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Nutrient fluxes via litterfall and leaf litter decomposition vary across a gradient of soil nutrient supply in a lowland tropical rain forest

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Abstract The extent to which plant communities are determined by resource availability is a central theme in ecosystem science, but patterns of small-scale variation in resource availability are poorly known. Studies of carbon (C) and nutrient cycling provide insights into factors limiting tree growth and forest productivity. To investigate rates of tropical forest litter production and decomposition in relation to nutrient availability and topography in the absence of confounding large-scale variation in climate and altitude we quantified nutrient fluxes via litterfall and leaf litter decomposition within three distinct floristic associations of tropical rain forest growing along a soil fertility gradient at the Sepilok Forest Reserve (SFR), Sabah, Malaysia. The quantity and nutrient content of small litter decreased along a gradient of soil nutrient availability from alluvial forest (most fertile) through sandstone forest to heath forest (least fertile). Temporal variation in litterfall was greatest in the sandstone forest, where the amount of litter was correlated negatively with rainfall in the previous month. Mass loss and N and P release were fastest from alluvial forest litter, and slowest from heath forest litter. All litter types decomposed most rapidly in the alluvial forest. Stand-level N and P use efficiencies (ratios of litter dry mass to nutrient content) were greatest for the heath forest followed by the sandstone ridge, sandstone valley and alluvial forests, respectively. We conclude that nutrient supply limits productivity most in the heath forest and least in the alluvial forest. Nutrient supply limited productivity in sandstone forest, especially on ridge and hill top sites where nutrient limitation may be exacerbated by reduced rates of litter decomposition during dry periods. The fluxes of N and P varied significantly between the different floristic communities at SFR and these differences may contribute to small-scale variation in species composition.

Keywords Habitat association · Nutrient cycling · Plant soil interactions · Sepilok Forest Reserve · Soil fertility gradient

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Introduction

Spatial partitioning of tree species in response to soil type and topography is frequently observed in tropical lowland rain forests (e.g. Debski et al. 2002; Potts et al. 2002; Paoli et al. 2006). Topographic and edaphic variations may be associated with differences in the availability of nutrients and water (Gibbons and Newbery 2003; Itoh et al. 2003), but there has been limited research linking local edaphic variation to the differential performance and traits of species (e.g. Palmiotto et al. 2004; Russo et al. 2005; Baltzer et al. 2005). Consequently, our understanding of how heterogeneity in belowground resource availability maintains tree species richness remains limited. Plants specialised to infertile or dry habitats may exhibit traits that can have direct or indirect feedback effects on ecosystem processes such as nutrient cycling (Aerts and Chapin 2000). However, the importance of these feedback mechanisms to the control of plant species distributions is poorly investigated.

Nutrient availability has a direct effect on the amount and chemical composition of litter. Plants associated with infertile soils typically have slow maximum growth rates and long-lived leaves with low concentrations of nutrients and high concentrations of secondary compounds (Aerts and Chapin 2000). These traits could all limit litter production and reduce its nutrient concentrations where nutrient availability is poor, and thus high stand-level nutrient-use-efficiencies are associated with nutrient poor environments (Vitousek 1997). However, the elements that limit the productivity of tropical forests are debated (Burslem et al. 2005). Whilst P is often reported as being the primary limiting nutrient throughout tropical lowland forests (Vitousek 1984), studies have linked the distribution of dipterocarp species of lowland tropical forests in Southeast Asia to concentrations of soil Mg (Baillie et al. 1987; Potts et al. 2002) and K (Shariff and Miller 1990). Additionally, available evidence suggests that tropical heath forests may be limited by N, not P, as in many other lowland tropical forests (Vitousek 1984; Moran et al. 2000).

However, nutrient cycling is dependent on litter decomposition as well as production, and the rate of decomposition is determined by litter quality and the physical environment (Swift et al. 1979). Litter "quality" reflects the concentrations of nutrients and structural and defense compounds; more nutrient-rich leaves with fewer chemical and physical defenses decompose more rapidly than tougher, nutrient-poor leaves (Swift et al. 1979; Swift and Anderson 1989). Thus, traits associated with high stand-level nutrient-use efficiency (sensu Vitousek 1982) are also associated with low decomposition rates (Vitousek 1997). The result is a feedback mechanism, whereby, at nutrient-limited sites, plants produce small amounts of low quality litter that decomposes slowly and exacerbates nutrient limitation in this environment (Swift et al. 1979; Vitousek 1984; Heal et al. 1997). Therefore, environment affects litter decomposition both indirectly, by influencing species composition and litter quality, and directly by controlling litter decomposition rates (e.g. increased decomposition rates during wetter periods; Villela and Proctor 2002).

Water availability may also limit species distributions and nutrient cycling, even in ever-wet aseasonal forests (Gibbons and Newbery 2003). Variation in water availability can affect nutrient cycling via increased litterfall during wet periods (Rai and Proctor 1986; Green 1998) and decreased decomposition rates during dry periods (Villela and Proctor 2002). Furthermore, the effect of drought periods on litterfall may vary with local topography, such that forest on well-drained soils over ridges or hill tops experience a more acute water shortage during dry months than adjacent forest on poorly drained slopes or flat areas (Daws et al. 2002; Gibbons and Newbery 2003; Baltzer et al. 2005).

Understanding the role of variation in soil conditions in driving fine-scale heterogeneity in nutrient cycling requires landscape-level comparison of sites where different forests have developed on contrasting soils but under a relatively uniform climate. This condition is satisfied by the mosaic of soil types and forests occurring within the Sepilok Forest Reserve (SFR), Sabah, Malaysia (Fox 1973). At Sepilok, alluvial forest, sandstone hill forest and heath forest co-occur within a single watershed in association with changes in underlying geology and soil conditions.

The soils differ in available soil nutrients and there is evidence of a generally decreasing gradient of soil fertility from alluvial to sandstone to heath forest (Table 1). Water availability may be lowest during dry spells on sandstone ridges and rarely limiting in flat alluvial areas (Baltzer et al. 2005). In this paper, we describe the nutrient status of the soils underlying the three forest types and identify the effects of litter quality and environment on nutrient cycling. Specifically we tested the hypotheses that:

1. Rates of litter production and nutrient fluxes via litterfall increase and stand-level nutrient-use efficiencies decrease along the increasing gradient of soil fertility at SFR.
2. Stand-level nitrogen-use efficiency is greater in the N-limited heath forest than the forest communities on more nutrient rich ultisols.
3. Temporal variation in the rate of litter production occurs in response to variation in rainfall.
4. Rates of litter decomposition (mass loss and nutrient release) respond to an interaction between the litter source and its decomposition environment.

Materials and methods

Study site

The Kabili-Sepilok Forest Reserve (5°10′ N 117°56′ E) is on the east coast of Sabah, Malaysia. The reserve is a 4475 ha patch of lowland dipterocarp, heath and mangrove forests ranging between 0 m and 170 m a.s.l (Fox 1973). In 1957, logging was banned in the reserve and extensive areas remain unexploited. Mean annual rainfall for the period 1976–1995 was 2,975 mm, with no month receiving less than 100 mm on average (Malaysian Meteorological Department, unpublished data). April is generally the driest month and December or January the wettest; 45% of the annual precipitation falls from early November to mid-February (Fox 1973). Occasional severe droughts can occur in association with El Niño—Southern Oscillation (ENSO) events.

Table 1 Mean (standard errors of means) for soil chemistry and physical properties between 0–5 cm and 5–20 cm depth intervals, and forest structure and species richness data for alluvial, sandstone and heath forest soils at the Sepilok Forest Reserve

	Alluvial forest		Sandstone forest		Heath forest	
	0–5 cm	5–20 cm	0–5 cm	5–20 cm	0–5 cm	5–20 cm
Soil chemical and physical properties						
pH (water)	4.6 (0.3)	4.5 (0.3)	4.5 (0.3)	4.8 (0.3)	4.1 (0.3)	4.7 (0.3)
Soluble P (mg kg^{-1})	7.79 (2.69)	3.08 (1.05)	4.64 (1.34)	2.70 (1.14)	9.23 (6.39)	4.04 (1.72)
Total N (%)	0.16 (0.06)	0.10 (0.02)	0.09 (0.02)	0.06 (0.02)	0.10 (0.04)	0.05 (0.02)
Nitrate (mg kg^{-1})	10.47 (5.14)	5.22 (2.00)	1.13 (0.81)	1.06 (0.67)	1.16 (1.09)	1.34 (1.89)
Ammonium (mg kg^{-1})	6.65 (5.02)	4.54 (4.62)	12.05 (5.30)	7.22 (4.52)	3.74 (2.78)	1.59 (0.66)
Exchangeable acidity (%)	4.44 (1.84)	6.13 (2.10)	3.76 (1.09)	3.25 (1.62)	2.96 (1.36)	1.59 (0.79)
Exchangeable Al (%)	3.92 (1.73)	5.54 (1.96)	3.03 (0.98)	2.70 (1.43)	1.64 (1.08)	1.15 (0.68)
Ca (meq. %)	1.57 (2.29)	0.40 (0.44)	0.07 (0.05)	0.03 (0.03)	0.23 (0.11)	0.10 (0.08)
Mg (meq. %)	1.77 (1.32)	1.12 (1.12)	0.23 (0.11)	0.09 (0.07)	0.75 (0.63)	0.12 (0.12)
K (meq. %)	0.32 (0.15)	0.18 (0.08)	0.14 (0.05)	0.08 (0.03)	0.22 (0.22)	0.07 (0.04)
ECEC (meq. %)	8.16 (2.72)	7.89 (2.86)	4.28 (1.18)	3.50 (1.69)	4.24 (1.96)	1.90 (0.88)
Clay (%)		34.7 (9.6)		19.8 (5.6)		14.5 (4.7)
Silt (%)		24.9 (7.2)		12.4 (4.2)		10.3 (3.6)
Sand (%)		40.4 (14.7)		67.8 (7.7)		75.4 (6.2)
Forest structure and species richness						
Stem density (ha^{-1})		941		1,343		1,656
Mean basal area (m^2 tree^{-1})		0.037		0.029		0.017
Species No.		434		368		194

Soil data are mean values from samples taken at the centre of every 20 m^2 sub-plot within three 4 ha plots in each of three forest types (Majalap et al. unpublished data). Floristic data are means based on stems ≥5 cm diameter at breast height growing on three 4 ha plots in each floristic association (Nilus 2003)

Three floristic associations of lowland evergreen tropical rain forest were studied at SFR: alluvial forest, sandstone hill forest and heath forest (known locally as kerangas). These three communities have analogues across Borneo wherever appropriate soil conditions exist. Underlying the western part of the reserve is sandstone bedrock inter-bedded with mudstone. In this area alluvial forest occurs on the ultisols (US Taxonomy) overlying alluvial flats and gently sloping, low mudstone and sandstone hills and is dominated by large, fast-growing dipterocarps such as *Parashorea tomentella* (Fox 1973). The sandstone hill forest occurs on well-drained ultisols on steeply sloping sandstone ridge and valley formations. The most common species are slow growing dipterocarps such as *Shorea multiflora* (Fox 1973). In sandstone forest tree species diversity is lower than in the alluvial forest but stem density is greater (Table 1; Nilus 2003). In this study, the sandstone hill forest was divided into that occurring on ridges and that at the base of gullies dissecting the sandstone ridges, to determine whether litter deposition and decomposition differ in these contrasting microhabitats. Sandstone cuesta landforms predominate in most of the eastern part of the reserve where spodozols (US Taxonomy) occur in association with small-crown heath forest (Fox 1973). The tree community is relatively species-poor and dominated by *Shorea multiflora*, *Cotylelobium melanoxylon* (Dipterocarpaceae), *Garcinia miequellii* (Clusiaceae) and *Tristaniopsis merguensis* (Myrtaceae).

Measurement of litterfall production

In each of the three principle floristic communities of the SFR (alluvial, sandstone and heath forest) there are three 4 ha plots within which all stems >5 cm diameter breast height have been measured and identified (Nilus 2003). Twenty-one 1 × 1 m litter traps were positioned within these plots in each of the four habitats defined by parent material and topography (alluvial forest, ridges underlain by sandstone, gullies between adjacent sandstone ridges and heath forest). Sampling was based on a stratified random design to maintain a minimum distance of 20 m between traps and to avoid positioning traps below canopy gaps. The traps were made by suspending a 2 × 2 mm nylon mesh inside a square frame of PVC tubing positioned 0.4 m above the ground. Traps were occasionally damaged (approximately one per month). When possible, traps were repaired immediately; more severe damage was repaired within 1 week and, if necessary, the litter collected from the damaged trap was excluded from analysis. Litter was collected twice monthly from 15 November 2000 to 1 November 2002. Litter samples collected during the first year of the study (15 November 2000–1 November 2001) were air-dried and sorted into four fractions as defined by Proctor et al. (1983): leaves (including stipules and petioles); small wood (twigs ≤20 mm diameter and bark ≤20 mm length); reproductive parts; and trash (any material passing through a 2 mm sieve, damar and faeces). Samples from the second year were air-dried and sorted into two fractions: reproductive parts and all other litter. Each fraction was weighed and sealed into plastic bags. For each bimonthly collection 10% of the samples from each habitat were randomly selected, dried to 105°C and reweighed to estimate moisture content. Litterfall production was expressed on an oven-dry basis by adjusting values for habitat-specific differences in the moisture content of the air-dried material.

Measurement of litter standing-crop and depth

Forest floor small litter was collected at 3-month intervals during the first year of the study (on 15 November 2000, 14 February 2001, 15 May 2001, 15 August 2001). A 0.5 × 0.5 m quadrat was placed in a predetermined direction 2 m from a randomly selected corner of each litterfall trap. The depth of the standing litter was measured at each corner of the quadrat and the litter within the quadrat was collected. No area of forest floor was sampled twice. The litter samples were air-dried, sorted, weighed and corrected for moisture content. The trash fraction was discarded, as it was not possible to differentiate between trash and mineral soil particles.

Measurement of leaf litter decomposition rate

Ten 2 × 1 m sheets of 2 × mm nylon mesh were pegged onto the forest floor at randomly selected sites in each of the four habitat types. Leaf litter was collected weekly from the mesh sheets for 2 months (1 May 2001–30 June 2001), air-dried and bulked by forest type. For each litter type, 200 0.25 × 0.25 m bags made from 2 × 2 mm nylon mesh were each filled with 10 g (±0.5 g) of air-dried leaf litter. Sub-samples of the air-dried leaf litter were taken at the start of the experiment to determine nutrient concentrations and moisture content. On 14–15 September 2001, 20 litter bags (five of each litter type) were placed onto the soil surface as a grid of 4 × 5 randomly placed bags at 10 randomly selected sites in each of the four habitat types. Four bags (one bag of each litter type) were collected from each site 21, 42, 84, 168 and 336 days after the experiment began. The leaves were removed from the bags, brushed clean of all soil and root particles, air-dried and weighed to determine mass loss. Samples were then ground and stored in sealed plastic bags.

Chemical analysis

The litterfall leaf and small wood fractions were bulked separately by month and samples from the November 2000 and February 2001 collections were oven-dried at 60°C and ground. Total N, P, K, Ca and Mg concentrations were determined for the November 2000 samples at the Forest Research Centre, Sabah, and for the February 2001 samples at the University of Aberdeen, UK. A 10% sub-sample of the February 2001 samples was also analysed at the Forest Research Centre as a cross-laboratory consistency check. Concentrations of N, P, K, Ca and Mg in leaf and small wood fractions from the two litterfall collections were not significantly different. Leaf litter samples collected from the litter decomposition bags and those taken before the start of the experiment were redried at 60°C, ground, and transferred to the University of Aberdeen, UK, for analysis.

About 0.1–0.2 g sub-samples of plant material dried to 60°C were digested using the sulphuric acid–hydrogen peroxide–lithium sulphate digest procedure for vegetation (Allen 1989). At the Forest Research Centre, Sabah, total P and N concentrations were determined using spectrophotometry (Hitachi Ltd., Tokyo, Japan), and flow-injection analysis (SFA2, Burkhard Scientific Ltd., Rickmansworth, UK), respectively. K, Ca and Mg concentrations were determined using an atomic absorption spectrophotometer (GBC Scientific Equipment, Danderong, Victoria, Australia). At the University of Aberdeen total P and N concentrations were determined using flow-injection analysis (FIA Star 5010 Analyser, Tecator, Höganäs, Sweden) and continuous-flow analysis (Auto-analyser II, Technicon Ltd., Dublin, Ireland), respectively. K, Ca and Mg concentrations were determined using an atomic absorption spectrophotometer (Atomic Absorption Analyst 100, Perkin–Elmer GmbH., Ueberlingen, Germany).

For the extraction of condensed tannins, 30 ± 0.01 mg samples of ground plant material dried to 60°C was added to 50% aqueous methanol, centrifuged and the solvent decanted (Waterman and Mole 1994). The concentration of condensed tannins was determined by spectrophotometry (CE 373 spectrophotometer, Cecil Instruments, UK). The acid detergent fibre method was used to determine lignin content of 1 g of ground dried (60°C) plant material (Van Soest 1963).

Data analysis

Coefficients of temporal and spatial variation in litterfall and litter standing crop were calculated and adjusted for population bias using the equation (Sokal and Rohlf 1995):

$$\mathrm{CV}^* = \mathrm{CV}[(1 + (1/4n)]$$

where CV* is an unbiased estimate of population variation, CV is the biased estimate and n the sample size. The turnover rate (K_L) of litter standing crop was calculated as (Olson 1963):

$$K_\mathrm{L} = \mathrm{LF}/\mathrm{SC}$$

where LF is the yearly litterfall mass production and SC is the litter standing crop at any time point. This method estimates only the turnover rate of recognisable plant tissues, and should be used only as a decomposition rate index for comparative studies (Swift et al. 1979; Anderson and Swift 1983). The decomposition rate constants of leaf litter from decomposition bags (K) were calculated by solving the equation (Olson 1963):

$$X_t/X_0 = e^{-Kt}$$

for K, where X_0 is the original dry mass of leaf litter, X_t is the leaf litter dry mass remaining at time t, t the time interval of sampling X_t (days) and K the decay coefficient (day^{-1}). The time periods to 50% litter mass loss ($t_{0.5}$) were calculated from (Bockheim et al. 1991):

$$t_{0.5} = \ln(0.5)/-K = 0.693/-K$$

K values derived from the decomposition bags were based solely on rates of leaf litter decomposition, whilst K_L values can include leaf and wood fractions but excluded the trash fraction.

A one-way analysis of variance was used to test for differences in annual litterfall and in nutrient concentrations of litter across habitat types. Total small litter dry mass falling per month was analysed per forest type using a univariate analysis of variance with month as the factor. Repeated-measures analysis of variance was used to test for differences in LF, SC, K_L and the proportion of original dry mass and nutrient mass remaining in the litter bags. Time was the within-subjects factor and habitat or litter type was the between-subject factor. Mauchly's test of sphericity was used to test if variances of all variables within a repeated-measures analysis were equal (von Ende 2001). If the sphericity assumption was violated the numerator and denominator degrees of freedom were adjusted using the Greenhouse-Geisser epsilon (von Ende 2001). All multiple comparisons between means were made using Tukey HSD tests (adjusted to maintain significance at $P = 0.05$). Data were tested for normality of residuals before analysis and, where necessary, were transformed using natural logs, with the exception of proportion data, which were all arcsine transformed. All analyses were carried out using SPSS v. 11.5.2 (SPSS Inc., Chicago, Illinois, USA).

Results

Litterfall

Mean total small litterfall production over 2 years ranged from 5.7 t ha^{-1} yr^{-1} in the heath forest, to 7.7 t ha^{-1} yr^{-1} in the alluvial forest (Table 2). Forest type, date of collection and their interaction all influenced the total mass of litter falling per day ($F_{3,80} = 14.12$, $P < 0.001$; $F_{23,1840} = 32.73$, $P < 0.001$; $F_{69,1840} = 3.12$, $P < 0.001$ for forest type, month and the month by forest type interaction, respectively). The alluvial forest produced more small litter than the other forest types and the heath forest less ($F_{3,83} = 20.22$, $P < 0.001$). The two sandstone forests produced intermediate amounts of small litterfall that were not significantly different. Leaf fractions followed the same patterns as the total litterfall but other fractions varied from this hierarchy (Table 2).

The proportions of litter represented by the different fractions (calculated by dry mass) did not vary significantly among forest types. The main component of litterfall was leaf material (81%), wood comprised ~17% of total litterfall, and the trash and fruit and flowers fractions each comprised ~1%. Spatial variation in total litterfall was lower in the heath forest than in the other three forest types ($F_{3,95} = 4.09$, $P < 0.05$; Table 2). Temporal variation was greater during the first year of the study than the second in all forest types, possibly because of the extremely large litterfall in May 2001, coinciding with a period of low rainfall following 2 months of abnormally heavy rain (Fig. 1). Temporal variation was greater in the two sandstone forests than in the alluvial or heath forests ($F_{3,167} = 10.24$, $P < 0.001$; Table 2, Fig. 1). Daily litterfall in the sandstone ridge and valley forests (L in g m^{-2} day^{-1}) decreased linearly with the amount of rainfall (Rf in mm) recorded for the previous month ($F_{476} = 36.98$, $P < 0.001$, $L = 2.25 - 0.0013\text{Rf}$; $F_{476} = 14.19$, $P < 0.001$, $L = 1.97 - 0.0007\text{Rf}$, for sandstone ridge and valley habitats, respectively).

Table 2 Estimated dry weights of mean litterfall production ($t\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$) and temporal ($n = 42$) and spatial ($n = 24$) coefficients of variation (CV) of total litterfall ±95% confidence limits from 21 forest traps in each of four habitat types in Sepilok Forest Reserve, Sabah

	Alluvial	Sandstone ridge	Sandstone valley	Heath
Nov 2000–Oct 2001				
Leaves	$6.7^{a} \pm 0.26$	$5.6^{b} \pm 0.22$	$5.3^{b} \pm 0.20$	$4.5^{c} \pm 0.14$
Small wood	$1.5^{a} \pm 0.14$	$1.2^{ab} \pm 0.14$	$1.3^{ab} \pm 0.16$	$1.0^{b} \pm 0.12$
Reproductive	$0.039^{ab} \pm 0.015$	$0.087^{a} \pm 0.021$	$0.059^{ab} \pm 0.020$	$0.025^{b} \pm 0.0085$
Trash	$0.14^{a} \pm 0.011$	$0.066^{b} \pm 0.0066$	$0.077^{b} \pm 0.0074$	$0.076^{b} \pm 0.0054$
Total litterfall	$8.3^{a} \pm 0.35$	$7.0^{b} \pm 0.28$	$6.7^{b} \pm 0.33$	$5.6^{c} \pm 0.22$
Nov 2000–Oct 2002				
Total litterfall	$7.7^{a} \pm 0.23$	$7.0^{b} \pm 0.17$	$6.5^{b} \pm 0.18$	$5.7^{c} \pm 0.12$
Temporal CV	$39.41^{a} \pm 1.63$	$50.29^{b} \pm 2.16$	$48.92^{b} \pm 2.11$	$38.77^{a} \pm 2.46$
Spatial CV	$37.33^{a} \pm 1.33$	$40.82^{a} \pm 4.09$	$41.98^{a} \pm 3.07$	$33.19^{b} \pm 3.95$

Mean values sharing the same superscript letter within a row are not significantly different, $P > 0.05$, Tukey's HSD test

There were large differences in nutrient concentrations in litterfall among the habitat types (Table 3). Leaf litter in the alluvial forest contained the highest N, P, K and Ca concentrations, and that in the heath forest the lowest concentrations of N and P. Concentrations of lignin, condensed tannins (CT) and their ratios to N concentration were greatest in the heath forest litter and lowest in the alluvial litter. The alluvial forest received more P (approximately 4-fold greater), and N and K (approximately 2-fold greater) per ha per year in litter than did the other three forest types (Table 4). The alluvial forest also received more Ca and Mg, but differences between the habitat types were less distinct. Stand-level N and P use efficiencies (ratios of litter dry mass to nutrient content) were greatest for the heath forest (145 and 5,844) followed by the sandstone ridge (123 and 4,492), sandstone valley (112 and 4,151) and alluvial (76.8 and 1,454) forests, respectively (Fig. 2). K and Ca use efficiencies were greatest for the sandstone ridge and valley forests, respectively (478 and 272) and lowest for the alluvial forest (263 and 90.8). Stand-level Mg use efficiency did not vary between habitat types (Fig. 2).

Litter standing crop and rates of litter turnover (K_L)

Mean annual standing litter mass was greatest in the sandstone ridge forest and smallest in the alluvial and sandstone valley forests ($F_{3,83} = 5.60$, $P < 0.001$, Table 5), and the litter layer was deepest in the sandstone ridge forest ($F_{3,83} = 23.49$, $P < 0.001$, Table 5). The largest temporal variation in total standing litter occurred in sandstone forests and the smallest in heath forest. The proportions of litter represented by three different fractions (leaves, small wood and fruit and flowers) did not vary among habitat types or over time. Leaves comprised the largest fraction of standing crop of litter, representing 67% of dry mass. Small wood was ~33% of total dry mass and the fruit and flowers fraction <0.5%.

Annual K_L varied between forest types ($F_{3,83} = 16.507$, $P < 0.001$, Table 5). The alluvial forest had the most rapid annual litter turnover, followed by the sandstone valley, the sandstone ridge and the heath forests; this was true for both leaf and wood litter (Table 5). Values of K_L calculated for 3-month intervals were similar to the annual K_L in each forest type except the sandstone valley forest. There, it exceeded the annual mean by 31%, but only between February and May.

Leaf litter decomposition

Mass losses from all litter types over time were greatest in the alluvial forest and there was no significant effect of litter type in this habitat ($F_{3,30} = 1.89$, $P = 0.152$; see Supplementary Material Table 1). However, decomposition rate differed among litter types in the other three habitats ($P = 0.001–0.031$) and mean squared

Fig. 1 Seasonality of total monthly rainfall (**a**) and litter fall production for four forest communities; (**b**) alluvial, (**c**) sandstone ridge, (**d**) sandstone valley and (**e**) heath. All bars are mean ± SE (*n* = 21)

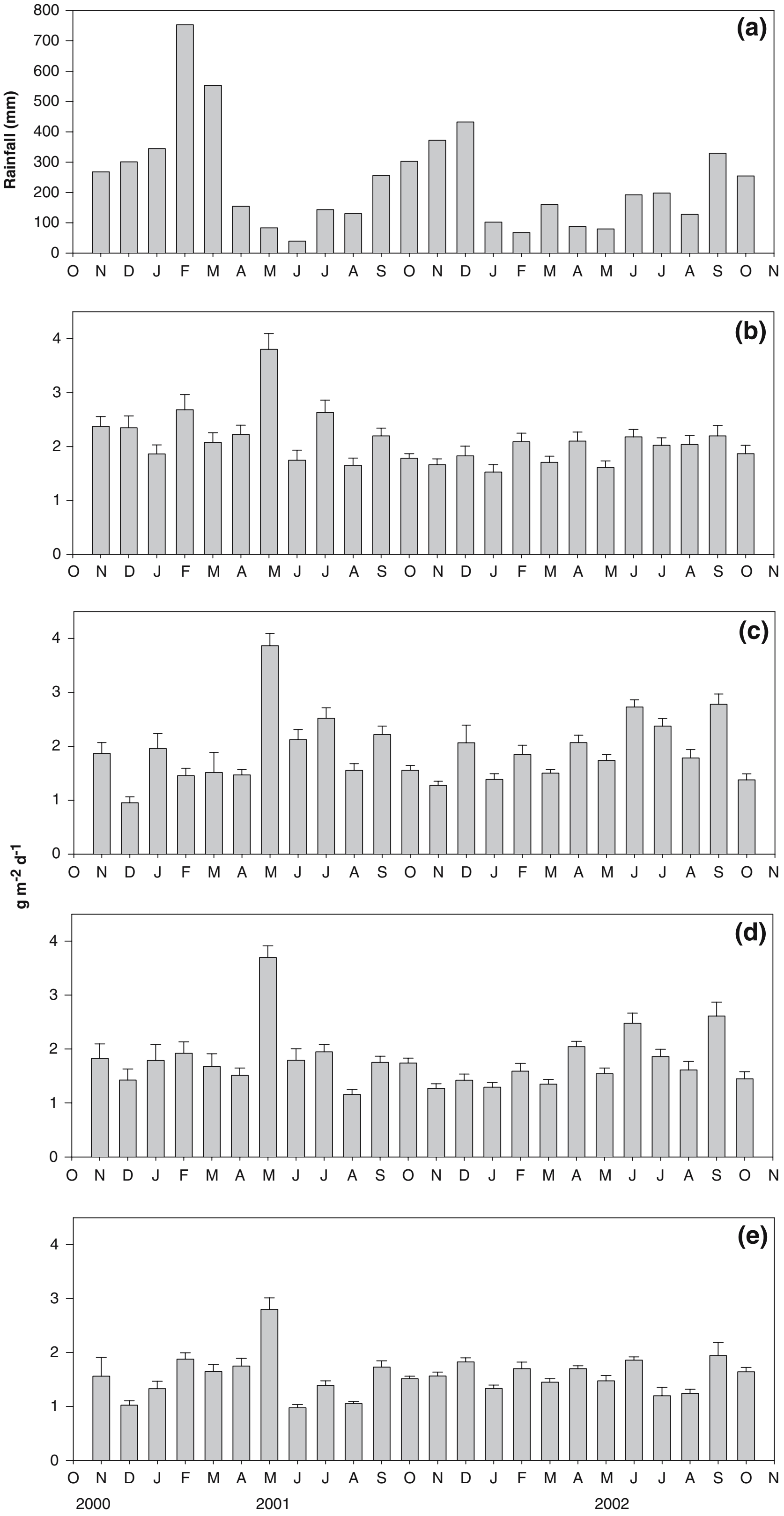

Table 3 Nutrient concentrations (mg g^{-1}) in both leaf and wood fractions, and secondary compound concentrations in leaf fractions of small litterfall in four forest types within the Sepilok Forest Reserve. Data are from litterfall collection from 21 forest traps in each forest type (all values are mean ± SE)

		Alluvial	Sandstone ridge	Sandstone valley	Heath
P	Leaves	$0.84^{a} \pm 0.061$	$0.44^{b} \pm 0.021$	$0.29^{b} \pm 0.028$	$0.20^{c} \pm 0.016$
	Wood	$0.31^{a} \pm 0.036$	$0.12^{b} \pm 0.012$	$0.10^{bc} \pm 0.014$	$0.077^{c} \pm 0.013$
N	Leaves	$13.5^{a} \pm 0.328$	$9.13^{b} \pm 0.257$	$9.18^{b} \pm 0.348$	$7.17^{c} \pm 0.315$
	Wood	$8.20^{a} \pm 0.414$	$5.87^{b} \pm 0.345$	$6.28^{b} \pm 0.276$	$5.17^{b} \pm 0.319$
K	Leaves	$3.80^{a} \pm 0.450$	$1.98^{b} \pm 0.127$	$2.62^{b} \pm 0.116$	$2.20^{b} \pm 0.170$
	Wood	$2.89^{a} \pm 0.339$	$1.17^{b} \pm 0.256$	$1.22^{bc} \pm 0.142$	$0.945^{c} \pm 0.151$
Ca	Leaves	$9.78^{a} \pm 0.615$	$3.61^{b} \pm 0.539$	$4.46^{bc} \pm 0.264$	$6.73^{c} \pm 0.725$
	Wood	$11.7^{a} \pm 1.20$	$4.08^{b} \pm 0.635$	$4.60^{b} \pm 0.496$	$5.47^{b} \pm 0.550$
Mg	Leaves	$1.98^{a} \pm 0.067$	$2.14^{b} \pm 0.09$	$2.27^{c} \pm 0.133$	$2.27^{c} \pm 0.136$
	Wood	$1.72^{a} \pm 0.129$	$1.24^{b} \pm 0.103$	$1.33^{b} \pm 0.140$	$1.23^{b} \pm 0.092$
Lignin (%)		$53.11^{a} \pm 0.011$	$57.62^{ab} \pm 0.012$	$63.31^{bc} \pm 0.021$	$65.94^{c} \pm 0.025$
Condensed tannin		$0.9^{a} \pm 0.271$	$2.97^{b} \pm 0.243$	$3.54^{b} \pm 0.235$	$3.75^{b} \pm 0.328$
Lignin/N ratio		$3.94^{a} \pm 0.10$	$6.13^{ab} \pm 0.20$	$7.99^{b} \pm 0.67$	$13.8^{c} \pm 1.25$
CT/N ratio		$0.07^{a} \pm 0.02$	$0.32^{b} \pm 0.03$	$0.44^{b} \pm 0.04$	$0.77^{c} \pm 0.07$

Mean values sharing the same superscript letter within a row are not significantly different, $P > 0.05$, Tukey's HSD test

Table 4 Nutrient addition (kg ha^{-1} yr^{-1}) from leaf and small wood litter fall combined, for four forest types in the Sepilok Forest Reserve

	Alluvial	Sandstone ridge	Sandstone valley	Heath
P	$5.41^{a} \pm 0.621$	$1.27^{bc} \pm 0.080$	$1.56^{b} \pm 0.0883$	$1.22^{c} \pm 0.069$
N	$103^{a} \pm 3.72$	$47.6^{b} \pm 1.92$	$56.9^{b} \pm 2.55$	$48.9^{b} \pm 2.43$
K	$29.9^{a} \pm 1.90$	$11.5^{c} \pm 0.631$	$18.4^{b} \pm 1.22$	$14.6^{bc} \pm 0.759$
Ca	$86.9^{a} \pm 7.23$	$19.6^{d} \pm 1.93$	$29.4^{c} \pm 2.69$	$43.9^{b} \pm 3.77$
Mg	$17.5^{a} \pm 1.04$	$11.7^{b} \pm 0.682$	$14.7^{ab} \pm 1.12$	$14.8^{a} \pm 0.607$

Calculated as nutrient concentrations of leaf and wood litter (mg kg^{-1}) multiplied by total dry mass of leaf and small wood litterfall (kg ha^{-1} yr^{-1}). The trash and reproductive fractions were not included as their contribution to small litterfall was negligible. All values are means ± SE

Mean values sharing the same superscript letter within a row are not significantly different, $P > 0.05$, Tukey's HSD test

values suggested that litter type had a greater effect on decomposition rates in these environments than in the alluvial forest. Different rates of dry mass loss from different litter types were most evident in the sandstone forests (Fig. 3). Proportionately more mass was lost from alluvial litter than from any other litter type across all four habitats (Fig. 3). However, there was no consistent hierarchy in decay rates of the different litter types across all environments and the rank order of K was different in each of the four forest types (Table 6).

Annual rates of decomposition (K) for alluvial forest litter were consistently greater, and therefore half-lives shorter, than for other litter types in the alluvial, sandstone ridge and sandstone valley forests (Table 6). The K value of alluvial leaf litter decomposing in its native habitat was 2.55 yr^{-1}; the corresponding K values of litters from the sandstone ridge, sandstone valley and kerangas forests were all 1.35 yr^{-1} when decomposing in their native environments. Annual rates of litter turnover (K_L) derived from measurements of leaf litterfall and standing crop, exceed these experimentally derived K values in all cases but alluvial forest (Tables 5 and 6).

Initial nutrient concentrations of leaf litter were not significantly different from those of leaf litter collected in litterfall traps (Table 3). Litter type and decomposition environment both

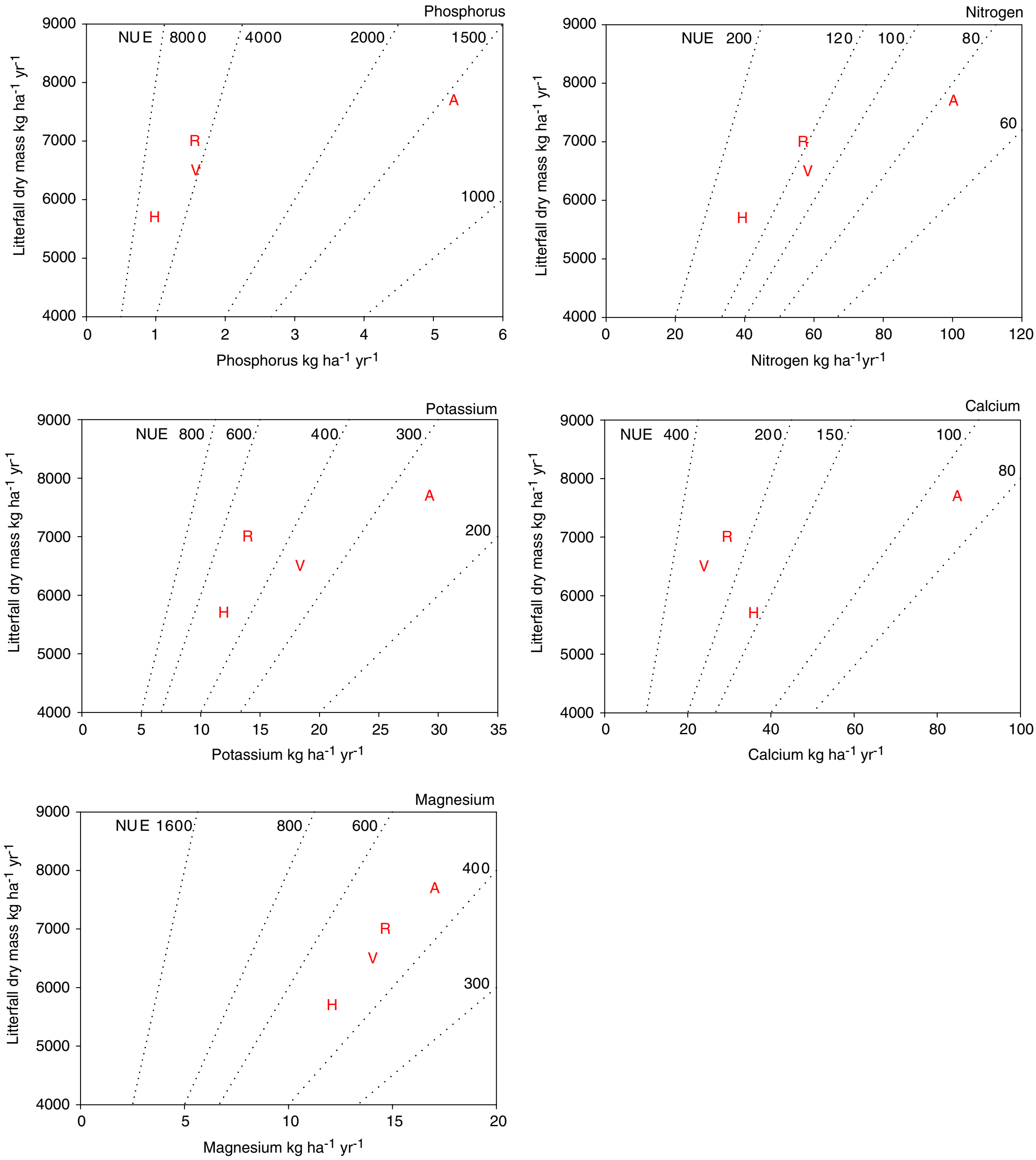

Fig. 2 The relationship between litterfall dry-mass production (kg ha^{-1} yr^{-1}) and total nutrient returns through litterfall (kg ha^{-1} yr^{-1}) for alluvial (A), sandstone ridge (R), sandstone valley (V) and heath (H) communities. Dotted lines indicate constant stand-level nutrient-use efficiency (NUE)

significantly influenced the proportions of nutrients remaining in litter over time ($F_{3,36} = 7.5$, $P < 0.001$; $F_{3,36} = 76.2$, $P < 0.001$; $F_{3,36} = 10.1$, $P < 0.001$; $F_{3,36} = 79.7$, $P < 0.001$; for the effect of environment and litter type on loss of N and P, respectively; see Supplementary Material Table 2). N and P initially accumulated in litter before being released (Figs. 4 and 5). By the end of the

Table 5 Mean total standing litter dry mass and depth, and annual litter turnover rates (K_L yr^{-1}) for leaf and small wood litter fractions and total small litter for four forest types in the Sepilok Forest Reserve

	Alluvial	Sandstone ridge	Sandstone valley	Heath
Standing litter				
Mass (kg ha^{-1})	$4.78^a \pm 0.252$	$5.88^b \pm 0.254$	$4.67^a \pm 0.227$	$5.32^{ab} \pm 0.223$
Depth (cm)	$2.62^a \pm 0.207$	$5.22^b \pm 0.305$	$3.39^a \pm 0.234$	$2.88^a \pm 0.203$
K_L yr^{-1}				
Leaves	$2.27^a \pm 0.091$	$1.49^b \pm 0.057$	$1.73^b \pm 0.093$	$1.43^b \pm 0.065$
Small wood	$1.07^a \pm 0.136$	$0.68^b \pm 0.107$	$1.01^a \pm 0.163$	$0.59^b \pm 0.116$
Total	$1.85^a \pm 0.099$	$1.21^{bc} \pm 0.052$	$1.47^b \pm 0.074$	$1.10^c \pm 0.066$

Mean values sharing the same superscript letter within a row are not significantly different, $P > 0.05$, Tukey's HSD test

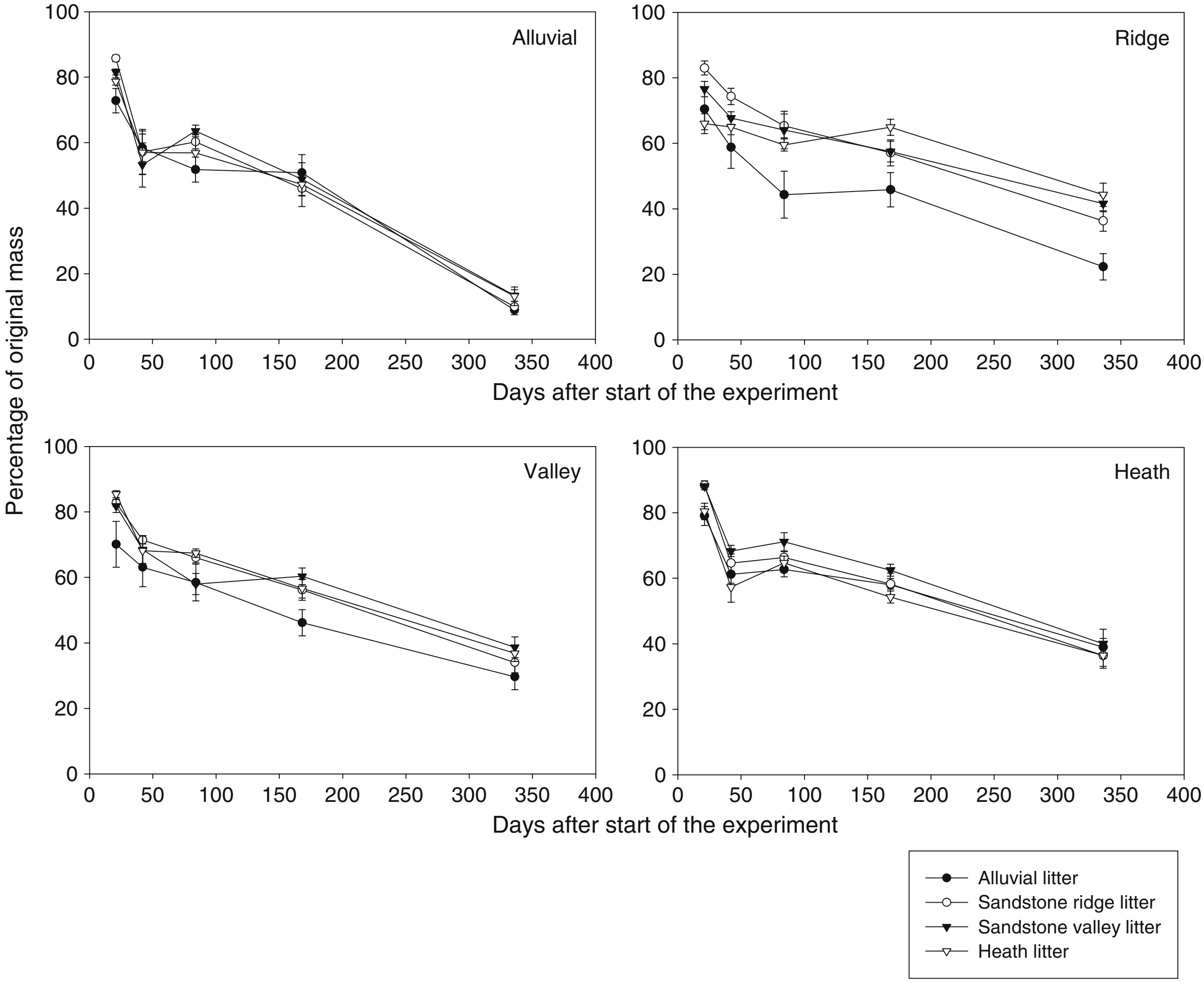

Fig. 3 Percentage of original litter mass remaining in litter decomposition bags over time. Four types of leaf litter (collected from alluvial, sandstone ridge, sandstone valley and heath sites) were positioned in four different habitats: alluvial, sandstone ridge, sandstone valley and heath within the Sepilok Forest Reserve. All values are means ± SE

experiment (336 days), less than 50% of the original N and P remained in the litters decomposing in the alluvial forest, but this was not true for the other three forest types where there was much more variability; the final percentages of N and P ranged from 22% to 85% and 12% to 91%,

Table 6 Annual rates of decomposition (*K*), half-lives and regression parameters for each of four types of leaf litter in four different forest types within the Sepilok Forest Reserve

Litter bag position and contents	R^2	*F*	Coefficient	*K* (yr^{-1})	$t_{0.5}$ (days)
Alluvial forest					
Alluvial litter	70	131	0.0070	2.55	99
S. Ridge litter	80	228	0.0057	2.08	122
S. Valley litter	80	229	0.0061	2.23	114
Heath litter	87	377	0.0060	2.19	116
Sandstone ridge forest					
Alluvial litter	53	62	0.0071	2.59	98
S. Ridge litter	50	53	0.0037	1.35	187
S. Valley litter	67	40	0.0034	1.24	204
Heath litter	75	160	0.0037	1.35	187
Sandstone valley forest					
Alluvial litter	47	50	0.0055	2.01	126
S. Ridge litter	55	69	0.0039	1.42	178
S. Valley litter	73	153	0.0037	1.35	187
Heath litter	79	213	0.0039	1.42	178
Heath forest					
Alluvial litter	46	49	0.0039	1.42	178
S. Ridge litter	68	123	0.0032	1.17	217
S. Valley litter	49	56	0.0042	1.53	165
Heath litter	72	145	0.0037	1.35	187

In all cases the intercept was 100 and $P < 0.001$ in all cases

respectively. The release of cations from leaf litter followed different patterns depending on decomposition environment and litter quality (see Supplementary Material Figs. 1–3). K was released rapidly from all litter types at all sites with <25% of initial K remaining after 336 days. There were two patterns of Ca release: the sandstone ridge and heath forest litters showed an initial phase of Ca accumulation, up to 174% of original Ca in the first 50 days, followed by a phase of net release, whereas alluvial and sandstone valley litters released Ca immediately with no accumulation phase. Total Mg in heath forest litter initially increased (approximately up to day 84) and then decreased across all habitat types. All other types of litter decreased immediately in total Mg. Initial leaf chemistry significantly affected rates of leaf litter decomposition (Table 7). However, the constituents most closely correlated with initial rates of biomass loss varied with decomposition environment. Decomposition rates were most strongly correlated with P and condensed tannin concentrations in the alluvial forest, with lignin in the sandstone ridge forest, N in the sandstone valley forest and with the condensed tannin: N ratio in the heath forest.

Discussion

Litterfall

The hypothesis that forests growing on nutrient-poor soils produce less, more nutrient poor, litter than those on relatively nutrient-rich soils (Vitousek 1997) is supported by the evidence that the alluvial forest produced the most small litter and the heath forest the least (Table 2). Additionally, the alluvial forest litter had the greatest concentrations of all nutrients except Mg and the litter produced by the heath forest had the lowest N and P concentrations. The soils underlying the alluvial forest have the highest concentrations of all nutrients except available P and the highest nitrification rates (Uchida, unpublished data), while the heath forest soils have very low concentrations of nitrate and ammonium. We conclude that differential nutrient supply drives landscape-level variation in small litter production.

The alluvial forest at Sepilok produces similar amounts of litter to a number of other lowland dipterocarp forests in Borneo, but litter production in the sandstone ridge, sandstone valley and heath forests is lower than most comparable sites in Borneo (Proctor et al. 1983; Burghouts et al. 1992). For example, a heath forest in Brunei produced almost 50% greater amounts of small litter than the heath forest at Sepilok (Moran et al. 2000). Small litter production in the Sepilok heath forest was more comparable to values estimated in caatinga heath forest on extremely infertile spodosol soils at San Carlos, Venezuela (Herrera 1979; Jordan and Murphy 1982).

The alluvial forest returned leaf litter with N and P concentrations at the upper limit of the range of values from Southeast Asian forests (c.f. Proctor et al. 1983; Clark et al. 2001). Stand-level N use efficiency (NUE) was greatest in the heath forest (142) and lowest in the alluvial forest (79.2), which supports the hypothesis that tropical heath forests overlying spodosols display greater N limitation than tropical forests growing on

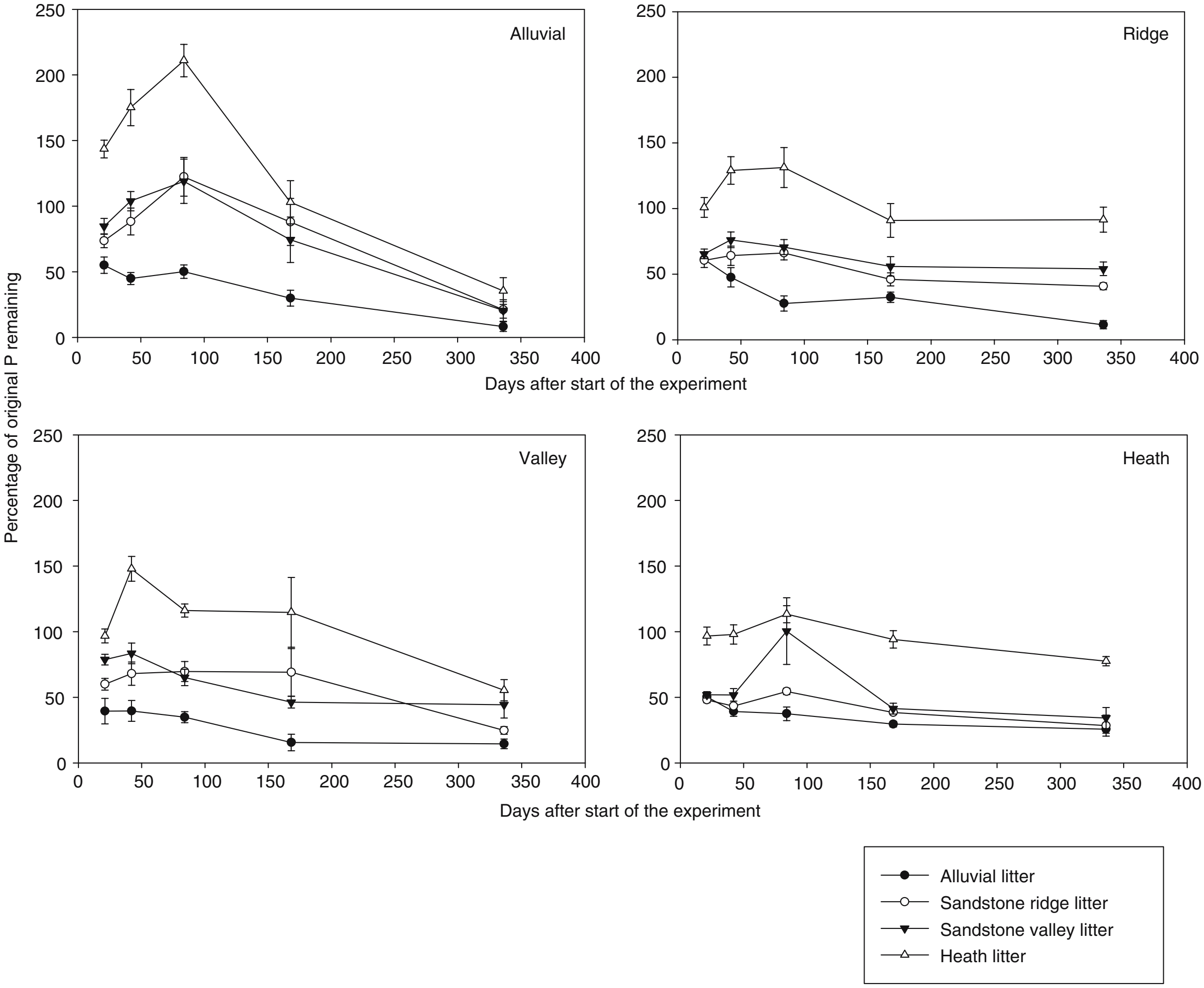

Fig. 4 Percentage of original P (by mass) remaining in litter contained in litter decomposition bags. Litter was collected from four habitats (alluvial, sandstone ridge, sandstone valley and heath) and positioned in each of these habitats in the Sepilok Forest Reserve. All values are means ± SE

ultisols (Vitousek 1984). The alluvial forest at Sepilok had low NUE and high rates of N deposition per year, which suggests that it did not suffer extreme N limitation and may be less limited by N than any of the other forest communities we studied at Sepilok. The flux of P via litterfall in the alluvial forest community was approximately four times greater than in the other three communities. At SFR, the heath forest and the forests positioned over sandstone ridges and valleys cycle P extremely efficiently (Fig. 3). The litterfall mass to P quotient is highest for these sites and at the upper limit of values observed for tropical evergreen forests (Vitousek 1984). We conclude that both N and P might limit litterfall in the heath forest, which contradicts the classical hypothesis that heath forests are limited principally by the availability of N rather than P (Proctor et al. 1983; Moran et al. 2000). However, Vitousek and Sanford (1986) state that forests found on spodosols “efficiently cycle small quantities of N (and in some cases P)”, which implies that co-limitation by N and P may occur. Not only was the heath forest litter the most nutrient poor, it also had the highest values for concentrations of lignin and condensed tannins and the quotients of these constituents to N, which indicates a gradient in litter quality from

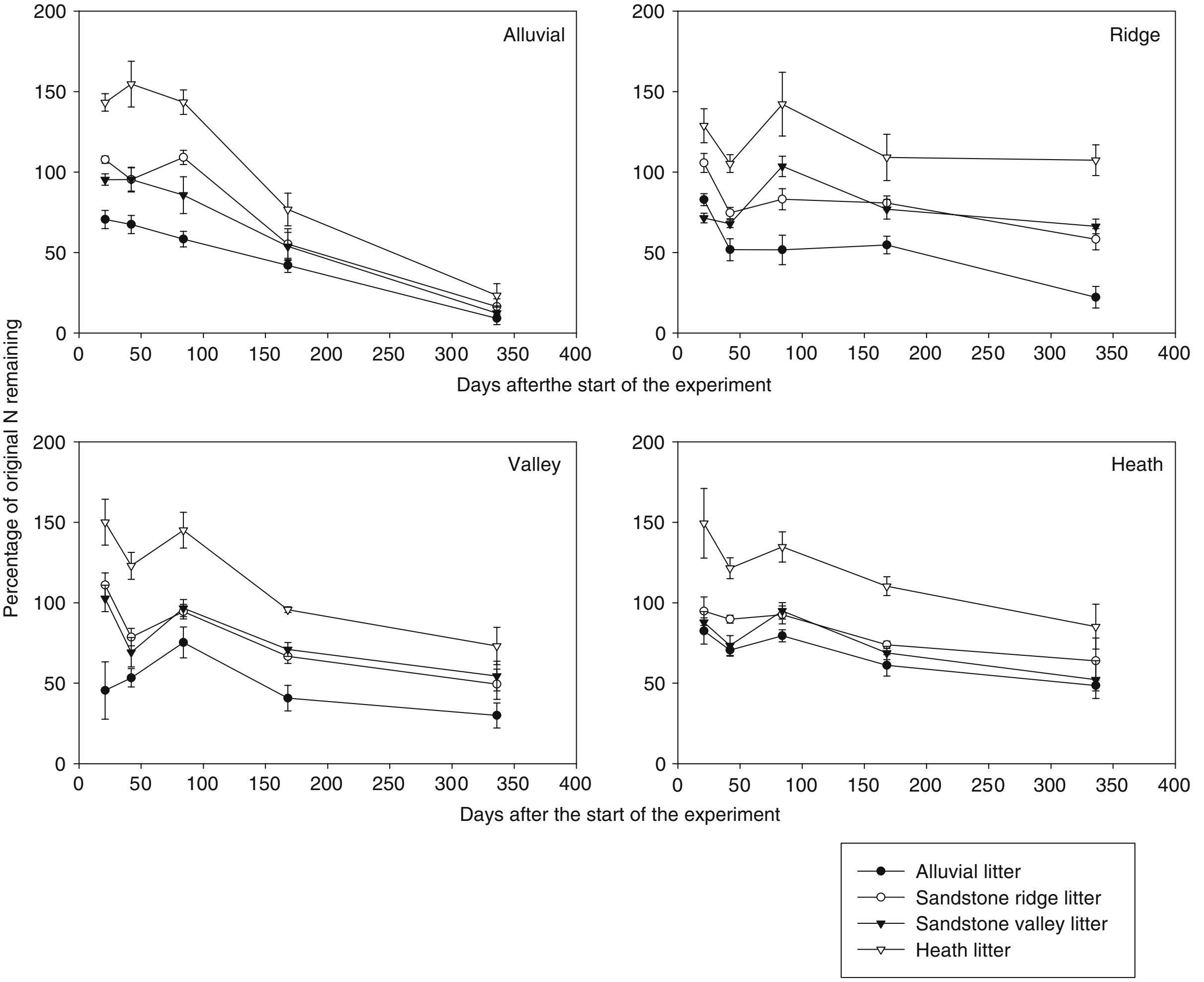

Fig. 5 Percentage of original N (by mass) remaining in litter contained in litter decomposition bags. Litter was collected from four habitats (alluvial, sandstone ridge, sandstone valley and heath) and positioned in each of these habitats in the Sepilok Forest Reserve. All values are means ± SE

alluvial to sandstone to heath forest that is directly associated with the soil fertility gradient (Melillo et al. 1993; Aerts 1997; Loranger et al. 2002).

The forests overlying sandstone soils cycle smaller amounts of Ca than the alluvial and heath forests. However, Ca is rarely a limiting nutrient and plants usually take up Ca in excess of that needed for cell metabolism (Rorison and Robinson 1984). Therefore, the low Ca concentrations in litterfall may be a product of the low Ca concentrations in sandstone soils and yet not an indication of Ca limitation (Table 1). Although litterfall can be used as an indicator of K and Mg cycling, K and, to a lesser extent, Mg are so readily leached that they are principally returned to the forest floor via throughfall (Cole and Rapp 1981; Parker 1983). Concentrations of K were highest in alluvial forest litter, but the lowest concentrations were found in the sandstone ridge, and not heath, forest litter as may be expected from the soil nutrient data (Table 1). Stand level K use efficiency data suggest that the K status of the sandstone valley and the sandstone ridge sites were very different, possibly because the valley sites receive soluble K in water draining from adjacent hills and ridges.

All habitat types showed large temporal variation in total daily litterfall. Litterfall for individual species may vary over time in response to climate even in the aseasonal tropics

Table 7 R^2 and *P* values from correlations of leaf litter nutrient and secondary compound concentrations with biomass remaining for all types of leaf litter in each of four different decomposition environments within the Sepilok Forest Reserve ($n = 4$)

	Decomposition environment			
	Alluvial	Sandstone Ridge	Sandstone Valley	Heath
N (mg g^{-1})	–21.3 0.002	NS	–14.6 0.009	–12.5 0.018
P (mg g^{-1})	–38.4 < 0.001	NS	NS	–17.4 0.006
Lignin (%)	+18.2 0.004	+20.7 0.003	NS	+21.0 0.003
Condensed tannins (mg g^{-1})	+29.6 0.004	+8.5 0.047	NS	+23.1 0.002
Lignin/N	+18.6 0.003	+17.1 0.007	NS	+14.9 0.010
Condensed tannins/N	+26.8 < 0.001	+15.0 0.011	NS	+25.6 < 0.001

– indicates a negative and + a positive relationship

(Burghouts et al. 1994; Chuyong et al. 2000). Monthly rainfall ranged from < 100 mm to >700 mm per month in 2001 at Sandakan Airport 11 km west of SFR. Peaks in tropical forest litter production in response to drought periods are commonly reported (Proctor 1984). Both sandstone forests showed a negative relationship between litter production and rainfall in the previous month. The absence of these responses from the alluvial and heath forests may indicate that drainage of water from sandstone soils, especially from ridges, increases the possibility of water shortage during dry periods (Becker et al. 1988; Daws et al. 2002). The low tree species diversity of the heath forest (Table 1; Nilus 2003) may explain the lower spatial variation of litterfall in this community; if rates of litter production vary between tree species then reduced species richness would result in a more spatially homogenous litterfall (Burghouts et al. 1994).

Litter standing crop and rates of litter decomposition and turnover (K_L)

The rates of leaf litter decomposition were consistent with other tropical forest studies that have used leaf litter bags with similar mesh sizes that exclude soil macrofauna: K_L values of 1.17–2.22 (1 mm mesh; Rogers 2002); 1.30 (1.5 mm mesh; Klinge 1977); 1.30–1.60 (1.5 mm mesh; Bloomfield et al. 1993) and 2.93 (3 mm mesh; Didham 1998). Litter turnover rates were similar to the rates derived from the litter bag experiment and showed the same pattern of variation between forest types.

The sandstone ridges had the greatest mass and depth of standing small litter despite there being greater inputs through litterfall in the alluvial forest. Estimates for litter turnover suggest that decomposition rates were much greater in the alluvial forest than the other forest types, a pattern that was confirmed in the decomposition experiment. The litter bag experiment suggested that this pattern was caused by differences in both the physical environment and litter quality. To our knowledge there are no comparable data on landscape-level variation in leaf litter decomposition within the lowland tropics.

Although the forest communities in Sepilok experience the same climate, differences in soil type and topography can create very different environments for decomposition. Small-scale variation in topography may reduce the moisture content of soil and litter, especially on the well drained ridge tops (Daws et al. 2002; Gibbons and Newbery 2003; Baker et al. 2003). In contrast the alluvial forest areas are flat and poorly drained, and standing water is seen there at certain times of year (Fox 1973), and studies of soil moisture have indicated higher gravimetric water content of alluvial than sandstone soils within SFR (Dent 2004). Limited water availability can inhibit the metabolism of fungi and bacteria (Aerts 1997), thus reducing the rates of leaf litter decomposition in sandstone forest in comparison to wetter alluvial forest areas.

The alluvial forest litter had the highest nutrient concentrations, the lowest concentrations of tannins and lignins, and decomposed more quickly than any other litter type at the sandstone sites (Table 3, Fig. 5). Thus the $t_{0.5}$ estimates for alluvial litter at sandstone sites were considerably shorter than the estimates for other litter types (Table 6). This supports the hypothesis that faster decomposition rates in tropical forests are associated with higher nutrient concentrations and lower secondary compound concentrations in litter (Swift et al. 1979; Melillo et al. 1982; Proctor et al. 1983; La Caro and Rudd 1985; Mesquita et al. 1998; Loranger et al. 2002). However, the leaf constituents most strongly correlated with rates of decomposition were not consistent across all decomposition environments.

In this study the decomposition rates of different litter types did not vary significantly in the alluvial forest habitat, and rates of decomposition for all litter types were considerably faster in the alluvial sites than in any other habitat. We conclude that litter quality had an important influence on the rate of litter decomposition but that the decomposition environment could override differences in litter quality.

Different litter types had significantly different patterns of nutrient loss. The alluvial forest leaf litter released N and P rapidly in all four forest types and the sandstone litters followed a similar but slower pattern of N and P release. However, leaf litter from the heath forest initially accumulated both N and P and released these nutrients only after 50–100 days. Therefore the pattern of early N and P accumulation followed by net release (Vitousek and Sanford 1986; Upadhyay and Singh 1989) was found only in the most nutrient-poor litter. The patterns of nutrient release seen in this study support the hypothesis that initial concentrations of N and P are positively related to the rates of N and P release (Upadhay and Singh 1989; Chuyong 1994; Cornu et al. 1997).

The decomposition environment had a significant effect on the release of N and P from all litter types. Percentages of N and P in leaf litter decomposing in the alluvial forest habitat were higher than in any other habitat up to 100 days from the start of the experiment, but at the end of the experiment were the lowest observed. Nutrient losses from litter at the sites with lower nutrient availability may be more rapid initially because competition for the new nutrient source, by plants and microorganisms, is more pronounced than at nutrient-rich sites. However, because of the rapid loss of leaf litter mass at the alluvial site the final percentages of original N and P were lower than in litter that decomposed in the sandstone or heath forest sites, where the dry mass loss rate was low.

K is readily leached and was lost rapidly from all types of leaf litter in all habitats (O'Connell and Sankaran 1997). However, there were still significant differences between litter and habitat types which followed similar patterns to those seen for N and P, i.e. leaf litter from the heath forest lost K more slowly than the other types of litter and the initial phase of K release from litter was slower in the alluvial habitat. The initial accumulation of Ca in leaf litter followed by a phase of net release has been reported for lowland tropical forests on Maraca Island, Brazil (Luizao et al. 1998) and at Gunung Mulu, Sarawak (Anderson et al. 1983). However, this pattern of Ca release is not always seen, and other tropical forest studies have reported different patterns of Ca release over time (Upadhay and Singh 1989; Cornu et al. 1997). At Sepilok, the sandstone ridge and heath forest litters showed an initial phase of Ca accumulation with a subsequent phase of net release, whereas leaf litter from the two wetter forest communities (alluvial and sandstone valley) released Ca immediately with no accumulation phase. The pattern of Ca release was unrelated to initial Ca litter concentration (Chuyong 1994).

Conclusions

As predicted, litter production, N and P concentrations increased and stand-level nutrient-use efficiencies decreased along a gradient of increasing soil fertility. Nutrient-use efficiencies indicated that the alluvial forest, which occurs over the most nutrient rich soils, was least limited by N and P, and that both N and P might limit litterfall in the heath forest, which contradicts the hypothesis that heath forests are limited principally by N rather than P. Litterfall production in the forests overlying well-drained sandstone soils increased linearly with decreased rainfall in the previous month, but this trend was not seen in the alluvial or heath forests. Therefore, although all forest types experienced a similar climate there were local differences in water availability mediated by soil type and topography. Rates of litter decomposition responded to both the litter quality and its decomposition environment and the most nutrient rich litter decomposed most quickly in all environments. However, increased water availability and high soil fertility in the alluvial forest habitat resulted in the fastest rates of litter decomposition and reduced differences between litter types in this environment.

The findings from the SFR are largely consistent with general patterns of increased litterfall production and decomposition in relation to increased soil fertility. However, we find local-scale site dependent variations within the SFR that are associated with the availability of water and differences in litter structure and chemical composition, and these might be important as determinants of differential species distributions between habitats.

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