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Research Article

Comparison of nutrient balance between a tropical lowland forest and a tropical montane forest in Malaysian Borneo

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ABSTRACT. To compare nutrient balances between lowland and montane tropical forests, water samples were collected for chemical analyses and hydrological observations over a 3-year period in Tower Large watershed in Lambir Hills National Park (LT; tropical lowland forest) and Mempening watershed in Kinabalu Park (KM; tropical montane forest) in Malaysian Borneo. We estimated the annual input flux by rainfall (AIF_R), annual input flux by throughfall (AIF_T) and annual output flux (AOF) of nutrients in these watersheds. The greatest difference in nutrient balance between LT and KM was manifested in the SO_4-S balance. Although no distinct difference in the AIF_R and AIF_T of SO_4-S was detected between KM and LT, the mean AOF of SO_4-S in LT was 65 times larger than that in KM. The AOF of SO_4-S was higher than the AIF_R and AIF_T in LT, whereas the AOF of SO_4-S was lower than the AIF_R and AIF_T in KM. No distinct differences in inorganic N balance were detected between LT and KM. The large differences in the AOFs of Na, K, Mg and Ca between KM and LT may be explained by the supply of each element in LT from chemical weathering of the bedrock.

Keywords: Borneo, Lambir Hills National Park, Kinabalu Park, Nutrient balance, Tropical forest.

INTRODUCTION

Nutrients enter forest ecosystems through rain, deposition of dust and aerosols, fixation by microorganisms above and below the ground (in the case of N) and weathering of the substratum (except for N). These nutrient inputs are provided to the forest floor by rainfall, throughfall and streamflow, and the chemical composition of the input varies depending on climate, vegetation and the sources of chemical transformation (Proctor, 2005). Bruijnzeel (1991) examined the balances of Ca, Mg, K, P and N fluxes in 25 tropical forests and concluded that annual input flux by rainfall (AIF_R) varies greatly with the location of the forest site and the amount of received dust and aerosols. He also demonstrated that nutrient losses per unit streamflow increased with increasing site fertility level, and indicated that the accuracy of annual output flux (AOF) is not high, because

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the methods used to estimate nutrient AOF vary among sites. To accurately compare nutrient balance between two sites, the observation period and AOF estimation method must be the same at both sites, but such comparable studies between lowland and montane tropical rainforests are lacking.

The objective of this study was to compare the nutrient balance between a lowland and a montane tropical forest using the same methods during the same period of observation in Malaysian Borneo. Nutrient AIF_R and AOF were estimated using comparative watershed-based study data obtained by sequential and event-based sampling of rainwater and streamwater, together with continuous hydrological observation data.

MATERIALS AND METHODS

Site description

This study was conducted in two experimental watersheds located in two national parks in Malaysian Borneo (Figure 1): Lambir Hills National Park (LHNP) and Kinabalu Park (MKNP). LHNP covers an area of 6,949 ha located about 25 km southwest of Miri, a city in eastern Sarawak, and its highest peak is Lambir Hill, 465 m above sea level (a.s.l.). MKNP extends over an area of 75,400 ha about 50 km east of Kota Kinabalu (KK), the state capital of Sabah, and includes the highest peak in Southeast Asia, Mount Kinabalu, the elevation of which is 4,095.2 m a.s.l. In LHNP, the annual mean temperature for the years years from 2000 to 2008 were 25.9℃ and 2,650 mm, respectively (Gomyo, 2010). The annual rainfall observed at site in MKNP is normally around 3,000 mm, but it was extraordinarily low in 1997 and 1998, which were years associated with El Niño events. The annual mean temperature at site in MKNP is normally around 18℃. But slightly higher values were recorded in 1997 and 1998 (Gomyo, 2010).

Tower Large watershed

The Tower Large (LT) experimental watershed in the LHNP was used as the lowland experimental site (Table 1). LT is characterized by rugged topography, with several waterfalls and exposed alternate layers including mudstone and sandstone. This area was uplifted and gently folded about 1.6 million years ago at the onset of the Pleistocene

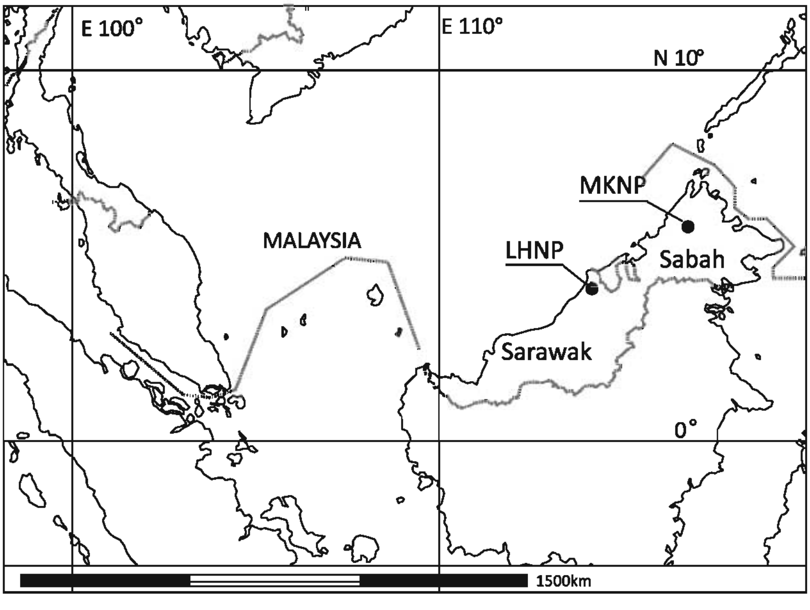

Figure 1. Map showing the study sites.

(Wilford, 1961). No gypsum or hydrothermal activity has been reported in LHNP, where clay udult ultisol soils developed over shale and on sandy humult ultisols (Hazebroek & Aband Kashim, 2001). The forests in LHNP are classified into two indigenous vegetation types common throughout Borneo: mixed dipterocarp forest and tropical heath forest (Yamakura *et al.*, 1995, Ashton, 1998, Potts *et al.*, 2002). The study site was established within a mixed dipterocarp forest on red-yellow podsols (ultisols). The lowest elevation point of LT is 90.4 m a.s.l., located about 13.7 km from the nearest coast. The weather station and rainwater sampling point (4°20'N, 113°50'E) used were about 2.3 km from LT.

Table 1. Features of the LT and KM watersheds.

Watershed name	Location	Distance from the nearest coast (km)	Elevation at acral area (m.a.s.l.)	Annual mean rainfall (mm)	Annual mean air temperature (℃)	Area (ha)	Vegetation	Soil (USDA)	Geology
Tower Large (LT)	4°11' 23" N, 114°01' 09" E	13.7	90.4	2650 (2000-2008)	25.9 (2000-2007)	23.25	Dipterocarpaceae	Ultisol	Tertiary sedimentary rocks
Mempening (KM)	6° 00' 42" N, 116°32' 27" E	42.6	1697.7	1709 (1997-1998) 3168 (1996,1999-2008)	18.6 (1997-1998) 17.2 (1996, 1999-2008)	1.78	Tristaniopsis, Dacrycarpus, Podocarpus	Spodosol	Tertiary sedimentary rocks

Mempening watershed

The Mempening watershed (KM) in MKNP was used as the highland experimental site (Table 1). Soils in KM are derived from sedimentary rocks (Trusmadi and Crocker formations) folded in the Tertiary period (Jacobson, 1970). These sedimentary rocks were intensely folded during the orogeny that culminated in the middle of the Miocene (Jacobson, 1970). The soil is classified as spodosols (Kitayama *et al.,* 2004). The most abundant canopy tree species are *Tristaniopsis* sp. (Myrtaceae) and the conifers *Dacrycarpus* and *Dacrydium* spp. (Podocarpaceae) (Kitayama *et al.,* 2004). The elevation of the lowest point of KM is 1,697.7 m a.s.l., the location of which is about 42.6 km from the nearest coast. The weather station and rainwater sampling points used were about 1.4 km from KM.

Rainfall and discharge observations

Rainfall was measured using a tipping-bucket rain gauge (20-cm diameter, tips every 0.5 mm; Ohta Keiki Co., Tokyo, Japan) and a data logger (1-s time resolution; KADEC-PLS, Kona System Co., Sapporo, Japan). Discharges at LT were measured by recording the water depth at a site over bedrock where rapid stream flow was generated from a pool with no flow velocity (Shiraki & Wakahara, 2005). Discharges at KM were measured at a V-notch weir at 10-min intervals using an automatic water level recorder (SE-TR/WT500, TruTrack Co., Christchurch, New Zealand).

Rainwater, throughfall, and streamwater sampling

Rainwater was collected for chemical analysis from both LT and KM using bulk samplers consisting of a PVC funnel (20-cm diameter) installed 0.5 m above the ground and connected to a 18-L container. A glass wool filter was placed at the bottom of the funnel to prevent water contamination by particulate matter and insects. These bulk samplers were also installed on the forest floor to collect throughfall. Rainwater and throughfall were transferred from the bulk samplers into 100-mL polyethylene bottles twice a week. To identify spatial variations in nutrient deposition, rainfall at KM was sampled in August 2008 using 10 bulk samplers located around the rain gauge. For the same purpose, throughfall at KM was sampled in June 2007 using 20 bulk samplers located randomly around the throughfall sampler. Standard variations in rainfall and throughfall were assessed as 3% of the rainfall or throughfall.

Streamwater was collected from the discharge observation points of the two watersheds into 100-mL polyethylene bottles twice a week for chemical analysis. Intensive streamwater sampling during stormflow events was performed four times in KM and once in LT at the discharge observation points using an automatic liquid sampler (Model 900, Sigma Co., NY, USA) at sampling intervals ranging from 10 to 120 min.

Chemical analyses

Sampled water was transferred to a field laboratory within 30 min and refrigerated at 2°C. All samples were filtered through a 0.2-μm filter (Minisart RC15, hydrophilic regenerated cellulose) within 2 months of sampling. The concentrations of cations (Na^+, NH_4^+, K^+, Mg^{2+} and Ca^{2+}) and anions (Cl^-, NO_3^- and SO_4^{2-}) were analysed using ion chromatography (HIC-6A; Shimadzu Co., Kyoto, Japan). The precision of the ion chromatography results was assessed as ±5%, based on standard solutions. Due to this procedure, the recorded levels of volatile NO_3^- and NH_4^+ may not be as accurate as those of the other ions.

Annual input fluxes by rainfall (AIF_R) and throughfall (AIF_T)

Annual input fluxes by rainfall (AIF_R) and throughfall (AIF_T) were calculated by summing the fluxes that were obtained for each sampling interval by multiplying the volume of water with the concentration of nutrients. Rainfall volume during the sampling period was obtained from automatic rain gauges. The volume of throughfall during the study period was not observed directly but was estimated using the following equations:

$$TF_{(LT)} = -1.825 + 0.899 * P_{(LT)} \quad P_{(LT)} > 2.03 \qquad (1)$$

$$= 0 \quad P_{(LT)} \leq 2.03$$

$$TF_{(KM)} = 0.940 * P_{(KM)} \qquad (2)$$

where $P_{(LT)}$, $P_{(KM)}$, $TF_{(LT)}$ and $TF_{(KM)}$ are rainfall at KM and LT and throughfall at LT and KM, respectively. Published data from Manfroi *et al.* (2004) was used for equation (1), and unpublished data collected from KM in June 2007 was used for equation (2).

Annual output fluxes (AOF)

A method introduced by Boy *et al.* (2008) was applied to compare AOFs between LT and KM. Discharge flow classes were defined as super dry (less than 25% of the 2-year mean discharge (MD2Y) of each watershed), baseflow (25–50%), intermediate (50–200%), and stormflow (discharge exceeding twice the MD2Y). The MD2Y of LT and KM was 0.1452 and 0.2496 mm/h, respectively.

RESULTS

Table 2 shows the AIF_R, AIF_T, AOF and AIF_R minus AOF (balance) of each element. For LT, we obtained AIF_R and AIF_T in 2006, and AOF in 2006 and 2007. For KM, we obtained AIF_R and AOF for three years (2006–2008) and AIF_T in 2008. Figure 2 shows the AIF_R, AIF_T and AOF of each element. Where more than two data points were available (AIF_R in LT and AOF in KM and LT), the standard deviation is shown at the end of the average bar.

Sulphur

The AOF of SO_4-S for LT in 2006 (61.4 kg/ha/year) was 9.4 times larger than the AIF_R (6.5 kg/ha/year) and 10.1 times larger than the AIF_T (6.1 kg/ha/year), while the AOF of SO_4-S for KM in 2006 and 2007 (0.9–1.1 kg/ha/year) was one-fifth to one-third of the AIF_R (3.3–4.8 kg/ha/year) (Table 2). Note that in KM in 2008, the AIF_T (6.5 kg/ha/year) was higher than the AIF_R (3.9 kg/ha/year). Although the AIF_R and AIF_T values showed no distinct difference between KM and LT, the mean AOF of SO_4-S in

LT (64.6 kg/ha/year) was 65 times higher than that in KM (1.0 kg/ha/year) (Figure 2, a and b). It is also notable that the mean AOF value was higher than the mean $\mathrm{AIF_R}$ and mean $\mathrm{AIF_T}$ in LT, whereas the mean AOF was smaller than the mean $\mathrm{AIF_R}$ and mean $\mathrm{AIF_T}$ in KM.

Inorganic Nitrogen

We define inorganic nitrogen as the total of NO_3-N and NH_4-N. The $\mathrm{AIF_R}$ and $\mathrm{AIF_T}$ of inorganic N in LT (5.8 and 5.2 kg/ha/year, respectively) were higher than the AOF (2.4

Table 2. $\mathrm{AIF_R}$, $\mathrm{AIF_T}$ and AOF from 2006 to 2008 in the LT and KM watersheds.

Watershed name	Year		SO_4-S	NO_3-N	NH_4-N	Inorg-N	K	Mg
					(kg/ha/year)			
LT	2006	$\mathrm{AIF_R}$	6.5	1.9	3.9	5.8	8.1	6.6
		$\mathrm{AIF_T}$	6.1	2.1	3.1	5.2	36.3	15.6
		AOF	61.4	2.2	0.2	2.4	35.4	34.3
	2007	AOF	67.8	2.3	0.2	2.5	38.1	36.1
KM	2006	$\mathrm{AIF_R}$	4.8	1.5	8.2	9.7	13.8	5.0
		AOF	1.1	0.9	0.7	1.6	10.5	9.6
	2007	$\mathrm{AIF_R}$	3.3	0.2	2.2	2.4	13.6	5.1
		AOF	0.9	0.7	0.6	1.3	10.1	9.0
	2008	$\mathrm{AIF_R}$	3.9	1.4	3.0	4.4	10.8	5.4
		$\mathrm{AIF_T}$	6.5	0.1	9.3	9.4	65.8	10.1
		AOF	1.0	1.1	0.9	2.1	13.9	10.6
LT	2006	$\mathrm{AIF_R}$-AOF	-54.9	-0.3	3.7	3.4	-27.3	-27.7
KM	2006	$\mathrm{AIF_R}$-AOF	3.7	0.6	7.5	8.1	3.3	-4.6

Watershed name	Year		Ca	Na	Cl	Rainfall	Discharge
				(kg/ha/year)		(mm)	
LT	2006	$\mathrm{AIF_R}$	22.4	6.8	9.1	2867.0	
		$\mathrm{AIF_T}$	15.7	11.2	21.4		
		AOF	22.3	15.4	10.6		1165.7
	2007	$\mathrm{AIF_R}$	NA	NA	NA	2986.0	
		AOF	24.0	17.5	13.1		1377.9
KM	2006	$\mathrm{AIF_R}$	31.1	5.2	6.5	3203.0	
		AOF	7.8	4.9	5.3		2350.5
	2007	$\mathrm{AIF_R}$	106.6	5.3	6.1	3109.0	
		AOF	7.3	4.0	4.7		2022.3
	2008	$\mathrm{AIF_R}$	126.3	4.3	4.1	3338.0	
		$\mathrm{AIF_T}$	21.9	4.0	6.4		
		AOF	10.0	5.1	5.8		2731.7
LT	2006	$\mathrm{AIF_R}$-AOF	0.1	-8.5	-1.5		
KM	2006	$\mathrm{AIF_R}$-AOF	23.2	0.4	1.2		

Note: $\mathrm{AIF_R}$ = Annual Input Flux by Rainfall; $\mathrm{AIF_T}$ = Annual Input Flux by Throughfall; AOF = Annual Output Flux

$\mathrm{AIF_R} = \sum C_R P_E$, C_R:Concentration of rainwater; P_E:The volume of rainfall in each sampling interval

$\mathrm{AIF_T} = \sum C_T T_E$, C_T:Concentration of throughfall ; T_E:The volume of throughfall in each sampling interval

NA= Not available

kg/ha/year) in 2006 (Table 2). In KM, the AIF_R (2.4–9.7 kg/ha/year) was also higher than the AOF (1.3–2.1 kg/ha/year), and in 2008, the AIF_T (9.4 kg/ha/year) was 2.1 times higher than the AIF_R and 4.5 times higher than the AOF. Figure 2 (c, d, e, f, g and h) shows that the mean AIF_R and AIF_T of NH_4-N were greater than those of NO_3-N, and the mean AOF of NO_3-N was greater than that of NH_4-N in both watersheds.

Potassium

In 2006, the AOF of K in LT (35.4 kg/ha/year) was 4.6 times higher than the AIF_R (8.1 kg/ha/year) (Table 2). In contrast, the AIF_R in KM (10.8–13.8 kg/ha/year) showed a level similar to that of the AOF (10.1–13.9 kg/ha/year). The AIF_T in KM in 2008 was 65.8 kg/ha/year, which was 6.0 times higher than the AIF_R and 4.7 times higher than AOF, whereas

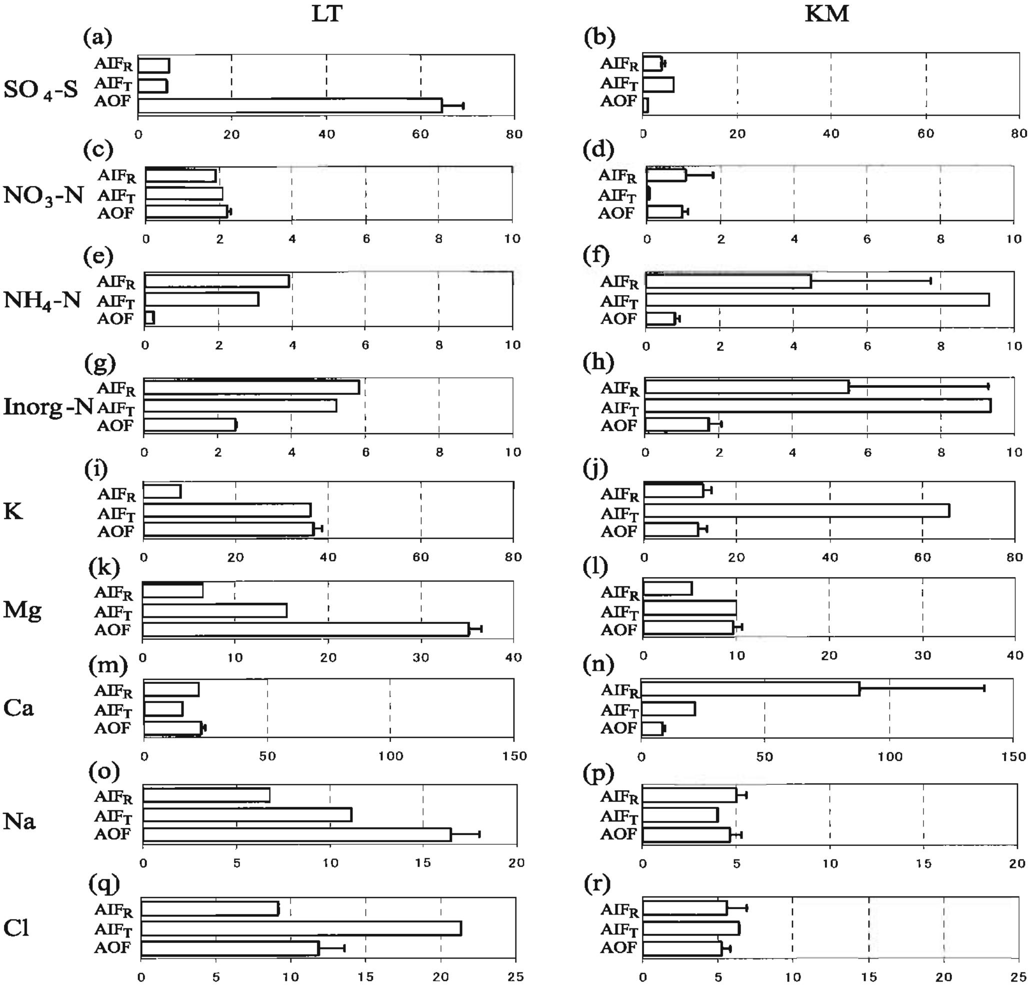

Figure 2. Mean AIF_R, AIF_T, and AOF of (a and b) SO_4-S, (c and d) NO_3-N, (e and f) NH_4-N, (g and h) Inorg-N, (i and j) K, (k and l) Mg, (m and n) Ca, (o and p) Na, and (q and r) Cl from 2006 to 2008 in the LT and KM watersheds. The bars are standard deviation. The dimensions of the x-axis of all Graphs are Kilogram per hectare per year [kg/ha/year].
AIF_R = Annual Input Flux by Rainfall; AIF_T = Annual Input Flux by Throughfall; AOF = Annual Output Flux.

the AIF_T in LT (36.3 kg/ha/year) was almost the same as the AOF. The mean AOF of K in KM was about one fifth of the mean AIF_T; the mean AOF and the mean AIF_T of K in LT showed less difference (Figure 2, i and j).

Magnesium

The AOF of Mg in LT (34.3 kg/ha/year) was 2.2 times higher than the AIF_R (6.6 kg/ha/year) and 5.2 times higher than the AIF_T (15.6 kg/ha/year) in 2006 (Table 2). The AOF of Mg in KM (9.0–10.6 kg/ha/year) was 1.7–2.1 times higher than the AIF_R (5.0–5.4 kg/ha/year). In 2008, the AIF_T was 10.1 kg/ha/year, which was higher than the AIF_R but almost the same as the AOF. The mean AIF_R and AIF_T of Mg showed small differences between LT and KM. The mean AOF of Mg in LT was 3.2–4.0 times higher than that in KM (Figure 2, k and l).

Calcium

The AIF_R of Ca in KM was 31.1, 106.6 and 126.3 kg/ha/year in 2006, 2007 and 2008, respectively, and the respective AOF values were 7.8, 7.3 and 10.0 kg/ha/year (Table 2). Inter-annual variations in AIF_R were much larger than those in AOF. The AOF of Ca in 2008 was 10.0 kg/ha/year, which was only 17.3% of the AIF_R and 50% of the AIF_T. The AOF of Ca at LT in 2006 (22.3 kg/ha/year) was the same as the AIF_R (22.4 kg/ha/year) and 1.4 times higher than the AIF_T (15.7 kg/ha/year). The mean AIF_R of Ca was higher than the mean AOF in KM, while the mean AOF was higher than the mean AIF_R in LT (Figure 2, m and n).

Sodium and Chloride

The AOF of Na in LT (17.5 kg/ha/year) was 2.3 times higher than the AIF_R (6.8 kg/ha/year) and 1.4 times higher than the AIF_T (11.2 kg/ha/year) in 2006. The AOF of Na in KM (4.0–5.1 kg/ha/year) showed almost the same values as the AIF_R (4.3–5.3 kg/ha/year). The AIF_T in 2008 was 4.0 kg/ha/year, which was almost the same as the AIF_R.

The AOF of Cl in LT (10.6 kg/ha/year) was 1.2 times higher than the AIF_R (9.1 kg/ha/year) and was one-half of the AIF_T (21.4 kg/ha/year) in 2006. The AOF of Cl in KM (4.7–5.8 kg/ha/year) showed almost the same values as the AIF_R (4.1–6.5 kg/ha/year). The AIF_T in 2008 was 6.4 kg/ha/year, which was higher than the AIF_R but almost the same as the AOF. The mean AIF_R, AIF_T and AOF values of Na and Cl showed no distinct differences in KM, but were higher in LT than in KM, particularly for Na (Figure 2, o, p, q and r).

DISCUSSION

Water balance

Table 2 shows rainfall and discharge in LT for 2006 and 2007, and in KM from 2006 to 2008. The mean annual loss (rainfall minus discharge) of rainfall and discharge were 1654.7 and 848.5mm, respectively. The water balance in KM has already been reported by Gomyo *et al.*, (2001) as the smallest value compared to other experiments in Peninsular Malaysia. They discussed that the annual evapotranspiration in KM may be less than that of other sites, due to the higher altitude and lower temperature. Kume *et al.* (2011) studied evapotranspiration in LT for 10 years (from 2000 to 2009) and the estimated mean annual evapotranspiration during this period was 1,323 mm. The loss of water in LT obtained in this study was about 330mm greater than the mean annual evapotranspiration and this difference may be due to groundwater flow which cannot be captured by our surface water measuring system. The following nutrient balance in LT did not include nutrient flux through the groundwater because we could not sample groundwater.

AOF estimation methods

The determination of nutrient balances in forested watersheds requires the characterization of hydrological nutrient outputs. Determination of AOF is particularly complicated because the ion concentrations in discharge waters vary greatly (McDowell & Asbury, 1994; Godsey *et al.*, 2004; Boy *et al.*, 2008). In southern Ecuador, for example, concentrations of nitrates (NO_3-N), dissolved organic carbon, dissolved organic nitrogen, and in some cases ammonium nitrate (NH_4-N) are reported to increase when streamwater discharge is high; concentrations of these chemical constituents are highest during periods of heavy rain (Wilcke *et al.,* 2001; Goller *et al.,* 2006; Boy *et al.,* 2008). In Peninsular Malaysia, Zulkifli *et al.* (2006) reported that the concentrations of K^+, NO_3-N and Mg^{2+} increase during storm events.

However, in most previous studies, nutrient AOF has been calculated by multiplying annual discharges with the volume-weighted mean concentrations of nutrients or by using the relationship between ion concentration and discharge (C–Q curve; McDowell, 1998; Markewitz *et al.,* 2006). Some studies using C–Q curves do not indicate the equations used or how the coefficients of the C–Q curves are determined. To estimate the contributions of different flow classes to AOF, Boy *et al.* (2008) developed a model in which they classified hourly discharges (obtained with TOPMODEL) into flow classes. They multiplied the cumulative discharge for a given flow class during a 5-year period with the mean concentration of each chemical constituent studied in the same flow class, although their analyses did not include continuous discharge data or intensive water sampling during stormflow periods (Boy *et al.,* 2008; Wilcke *et al.,* 2009). Studies that have used both hydrological and biogeochemical approaches to elucidate the stormflow-related elements of AOF are limited, particularly in the tropics (Saunders *et al.,* 2006). Our study provides a solution to this issue by estimating AOF with continuous discharge data and sequential and stormflow event-based water sampling.

Sulphur

The absolute AOF values and nutrient balance of SO_4-S showed greater differences between LT and KM compared to other nutrients. This may be the case as in KM, the AIF_R of SO_4-S in the soil pool is converted into insoluble sulphate (organic S) and insoluble sulphide in soil S pools or to gaseous S by microorganisms (Johnson, 1984; Alewell *et al.,* 1999). The AOF value obtained for SO_4-S in LT is too high to be explained by the AIF_R of SO_4-S, and thus the SO_4-S in streamwater may be released from a terrestrial source within the watershed. The oxidation of sulphide may also be a principal source of SO_4-S (e.g., Strauss, 1997; Fitzhugh *et al.,* 2001; Kohfahl *et al.,* 2008). The high AOF of SO_4-S in LT is likely a result of sulphide production due to chemical weathering.

Inorganic Nitrogen

In tropical montane forests, the relatively slow decomposition rate of organic matter caused by relatively low temperatures at high elevations may be a factor restricting N cycles. The N cycle in tropical lowland forests, in contrast, may not be restricted in the same way because of the higher decomposition rate of organic matter that occurs under high temperatures at low elevations (Grubb, 1989). Some studies which have suggested that the AOF of N in tropical montane forests is less than that in tropical lowland forests may have led to the perception that N cycling differs between tropical montane and lowland forests (Grubb, 1989). However, a review of 25 case studies by Bruijnzeel (1991) showed that the AOF of N in tropical montane forests is not necessarily smaller than that in tropical lowland forests. The review revealed that the methods used to estimate nutrient AOF varied among sites, suggesting that the large variation of N balances in both tropical lowland and montane forests may be attributed to the accuracy of AOF estimates.

In the present study, no distinct differences in inorganic N balances were detected between the tropical lowland forest (LT) and the tropical montane forest (KM). Schnur (2001) studied N balances at several sites in Hawaii with the same altitude and temperature but different rainfall, and showed that the AOF of N was greater at sites with significantly higher rainfall. He suggested that decomposition rates and N availability are dominated by soil water status rather than temperature. Based on his findings, we suggest that the inorganic N balance in KM is comparable with that in LT because humidity is higher in KM than in LT, due to higher rainfall and lower evapotranspiration. McDowell (1998) reported that the AIF_R, AIF_T and AOF of inorganic N in a tropical montane forest in the Luquillo Mountains, Puerto Rico, were 1.89, 3.52 and 1.29 kg/ha/year, respectively. These values are comparable with those obtained in our study (2.4–9.7, 9.4 and 1.3–2.1 kg/ha/year for AIF_R, AIF_T and AOF, respectively). Like McDowell (1998), we also assumed that AIF_R is balanced with AOF, and that almost all the additional N provided by AIF_T is absorbed by vegetation.

Potassium

Input flux of K to forest ecosystems mostly occurs via rainfall, dry deposition and leaching from leaves and branches (Vitousek & Sanford, 1986). Our finding that the AIF_T of K was 4.5–5.2 times higher than the AIF_R in both watersheds indicates washout of dry deposition on canopies and leaching from leaves and branches takes place. The AIF_T of K was the highest of all nutrients in KM and LT, which is in accordance with previous studies on tropical rain forests (Vitousek & Sanford, 1986).

Kitayama *et al.* (2004) reported that the annual reabsorption flux of K was 20.3 kg/ha/year in KM, and noted that trees absorb some K supplied by throughfall. Assuming that K reabsorption by the vegetation occurred in LT and KM, and given that 69% of the AOF in LT occurred during stormflow class discharges, it is likely that other K supply routes exist in LT in addition to rainfall and throughfall. Because of the small difference between AOF and AIF_T in LT, we postulate that K is supplied through chemical weathering of the bedrock. In KM, we assume that chemical weathering contributed minimally to the K supply, and that vegetation absorbs most of the K from rainfall and throughfall. This is in accordance with previous reports from the Luquillo Experimental Forest, Puerto Rico (McDowell, 1998).

Magnesium

The AIF_T of Mg was smaller than that of K or Ca, which is similar to results reported for other sites. Kitayama *et al.* (2004) observed that the leaf litter concentrations of K, Ca and Mg in KM were 2.71, 4.26 and 1.70 mg/g, respectively, suggesting that the leaching of Mg from leaves and branches is less than that of Ca and K.

Input of Mg into forest ecosystems can occur through rainfall, throughfall and the chemical weathering of bedrock (Bruijnzeel, 1991; Grip *et al.*, 1994; McDowell, 1998). In tropical forests, Mg output is higher than input, something that has been discussed mainly in relation to weathering flux. Although small differences were observed between LT and KM with respect to the AIF_R and AIF_T of Mg, the AOF of Mg in LT was 3.2–4.0 times higher than that in KM. This suggests that, like K input flux, the contribution of chemical weathering to Mg flux is greater in LT than in KM. The high AOF of SO_4^{2-} in LT, which may have been due to FeS_2 oxidization, also supports this hypothesis.

Calcium

The AIF_R of Ca was higher in KM than in LT. Zulkifli *et al.* (1988) observed a high AIF_R value for Ca (52.2 kg/ha/year) and a high AIF_R value for Mg (18.6 kg/ha/year) at Berembun in Peninsular Malaysia, and suggested that these high values were related to sample contamination by local dust. The high Ca input in KM may also be due to aerosols generated by shifting cultivation and large-scale agriculture around Kinabalu Park. Dust is deposited on leaves and branches before being washed out by rainfall. In LT, the high AOF of Ca may be the result of chemical weathering, as for K and Mg. Taken together, we postulate that the differences in K, Mg and Ca nutrient balances between KM and LT are attributable to differences in chemical weathering.

Sodium and Chloride

Distance from the sea is the primary factor determining the AIF_R of Na and Cl. Even though the distance between LT and the coast is only 13.7 km, the AIF_R of Na and Cl were relatively low compared to values recorded at other sites located less than 20 km from the coast, i.e. four sites in Queensland, Australia (Brasell & Gilmour, 1980) and four sites in Fiji (Waterloo *et al.,* 1997). The Lambir Hills lie between the LT observation site and the coast, and the hills may block rainfall from the sea. In Turrialba, Costa Rica (Hendry *et al.,* 1984), another tropical rainforest located less than 20 km from the coast, a strong relationship was detected in the AIF_R of Na and Cl. However, at Berembun, Malaysia (Zulkifli *et al.,* 1988) and Mt. Kilimanjaro, Tanzania (Schrumpf *et al.,* 2006), where research sites were located more than 20 km from the coast, no correlations were found in the AIF_R of Na and Cl. The AOF of Na was higher in LT than in KM. This may have been the result of chemical weathering, as for Mg, Ca and K. We consider that the difference in the Na nutrient balance between KM and LT is attributable to differences in chemical weathering.

CONCLUSION

The greatest difference in nutrient balances between LT and KM was in the SO_4-S balance. Although no distinct differences in the AIF_R of SO_4-S were detected between KM and LT, the mean AOF of SO_4-S in LT was 65 times larger than that in KM. The AOF of SO_4-S was higher than the AIF_R and AIF_T in LT, whereas the AOF of SO_4-S was lower than the AIF_R and AIF_T in KM. The AIF_R and AIF_T of NH_4-N were greater than those of NO_3-N, and the AOF of NO_3-N was greater than that of NH_4-N in both LT and KM. This suggests that microorganisms nitrify most of the NH_4-N and organic N supplied by rainfall. The large differences in the AOFs of Na, K, Mg and Ca between KM and LT may be explained by the supply of each element in LT from chemical weathering of the bedrock.

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