

Rainfall partitioning into throughfall and stemflow and associated nutrient fluxes: land use impacts in a lower montane tropical region of Panama

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Abstract Land-use change alters catchment hydrology by influencing the quality and quantity of partitioned rainfall. We compared rainfall partitioning (throughfall, stemflow and interception) and nutrient concentrations in rainfall, throughfall and stemflow in three land-use types [primary forest (PF), secondary forest (SF) and agriculture (A)] in Panama. Measurements of throughfall were highly variable which may have masked seasonal and land use differences but it was clear that throughfall at agricultural sites made up a larger proportion of gross precipitation than at forest sites. Of incident precipitation, 94% became throughfall in agriculture sites while 83 and 81% of gross precipitation became throughfall in PF and SF, respectively. The size of the precipitation event was the main driver of variation in throughfall and stemflow. Consistent patterns in nutrient cycling were

also difficult to identify. Vegetation has a vital role in delivering nutrients as throughfall deposition of K was often larger than precipitation deposition. A canopy budget model indicated that canopy exchange was often more dominant than dry deposition. Throughfall was generally enriched with nutrients, especially K and Mg, with enrichment factors of up to 17 and 5 for K and Mg, respectively, in PF. In contrast, Ca was sometimes taken up by the canopy. Values of nutrient deposition were high (with up to 15, 3, 30 and 15 kg ha⁻¹ month⁻¹ in stand deposition of Ca, Mg, K and Na, respectively in PF), possibly due to the slash-and-burn agricultural practices in the area or marine inputs. Throughfall and stemflow are vital sources of nutrients in these ecosystems.

Keywords Agriculture · Canopy budget model · Canopy exchange · Dry deposition · Ion fluxes · Nutrient leaching · Primary and secondary forests

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Introduction

Water balance studies in different land-use types provide information on the delivery of water to rivers and streams in catchments with different vegetation cover. When rainfall reaches a vegetated area, it has three possible fates: throughfall, stemflow and interception. Gross precipitation is measured above the canopy or in a clearing while throughfall is the

rainfall measured falling through the canopy. Stemflow is the rainfall running down plant stems and trunks to the forest floor, and finally, interception is measured as the difference between gross precipitation and the sum of throughfall and stemflow (Crockford and Richardson 2000; Levia and Frost 2003; Levia et al. 2011). Interception of rainfall by the forest canopy represents a significant proportion of the water balance of rainforests (McJannet et al. 2007).

Land-use change has a significant impact on catchment hydrology. Forested catchments have larger interception losses than pastures due to increased leaf area index (LAI) in forests (Hodnett et al. 1995). Other forest factors which influence the proportion of rainfall that is intercepted include stem density, canopy density, branch angle, the structure of the crown and crown height (uniform or variable), thickness of bark, leaf shape and inclination (Crockford and Richardson 2000; Huber and Iroumé 2001; Fleischbein et al. 2005; Brauman et al. 2010; Carlyle-Moses et al. 2010; Mair and Fares 2010). However, spatial patterns in throughfall are highly dependent on the ecosystem and in many ecosystems there are no identifiable relationships between forest canopy and throughfall (Levia et al. 2011). Climatic factors which influence interception are the volume and intensity of rainfall, the duration of the rainfall event and conditions after rain has finished such as wind speed, air temperature and humidity (Crockford and Richardson 2000; Huber and Iroumé 2001; Zimmermann et al. 2009). Differences in rainfall partitioning are likely to impact on physical, chemical and biological processes of ecosystems (Krämer and Hölscher 2009). Soil moisture, the concentration of solutes in soil, leaf litter decay, understorey vegetation and distribution of fine roots could all be influenced by changes in throughfall (Krämer and Hölscher 2009). Furthermore, differences in interception from different vegetation types influence the regional climate (Lloyd et al. 1988).

In addition to influencing throughfall volume, forest structure and function also modify the quality of throughfall by influencing nutrient concentrations reaching soils via precipitation (Lilienfein and Wilcke 2004; Staelens et al. 2008). The process known as wet deposition is a function of the volume and chemistry of precipitation (Ponette-González et al. 2010b). Plant canopies alter the chemistry of precipitation through the processes of leaching and uptake (Hölscher et al. 2003; Zimmermann et al. 2008) which are influenced

by the physiology and ion status of trees (Talkner et al. 2010). For instance, when ion uptake is the prevalent process, nutrient concentrations in soils can increase below canopy gaps due to the absence of leaves to take up nutrients, thereby improving the nutrient supply for regrowth in clearings (Wilcke et al. 2009). However, where leaching is occurring, stand deposition (SD) (the sum of nutrients in throughfall and stemflow) can be higher in mixed plots than single species plots due to differences in rates of leaching (Talkner et al. 2010). Regardless of the influence of the canopy, throughfall is a vital pathway for the distribution of nutrients to the forest floor, particularly in systems with weathered soils such as tropical forests (Parker 1983). Identifying and quantifying the source of nutrients in precipitation and throughfall as dry deposition (DD) or canopy exchange (CE) is difficult because micrometeorological methods are expensive (Lilienfein and Wilcke 2004). An alternate approach is to use a canopy budget model based on the assumption that leaching and uptake of Na and Cl are minimal and either of these can be used as a tracer ion to estimate the contribution of DD and CE to net throughfall deposition (NTD) (Staelens et al. 2008).

There are a number of studies reporting rainforest interception, throughfall and stemflow (e.g. Huber and Iroumé 2001; Loescher et al. 2002; McJannet et al. 2007), particularly in tropical lowland rainforests (Zimmermann et al. 2008, 2009) and tropical montane forests (Wilcke et al. 2009; Wullaert et al. 2009; Mair and Fares 2010; Ponette-González et al. 2010a, b) but few have recorded the hydrological characteristics of lower montane forests (Cavelier et al. 1997; Fleischbein et al. 2005). Nutrient cycle studies in tropical areas have quantified amounts of nutrients delivered by throughfall (Cavelier et al. 1997; Hölscher et al. 2003; Zimmermann et al. 2007, 2008; Wilcke et al. 2009; Scheer 2011), but few studies have compared the influence of different land use types on nutrient cycling (Lilienfein and Wilcke 2004; Dezzeo and Chacón 2006; Ponette-González et al. 2010a). This study considers rainfall redistribution together with nutrient deposition for three different land use types across seasons.

The aims of this research were to quantify rainfall partitioning (throughfall, stemflow and interception loss) in three land use types [primary forest (PF), secondary forest (SF) and agricultural land (A)] across wet and dry seasons. In addition to rainfall

partitioning, concentrations of nutrients in the various rainfall compartments were measured to investigate any changes in water quality due to changes in DD and leaching or uptake of solutes by leaves and stems.

The main land-use types of the study region are grazing, shrubs and farming with slash and burn used in land management (Flores de Gracia 2005), however, PF remains the dominant vegetation type within the Santa Fe National Park. Agricultural plantations and pastures occur where PF has been displaced but where these have not been established, the area becomes SF. SF establishes on abandoned pastures and also constitutes the fallow vegetation in the slash and burn process but it does not have the same structure and function as PF due to the depletion of soil nutrients during the removal of pristine forest. Fertilisers are not used in the region due to inhibitive costs. Despite the variation in land use types in this region, there is little information about the influence of different vegetation types on catchment hydrology. The effect of changes in vegetation on the water cycling and water quality remains poorly understood but such information is vital for an adequate understanding of the effect of changing vegetation and climate on regional water resources.

Methods

Study sites

All study sites were located in or near the recently formed Santa Fe National Park in the central Cordillera region, Veraguas province, Panama (Fig. 1). The national park was established in 2001 to halt further deforestation and conserve the rich biodiversity of this part of the Mesoamerican Biological Corridor. The sites were located within the Bulaba River sub-basin which is part of the Santa Maria River catchment, a vital water supply in the region.

The landscape is mountainous with some very steep terrain and some more level areas. The elevations of study sites ranged between 420 and 950 m above sea level and slopes ranged between 5 and 55° (Table 1). All measurements were taken during the period September 2007–November 2008. The mean annual rainfall for the nearest weather station in Santa Fe (elevation 463 m) was 2250 mm for the years

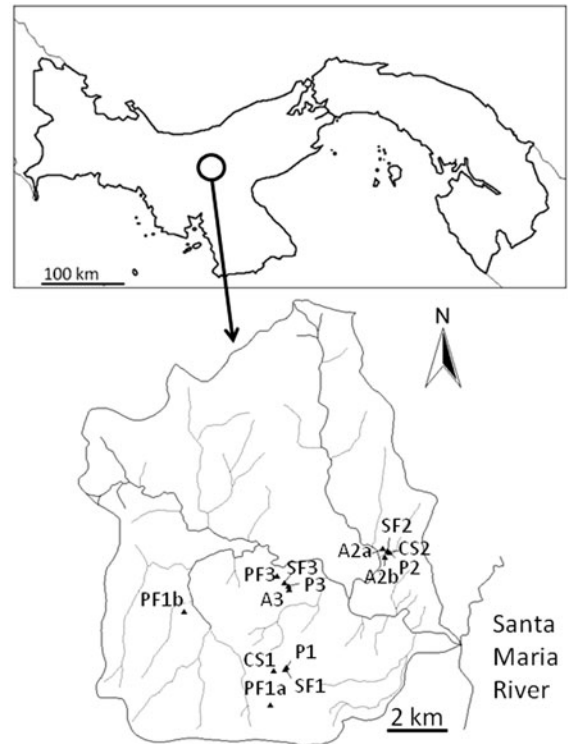


Fig. 1 Location of study sites in Panama

1996–2007 and the range was 1300 mm to 3090 mm (ETESA 2008). All study sites had distinct wet and dry seasons with the majority of rain falling between the months of June and December. We observed large spatial variability in rainfall due to the terrain of the region and some fog in the early morning in the higher plots at Alto de Piedra.

The natural vegetation at the site was lower montane tropical rainforest according to the classification system of the vegetation of Panama (ANAM 2000), yet Carrasquilla (2006) lists tropical lowland forests as the native vegetation between sea level and 700 m elevation on the Pacific side of Panama. Many plant species present at the plots were common in lowland and midland habitats (e.g. *Hampea appendiculata* (Donn. Sm.) Standl. and *Virola sebifera* Aubl.) while others are reported in lowland habitats only (e.g. *Jacaranda copaia* (Aubl.) D. Don) (Carrasquilla 2006). Crops cultivated on the agriculture plots in this study included plantain, orange and fruit palm (A2a), yuca (also known as manioc or cassava) and plantain (A2b) and yuca, plantain and beans (A3).

Table 1 Description of study plots

Land-use type	Name of location	Site abbreviation	UTMX	UTMY	Elevation (m)	Aspect	Inclination (°)
Primary forest	Alto de Piedra	PF1a	487,288	940,241	950	E	25
	Primer Brazo	PF1b	484,985	942,765	678	NE–SE	45
	Muelas	PF3	487,478	943,729	526	S	50
Secondary forest	Alto de Piedra	SF1	487,702	941,192	842	N–NE	10
	Bermejo	SF2	490,519	944,348	483	NW–SW	55
	Muelas	SF3	487,673	943,544	507	NW	10
Agriculture	Bermejo banana	A2a	490,338	944,449	420	NW–SW	20
	Bermejo yuca	A2b	490,382	944,208	445	SW–W	30
	Muelas	A3	487,808	943,363	542	SW–SE	15
Pasture	Alto de Piedra	P1	487,738	941,260	819	N	10
	Bermejo	P2	490,457	944,371	481	W	40
	Muelas	P3	487,779	943,448	555	N	40
Climate stations	Alto de Piedra	CS1	487,395	941,164	858	E	5
	Bermejo	CS2	490,457	944,371	481	W	15

Sites were selected using satellite images, vegetation maps, ground surveys and local information on historical land-uses to assess the accessibility of plots and stability of vegetation. The sites were chosen to represent the prevailing land-use types of the region, including natural and anthropogenic vegetation. The four land-use types were PF, SF, agriculture (A) and pasture (P), with three replicates of each type (Table 1). Circular plots of 20 m radius were established in the forests, while plots of 10 m radius were established in the agriculture and pasture sites. Data were collected for each plot using a GPS (Table 1).

Vegetation survey

Diameter at breast height (DBH at 1.3 m) and tree height were measured for all trees with a DBH of ≥ 10 cm in each forest plot using a metric measuring tape and Vertex III ultrasonic hypsometer (Haglöf, Långsele, Sweden). Plants with a DBH of 3–10 cm were measured in the 10 m radius of the plot and shrubs and trees with a DBH smaller than 3 cm were measured in five 1 m radius sub-plots (one in the centre and one at each cardinal point) within the 20 m radius. Tree height was estimated where the canopy was too dense.

Crown dimensions of trees sampled for stemflow were measured in eight directions according to the method of Dietz (2007). The height of the first branch was measured and the crown length was calculated as

the difference between this measurement and the total tree height.

Leaf area index was estimated with a Minolta digital camera fitted with a Nikon FC-E8 fisheye converter of $2,048 \times 1,536$ pixel resolution mounted on a Hemi View levelling device (Regent Inc., Ontario, Canada) in September 2007. Photographs were taken with a remote control at 1.3 m above the ground and vegetation directly above the lens was removed. Fifty images were collected at each primary and SF plot and 15 were taken at the agricultural plots adjacent to the randomly located throughfall collection points, in addition to two transects of 20 images at five m intervals in the forest plots. All photographs were collected between early morning and noon. Images were analysed with Can-Eye version 5.0 (French National Institute for Agricultural Research, INRA) to obtain LAI and canopy cover estimates (Weiss et al. 2004; Demarez et al. 2008).

Rainfall measurements

Two automatic weather stations equipped with air temperature (CS215), humidity (CS215), radiation (CS300, Apogee Si-Fotodiod) and precipitation (ARG100) sensors all supplied by Campbell Scientific (Shepshed, UK) were placed in open sites at Alto de Piedra and Bermejo (Table 1). Data were logged at half-hourly intervals using a Campbell data logger (CR 200, Campbell Inc. Logan, UT, USA) housed in a

weatherproof box for the period September 2007–October 2008. The Alto de Piedra station (CS1) was in a clearing of approximately 400 m² and was closest to sample locations SF1 and P1. The Bermejo climate station was installed on pasture P2 in the absence of a more suitable clearing and was close to SF2 and about 100–300 m away from A2a and A2b.

The tipping bucket rain gauges attached to the climate stations were placed on horizontal ground and had a resolution of 0.2 mm with an opening of 25.4 cm diameter. Gauges used to measure throughfall (described below) were also placed in a cleared area at pasture sites and adjacent to each climate station to verify agreement between the commercial tipping bucket gauge and the rain collectors and allow direct comparisons between the throughfall data and the gross precipitation. Three collectors were placed at each climate station.

Throughfall was measured using rainfall collectors consisting of a plastic funnel connected to an enclosed 18 L plastic bucket with a plastic tube. The funnel openings were 0.25 m in diameter, the vertical rim was 3 cm high and the total height of each gauge was 0.95 m. The steep angle of the funnels and the vertical rim minimised the chance of rain splashing out of the gauges, while the height of the gauges prevented rain splashing into the gauges from the forest floor.

A plastic net was fitted across each funnel to prevent build-up of leaves plugging the funnel and a tennis ball was placed on each net to reduce evaporation of collected water. Gauges were installed horizontally and on steep slopes, the gauges were held in place with sticks. Understorey vegetation directly above the samplers was removed so throughfall of the tree canopy was collected. Throughfall collectors were positioned randomly along 50 m transects in the forest sites and 30 m transects in the agriculture sites. There were three parallel transects which were 10 m apart at each site. The minimum distance between each gauge was 2 m and ten collectors were placed on each forest transect while five collectors were placed on each agriculture transect. Therefore, there were a total of 30 collectors at each forest plot and 15 collectors at each agriculture plot. We used a similar number of gauges to Wullaert et al. (2009), who found no difference between throughfall datasets collected with troughs and funnel gauges. The transect approach was favoured over a grid design to minimise damage to vegetation and

protect the forest floor. Three gauges were randomly located on each pasture plot.

Due to the large number of gauges, the distances between the sites and the inaccessible nature of the sites, the amount of water in each throughfall collector was measured once a week. A one litre graduated cylinder accurate to 10 mL was used to measure the volume of water in each bucket.

Stemflow was measured on one primary forest (PF1a) and one secondary forest (SF1) plot with eleven and fourteen trees chosen at each plot, respectively to represent a range of DBH classes and species present. Collar gauges were installed on the sample trees by creating a spiral from plastic hoses cut in half lengthwise around the stem. Trees with a larger DBH were fitted with a hose of 24 mm in diameter while smaller trees were fitted with a hose of 15 mm in diameter. Hose spirals were attached to trees with nails and then sealed along the length of the spiral with silicon sealant (McJannet et al. 2007). Each spiral collar was connected to a 45 L reservoir. Moss, climbers and loose bark were removed from each tree prior to installation and the integrity of each collar was checked once a month to ensure it was still properly fitted. The diameter of the collars did not exceed 25 mm to avoid collection of direct rainfall and water dripping from leaves. Inspections during high rainfall events did not reveal any water overflowing from the collars. The volume of water in each reservoir was measured each week at the same time as the throughfall data and stemflow measurements were included in the intensive campaign. Unavoidably, the reservoirs on the two largest trees overflowed several times during large rainfall events.

Analysis of rainfall partitioning data

Throughfall and rainfall data were scaled to the plot level. Basal area was used to scale stemflow amounts for individual trees to stemflow for the entire plot according to the following equation (Eq. 1):

$$\begin{aligned} \text{stemflow of plot} \\ = \frac{\text{measured stemflow} \times \text{basal area of plot}}{\text{basal area of trees with measured stemflow}} \end{aligned} \quad (1)$$

where rainfall events were large, throughfall values were normally distributed, however during the dry

season, throughfall values for some weeks were not normally distributed. Because the majority of cases were normally distributed, we used mean and coefficient of variation (CV) values to represent the throughfall. All statistical analysis was carried out using PASW Statistics v. 18 (SPSS).

Nutrient measurements

Water samples were collected from throughfall and stemflow (where available) of each land-use type for nutrient analysis. Throughfall samples collected at the pasture sites were used as gross precipitation values for other sites. Throughfall and stemflow water samples were collected once the volume in each reservoir was recorded. Samples were pooled from each site. These samples were tested for pH and concentrations of Ca, Mg, K and Na using an atomic absorption spectrophotometer (Spectra AA 300, Varian Pty Ltd., Clayton South, Australia). Concentrations of P were also determined but these were often below detection limits for the instrument (approximately 0.05 mg L^{-1} continuous-flow method) so values are not reported here. Values presented are means and standard errors for each land-use type. Nutrient fluxes were calculated by multiplying water fluxes (precipitation, throughfall or stemflow) with the respective concentrations.

Canopy budget model

The amount of nutrients entering the ecosystem by stand deposition [SD; defined as the sum of throughfall deposition (TD) and stemflow deposition (SFD)] result from total atmospheric depositions and canopy exchange (CE) processes (Lovett et al. 1996; Staelens et al. 2008; Talkner et al. 2010) and can be written as (Eq. 2):

$$\text{TD} + \text{SFD} = \text{PD} + \text{DD} + \text{CE} \quad (2)$$

where PD is precipitation deposition and DD is dry deposition. Since stemflow was only collected at the PF and SFs at Alto de Piedra (PF1a and SF1), full nutrient delivery analysis was confined to these sites.

The canopy budget model developed by Ulrich (1983) and Bredemeier (1988) was used to determine net throughfall deposition (NTD), DD and CE. The NTD is defined as (Eq. 3):

$$\text{NTD} = \text{TD (or SD for PF1a and SF1)} - \text{PD} \quad (3)$$

Na is often used as a tracer ion as it is only deposited in particles and CE rates for Na are low (Bredemeier 1988; Staelens et al. 2008). The DD of an element X (Ca, Mg, K) was calculated as follows (Eq. 4):

$$\text{DD} = \frac{\text{NTD}_{\text{Na}}}{\text{PD}_{\text{Na}}} \times \text{PD}_x \quad (4)$$

The CE of Ca, K and Mg was then estimated by subtracting DD (Eq. 4) from NTD (Eq. 3).

Nutrient enrichment factors were calculated as the amount of nutrient delivered as SD or TD (depending on whether SFD was available for the site) divided by the PD for that site.

Results

Seasonal patterns in rainfall

Rainfall was highly seasonal at the study sites with most of the rain falling during the period May to November and very little rain falling during the period December to April according to the data measured at the three pastures (Fig. 2). Rainfall was generally above long-term average each month for all three sites, with annual totals almost double long-term average values (Fig. 2). The wettest site during the 2007 wet season was Alto de Piedra, while more rainfall was collected at Bermejo in the 2008 wet season. Muelas was the driest site but there were some heavy falls during the drier months of March, May, June at Muelas (Fig. 2).

Tree characteristics in the forests

Detailed analysis of the structure of the stands at PF1a and SF1 indicates that the PF had a greater stem density, DBH, basal area and tree height (Table 2) for all DBH classes. In addition to this, all PFs had a larger number of species and higher Shannon index than the SFs (Table 3). These values indicate greater biodiversity, structural complexity and total biomass in the PFs when compared to SF. Despite this, there was no difference in the LAI values recorded at the primary and SFs at Muelas (PF3 and SF3, Table 3). Canopy cover was larger in the PF, however and in general, the mean LAI was slightly larger for the PF than the SF (Table 3), while the agricultural sites had the smallest LAI values.

Fig. 2 Monthly rainfall patterns for September 2007–October 2008 recorded at the Alto de Piedra, Bermejo and Muelas pasture sites, compared to long-term averages collected at the government climate station at Santa Fe. There were no data available for Muelas for the months of November and December 2008 and the September 2007 rainfall collection was incomplete because equipment was not set up until part way through the month

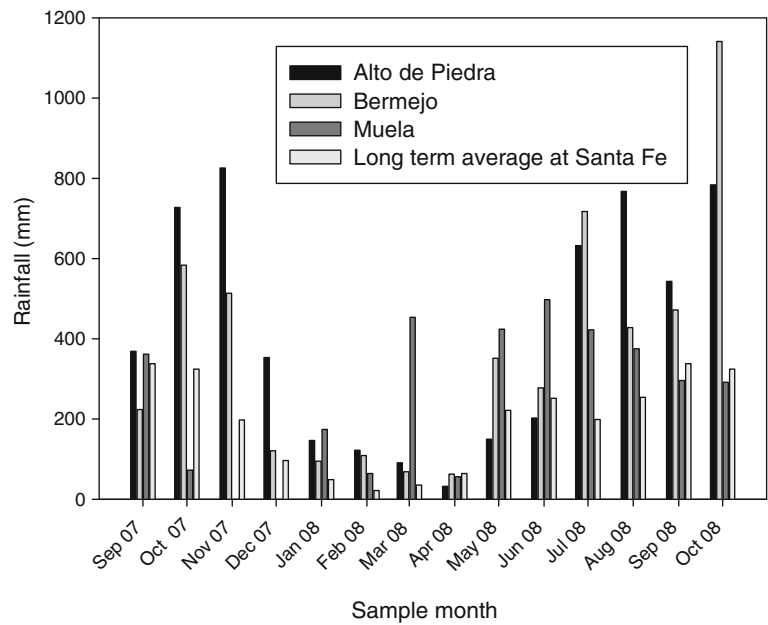


Table 2 Stand structural characteristics in the primary and secondary forest at Alto de Piedra (PF1a and SF1) for different DBH classes

Characteristic	DBH class	PF	SF
Stem density (n/ha)	DBH ≥ 3 cm	3,889 (1,742)	2,928 (678)
	DBH ≥ 10 cm	990 (450)	683 (296)
	DBH ≥ 50 cm	77 (16)	8 (14)
Basal area (m ² /ha)	DBH ≥ 3 cm	79.8 (20)	21.6 (10)
	DBH ≥ 10 cm	73.1 (16)	16.5 (11)
DBH (cm)	DBH ≥ 3 cm	17.6 (1.6)	11.0 (2.7)
	DBH ≥ 10 cm	26.1 (3.8)	15.3 (2.2)
Tree height (m)	DBH ≥ 3 cm	12.7 (0.3)	7.2 (0.6)
	DBH ≥ 10 cm	17.9 (1.3)	9.3 (0.5)

Data are means of three plots with standard deviations in parentheses

Table 3 Leaf area index (m² of leaf per m² of ground), canopy cover (on a scale of 0–1) and tree species diversity for primary and secondary forest plots, reported as Shannon Index and number of species per plot (measured during the wet season in 2007)

	PF1a	PF1b	PF3	SF1	SF2	SF3	A2a	A2b	A3
LAI	5.4	5.0	5.4	4.0	5.2	5.4	5.1	3.0	3.4
Canopy cover	0.83	0.87	0.86	0.79	0.76	0.79	0.83	0.41	0.74
Shannon index	2.8	3.0	3.2	2.7	2.3	2.2	nd	nd	nd
Number of species	35	46	69	28	24	21	12	16	20

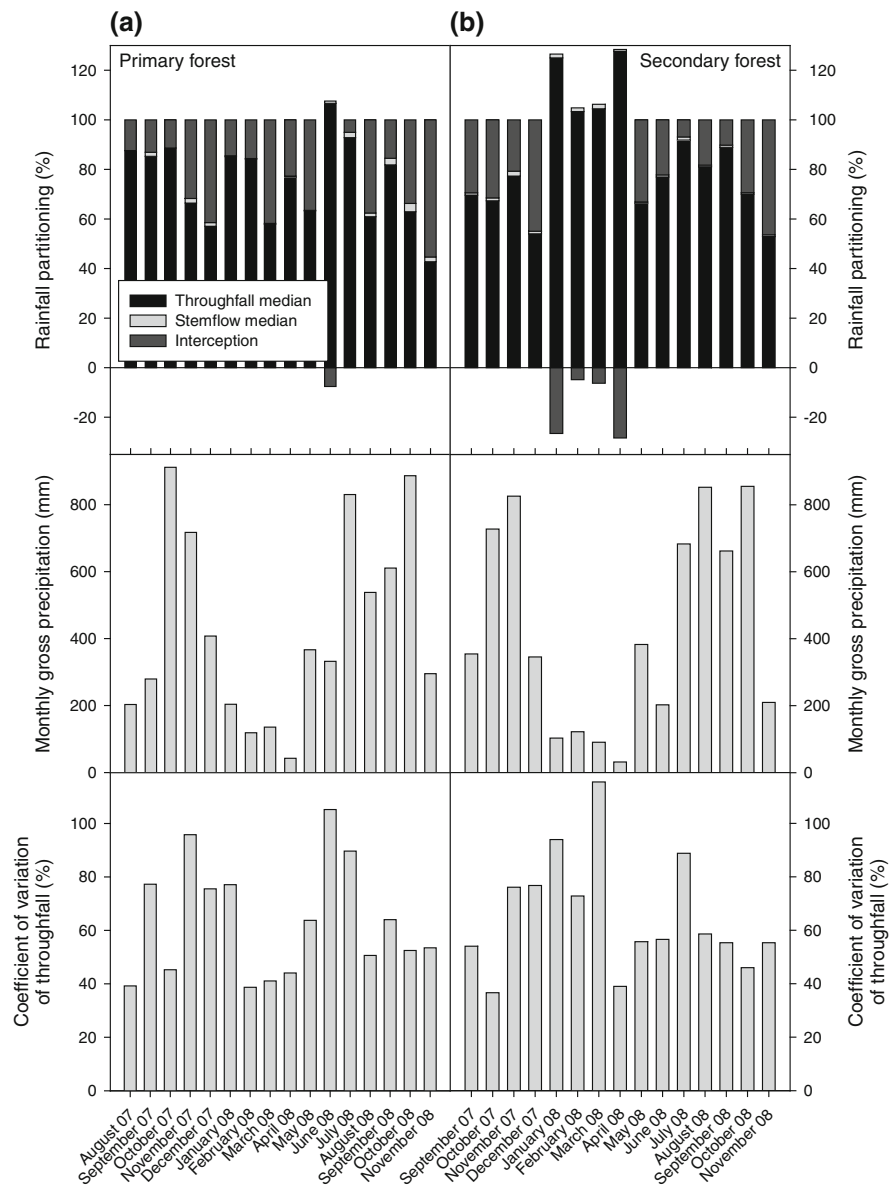
nd not determined

Rainfall partitioning

Rainfall partitioning for the primary and SFs at Alto de Piedra (sites PF1a and SF1, respectively) is shown as monthly values in Fig. 3, while seasonal values of throughfall and stemflow for every site are reported in

Table 4. When total gross precipitation was divided into throughfall, stemflow and interception, there were four occasions in the SF (Fig. 3b) and one in the PF (Fig. 3a) where the throughfall exceeded the gross precipitation (P_g), resulting in negative interception values. In the SF, these months had the least rainfall

Fig. 3 Rainfall partitioning, gross precipitation and CV for throughfall for the months of August 2007–November 2008 for the primary (left hand column) and secondary (right hand column) forests at Alto de Piedra. Rainfall partitioning is shown as % of gross precipitation and is divided into throughfall, stemflow and interception (the remaining water when throughfall and stemflow was subtracted from gross precipitation). Where the sum of throughfall and stemflow exceeded the gross precipitation, interception is shown as a negative value



and some had very high coefficients of variation. It was difficult to distinguish clear monthly patterns in the rainfall partitioning data because the CV values were so large (Fig. 3, lower panels). There was no relationship between the months with high CV and months with large or small rainfall (Fig. 3).

When the data were pooled into seasonal values for each site, there were fewer instances of throughfall exceeding gross precipitation in the forests (Table 4). In the PF, wet season throughfall ranged between 68 and 95% of P_g while dry season values ranged between 50 and 119%, indicating the huge variation in

throughfall in the dry season. SF values were 68–89 and 75–89% in the wet and dry, respectively (Table 4). For agricultural sites, throughfall exceeded P_g at all sites in the 2007 wet season and only got as low as 78% in the 2008 wet season. Dry season throughfall values were 83–94% in the agricultural land use type.

Throughfall clearly increases as gross precipitation increases but there is no relationship between throughfall expressed as a percentage of precipitation and gross precipitation (data not shown). The relationship between total seasonal rainfall and total seasonal throughfall in mm was strong, with an R^2 value of 0.97.

Table 4 Throughfall and stemflow (where available) for different seasons at different land-use sites

Land-use type	Site name	Season	Total gross precipitation (P_g , mm)	Total throughfall (mm) (CV%)	Throughfall as a proportion of P_g (%)	Stemflow (mm and %)
Primary forest	PF1a	Wet 07	1,251	852 (82%)	68.1	37 (3.0%)
	PF1b	Wet 07	866	823 (45%)	95.0	
	PF3	Wet 07	434	412 (33%)	94.9	
	PF1a	Dry 08	808	571 (48%)	70.6	13 (1.6%)
	PF1b	Dry 08	848	1,005 (65%)	118.5	
	PF3	Dry 08	645	319 (165%)	49.5	
	PF1a	Wet 08	3,696	3,129 (49%)	84.7	118 (3.2%)
	PF1b	Wet 08	4,053	3,347 (53%)	82.6	
	PF3	Wet 08	2,458	1,979 (40%)	80.5	
Secondary forest	SF1	Wet 07	1,908	1,304 (42%)	68.4	21 (1.1%)
	SF2	Wet 07	1,430	1,142 (40%)	80.2	
	SF3	Wet 07	434	388 (42%)	89.2	
	SF1	Dry 08	694	617 (65%)	88.9	10 (1.5%)
	SF2	Dry 08	456	343 (78%)	75.2	
	SF3	Dry 08	645	507 (38%)	78.5	
	SF1	Wet 08	3,847	2,988 (47%)	77.7	34 (0.9%)
	SF2	Wet 08	3,387	2,994 (45%)	88.4	
	SF3	Wet 08	2,458	2,061 (45%)	83.8	
Agriculture	A2a	Wet 07	1,430	1,436 (48%)	100.5	
	A2b	Wet 07	1,430	1,475 (38%)	103.2	
	A3	Wet 07	434	464 (20%)	106.8	
	A2a	Dry 08	456	417 (90%)	91.5	
	A2b	Dry 08	456	379 (94%)	83.2	
	A3	Dry 08	748	701 (27%)	93.8	
	A2a	Wet 08	3,355	2,674 (56%)	79.7	
	A2b	Wet 08	3,211	2,783 (48%)	86.7	
	A3	Wet 08	2,458	2,411 (34%)	98.1	

Values presented are medians for each site/season with coefficients of variation in brackets (calculated as standard deviation/median*100). Dry season is defined as the months December 2007–April 2008. Site abbreviations are defined in Table 1

In contrast, the regression between gross precipitation (mm) and throughfall (%) produced an R^2 of 0.01. This demonstrates that changes in proportional throughfall are not associated with the size of the rainfall event, however, variation in proportion of throughfall declined as the seasonal rainfall increased, converging on approximately 80% throughfall for large seasonal totals of P_g (data not shown). Individual land-use types were also considered for this analysis and splitting the dataset did not improve the relationship measurably. We investigated the role of LAI, canopy cover, Shannon Index and species number on throughfall variability and did not find substantial relationships between any of these factors and throughfall amount.

Stemflow was about 3% of P_g in the wet seasons in the PF and 1.6% in the dry season (Table 4). Stemflow for the SF was smaller in the wet season (about 1%) compared to that of the dry season (1.5%). Analysis of the drivers of monthly stemflow indicated only weak correlations between plant structure and volume of stemflow (data not shown).

Dry deposition and canopy exchange of nutrients

Samples analysed for pH were only collected in the first few months of the study and there were no clear patterns to report so data are not shown. Similarly, patterns of solute concentrations in stemflow samples

were unclear so reporting and analysis of nutrient inputs is focussed on throughfall results (Fig. 4; Tables 5, 6).

The concentrations of Ca, Mg, K and Na in rainfall (pasture throughfall) were consistent throughout the year, except in January when Ca concentration increased as the dry season began (Fig. 4). The concentration of Na in rainfall was also slightly elevated in December. Concentrations of solutes in throughfall were generally similar to those in the incident rainfall (Fig. 4), with the following exception. In PF, Ca concentrations in throughfall were elevated above those of incident rainfall in October 2008. Concentrations of Mg were elevated in throughfall of several land-use types in December 2007, January and September 2008 (Fig. 4). Concentrations of K were larger than all other solutes and elevated in throughfall in December 2007, January, and September 2008. Finally, Na concentrations were elevated in SF in January 2008 and elevated in PF in October 2008 but reduced in all throughfalls in September 2008 (Fig. 4).

Deposition of nutrients varied between land-use types and seasons (Table 5). Total annual PD, in $\text{kg ha}^{-1} \text{ year}^{-1}$ for Alto de Piedra was $\text{Na (127.8)} > \text{Ca (79.2)} > \text{K (53.4)} > \text{Mg (10.2)}$. For Bermejo, the annual PD was $\text{Na (64.8)} > \text{Ca (62.4)} > \text{K (34.2)} > \text{Mg (9.6)}$ and for Muelas annual PD based on wet season estimates only was $\text{Ca (24)} > \text{K (21.6)} > \text{Na (10.8)} > \text{Mg (2.4)}$. Wet season delivery of nutrients via PD was larger than dry season fluxes for all nutrients with the exception of Mg (Table 5). Throughfall deposition (TD) and stand deposition (SD, used where stemflow values were available) often delivered more nutrients than PD and wet season inputs are often (but not always) larger than dry season values. TD is consistently larger than PD for all solutes at the Alto de Piedra sites and for K at all three localities (Table 5).

Net throughfall deposition is largest for K at the Alto de Piedra sites. Proportioning NTD into DD and CE using the approach of Ulrich (1983) indicates that the contribution of CE was generally higher than DD inputs. Furthermore, CE is most often positive,

Fig. 4 Seasonal variation in concentrations of Ca, Mg, K and Na in throughfall for the four land-use types, pasture, primary forest, secondary forest and agriculture. Values shown are means across each land use type \pm standard error of the mean

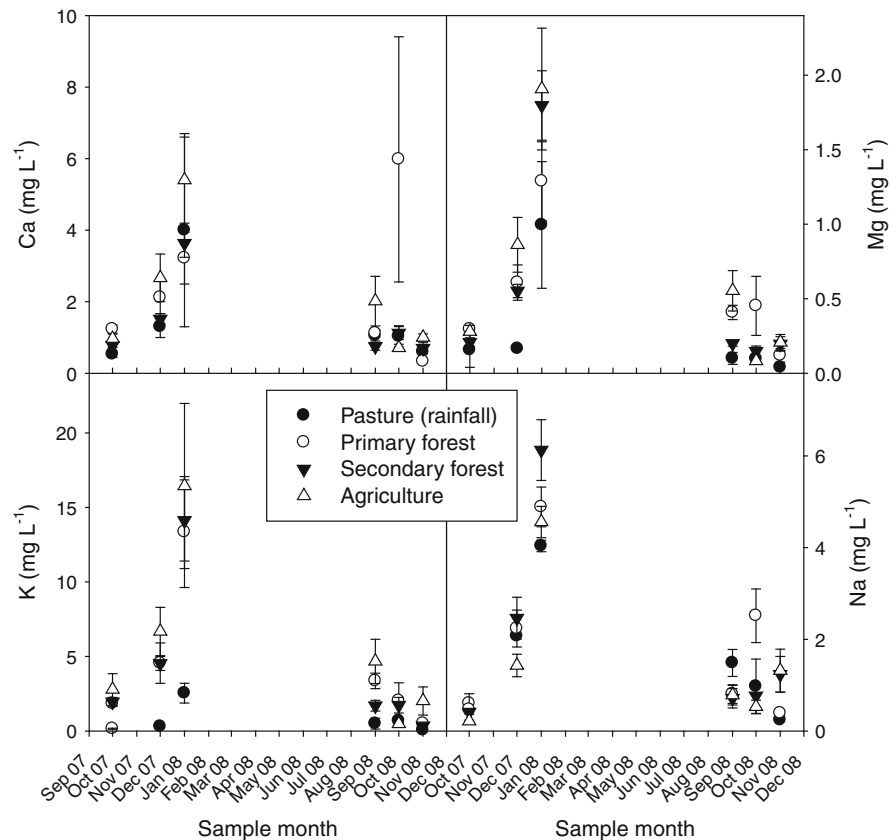


Table 5 Bulk precipitation deposition shown as precipitation deposition (PD), stand deposition (SD), including stemflow, where available) and throughfall deposition (TD), Net throughfall deposition (NTD), dry deposition (DD) factor, DD and canopy exchange (CE)

Season	PD, SD, TD (kg ha ⁻¹ month ⁻¹)	NTD (kg ha ⁻¹ month ⁻¹)			DD factor			CE (kg ha ⁻¹ month ⁻¹)			
		Ca ²⁺	Mg ²⁺	K ⁺	Na ⁺	Ca ²⁺	Mg ²⁺	K ⁺	Ca ²⁺	Mg ²⁺	K ⁺
Alto de Piedra PD	Dry 08	3.4 ± 0.2	0.9 ± 0.3	4.2 ± 1.4	8.2 ± 0.2						
	Wet 08	9.8 ± 4.3	0.8 ± 0.4	4.7 ± 3.9	13.1 ± 5.9						
PF1a SD	Dry 08	8.4 ± 1.3+	2.7 ± 0.5+	27.1 ± 7.5+	9.2 ± 1.5	5.0	1.8	22.9	1.0	0.12	0.4
	Wet 08	14.2 ± 1.2+	2.9 ± 0.2+	24.0 ± 5.3+	11.5 ± 2.6	4.4	2.1	19.3	-1.6	0	0
PF2b TD	Dry 08	5.4 ± 0.5+	2.0 ± 0.3+	13.0 ± 2.5+	9.2 ± 1.5	2.0	1.1	8.8	1.0	0.12	0.4
	Wet 08	4.1 ± 0.6-	3.4 ± 0.7+	17.0 ± 5.2+	12.7 ± 3.7	-5.7	2.6	12.3	-0.4	0	0
SF1 SD	Dry 08	6.2 ± 1.0+	1.9 ± 0.2+	18.4 ± 5.5+	10.7 ± 1.7+	2.8	1.0	14.2	2.5	0.30	1.0
	Wet 08	7.8 ± 0.7	1.0 ± 0.1	9.8 ± 4.3+	4.5 ± 1.1-	-2.0	0.2	5.1	-8.6	0	0
Bermejo PD	Dry 08	4.1 ± 2.2	0.8 ± 0.6	1.7 ± 1.3	3.2 ± 0.7						
	Wet 08	6.3 ± 0.6	0.8 ± 0.2	4.0 ± 0.1	7.6 ± 0.8						
SF2 TD	Dry 08	2.2 ± 0.1	1.3 ± 0.1	8.4 ± 1.6+	3.1 ± 0.4	-1.9	0.5	6.7	-0.1	0	0
	Wet 08	4.2 ± 0.9-	1.1 ± 0.1	8.0 ± 2.3+	4.5 ± 1.4-	-2.1	0.3	4.0	-3.1	0	0
A2a TD	Dry 08	4.8 ± 1.4	1.6 ± 0.4	11.6 ± 1.2+	3.0 ± 0.4	0.7	0.8	9.9	-0.2	0	0
	Wet 08	9.8 ± 3.6	2.4 ± 0.7+	12.5 ± 8.3+	4.2 ± 0.8-	3.5	1.6	8.5	-3.4	0	0
A2b TD	Dry 08	4.4 ± 1.5	1.5 ± 0.5	14.0 ± 3.7+	3.4 ± 0.4	0.3	0.7	12.3	0.2	0.06	0.3
	Wet 08	7.5 ± 1.7	1.6 ± 0.2	20.2 ± 5.6+	8.2 ± 3.0	1.2	0.8	16.2	0.6	0.08	0.5
Muelas PD	Wet 08	2.0 ± 0.6	0.2 ± 0.0	1.8 ± 0.3	0.9 ± 0.3						
	Wet 08	1.1 ± 0.2-	0.4 ± 0.2	3.2 ± 1.6+	1.7 ± 0.9	-0.9	0.2	1.4	0.8	0.89	1.8
SF3 TD	Wet 08	2.9 ± 1.0	0.6 ± 0.2+	4.6 ± 1.1+	2.0 ± 0.6+	0.9	0.4	2.8	1.1	1.22	2.4
	Wet 08	3.1 ± 0.3+	0.5 ± 0.1	4.3 ± 1.9+	2.2 ± 0.7+	1.1	0.3	2.5	1.3	1.44	2.9

Values shown for PD, SD and TD are means ± standard error for values in kg ha⁻¹ month⁻¹. A + or - indicates a significant increase or decrease when SD or TD are compared to PD for the same location and season. NTD is calculated as TD (or SD for PF1a and SF1) - PD. DD factor indicates the proportionality of Na in NTD and PD. DD = DD factor*PD and CE = TD (or SD) - DD [following the method of Ulrich (1983)]. Negative CE indicates canopy uptake and positive CE indicates canopy leaching of that ion. Site abbreviations are described in Table 1

PF primary forest; SF secondary forest; A agriculture

indicating leaching of ions (Staelens et al. 2008) but there are cases of uptake of Ca, indicated by negative CE values (Table 5).

Patterns in PD, SD and TD are reflected in nutrient enrichment factors across the sites (Table 6). Enrichment factors were consistently close to 1 for Na. Smallest enrichment factors were calculated for Ca but large and also highly variable values were reported for K. Enrichment factors for Mg were intermediate. The sites with the most nutrient enrichment as water passes through the canopy were PF1a, A2a, A3 and A2b. The sites with the least nutrient enrichment were PF3, SF2 and SF3 (Table 6).

Discussion

Seasonality and impacts of land-use type on hydrological characteristics

Throughfall

Estimation of throughfall is notoriously difficult because values for any one rain event are highly variable (Crockford and Richardson 2000; Levia and Frost 2006). As a consequence, values of coefficients of variation (CV) are very large in this study, ranging from 40 to 120% on a monthly scale (Fig. 3) and 20–165% on a seasonal scale (Table 4). This large variation makes identifying and interpreting seasonal and land use responses challenging as any patterns may be masked by the variability of the dataset. However, the large variation recorded here is within

the range reported by other studies such as Huber and Iroumé (2001), Dezzeo and Chacón (2006), Keim et al. (2005) and Zimmermann et al. (2007) and the number of gauges used is consistent with previous studies reviewed by Levia and Frost (2006). Large spatial variability of throughfall has been attributed to the complexity of the structure of tropical forest canopies and high species diversity (Herwitz 1985), as well as climatic factors such as wind speed and direction and topography of a site (Crockford and Richardson 2000). Levia and Frost (2006) identified a suite of biotic and abiotic factors which influence temporal and spatial variation of throughfall volume, many of which may have contributed here but are difficult to evaluate.

When the overall proportion of throughfall is calculated by pooling all plots within a land-use type across the entire sampling period (Table 4), the throughfall for PF and SFs is very similar (83 and 81%, respectively) but the throughfall for agriculture is 94% of gross precipitation. This is consistent with increased throughfall in coffee agroforestry compared to montane cloud forest throughfall in eastern Mexico (Ponette-González et al. 2010b) which was associated with weak but significant inverse relationships amongst LAI, stand basal area and net throughfall. Other contributing factors could include species composition, meteorological conditions and canopy structure (Levia and Frost 2006). We recorded a smaller LAI for agriculture plots (Table 3). However, despite extensive statistical analysis of vegetation structure, number of species and rainfall characteristics, we were not able to identify the drivers of throughfall, because the dataset was so variable.

Table 6 Nutrient enrichment factors for throughfall and stand deposition (SD) at each site

Values are calculated as TD divided by PD and are therefore unitless. Each value is the mean of the sampling events \pm standard error of the mean. The mean value for primary forests, secondary forests and agriculture sites is also presented. There were no significant differences between land use types

Site	Ca	Mg	K	Na
PF1a (SD)	2.4 \pm 0.4	5.8 \pm 1.9	17.5 \pm 6.0	1.1 \pm 0.1
PF1b	0.9 \pm 0.2	3.3 \pm 0.6	7.3 \pm 1.9	0.8 \pm 0.1
PF3	0.9 \pm 0.4	1.8 \pm 0.6	5.7 \pm 4.1	2.0 \pm 1.3
PF mean	1.4 \pm 0.5	3.6 \pm 1.2	10.2 \pm 3.7	1.3 \pm 0.4
SF1 (SD)	1.4 \pm 0.4	2.2 \pm 0.4	7.1 \pm 1.9	0.9 \pm 0.2
SF2	0.8 \pm 0.2	2.4 \pm 0.7	6.6 \pm 2.6	0.8 \pm 0.1
SF3	1.5 \pm 0.1	2.1 \pm 0.5	7.1 \pm 4.6	1.6 \pm 0.6
SF mean	1.2 \pm 0.2	2.2 \pm 0.1	6.9 \pm 0.2	1.1 \pm 0.3
A2a	2.0 \pm 0.6	4.8 \pm 1.7	17.3 \pm 9.0	0.7 \pm 0.1
A2b	1.4 \pm 0.2	3.4 \pm 1.1	7.6 \pm 1.8	1.0 \pm 0.2
A3	1.7 \pm 0.4	1.8 \pm 0.3	9.7 \pm 7.5	1.5 \pm 0.9
A mean	1.7 \pm 0.2	3.3 \pm .0.9	11.5 \pm 2.9	1.1 \pm 0.2

There were patterns in the seasonality of variability in the SF (Table 4; Fig. 3) and agriculture sites (Table 4). The CV was generally smaller in the wet season than the dry season in these land use types. But this pattern was less clear in the PF sites. The pattern of increased CV occurring in the dry season at the SF and agriculture sites, while not at the PF sites may be due to the less complex canopy structure and smaller LAI at the disturbed sites (Levia and Frost 2006) or different crown characteristics (Crockford and Richardson 2000). As the amount of rainfall decreased during the dry season the CV of throughfall increased, indicating a large signal-to-noise ratio, consistent with the findings of Carlyle-Moses et al. (2004) that smaller rainfall events had larger CV values. Therefore, when rainfall volumes are large in these two land use types, measurements of throughfall are more reliable during the wet season than values collected for drier periods.

Whatever the reason for variation in throughfall, the use of land for agricultural purposes has clear impacts in the hydrology of a catchment through increases in throughfall. Despite the increase in throughfall under agriculture, these plots fell on the same line as other plots when comparing the relationship between the size of a precipitation event and throughfall volume (data not shown). Therefore, the overriding driver of throughfall volume was precipitation volume, not land-use type.

Stemflow

Stemflow ranged between 0.9 and 3.2% of gross precipitation (P_g) for PF and SFs (Table 4), slightly higher than many values reported for tropical forests (0.8–1.8%, Levia et al. 2011) but well below the value for a tropical montane rainforest reported by Herwitz (1986) of 13.6% and values of 12–57% for corn (Lilienfein and Wilcke 2001). Stemflow as a percentage of P_g halved in the dry season in the PF, consistent with many previous studies (Levia and Frost 2003) but increased by about 50% in the dry season in the SF (Table 4). Monthly values of stem flow show stemflow declined during the dry season at the PF but increased through most of the dry season at the SF (data not shown). These subtle seasonal differences in stemflow in the PF and SFs may have implications for water and nutrient delivery to roots during the dry season. While stemflow was not measured in agriculture plots, it is likely that stemflow would have been higher in these

plots as it was 18–26% of P_g in banana plots (Cattan et al. 2007).

The volume of stemflow running down each tree was predominantly driven by the volume of gross precipitation (Table 4). In PF, there was also a weak negative relationship between stemflow and crown length and in SF, there was a weak positive relationship between crown dimension and stemflow volume (Levia and Frost 2003). Therefore, there is a difference between the tree characteristics and their influences on stemflow in PF and SFs, which may be governing the differences in seasonality of stemflow in the two forest types described above.

Dry deposition and canopy exchange of nutrients

Fluxes of base cations were high in this study (e.g. Hölscher et al. 2003; Dezzeo and Chacón 2006; Wilcke et al. 2009; Scheer, 2011) and such values have been attributed to marine influences and burned materials (Talkner et al. 2010; Scheer 2011). Local farmers clear and burn their SF at the onset of the rainy season in late April to early May (Suman 1989). Nutrient enrichment factors were also high, emphasising the role of net throughfall in nutrient cycling, especially for K and Mg. Seasonally, nutrients were more concentrated in throughfall samples collected during the dry season (Fig. 4). This is analogous to the finding of Robson et al. (1994) that ionic concentrations were higher in small rain events than larger rain events because leaching and washing of leaves is proportionally larger at the beginning of a storm or because of dilution of solutes in the wet season (Scheer 2011). Despite higher concentrations of ions in throughfall during the dry season, deposition of nutrients is generally larger in the wet season (Table 5) because the volume of water is the overriding factor in deposition rates (Levia and Frost 2006).

Vegetation enhances delivery of K to the soil because TD and SD of this ion was significantly larger than PD (Table 5). However, patterns in nutrient delivery via throughfall and SD associated with land use were difficult to distinguish in this study. Land cover significantly impacted on quantity and spatial variability of deposition of S, Cl and N in clearings, forest and agroforestry in Mexico (Ponette-González et al. 2010a) due to canopy-induced changes in fog and dry-deposition. The presence or absence of vegetation was more important than the type of vegetation.

Furthermore, Ponette-González et al. (2010a) found topography and climate interact with vegetation effects on nutrient deposition. The roles of topographic exposure, elevation and aspect in atmospheric deposition were highlighted by Lovett et al. (1997) and listed by Levia and Frost (2006) as highly influential in throughfall chemistry. Nutrient fluxes are generally higher at lower elevations and higher when a site faces urban sites or oceans (Levia and Frost 2006). The location of sites within the catchment appears to be influencing deposition in the present study. TD and SD are largest at the Alto de Piedra sites and lowest at the Muelas sites. The aspect, elevation and slopes of these sites are highly variable (Table 1) and it is unclear which of these is causing the differences between depositions at various sites but it is clear that site location is interacting with vegetation influences on TD and SD (Lovett et al. 1997; Levia and Frost 2006; Ponette-González et al. 2010a).

Assumptions associated with the tracer ion approach to calculating DD and CE are that the canopy input of tracer ions is negligible and the efficiency of deposition of the tracer ion and the ion being investigated is equivalent (Bredemeier 1988; Staelens et al. 2008). Furthermore, when NTD of the tracer ion (Na in this case) is negative, DD is zero. Calculated nutrient enrichment factors for Na were very close to 1 (Table 6), indicating limited CE for our tracer ion (Hölscher et al. 2003). While this approach does have limitations, the simplicity and low cost of these calculations provide a convenient alternative to micrometeorological techniques and it is most effective for the ions investigated in the present study (Talkner et al. 2010; Scheer 2011).

At Alto de Piedra and Bermejo sites, DD was generally less than 10% (although it did reach 37% for Ca at SF1 in the dry season). In contrast, DD was most often the dominant input of ions at the Muelas sites. Differences between locations highlight the importance of position within the catchment (influencing aspect, slope and elevation) above land-use type in nutrient deposition. Canopy exchange involves leaves, branches and stems acting as sources or sinks of ions passing through the canopy as throughfall and along the stem as stemflow (e.g. Lovett et al. 1996). The sign of CE indicate processes of leaching (positive CE, when the canopy is a source) and uptake (negative CE, when the canopy is a sink) of ions. There were many

examples of ion leaching in the PF and SFs. In the case of Ca, the canopy of the PF and SFs was a source of ions throughout much of the study period (Table 5). Plant processes which contribute to leaching of Ca include loss of ions from senescent leaves during autumn and cation exchange in the leaf tissue (Talkner et al. 2010).

Differences between leaching patterns of the four nutrients are consistent with previously reported patterns in a tropical montane forest in Ecuador (Wilcke et al. 2009), German beech forests (Talkner et al. 2010), and a lowland Atlantic rainforest in Brazil (Scheer 2011), whereby Na undergoes the smallest enrichment while K is the most enriched and Mg and Ca are intermediately enriched as rainfall passes through the canopy. The mobility of K in plant tissues is widely recognised, resulting in significant CE across a variety of forest types (Dezzeo and Chacón 2006; Scheer 2011).

Dezzeo and Chacón (2006) found that mean annual concentrations of nutrients in throughfall and stemflow did not differ between PF and SFs and Hölscher et al. (2003) found only minor differences in the nutrient transfer via stemflow and throughfall for three successional stages of forest. Yet direct comparison of PF and SF at Alto de Piedra (data not shown) demonstrated larger SD in the former and this was confirmed by larger enrichment factors of all nutrients in the PF (Table 6). Ponette-González et al. (2010a) found that Cl fluxes were enhanced in coffee plantations, indicating that land-use type influences biogeochemical cycles. Similarly, comparisons of sites A2a and SF2 show that for a similar LAI, nutrient enrichment of Ca, Mg and K is approximately twice as large in the agricultural site as it is in the SF (Table 6). Site A2b was less enhanced, possibly because of the smaller LAI or the different planted species (yuca versus banana). Ponette-González et al. (2010b) attributed changes in ion cycling to changes in fog and DD caused by an altered canopy, together with interactions with topography and climate creating deposition ‘hotspots’.

Concentrations of nutrients were often more highly concentrated in stemflow than throughfall, particularly for Ca and Na (data not shown), possibly indicating leaching of these nutrients by epiphytes and lichens on the bark. Given the small volume of stemflow, SFD only made up approximately 5% of total SD (data not shown) yet stemflow plays a role in delivering nutrients

to the base of trees which may be particularly important in tropical rainforests where nutrient availability is limited (Herwitz 1986; Dezzeo and Chacón 2006).

Conclusions

In conclusion, rainfall was a source of nutrients and also provided a vital cycling medium by moving ions from the canopy to the soil via throughfall at all of these sites. The huge variability of throughfall may have been masking seasonal and land use differences but it was clear that throughfall in agricultural sites made up a larger proportion of gross precipitation than forest sites. The main driver of variation in throughfall and stemflow was the size of the precipitation event. Consistent patterns in nutrient cycling were also difficult to identify. Throughfall was generally enriched with nutrients, especially K and Mg, while Ca was sometimes recorded at lower concentrations in throughfall than precipitation. Using the ion tracer technique, we found CE processes were proportionally larger than DD, especially during the wet season. However, we emphasise the importance of understanding the underlying assumptions of calculating DD and CE using the ion tracer approach when interpreting this result. Nutrient delivery was more strongly influenced by locality in the catchment than land-use type, indicating the importance of elevation, topography and aspect. Values of nutrient deposition were high, possibly due to the slash-and-burn agricultural practices in the area.

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