

LEAF LITTER DECOMPOSITION AND SOIL CARBON DIOXIDE FLUXES ACROSS CLIMATIC GRADIENT IN TROPICAL MONTANE AND LOWLAND FORESTS

V Jeyanny^{1,*}, K Wan Rasidah¹, MH Ahmad Husni², B Siva Kumar², S Muhammad Firdaus³ & A Arifin⁴

¹Forest Research Institute Malaysia, 52109 Kepong, Selangor Darul Ehsan, Malaysia

²Faculty of Agriculture, Universiti Putra Malaysia, 43400 Serdang, Selangor Darul Ehsan, Malaysia

³School of Environmental Sciences, University of Guelph, 50 Stone Road East Guelph, Ontario, N1G 2W1 Canada

⁴Faculty of Forestry, Universiti Putra Malaysia, 43400 Serdang, Selangor Darul Ehsan, Malaysia

Received January 2014

JEYANNY V, WAN RASIDAH K, AHMAD HUSNI MH, SIVA KUMAR B, MUHAMMAD FIRDAUS S & ARIFIN A. 2015. Leaf litter decomposition and soil carbon dioxide fluxes across climatic gradient in tropical montane and lowland forests. Leaf litter decomposition and soil respiration are of great interest in climate change studies due to their roles in recycling carbon and nutrients. These processes can be markedly different in tropical montane and lowland forests. Litterbag technique was used to determine the decomposition and nutrient dynamics of leaf litter in two different tropical forest types in Pahang, Malaysia for 480 days. Soil CO₂ fluxes were measured periodically for up to 360 days. Mass loss, total C, N, S, P, K, Mn, lignin, cellulose as well as C:N and lignin:N dynamics of decaying leaves were quantified. Various mathematical models and regression analysis were used to describe litter mass loss trends. Rapid decomposition (k : -0.004 day⁻¹) and weight loss (> 80%) took place in the lowland forest compared with the montane forest. Significant linear regression relationships between mass loss and litter quality were obtained for all sites except for cellulose (montane forest). Low soil CO₂ fluxes (two to three folds) and 38% slower decomposition due to reduced soil and air temperatures were found in the montane forest, suggesting its role as potential temporary C sink. Decomposition rate, C:N, lignin:N and soil respiration can be used as potential indicators to predict C balance in forests.

Keywords: Litter decay, carbon cycle, soil respiration, tropics, high altitudes

INTRODUCTION

Decomposition of leaf litter is a vital ecological process in C balance and nutrient cycling in terrestrial ecosystems (Scheffer et al. 2001). Mineralisation of litter contributes 50% of the CO₂ flux from soil and usually remains stable due to constant litter production (Cousteaux et al. 1995). In recent time, litter decomposition and soil respiration have taken centre stage due to their roles in global climate change. Tropical ecosystems which boast warmer climates are important sinks and source of atmospheric C. The need to investigate changes that take place during litter decomposition and soil CO₂ fluxes has been amplified due to the projected global temperature increase of 0.6 and 1.1 °C over the period 1880 to 2012 (IPCC 2013) with rising atmospheric CO₂ (Pitelka & Rojas 2001). Litter

decomposition is influenced by climate, litter quality and decomposers (Austin & Vitousek 2000, Jacob et al. 2009). Litter quality is the chemical properties of plant litter inclusive of nutrient ratios (i.e. C:N and lignin:N) (Strickland et al. 2009). The degradation of lignin is usually controlled by Mn which actively participates as manganese peroxidase enzyme (Berg & McClaugherty 2008).

Climatic variables such as soil, air temperature, relative humidity and rainfall as well as soil moisture content play more dominant roles in influencing litter decomposition in forests of different altitudes such as lowland and montane forests due to climatic gradients. Many researchers have studied the role of litter decomposition as an important process in

*jeyanny@frim.gov.my

nutrient turnover and maintaining soil fertility (Baggie et al. 2004, Perez-Corona et al. 2006, Uma et al. 2014) rather than for estimating C budgets. We tested a hypothesis concerning leaf litter decay in both climatic gradients whereby litter decomposition was influenced by litter quality and accelerated decomposition took place at low litter C:N and lignin:N ratios.

Soil respiration is the largest terrestrial source of CO₂ to the atmosphere and accounts for an annual flux that is one magnitude higher than fossil fuel combustion (Raich et al. 2002). Soil efflux rate at the soil surface is the sum of heterotrophic (microbial decomposition) and autotrophic (root) respiration whereby root usually constitutes almost half of the soil CO₂ fluxes (Luo & Zhou 2006, Berger et al. 2010). Soil respiration has been investigated in various ecosystems, namely, temperate, boreal and neotropical rainforests (Xu & Qi 2001, Adachi et al. 2006) but studies in relation to litter decomposition and its differences in montane forest and lowland tropical forest are still scarce. Soil respiration is influenced by various factors, particularly, soil temperature, soil moisture content (Adachi et al. 2006) and the presence of litter and root dynamics (Couteaux et al. 1995). Measurements of soil CO₂ emissions taken simultaneously with litter decomposition in forests of high and low altitudinal variations can be used to evaluate soil as sources or sinks of C. Furthermore, litter decomposition decay curves and soil respiration patterns due to elevation and litter quality may shed some light on the characteristics of C dynamics. This will help forest managers in understanding, managing and predicting the rate of soil organic C loss or sequestration in a changing climate. Thus, the objectives of this experiment were to detect leaf litter decomposition, changes in substrate quality, estimate mass loss and evaluate soil CO₂ fluxes in tropical montane forest and lowland forest that could potentially indicate soil C storage.

MATERIALS AND METHODS

Study site

The research was carried out at two different areas, each representing a montane forest and a lowland forest in Pahang, West Malaysia. The

first site is located at Sungai Kial Forest Reserve (FR), Tringkap, Cameron Highlands, Pahang (4° 31' N, 101° 25' E). The second site is located at a secondary lowland forest known as Jengka Virgin Jungle Reserve (Jengka VJR), Jengka 18, Pahang (3° 35' N, 102° 34' E). The detailed site description is explained in Jeyanny et al. (2013) and is briefly tabulated in Table 1. Jengka VJR was reported to be logged once in 1968–1969 and known as a secondary forest (Putz & Redford 2010) with minimal disturbances (Laidlaw 2011). Both sites with vast differences (Table 1) were selected to show changes that might take place (i.e. decomposition and soil CO₂ flux) at different forest types and altitudes.

Meteorological data

Data on mean temperature and rainfall were collected for both sites from Jun 2011 till November 2012 for Jengka VJR and July 2011 till November 2012 for Sungai Kial FR. The two stations which logged the data were the Felda Kampung Awah station (03° 31' N, 102° 30' E) and Tanah Rata station, Cameron Highlands (04° 28' N, 101° 22' E).

Litter decomposition and mass loss

Freshly fallen foliar litter were collected at random points within the study area for Jengka VJR and Sungai Kial FR (according to slope position). A 25 cm × 25 cm (PVC) frame was placed on the litter layer and litterfall material consisting of leaves and twigs less than 25 mm in diameter were collected. Live roots and fresh (green) leaves were omitted. Leaf litter samples were air dried at room temperature, cleaned of debris and mixed thoroughly in the laboratory instead of a single species so as to accurately represent site-specific decomposition rates under natural conditions which were heterogeneous (Borders et al. 2006). A total of 7.5 g leaves were weighed and inserted into polyethylene litterbags measuring 15 cm × 15 cm with 1-mm mesh size. The bags were sewn using nylon thread and tagged. Subsamples were reserved prior to litterbag preparation for initial chemical analysis. A total of 64 litterbags were prepared for Sungai Kial FR to represent two slope positions, i.e.

Table 1 Site description of research area

Characteristic	Sungai Kial Forest Reserve	Jengka Virgin Jungle Reserve
Elevation (m asl)	1400–1600	50–90
Slope (°)	22–40	2–18
Soil series	Ringlet	Durian
Typic	<i>Haplohumult</i>	<i>Paleudult</i>
Soil texture	Clay loam	Silty clay loam
Common tree families	Myrtaceae, Lauraceae Polygalaceae	Phyllanthaceae, Dipterocarpaceae

asl = above sea level

summit and toeslope. The bags were placed horizontally on the forest floor and lightly covered with natural litter layer in July 2011 and tagged. Eight litterbags were retrieved every 4 months from each slope position for a period of 16 months starting from November 2011. However for Jengka VJR, 32 (8 replications $\times$ 4 collections) litterbags were placed beginning June 2011 and retrieved accordingly. Upon arrival at the laboratory, litterbags were air dried, carefully brushing off contaminants and oven dried at 65 °C until constant weight. The weights of samples were recorded. The percentage of dry mass loss was calculated according to Olson (1963) and the decomposition rate constant k was calculated from the decay curve using equation 1 (Berg & McClaugherty 2008).

$$\ln(M_0/M_t) = kt \quad (1)$$

where M_0 = mass of litter (g) at time 0, M_t = mass of litter (g) at time t , t = time of incubation (days) and k = decomposition rate constant.

Nutrient analyses of C, N, S, P, K, Mn, lignin and cellulose

Tissue samples collected initially and periodically were ground to < 1 mm size particles and analysed for C, N, P, K, S, Mn, lignin and cellulose. The values for total C, N and S were determined using CNS analyser. Total P, K, and Mn were determined using the dry ashing method, followed by determination of element concentration using inductively coupled plasma spectrometer. The Van Soest (1963) acid detergent method was used to determine substrate quality of lignin and cellulose.

Soil respiration measurements

An automated soil CO₂ flux system was used to measure soil CO₂ fluxes with the atmosphere. The instrument was calibrated using the zero and span procedure before measurements were recorded. Measurements were taken between 10 a.m. and 12 noon, when daily soil CO₂ fluxes were assumed to be at the highest rate (Luo & Zhou 2006). Sampling replications were constrained by time whereby unequal numbers of replications were obtained at Jengka VJR as well as summit and toeslope of Sungai Kial FR. A total of 11 measurements were taken for Jengka VJR. Both the summit and toeslope plots in Sungai Kial FR had six replicates each. Prior to measurement, a 10 cm $\times$ 10 cm PVC pipe soil collar was placed on soil surface and inserted into the soil, leaving a headspace of 3 cm. Flux measurements were made approximately 1 m from the stem of the nearest tree on bare soil and soil disturbance during collar insertion was minimised. During measurement, the lid of the chamber was closed and air was circulated in a gap between the collar headspace and the chamber. Once the CO₂ concentration in the chamber had stabilised (approximately 30 s), the concentration was recorded for about 60 s. Each measurement was repeated twice at each sampling point. The flux rate was determined by the software of the system by calculating the initial slope of a fitted exponential curve at ambient CO₂ concentration.

Ancillary measurements

Six replicates of bulk density samples at 5 cm depth were retrieved using core rings of

100 cm³, close to the soil flux measurement sampling point (5 cm depth) to determine soil porosity and volumetric soil water content. The core rings were recorded for initial weight and placed in a three-phase meter to determine volume of solid soil particles, and later oven dried at 105 °C for 24 hours for soil bulk density and soil water content measurements. Soil water content was expressed as percentage of water filled pore space, which was the ratio of volumetric water content to the total porosity of soil. Air filled pore space was equivalent to 1 minus water filled pore space.

Soil temperature was determined using additional temperature probe that was fitted with the pH meter. The probe was inserted into the soil at 5 cm depth and measurement was taken when values stabilised. Relative humidity values were obtained from CO₂ flux system.

Statistical analysis

The trends of mass loss, total C, N, S, P, K, Mn, lignin, cellulose, C:N and lignin:N over time were determined using either a single exponential model or double exponential model in Sigmaplot version 12.0 Software. The goodness of fit of the regression models were tested using adjusted coefficient of determination (r^2), normality test and mean squared error (MSE) values of the actual and predicted values. Selections of models were based on significance of r^2 at $p < 0.05$, normalised data distribution and the lowest MSE values (Mason et al. 2006, Parsons & Congdon 2008). Pearson linear correlation between mass loss and litter quality from 0 to 480 days were also computed to identify which litter quality variable had the most significant effect on mass loss. Analysis of variance (ANOVA) for soil CO₂ fluxes, water filled pore space and air filled pore space were done in Statistical Analysis System version 9.2 and the treatment means were compared according to Student–Newmann–Keul test.

RESULTS AND DISCUSSION

Meteorological data

Mean temperatures in Sungai Kial for 2011 and 2012 were 17.7 and 18.1 °C, generally showing an increasing trend (Figure 1). A slight increase in temperature was observed from March till May

2012 and from September till November 2012. Rainfall ranged from 110 to 450 mm, where heavy precipitation occurred in August 2011, October 2011 as well as November 2011 and 2012. Dry season was recorded from December 2011 till February 2012. Annual rainfall ranged from 2800 to 3310 mm for 2011 and 2012.

The mean temperature for Jengka VJR (Figure 2) ranged from 25 to 28 °C except for August and December 2011 when temperature surged to above 30 °C. Values were not available for the periods of June–July 2011, September–November 2011, January 2012 and June 2012. High precipitation was apparent during the months of October and November 2011 (250–350 mm). June till September (2011 and 2012) were considered dry as rainfall was less than 200 mm.

Changes in temperature in Sungai Kial FR were related to lower rainfall during March till June 2012 and September till October 2012, which destabilised air temperature. Annual rainfall above 2000 mm was common in Sungai Kial according to rainfall data from 1965 till 1998 (DOA 2000) with wet seasons occurring in October and November (DOA 1989). Poore (1968) reported similar mean temperature of 25.8 °C for Jengka VJR. The typical dry season from June till September was common due to the south-west monsoon and the inter monsoonal period in October, leading to heavy rainfall (Poore 1968). Generally, mean temperatures in Sungai Kial FR were relatively lower compared with Jengka VJR. The precipitation trends in the montane forest were also on the higher side due to periodic cloud formations in mountainous terrain (Hafkenscheid 2000).

Initial nutrient analysis

Carbon constitutes more than 40% of the leaf nutrients (Table 2). Values for total N, S, P, K and Mn were all relatively higher in the summit and toeslope plots of Sungai Kial compared with those of Jengka VJR. Values for proximate cellulose and lignin were 33–41%. Leaf litter C:N and lignin:N were relatively higher for Jengka VJR (56) compared with Sungai Kial, which recorded levels ranging from 20 to 25.

High C stimulates lignin degradation (Baggie et al. 2004) but high N suppresses lignolytic activity by at least 83% in *P. chrysosporium*. On

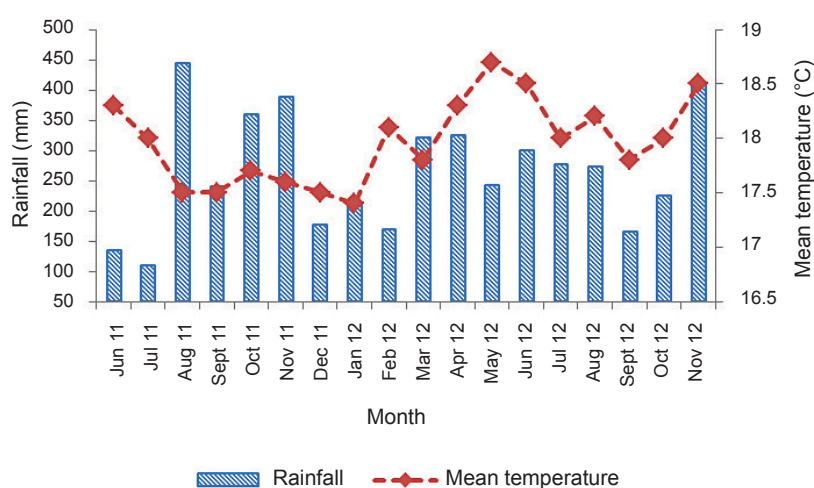


Figure 1 Changes in mean temperature and rainfall from July 2011 till November 2012 in Sungai Kial Forest Reserve

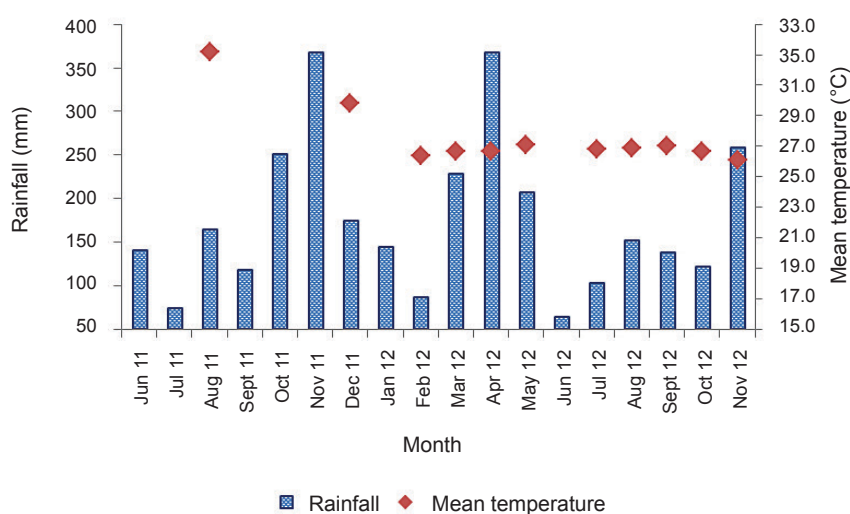


Figure 2 Changes in mean temperature and rainfall from July 2011 till November 2012 in Jengka Virgin Jungle Reserve

the other hand, elevated levels of Mn in Sungai Kial litter may potentially enhance the activity of Mn-peroxidase, which takes part in lignin degradation (Perez & Jeffries 1992). Increased P content is usually dependent on the amounts of C, N and its ratio as well as cellulose, lignin and polyphenols. Its increment positively stimulates decomposition and facilitates P release (Baggie et al. 2004). Nevertheless, values for N, P and K for both the lowland and montane forest were similar to leaf nutrient fractions in Sepilok Forest Reserve, Sabah (Dent et al. 2006). Levels of proximate lignin and cellulose corroborated

with reports by Scherer-Lorenzen et al. (2007) in a tropical forest in Panama. Values for C:N and lignin:N were unique depending on their respective inert qualities of leaf litter as our results varied with other researchers (Parsons & Congdon 2008, He et al. 2009).

Decomposition decay, mass loss and substrate quality

Figures 3a–c show the relationship between percentage of litter remaining, which is negatively correlated with time (days) based on a single

Table 2 Initial nutrient concentration of leaf litter analysis

Study site	C	N	S	P	K	Mn	Proximate cellulose (%)	Proximate lignin (%)	C:N	Lignin:N
	←	←	(%)	→	→	(mg g ⁻¹)				
Sungai Kial Forest Reserve										
Summit	43.98 (0.63)	1.81 (0.03)	0.07 (0.00)	0.04 (0)	0.21 (0)	0.6 (0)	33.14 (1.39)	36.97 (1.12)	24.26 (0.36)	20.38 (0.33)
Toeslope	43.20 (0.44)	1.72 (0.07)	0.07 (0)	0.04 (0)	0.23 (0)	0.6 (0)	37.13 (0.96)	33.87 (6.08)	25.20 (1.23)	21.61 (0.50)
Jengka Virgin Jungle Reserve	42.64 (0.03)	0.73 (0.03)	0.03 (0)	0.01 (0)	0.17 (0)	0.3 (0)	33.24 (1.29)	41.64 (0.77)	56.22 (1.99)	56.96 (1.90)

Values in parentheses represent standard errors

exponential model. Significant regression coefficients ($p < 0.01$) were shown for all three models. The goodness of fit for both summit and toeslope were 87% and for Jengka VJR, 76%. The decomposition decay constant k was -0.0026 day^{-1} for toeslope, the lowest compared with summit (-0.0032 day^{-1}) and Jengka VJR (-0.0040 day^{-1}).

Weight loss for Jengka VJR was the fastest compared with summit and toeslope, where rapid decomposition took place at 120 and 240 days (Figure 3c). The annual k values (365 days) were -0.0019 , -0.0016 and $-0.0045 \text{ year}^{-1}$ for summit, toeslope and Jengka VJR respectively (results not shown). After 480 days, the remaining litter was close to 20% for all sites. Thus the single exponential model decay according to Olson (1963) was adapted for this study. The single exponential model provides simplicity and better goodness of fit for initial decomposition stage (Berg & McClaugherty 2008). It gave the most significant adjusted r^2 and lowest MSE values (Table 3). Moreover, the model was chosen as it passed the normality test. The prediction percentage of leaf litter remaining can be done for all sites based on the given equation if an x value (t , days) is introduced, and the y value falls within the 95% confidence band (dotted line) in Figure 3.

Litter mass loss was not drastic in Sungai Kial FR owing to low temperatures and heavy precipitation encountered in the montane forests that might have slowed down decomposition. The wider confidence interval band for litter mass remaining in toeslope (Figure 3b) as opposed to summit (Figure 3a) indicated that increased amount of replications at the toeslope would have enhanced precision on decomposition trends. He et al. (2009) investigated litter decomposition in Jiang Fengliang montane forest, China above 800 m asl and concluded that the litter decay constant was $0.08\text{--}0.1 \text{ month}^{-1}$ at 20°C at higher altitudes. Majila et al. (2005) also confirmed values for high elevations were between -0.0026 and -0.0042 day^{-1} as found in our study. Values were reported to be lower in temperate forests (-0.05 month^{-1}). The k values for Jengka VJR concurred with Nahrawi et al. (2011) for sago leaves at lowland temperatures as elevated temperatures increased decomposition processes (Vitousek et al. 1994, Yanai et al. 2003). The extreme litter mass loss encountered at 120

and 240 days in Jengka VJR probably were also influenced by soil water filled pore space besides precipitation, whereby moisture conditions at the litter surface allowed rapid decomposition (Valentini et al. 2008). Decomposition rates in the Sepilok Forest Reserve were also reported to be -0.004 day^{-1} in the sandstone ridge and valley forest (Dent et al. 2006) of Borneo. Accelerated decomposition processes in lowlands may provide better nutrient turnover in soil, leading to increased net primary production of aboveground biomass.

Carbon levels for Sungai Kial FR were relatively stable from the start (Table 2) but levels decreased with time for Jengka VJR during the decomposition process (Table 4). Both N and P increased positively during decomposition in both forest reserves, compared with the initial levels, especially for N. Values for S showed similar trend except for summit at 480 hours, which slightly decreased from 0.19 to 0.13%. Potassium levels were markedly reduced during decomposition as opposed to initial concentrations in leaf litter (Tables 2 and 4). There were also no distinctive trends for Mn concentration during decomposition. Lignin levels were in the range of 37–51% in Sungai Kial FR, increasing during the first stage of decomposition compared with initial levels (Table 2) but decreased for Jengka VJR with values ranging from 28 to 38%. Cellulose levels increased with time in Jengka VJR and stabilised but values for Sungai Kial FR were in the range between 17 and 32%. Levels of lignin and cellulose shared an antagonistic relationship in both forest sites, whereby low levels of lignin were recorded when cellulose increased (Table 2). Both leaf litter C:N and lignin:N decreased with time for summit and Jengka VJR whereby decrease was more prominent in Jengka VJR.

Significant correlations (Table 5) were apparent for N, P, K, Mn, C:N and lignin:N for summit, whereby most variables showed highly significant r values of 0.7 ($p < 0.001$). Mass loss of litter was positively correlated with the release of all corresponding nutrients at toeslope except for P, proximate cellulose and lignin:N. Decreasing K release as opposed to initial K contents was indicated by negative slopes for all sites. Correlations for N and P were significant for most sites, whereas proximate cellulose was least correlated except for Jengka VJR.

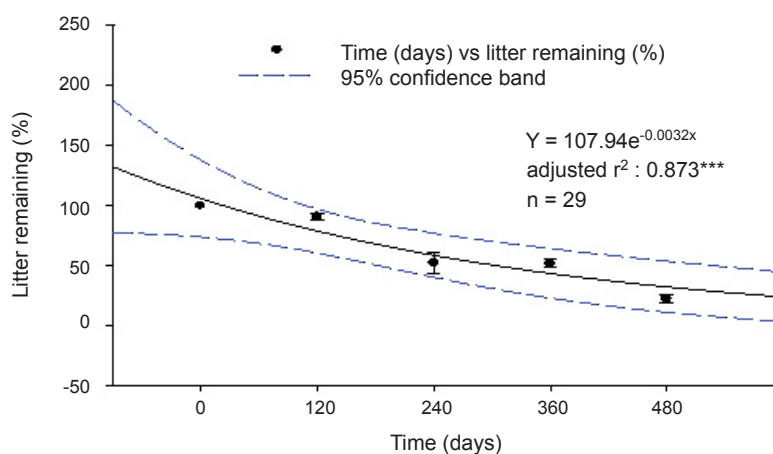


Figure 3a Trend of litter remaining against time at summit of Sungai Kial Forest Reserve

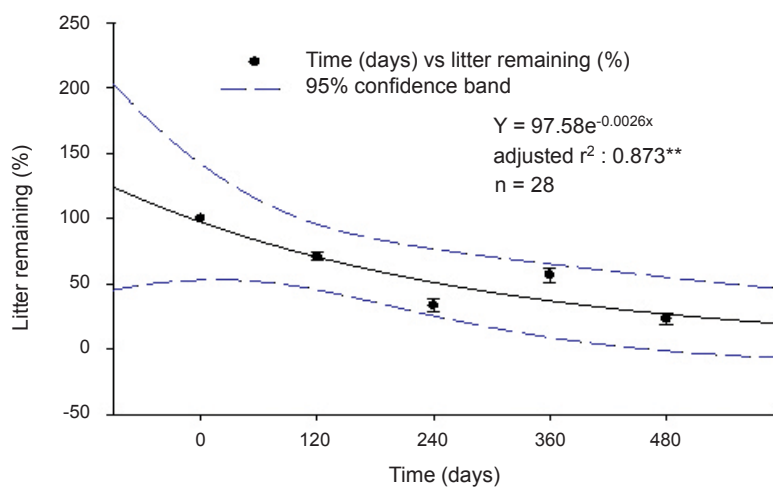


Figure 3b Trend of litter remaining against time at toeslope of Sungai Kial Forest Reserve

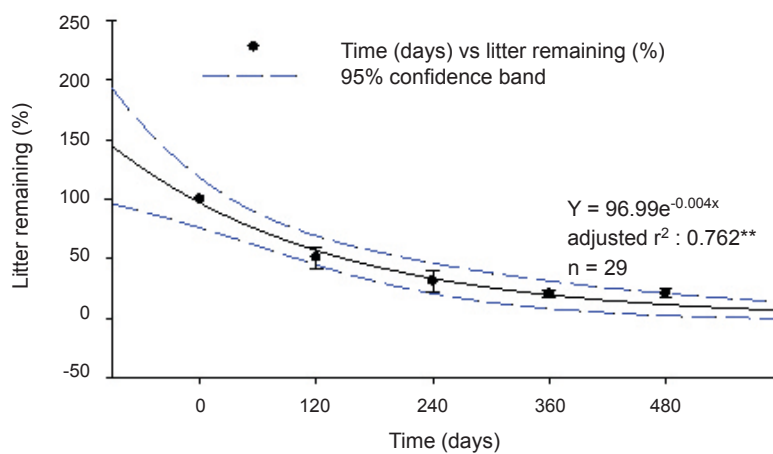


Figure 3c Trend of litter remaining against time in Jengka Virgin Jungle Reserve

Table 3 Cross validation of litter decay models

Site	Single exponential model			Double exponential model		
	MSE	Adjusted r^2	Normality test	MSE	Adjusted r^2	Normality test
Sungai Kial Forest Reserve						
Summit	151.14	0.87**	Passed	367.05	0.88**	Passed
Toeslope	236.41	0.87**	Passed	243.68	0.72**	Passed
Jengka Virgin Jungle Reserve	232.43	0.79**	Passed	218.39	0.80**	Failed

MSE = mean squared error, **significant at $p < 0.01$

Carbon is an important constituent in litter and is usually related to lignin degradation (Berg & McClaugherty 2008). Stable values for C in Sungai Kial FR may suggest that degradation of lignin is slow (Table 2) but reducing levels in the lowland facilitates soil C mineralisation processes with increasing temperatures (Couteaux 1995). This further substantiated an earlier investigation done in the same plots where Jengka VJR was only able to sequester 23 Mg C ha⁻¹ in soil compared with 98–126 Mg C ha⁻¹ in montane forest (Jeyanny et al. 2013). The increase of N at the early stage of decomposition is quite common due to immobilisation (Domisch et al. 2006). Both N and P are reported to be actively involved in translocation, microbial growth and its metabolites, thus giving increasing levels during decomposition (Parsons & Congdon 2008) and positive linear correlations in most of the sites (Table 5). Sulphur levels were more related to nucleic acid formation and were reported to increase linearly during decomposition (Berg & Laskowski 2006) (Table 5). Potassium is highly soluble, vulnerable to leaching and easily utilised for microbial growth, thus giving decreasing values (Berg & McClaugherty 2008). However, K losses were insignificant in the lowland forest when plotted against mass loss due to environmental characteristics of Jengka VJR, exhibiting reduced precipitation and a flat terrain that delayed leaching processes. Manganese is an important constituent in the activity of Mn–P, a lignin degrading enzyme (Perez & Jeffries 1992). It was reported to affect C release via soil respiration due to consumption of labile C (Trum et al. 2010). Although the values for Mn were irregular during decomposition, it was noticed that C and Mn shared an antagonistic relationship for the summit and toeslope plots

(Table 4), suggesting C loss with increasing Mn for the summit. Similarly, proximate lignin during decomposition was antagonistic to Mn trends in the summit (Sungai Kial FR) and Jengka VJR. Lignin represents 30% of the carbon sequestered in plant materials annually (Austin & Ballare 2010). Increased lignin in Sungai Kial during early stages was due to decomposition of easily degradable compounds that left lignin levels intact to enrich the decomposing litter layer (Berg & McClaugherty 2008). However, the attributes of lignin during decomposition were inconclusive as it did not show any concrete correlation trends. A possible assumption is that lignin degradation is amplified during warmer climates in Jengka VJR by microbial activities and its resilience is influenced by litter quality and composition (Fioretto et al. 2005). The importance of lignin is also closely related to lignin: N, which controls the amount of metabolic fraction in plant residues (Bernhard-Reversat & Schwartz 1997). It is a good predictor of mass loss during initial stage of decay (Adair et al. 2008, Nahrawi 2011) as shown in Table 4, especially for Jengka VJR. Besides lignin:N, litter C:N was also found to be useful in predicting decay trends especially in the summit and Jengka VJR. C:N values decreased with time (Table 4) and the results were concurrent with studies by workers in various crop litter such as oil palm, pineapple (Nahrawi et al. 2011), Spanish cedar (Scherer-Lorenzen et al. 2007) and rosewood (Vendrami et al. 2012). Both ratios also showed strong negative correlations with mass loss (Table 5), further substantiating their importance in controlling decomposition processes as a combined factor (Berg & McClaugherty 2008). However, initial low levels of C:N and lignin:N prior to decay process in the montane forest did not accelerate

Table 4 Changes in litter nutrient content during decomposition, 120 to 480 days (n = 3)

Study site	Time (days)	C	N	S	P	K	Mn (mg g ⁻¹)	Proximate cellulose (%)	Proximate lignin (%)	C:N	Lignin:N
Sungai Kial Forest Reserve											
Summit	120	44.57	2.49	0.08	0.04	0.06	0.11	17.16 (0.37)	50.78 (0.39)	17.95 (0.95)	20.43 (0.70)
	240	45.00	2.78	0.09	0.04	0.05	0.11	22.52 (2.16)	46.17 (0.87)	16.19 (0.55)	16.63 (0.67)
	360	42.70	2.55	0.19	0.04	0.06	0.08	27.25 (1.30)	37.55 (1.03)	17.01 (1.41)	14.97 (1.42)
	480	44.79	2.70	0.13	0.06	0.03	0.12	19.86 (4.34)	49.30 (4.99)	15.72 (0.88)	16.20 (2.65)
Toeslope	120	44.48	2.54	0.08	0.04	0.05	0.08	25.56 (0.66)	40.89 (0.41)	17.76 (0.50)	16.54 (0.69)
	240	45.20	2.57	0.09	0.04	0.04	0.04	22.29 (5.54)	49.66 (5.16)	17.62 (0.59)	19.33 (1.91)
	360	45.39	2.69	0.11	0.05	0.06	0.04	32.04 (6.16)	42.69 (1.79)	17.12 (1.34)	16.80 (1.56)
	480	44.75	2.67	0.13	0.06	0.06	0.03	27.19 (2.56)	39.80 (0.95)	17.13 (2.09)	15.36 (1.64)
Jengka Virgin Jungle Reserve	120	35.70	0.79	0.04	0.01	0.09	0.02	42.69 (0.41)	38.04 (0.83)	45.43 (1.35)	48.44 (0.57)
	240	29.93	0.95	0.05	0.02	0.08	0.02	46.69 (0.58)	29.77 (1.43)	31.79 (2.69)	31.70 (3.49)
	360	32.65	1.07	0.04	0.02	0.07	0.06	45.37 (2.48)	28.40 (4.14)	31.87 (4.96)	27.93 (6.72)
	480	30.07	1.15	0.05	0.02	0.18	0.01	40.27 (3.16)	32.00 (2.57)	26.06 (0.23)	25.83 (2.97)

Standard errors for C, N, S, P, K and Mn were < 0.02; values in parentheses represent standard errors

Table 5 Pearson linear correlation coefficients (r) between mass loss and litter quality from 0 to 480 days

Study site n = 15	C	N	S	P	K	Mn (mg g ⁻¹)	Proximate cellulose (%)	Proximate lignin (%)	C:N	Lignin:N
Sungai Kial Forest Reserve										
Summit	-0.04ns	0.69***	0.50ns	0.75***	-0.57*	0.52*	0.26ns	-0.09ns	-0.71***	-0.61**
Toeslope	0.70**	0.75**	0.81***	0.26ns	-0.76***	-0.60*	-0.48ns	-0.63*	0.70**	-0.39ns
Jengka Virgin Jungle Reserve	-0.47ns	0.58**	0.43ns	0.56*	-0.45ns	-0.04ns	-0.79***	-0.78***	-0.71***	-0.82***

indicates significant correlation between the two variables at 0.05 (), 0.01 (**) and 0.001 (***) probability levels, ns = not significant

decomposition processes. In addition, increased lignin loss was related to high cellulose content (Table 3) which alleviated C limitation during lignin degradation (Talbot & Treseder 2012). Cellulose levels in Sungai Kial were in the lower range probably due to increased precipitation that allowed faster cellulose degradation (Fioretto et al. 2005, Hilli et al. 2010).

Soil respiration

Soil CO₂ fluxes, soil temperature, soil bulk density, relative humidity, water filled pore space and air filled pore space were measured for all three sites (Table 6 and Figures 4a, b and c), concurrently during decomposition processes except for 480 days due to faulty soil CO₂ flux instrument. Soil bulk density ranged from 0.3 to 0.7 g cm⁻³ for the tropical montane forest and 1.3 to 1.4 g cm⁻³ for the lowland forest (Table 6). Soil temperature for summit and toeslope in Sungai Kial FR did not differ much from 0 to 360 days as the common range fell between 15 and 18 °C. Values for Jengka VJR were between 24 and 25 °C (Table 6). Relative humidity levels for all three plots were in the range of 85–95%.

Soil CO₂ fluxes were the same for all three sites at 0 and 120 days but significantly increased for Jengka VJR (two folds) at 240 days and three to four folds at 360 days compared with summit and toeslope respectively (Figure 4a). Decreased values for soil CO₂ fluxes were reported during heavy rainfall for Jengka VJR (120 days) in October/November 2011 (Figure 2) which were comparable with Sungai Kial FR. However, CO₂ fluxes plummeted drastically during dry periods at more stable temperatures in Jengka VJR and were positively correlated with water filled pore space (Figure 4b). Values for water filled pore space were in the range of 54–68% for toeslope and 52–80% for summit except for 240 days, which showed very high values (>100%). Jengka VJR reported water filled pore space values of 65–83% for 0, 120 and 360 days. The air filled pore space was less than 50% for all sites (Figure 4c). The values for air filled pore space were negatively correlated with water filled pore space. Values for water filled pore space correlated with rainfall data for Jengka VJR (Figure 2). Minimal values for water filled pore space were recorded for 0 and

360 days during the dry season from June till September 2012.

Soil bulk density levels concurred with a previous study (Jeyanny et al. 2013), where density levels were lower in the montane forest due to a complex mixed material of soil and organic. The silty clay loam texture of the Durian series soil (Jengka VJR) were found to have 50% silt content (data not shown) which would have filled in the soil pore spaces resulting in higher bulk densities. Previous logging activities might have caused soil compaction (Laidlaw 2011). The relative humidity levels in both forest types were within normal values due to the closed canopy forest ecosystem (Melling et al. 2005) in tropical forests and were not significant in influencing CO₂ fluxes. However, soil and mean air temperature played important roles in accelerating organic matter decomposition by microbes due to favourable environmental conditions (Table 6) and might have caused an increase in CO₂ respiration in Jengka VJR. Comparable results were found in a logged-over lowland forest in Pasoh, Negeri Sembilan, whereby values between 2.5 and 6.5 µg mol CO₂ m⁻² s⁻¹ were reported (Kosugi et al. 2007). In contrast, lower levels of CO₂ fluxes (2.0 µg mol CO₂ m⁻² s⁻¹) were found at higher altitudes of afro-montane forests in Ethiopia (Yohaness et al. 2011). McGroddy and Silver (2000) compared soil fluxes at 180 and 1000 m above sea level of a Puerto Rico experimental forest which gave values of 10.0 and 2.2 µg mol CO₂ m⁻² s⁻¹ respectively. Global soil respiration consists of 50 Pg C year⁻¹ from decomposition of litter and soil organic matter, and 18 Pg C year⁻¹ from live roots and mycorrhizae (Luo & Zhuo 2006). Although previous studies suggested fine roots, such as in montane forest, were responsible for 30–70% of soil CO₂ fluxes (Schlesinger 1977), low values of CO₂ fluxes were reported in our montane study site. We believe it is due to the low root turnover in highly saturated soil such as in the montane forest which is more dominant towards soil C accumulation, suppressing root respiration activities. Thus, soil moisture and temperature were important stimuli in initiating elevated soil CO₂ fluxes (Doff Sotta et al. 2004). Values for water filled pore space of Jengka VJR positively correlated with soil CO₂ flux measurements (Figures 4a and b) and rainfall (Figure 2) (Valentini et al. 2008) but not for Sungai Kial FR. Values above

Table 6 Soil bulk density, soil temperature and relative humidity of study area, n = 6

Time (days)	Soil bulk density (g cm ⁻³)			Soil temperature (°C)			Relative humidity (%)		
	Summit	Toeslope	Jengka VJR	Summit	Toeslope	Jengka VJR	Summit	Toeslope	Jengka VJR
0	0.5 (0.05)	0.5 (0.04)	1.3 (0.04)	16.5 (0.22)	15.6 (0.24)	25.0 (0)	88.0 (1.0)	93.4 (0.67)	93.7 (0.43)
120	0.5 (0.08)	0.4 (0.02)	1.4 (0.03)	17.3 (0.07)	17.9 (0.04)	25.1 (0.05)	85.9 (0.79)	84.8 (0.79)	89.1 (0.19)
240	0.3 (0.01)	0.4 (0.09)	1.3 (0.04)	18 (0.18)	17.9 (0.04)	25.07 (0.11)	89.9 (0.79)	90.9 (0.79)	85.6 (0.19)
360	0.6 (0.07)	0.7 (0.15)	1.4 (0.03)	15.8 (0.16)	16.0 (0)	24.8 (0.16)	na (0.75)	86.4 (0.75)	90.3 (0.42)

Values in parentheses represent standard errors; VJR = Virgin Jungle Reserve; na = not available

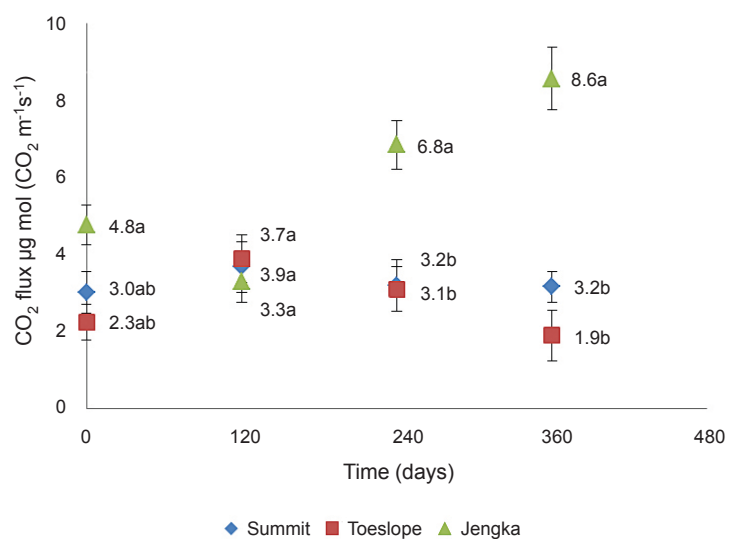


Figure 4a Soil CO₂ flux data at summit and toeslope of Sungai Kial FR and Jengka Virgin Jungle Reserve

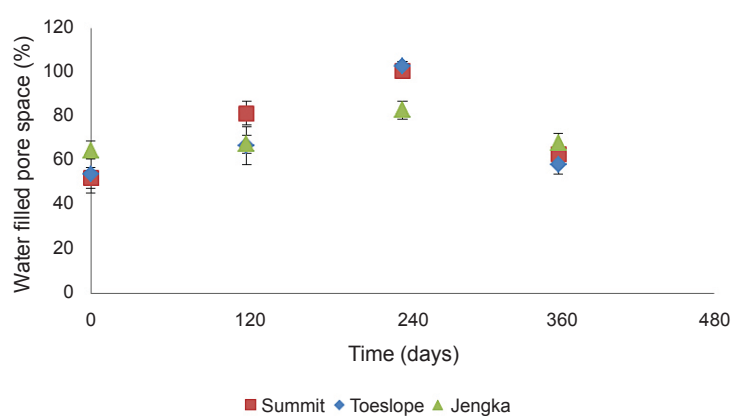


Figure 4b Soil water filled pore space values at summit and toeslope of Sungai Kial FR and Jengka Virgin Jungle Reserve

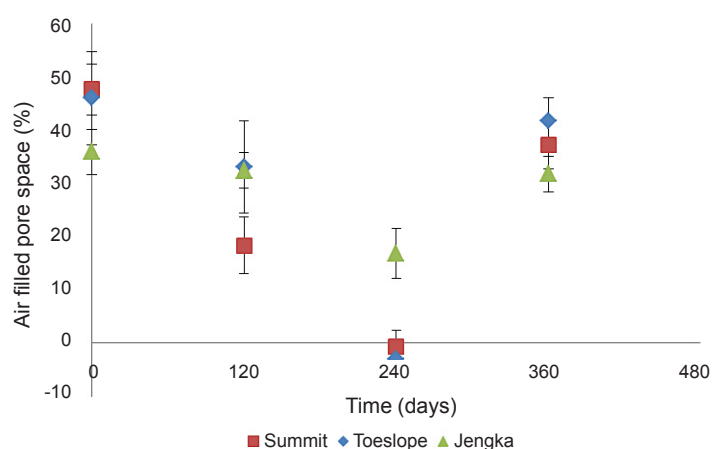


Figure 4c Soil air filled pore space values at summit and toeslope of Sungai Kial Forest Research and Jengka Virgin Jungle Reserve

100% obtained at 240 days could have been due to oversaturation of core samples during measurement or due to instrumental error. The effect of moisture content on soil CO₂ fluxes is complex and difficult to elucidate as it affects the respiratory activity of roots and microbes and gaseous transport via soil (Pingingtha et al. 2010). Soil water content could be as low as 31% and as high as 65% for lowland and upland forests respectively (McGroddy & Silver 2000).

CONCLUSIONS

The decomposition decay rate constant k ranged from -0.002 to -0.003 day⁻¹ for tropical montane forest and -0.004 day⁻¹ for lowlands, implying that accelerated decomposition in lowlands influenced rapid soil C mineralisation. Their decomposition rates and mass loss could be predicted and monitored using single exponential regression models, which recorded the highest mass loss (> 80%) at the lowlands due to favourable soil and air temperatures. Significant linear regression relationships were found between mass loss and litter quality except for cellulose at the montane forest. Initial low C:N and lignin:N in the montane forest did not contribute to faster decomposition but the indexes were useful to predict mass loss. Carbon, Mn and cellulose were observed to affect lignin degradation processes. Soil CO₂ fluxes were two folds higher in the lowlands during reduced precipitation and positively correlated with decomposition and water filled pore space. Minimal soil CO₂ fluxes in the highlands were attributed to lower temperatures that enabled soil C accumulation. The microclimatic conditions (i.e. soil and air temperatures, water filled pore space) of tropical forest ecosystems heavily influenced plant litter decomposition and soil respiration within the global C cycle. Montane forests may sequester more C compared with lowlands and on-going management strategies should also exploit the use of decomposition rate and soil respiration as potential indicators to predict C balance in forests. Litter decomposition model and soil respiration patterns in the tropical montane and lowland forests can be utilised to benchmark global C trends and predict soil C sinks.

ACKNOWLEDGEMENTS

This study was supported by the Ministry of Agriculture via the E-Science Fund (Project No. 05-03-10-SF1029). Thanks are due to the staff of Forest Research Institute Malaysia and Universiti Putra Malaysia for field and technical assistance.

REFERENCES

- ADACHI M, BEKKU YS, RASHIDAH W, OKUDA T & KOIZUMI H. 2006. Differences in soil respiration between different tropical ecosystems. *Applied Soil Ecology* 34: 258–265.
- ADAIR EC, PARTON EC, DEL GROSSO WJ ET AL. 2008. Simple three-pool model accurately describes patterns of long term litter decomposition in diverse climates. *Global Change Biology* 14: 2636–2660.
- AUSTIN AT & BALLARE CL. 2010. Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proceedings of the National Academy of Sciences* 107: 4618–4622.
- AUSTIN AT & VITOUSEK PM. 2000. Precipitation, decomposition and litter decomposability of *Metrosideros polymorpha* in native forests on Hawaii. *Journal of Ecology* 88: 129–138.
- BAGGIE I, ROWELL D, ROBINSON J & WARREN G. 2004. Decomposition and phosphorus release from organic residues as affected by residue quality and added inorganic phosphorus. *Agroforestry Systems* 63: 125–131.
- BERG B & LASKOWSKI R. 2006. *Litter Decomposition: A Guide to Carbon and Nutrient Turnover*. Academic Press, New York.
- BERG B & MCCLAUGHERTY C. 2008. *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration*. Springer Verlag, Berlin.
- BERGER TW, INSELBACHER E & ZECHMEISTER-BOLTENSTERN S. 2010. Carbon dioxide emissions of soils under pure and mixed stands of beech and spruce, affected by decomposing foliage litter mixtures. *Soil Biology and Biochemistry* 42: 986–997.
- BERNHARD-REVERSAT F & SCHWARTZ D. 1997. Change in lignin content during litter decomposition in tropical forest soils (Congo): comparison of exotic plantations and native stands. *Earth and Planetary Sciences* 325: 427–432.
- BORDERS BD, PUSHNIK JC & WOOD DM. 2006. Comparison of leaf litter decomposition rates in restored and mature riparian forests on the Sacramento River, California. *Restoration Ecology* 14: 308–315.
- COUTEAUX MM, BOTTNER P & BERG B. 1995. Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution* 10: 63–66.
- DENT DH, BAGCHI R, ROBINSON D, MAJALAP-LEE N & BURSLEM DF. 2006. Nutrient fluxes via litterfall and leaf litter decomposition vary across a gradient of soil nutrient supply in a lowland tropical rain forest. *Plant and Soil* 288: 197–215.

- DOA (DEPARTMENT OF AGRICULTURE). 1989. *Soil Correlation of Steepland Soils in Cameron Highlands*. DOA, Kuala Lumpur.
- DOA. 2000. *Agricultural Development Plan of Cameron Highlands*. DOA, Kuala Lumpur.
- DOF SOTTA E, MEIR P, MALHI Y, HODNETT M & GRACE J. 2004. Soil CO₂ efflux in a tropical forest in the central Amazon. *Global Change Biology* 10: 601–617.
- DOMISCH T, FINER L, LAINE J & LAIHO R. 2006. Decomposition and nitrogen dynamics of litter in peat soils from two climatic regions under different temperature regimes. *European Journal of Soil Biology* 42: 74–81.
- FIORETTO A, DI NARDO C, PAPA S & FUGGI A. 2005. Lignin and cellulose degradation and nitrogen dynamics during decomposition of three leaf litter species in a Mediterranean ecosystem. *Soil Biology and Biochemistry* 37: 1083–1091.
- HAFKENSCHIED RLLJ. 2000. Hydrology and biogeochemistry of montane rain forests of contrasting stature in the Blue Mountains of Jamaica. PhD thesis, Vrije Universiteit, Amsterdam.
- HE X, ZHANG P, LIN Y, LI A, TIAN X & ZHANG QH. 2009. Responses of litter decomposition to temperature along a chronosequence of tropical montane rainforest in a microcosm experiment. *Ecological Research* 24: 781–789.
- HILLI S, STARK S & DEROME J. 2010. Litter decomposition rates in relation to litter stocks in boreal coniferous forests along climatic and soil fertility gradients. *Applied Soil Ecology* 46: 200–208.
- IPCC (INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE). 2013. The physical science basis. In Stocker TF et al. (eds) *Summary for Policymakers: Climate Change 2013*. Cambridge University Press, Cambridge.
- JACOB M, WELAND N, PLATNER C, SCHAEFER M, LEUSCHNER C & THOMAS FM. 2009. Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity. *Soil Biology and Biochemistry* 41: 2122–2130.
- JEYANNY V, HUSNI MHA, WAN RASIDAH K, BALASUNDARAM SK, ARIFFIN A & FIRDAUS M. 2013. Comparison of selected soil chemical properties and forest floor depth in a tropical lowland and montane forest. In *Proceedings of the International Conference on Sustainable Forest Management—The 2nd Forest Science Forum*. 14–16 October 2012, Beijing.
- KOSUGI Y, MITANI T, ITOH M ET AL. 2007. Spatial and temporal variation in soil respiration in a Southeast Asian tropical rainforest. *Agricultural and Forest Meteorology* 147: 35–47.
- LAIDLAW RK. 2011. Effects of habitat disturbance and protected areas on mammals of Peninsular Malaysia. *Conservation Biology* 14: 1639–1648.
- LUO Y & ZHUO X. 2006. *Soil Respiration and the Environment*. Academic Press, Burlington.
- MAJILA BS, JOSHI GC & KALA CP. 2005. Patterns in litter fall and litter decomposition along an altitudinal gradient in the Binsar Wildlife Sanctuary, Central Himalaya. *International Journal of Sustainable Development and World Ecology* 12: 205–212.
- MASON IG, MCLACHLAN RI & GERARD DT. 2006. A double exponential model for biochemical oxygen demand. *Bioresource Technology* 97: 273–282.
- MCGRODDY M & SILVER WL. 2000. Variations in belowground carbon storage and soil CO₂ flux rates along a wet tropical climate gradient. *Biotropica* 32: 614–624.
- MELLING L, HATANO R & GOH KJ. 2005. Soil CO₂ flux from three ecosystems in tropical peat land of Sarawak, Malaysia. *Tellus B* 57: 1–11.
- NAHRAWI H, HUSNI MHA, OTHMAN R & BAH A. 2011. Decomposition of leaf and fine root residues of three different crop species in tropical peat under controlled condition. *Malaysian Journal of Soil Science* 15: 63–74.
- OLSON JS. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44: 322–331.
- PARSONS SA & CONGDON RA. 2008. Plant litter decomposition and nutrient cycling in north Queensland tropical rain-forest communities of differing successional status. *Journal of Tropical Ecology* 24: 317–327.
- PEREZ J & JEFFRIES TW. 1992. Roles of manganese and organic acid chelators in regulating lignin degradation and biosynthesis of peroxidases by *Phanerochaete chrysosporium*. *Applied and Environmental Microbiology* 58: 2402–2409.
- PEREZ-CORONA ME, HERNANDEZ MCP & DE CASTRO FB. 2006. Decomposition of alder, ash, and poplar litter in a Mediterranean riverine area. *Communications in Soil Science and Plant Analysis* 37: 1111–1125.
- PINGINTHA N, LECLERC MY, BEASLEY JR JP, ZHANG G & SENTHONG C. 2010. Assessment of the soil CO₂ gradient method for soil CO₂ efflux measurements: comparison of six models in the calculation of the relative gas diffusion coefficient. *Tellus B* 62: 47–58.
- PITELKA L & ROJAS AR. 2001. IPCC WGI Third Assessment Report, Chapter 3: The carbon cycle & atmospheric carbon dioxide. <http://www.ipcc.ch/ipccreports/tar/wg1/558.htm>.
- POORE M. 1968. Studies in Malaysian rain forest: I. The forest on triassic sediments in Jengka Forest Reserve. *The Journal of Ecology* 56: 143–196.
- PUTZ FE & REDFORD KH. 2010. The importance of defining ‘forest’: tropical forest degradation, deforestation, long-term phase shifts, and further transitions. *Biotropica* 42: 10–20.
- RAICH JW, POTTER CS & BHAGAWATI D. 2002. Interannual variability in global soil respiration, 1980–94. *Global Change Biology* 8: 800–812.
- SCHEFFER RA, VAN LOGTESTIJN RSP & VERHOEVEN JTA. 2001. Decomposition of *Carex* and *Sphagnum* litter in two mesotrophic fens differing in dominant plant species. *Oikos* 92: 44–54.
- SCHERER-LORENZEN M, LUIS BONILLA J & POTVIN C. 2007. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. *Oikos* 116: 2108–2124.

- SCHLESINGER WH. 1977. Carbon balance in terrestrial detritus. *Annual Review of Ecology and Systematics* 8: 51–81.
- STRICKLAND MS, OSBURN E, LAUBER C, FIERER N & BRADFORD MA. 2009. Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. *Functional Ecology* 23: 627–636.
- TALBOT JM & TRESEDER KK. 2012. Interactions among lignin, cellulose, and nitrogen drive litter chemistry–decay relationships. *Ecology* 93: 345–354.
- TRUM F, TITEUX H, DELVAUX B & GILKES R. 2010. Effects of manganese concentration on beech leaf litter decomposition: results from field and laboratory experiments. In Gilkes RJ & Prakongkep N (eds). *Proceedings of the 19th World Congress on Soil Science. Solutions for a Changing World*. 1–6 August 2010, Brisbane.
- UMA M, SARAVANAN TS & RAJENDRAN K. 2014. Growth, litterfall and litter decomposition of *Casuarina equisetifolia* in a semiarid zone. *Journal of Tropical Forest Science* 26: 125–133.
- VALENTINI CMA, SANCHES L, DE PAULA SRR ET AL. 2008. Soil respiration and aboveground litter dynamics of a tropical transitional forest in northwest Mato Grosso, Brazil. *Journal of Geophysical Research: Biogeosciences* 113: G00B10.
- VAN SOEST PJ. 1963. Use of detergents in analysis of fibrous feeds: a rapid method for the determination of fiber and lignin. *Journal of Association Official Analytical Chemists* 46: 829–835.
- VENDRAMI JL, JURINITZ CF, CASTANHO CT, LORENZO L & OLIVEIRA AA. 2012. Litterfall and leaf decomposition in forest fragments under different successional phases on the Atlantic Plateau of the state of Sao Paulo, Brazil. *Biota Neotropica* 12: 136–143.
- VITOUSEK PM, TURNER DR, PARTON WJ & SANFORD RL. 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawaii: patterns, mechanisms, and models. *Ecology* 75: 418–429.
- XU M & QI Y. 2001. Soil-surface CO₂ efflux and its spatial and temporal variation in a young ponderosa pine plantation in northern California. *Global Change Biology* 7: 667–677.
- YANAI RD, CURRIE WS & GOODALE CL. 2003. Soil carbon dynamics after forest harvest: an ecosystem paradigm reconsidered. *Ecosystems* 6: 197–212.
- YOHANNES Y, SHIBISTOVA O, ABATE A, FETENE M & GUGGENBERGER G. 2011. Soil CO₂ efflux in an afro-montane forest of Ethiopia as driven by seasonality and tree species. *Forest Ecology and Management* 261: 1090–1098.