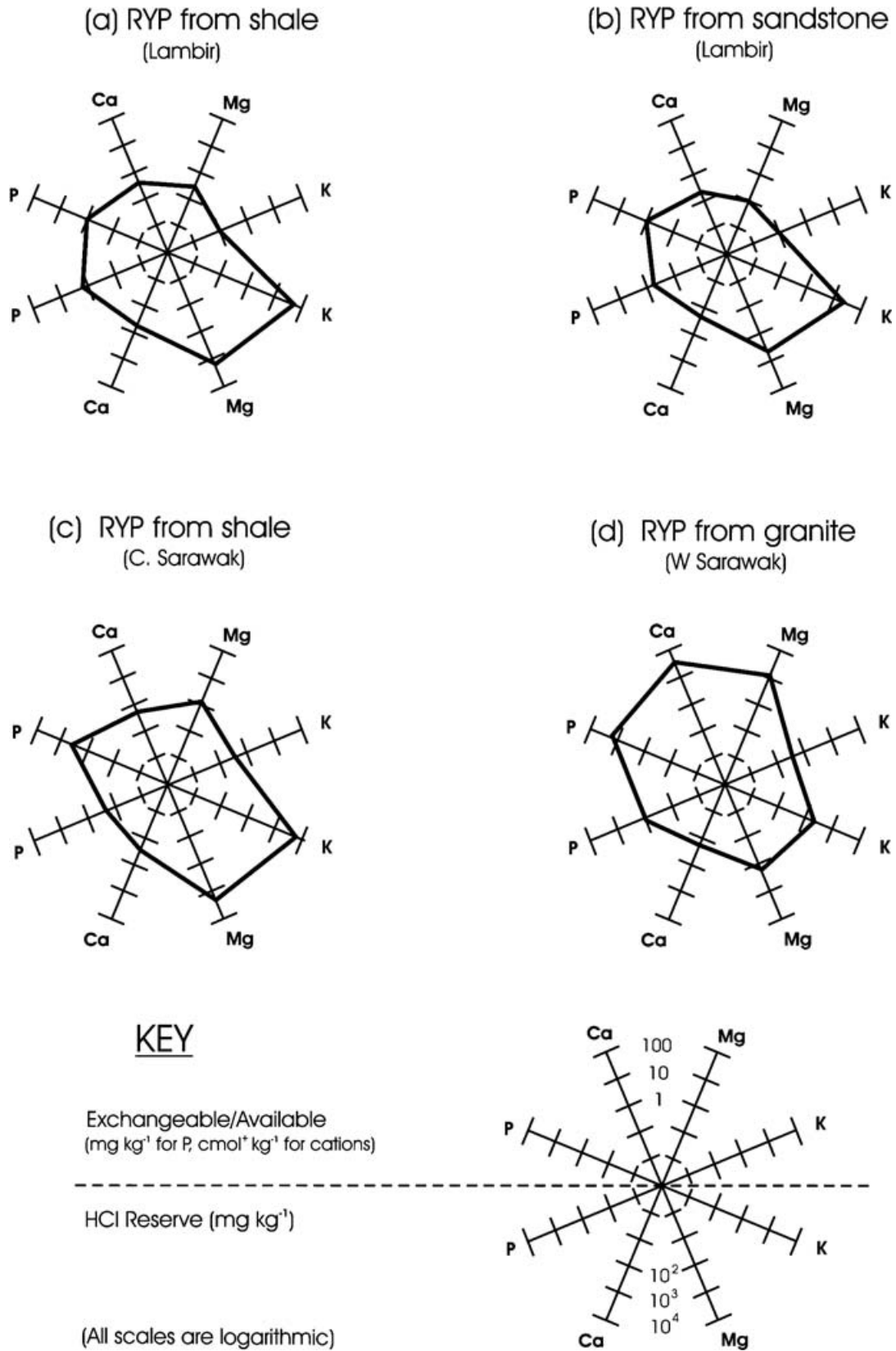
Figure 3. Stoichiometric roses showing available and reserve forms of mineral nutrients in topsoils of Lambir LTER plot and other Red Yellow Podzolic (RYP) soil in Sarawak. Comparative data for Central Sarawak from Baillie *et al.* (1987) and for West Sarawak from Andriesse (1972).

reserves in the routine analyses of agricultural soils in Sarawak (Chin 2002).

The importance of reserve nutrients is attributed to the buffering of nutrient cycles by small but significant releases during mineral weathering. Tectonic uplift and regolith truncation in landscapes like Lambir facilitate such replenishment because weathering and pedogenesis are reactivated and saprolites remain within rooting depth (Ghafur *et al.* 2004, Ross & Dyke 1996, Vitousek *et al.* 2003). Soil reserves of Ca are low at Lambir and it loads on a separate principal component from the other cationic nutrients. Its replenishment by weathering is thought to be of minor importance, and atmospheric inputs may be relatively significant (Chadwick *et al.* 1999).

A possible explanation for the observed associations of soils, forest and necromass at Lambir is that stochastic dispersal-assembly agglomerations of tree species had distinctive impacts on pedogenesis and generated characteristic soil profiles. However, permanent and crucial soil attributes, such as texture and mineral nutrient fertility, are associated with regolith lithology over large areas on clastic sedimentary rocks in Borneo, irrespective of land cover, and in places that have long been deforested (Andriesse 1972). Although the effects of forests on pedogenesis can be substantial (Cailleau & Braissant 2005, Dijkstra *et al.* 2003), we prefer a litho-physiographic explanation of the patterns, with soil texture and mineral nutrients inherited from source rocks, and the forest developing differently in response to edaphic variations. The spatial associations between soils and floristics in the Lambir MDF are therefore attributed to aggregations of edaphic specialist species on lithologically determined soils (Davies *et al.* 2005, Hirai *et al.* 1997, Russo *et al.* 2005). The differences in necromass dynamics and humus accumulation are attributed to the lower quality of the litter produced by the specialist flora on sandstone soils. Once the humus has developed, the differences in effective fertility between the soils are accentuated and perpetuated by the larger sequestration of nutrients in the less fertile soils.

The thickness and structure of necromass are facets and indicators of multivariate edaphic syndromes, which include physical dimensions, related to soil depth, stability, texture and hydrature, as well as nutrients. The syndromes are affected by the lithology, stratigraphy and tectonics of the bedrock, and by topogenesis and regolith formation. Different syndromes operate on the sandstone and shale at Lambir, and the development of humus layers is a response to, and a convenient field indicator of, these differences. Our findings on the implications of reserve nutrients to soil fertility and on the utility of humus layers as field indicators of edaphic conditions are likely to apply to large tracts of forest on Acrisol/Ultisols derived from Tertiary clastic sedimentary formations throughout the tropics (Driessen & Dudal 1991).

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