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Disproportionate single-species contribution to canopy-soil nutrient flux in an Amazonian rainforest

Disproportionate single-species contribution to canopy-soil nutrient flux in an Amazonian rainforest

Sonja Germer [a,*], Alexander Zimmermann [b], Christopher Neill [c], Alex V. Krusche [d], Helmut Elsenbeer [b]

[a] Helmholtz Centre Potsdam, German Research Centre for Geosciences (GFZ), Section Hydrology, Telegrafenberg, 14473 Potsdam, Germany
[b] Institute of Earth and Environmental Sciences, University of Potsdam, Karl-Liebknecht-Str. 24-25, 14476 Golm, Germany
[c] The Ecosystems Centre, Marine Biological Laboratory, 7 MBL St., Woods Hole, MA 02543, USA
[d] Centro de Energia Nuclear na Agricultura, University of São Paulo, P.O. Box 96, 13.400-970 Piracicaba, SP, Brazil

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ABSTRACT

Rainfall, throughfall and stemflow were monitored on an event basis in an undisturbed open tropical rainforest with a large number of palm trees located in the southwestern Amazon basin of Brazil. Stemflow samples were collected from 24 trees with a diameter at breast height (DBH) > 5 cm, as well as eight young and four full-grown babassu palms (Attalea speciosa Mart.) for 5 weeks during the peak of the wet season. We calculated rainfall, throughfall and stemflow concentrations and fluxes of Na^+, K^+, Ca^{2+}, Mg^{2+}, NH_4^+, Cl^-, SO_4^{2-}, NO_3^- and H^+ and stemflow volume-weighted mean concentrations and fluxes for three size classes of broadleaf trees and three size classes of palms. The concentrations of most solutes were higher in stemflow than in rainfall and increased with increasing tree and palm size. Concentration enrichments from rainfall to stemflow and throughfall were particularly high (81-fold) for NO_3^-. Stemflow fluxes of NO_3^- and H^+ exceeded throughfall fluxes but stemflow fluxes of other solutes were less than throughfall fluxes. Stemflow solute fluxes to the forest soil were dominated by fluxes on babassu palms, which represented only 4% of total stem number and 10% of total basal area. For NO_3^-, stemflow contributed 51% of the total mass of nitrogen delivered to the forest floor (stemflow + throughfall) and represented more than a 2000-fold increase in NO_3^- flux compared what would have been delivered by rainfall alone on the equivalent area. Because these highly localized fluxes of both water and NO_3^- persist in time and space, they have the potential to affect patterns of soil moisture, microbial populations and other features of soil biogeochemistry conducive to the creation of hotspots for nitrogen leaching and denitrification, which could amount to an important fraction of total ecosystem fluxes. Because these hotspots occur over very small areas, they have likely gone undetected in previous studies and need to be considered as an important feature of the biogeochemistry of palm-rich tropical forest.

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1. Introduction

Stemflow in forest ecosystems is often viewed as a minor pathway for water and nutrients frequently neglected in studies of forest water and nutrient balances (Levia and Frost, 2003). Because stemflow concentrates rainfall and canopy leachate into small areas, it may play a more important role in delivering solutes from the canopy to the forest floor than is generally recognized. As rainfall passes through forest canopies it is redistributed spatially and reaches the forest soil as throughfall and stemflow. Stemflow can account for more than 10% of incident rainfall for different vegetation types in tropical, temperate, semi-arid and arid regions (Levia and Frost, 2003).

In tropical forest, palms, such as babassu (Attalea speciosa Mart.) and peach palm (Bactris gasipaes Kunth), and small trees are most effective in funneling rainfall towards their trunks (Germer et al., 2010; Manfroi et al., 2004; Raich, 1983a; Schroth et al., 1999). Because the total basal area of trees occupies a comparatively small fraction of total forest area, stemflow is a point source of water (Manfroi et al., 2004). Therefore, the intensity and volume of stemflow can locally by far exceed that of rainfall or even throughfall (Germer et al., 2010; Herwitz, 1986b).

Stemflow often has higher solute concentrations than rainfall or throughfall (Levia and Frost, 2003; Parker, 1983). The combination of localized concentrated stemflow water and solute transfer creates hotspots of water and nutrient inputs to the forest floor. These hotspots can lead to areas around tree trunks that have soil water contents and soil solution concentrations distinct from the bulk soil (Chang and Matzner, 2000a; Falkengren-Grerup, 1989; Glatzel and Kazda, 1985; Jochheim and Schäfer, 1988; Ladekarl, 1998;

* Corresponding author. Tel.: + 49 331 288 1528; fax: + 49 331 288 1570.
E-mail address: sonja@germerweb.com (S. Germer).

Tanaka et al., 1996; Wolfe et al., 1987), which in turn influence local soil biogeochemical processes (Chang and Matzner, 2000b). Preferential flow near the trunks might also lead to a rapid influx of water and nutrient to the deeper soil zone, thereby influencing groundwater recharge and nutrient loading (Johnson and Lehmann, 2006; Taniguchi et al., 1996).

In this study we evaluated the relative importance of stemflow and throughfall solute concentrations and fluxes to the soil surface of an open rainforest in the southwest Amazon with a high density of understory trees and palms. We compared: (1) solute concentrations and fluxes in rainfall, throughfall and stemflow, and (2) solute concentrations and fluxes in stemflow of different size classes of broadleaf trees and palms.

2. Study area and methods

2.1. Study area

The study site of Rancho Grande is located approximately 50 km south of Ariquemes (10°18′S, 62°52′W, 143 m a.s.l.) in the Brazilian state of Rondônia, in the southwestern Amazon Basin of Brazil. The area is part of a morphostructural unit known as the Southern Amazon Dissected Highlands (Planalto Dissecado Sul da Amazônia, Peixoto de Melo et al., 1978), which is characterized by pronounced topography with an altitudinal range of up to 150 m. Remnant ridges of Precambrian basement rock composed of gneisses and granites of the Xingu (Leal et al., 1978) or Jamarí Complex (Isotta et al., 1978) are separated by flat valley floors of varying width. The dominant soil of the study area is a Kandiudult (US Taxonomy; Acrisol in the WRB Taxonomy; Zimmermann et al., 2006). The climate is tropical wet and dry (Köppen's Aw, Peel et al., 2007). The mean annual temperature between 1984 and 2003 was 27 °C. The mean annual precipitation during the same period was 2300 mm with a marked dry period from July to September (Germer et al., 2006).

The vegetation at this terra firme study site is old-growth open tropical rainforest (Floresta Ombrófila Aberta) with a large number of palm trees. Open tropical rainforest is the predominant vegetation type within the transition zone from dense rainforest to cerrado vegetation (savanna) in the southern Amazon (IBGE, 2004), and makes up 55% of the total vegetated area in Rondônia (Fernandes and Guimarães, 2001). It is characterized by a discontinuous upper canopy of up to 35 m height with emergent trees up to 45 m tall, permitting the sun light to reach the understory and thereby facilitating dense undergrowth. Roberts et al. (1996) determined a leaf area index (LAI) of 4.6 m^2 leaf/m^2 ground for an open tropical rainforest at the Jarú Reserve about 100 km east of Rancho Grande, compared to a LAI of 6.1 for a dense tropical rainforest measured 60 km north of Manaus. Within a 1.37 ha catchment our inventory of trees with DBH (diameter at breast height) >5 cm resulted in a total tree density of 813 trees ha^{-1}, including 108 palms (520 ha^{-1} for DBH > 10 cm, including 81 palms). Among the 94 species with DBH > 5 cm (89 species with DBH > 10 cm) in our study area, the most abundant were Pama verdadeira (Brosimum gaudichaudii Trecul., Moraceae) and Breu rosa (Protium sp., Burseraceae). The most common palm species in this region were Paxiuba bariguda (Iriartea deltoidea Ruiz & Pav.), followed by the babassu palm (A. speciosa Mart., synonym: Orbignya phalerata Mart., local name: babaçu) with a density of 36 full-grown and 115 young individuals (without stem and hence DBH < 5) per hectare.

2.2. Field measurements

We collected rainfall, throughfall and stemflow for nine rainfall events (02/11, 02/17, 02/19, 02/23, 02/27, 03/02, 03/05, 03/14, and 03/17) during the mid rainy season of 2005. There were 31 total rainfall events during this sampling period. All samples were collected either 2 h after every event or the next morning for events that ended after 21:00. To qualify as a rainfall event, at least 0.5 mm of rainfall must have been recorded in 30 min. Events were operationally defined as separated by at least 2 h without rain (Germer et al., 2006).

A tipping bucket rain gauge (Hydrological Services P/L, Liverpool Australia) with a resolution of 0.254 mm and a Campbell logger recorded five-minute rainfall intensity values in a pasture about 400 m from the forest. Incident rainfall and throughfall were collected on an event basis with trough-type collectors for chemical analysis. The collectors, installed on supports 1 m above ground, were made from 150 mm diameter PVC pipes, which were connected by flexible tubes to 20 L plastic canisters. Funnels with a thin-mesh nylon net pre-leached with deionized water (DIW) were installed between collector pipe and tubes and prevented coarse material entering the canisters. The total collecting area per collector was 980 cm^2 (7 ∗ 140 cm). Throughfall was collected with 20 collectors distributed randomly, but under the constraint of avoiding disturbances in the heavily instrumented 1.37 ha catchment (Germer et al., 2009). The collectors were cleaned of organic deposits after each event. The samplers collected wet deposition plus the gravimetrically settling coarse particulate deposition, which is low in Rondônia during the mid rainy season (Germer et al., 2007).

We knew from previous observations that babassu palms are effective at funneling rainfall towards their stems. Therefore we collected stemflow from 24 broadleaf trees and 12 babassu palms in an area of 1.37 ha. For each of three predefined broadleaf tree DBH classes of 5–10 cm (T_{5-10}), 10–20 cm (T_{10-20}), and >20 cm ($T_{>20}$) we randomly selected eight individuals. Because we observed that the fronds of young palms with short subterranean stems appeared to redistribute rainfall through their funnel-shaped petioles, we subdivided babassu palms into three classes and selected four young palms with a petiole diameter (PD) of 3–6 cm (P_{3-6}), four young (sub-canopy) palms with a petiole diameter of >6 cm ($P_{>6}$), and four mature (canopy) palms (P_A) with a DBH of 29.9–32.2 cm.

Collectors made of aluminum with an inner diameter of 4 cm were fitted around trunks at breast height (1.3 m above the forest floor) in a downward spiral. Triangular collectors were fitted around juvenile palm fronds. Acid-washed polyethylene inlays were sealed to the trunks and palm fronds, funnels with thin-mesh nylon nets pre-leached with DIW were attached to the lower end of collectors to prevent coarse material from entering the canisters, and flexible tubes diverted the water to canisters on the ground. Collectors were cleaned of litter, and polythene inlays were checked for leakage daily, which avoided any clogging of the collectors.

2.3. Laboratory analyses

Stemflow, rainfall and throughfall samples of up to one liter were collected in Nalgene polyethylene bottles that were pre-washed with dilute (5%) HCl then thoroughly rinsed with nanopure deionized water. All samples were transported to a field laboratory about 500 m from the catchments and stored on ice in coolers immediately after collection.

In the field laboratory, pH of unfiltered samples was measured with an Orion pH meter (Model 250A+) calibrated twice daily. For cation and anion determination, a 50 ml aliquot was filtered through pre-ashed glass fiber filters (Whatman, GF/F) pre-washed with 20 ml of sample. Samples were stored in acid washed polyethylene bottles, preserved with thymol (10 mg) and frozen. The frozen cation/anion samples were shipped in Styrofoam coolers to the Centro de Energia Nuclear na Agricultura – University of

São Paulo (CENA – USP) in Piracicaba. The samples were maintained frozen until analysis.

Concentrations of cations (Na^+, K^+, Ca^{2+}, Mg^{2+} and NH_4^+) and anions (Cl^-, SO_4^{2-} and NO_3^-) were analyzed using a Dionex ion chromatograph (model DX-500). Separate standard curves were prepared for each batch of 80 samples. In addition a certified reference sample of soft river water (Trois-94, Quebec, Canada, National Water Research Institute of Canada) was included in each sample run. The results were acceptable when the R^2 of the correlation between standards and peak areas was 0.99 or higher. Differences in concentrations determined daily for the certified water sample were maintained within 1% of that specified in the certificate. The detection limits were (in μM): Cl^- = 1.41, SO_4^{2-} = 0.52, NO_3^- = 0.81, Na^+ = 2.17, NH_4^+ = 2.77, K^+ = 1.28, Mg^{2+} = 2.06 and Ca^{2+} = 1.25. Analytical precision of solute concentrations was always less than 10%. Sample blanks of deionized water and deionized water passed through PVC collectors were below detection limits.

2.4. Data analysis

Volume-weighted means per event E were used to express mean solute concentration of individual events for stemflow per tree and palm class c ($VWM_{SF,E,c}$) and for stemflow SF and throughfall TF per entire tree population ($VWM_{SF,E}$ and $VWM_{TF,E}$, respectively).

The $VWM_{SF,E,c}$ and $VWM_{TF,E}$ per event were calculated as

$$VWM_E = \left(\sum_{n=1}^{i} C_{i,E} V_{i,E} \right) \left(\sum_{n=1}^{i} V_{i,E} \right)^{-1} \qquad (1)$$

for all sampled events, where $C_{i,E}$ and $V_{i,E}$ is the respective concentration and volume at collector i for event E.

Mean stemflow solute concentration of individual events and the entire tree population ($VWM_{SF,E}$) was calculated as

$$VWM_{SF,E} = \sum_{n=1}^{c} VWM_{SF,E,c} * SF_{share,c} \qquad (2)$$

where $SF_{share,c}$ is the share of total stemflow of the respective class c taking into account the relative frequency per hectare of trees.

The total stemflow solute fluxes per class $Flux_{SF,c}$ were calculated as

$$Flux_{SF,c} = \sum_{n=1}^{E} VWM_{SF,E,c} * SF_{H_2O,E,c} \qquad (3)$$

where $SF_{H_2O,E,c}$ is stemflow water volume of the respective event and class. $SF_{H_2O,E,c}$ is the product of rainfall water volume per event and the share per class of the 8% total stemflow quantity (Germer et al., 2010). Total throughfall and rainfall solute fluxes were calculated in the same way. The share of total throughfall water volume in relation to incident rainfall (89%) was taken from Germer et al. (2006).

The total stemflow solute fluxes for the entire tree population $Flux_{SF}$ were calculated as

$$Flux_{SF} = \sum_{n=1}^{c} Flux_{SF,c} \qquad (4)$$

where the young palms were excluded because they had no trunk and our sample size was too small to ensure reliable estimates of stemflow water flux generated by individual palm fronds.

Stemflow enrichment ratio per trunk basal area E was calculated according to Levia and Herwitz (2000) as

$$E = \frac{Flux_{SF}}{Flux_R B} \qquad (5)$$

where $Flux_R$ is the flux via rainfall and B is the total basal area of all trees per plot. The equivalent ratio for water fluxes was called the funneling ratio (Herwitz, 1986a).

The stemflow solute concentrations per event and class were tested for normality using the Shapiro–Wilk test (Shapiro and Wilk, 1965). Stemflow was not normally distributed for all classes. Therefore we used the nonparametric Kruskal–Wallis test to compare the stemflow concentrations of the six classes. Where this comparison revealed significant differences ($p < 0.05$), the nonparametric Mann–Whitney U-test was applied for pair-wise comparisons of classes.

For all data analyses we used the language and environment of R (Version 2.10.0).

3. Results

Annual rainfall from August 2004 to July 2005 was 2286 mm, and total rainfall during the sampling period amounted to 450 mm. Events with less than 10 mm of rainfall, which did not generate enough stemflow for collecting purposes, comprised 14% of annual rainfall (320 mm). The nine events sampled for rainfall, throughfall and stemflow had a total incident rainfall of 264 mm or 12% of annual rainfall and 59% of total rainfall during the sampling period. The sampled events covered the annual range of rainfall depth and maximal 10-min rainfall intensities except for the six largest and the four most intense events (Fig. 1). Because samples were taken only during the wet season, antecedent dry periods of all events were relatively short and ranged from 11 to 44 h. Stemflow quantity is, however, influenced significantly only by rainfall depth, but not by intensity or antecedent dry period for most events (Germer et al., 2010). Rainfall totals per event ranged from 10.7 to 57.7 mm. The highest mean rainfall intensity was 25.6 mm h^{-1} and maximum 10-min rainfall intensity was 83.8 mm h^{-1}. Stemflow accounted for 8% of total throughfall + stemflow.

Palms contributed to a disproportionate share of total stemflow. Full-grown palms made up 4% of stem numbers and 10% of basal area but 57% of total stemflow (Table 1). In contrast, large broad-
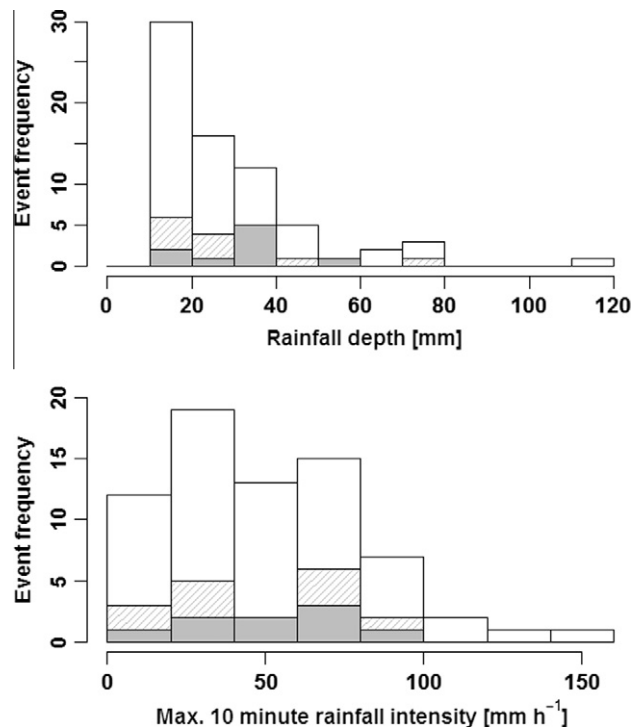

Fig. 1. Frequency of events sampled for stemflow, throughfall and rainfall (gray), sampled for throughfall and rainfall during the late wet season from January to April 2005 only (gray lines), and non-sampled events from August 2004 to July 2005 (white).

leaf trees (>20 cm DBH) made up 23% of stem numbers, 70% of basal area but only 16% of stemflow.

3.1. Solute concentrations

Concentrations of K^+, Mg^{2+}, Cl^-, SO_4^{2-}, and NO_3^- in throughfall and stemflow as well as concentrations of NH_4^+, Ca^{2+}, and H^+ in stemflow exceeded concentrations in rainfall (Table 2). In addition, concentrations of all solutes except Na^+ and NH_4^+ were more enriched in stemflow than in throughfall. The difference of throughfall and stemflow enrichment ratios, however, varied among solutes. For instance, K^+ concentrations increased 11-fold in throughfall but 46-fold in stemflow. Nitrate concentrations in throughfall increased 7-fold but stemflow NO_3^- concentrations increased 81-fold, the largest ratio of all analyzed solutes. We found other considerable concentration increases from rainfall to stemflow for H^+ (30-fold) and Cl^- (12-fold), while from rainfall to throughfall the concentration of Cl^- doubled and remained unchanged for H^+.

Our second comparison revealed that the stemflow concentrations of all solutes except Na^+, NH_4^+, SO_4^{2-}, and H^+ increased with increasing tree and palm size class (Table 3). For trees, this trend was particularly pronounced for K^+ and Ca^{2+}, with stemflow concentrations that differed significantly among all three size classes. For palms, stemflow concentrations of K^+, Ca^{2+}, Cl^-, NO_3^-, and H^+ increased significantly from smaller to larger palm size classes. Mature arborescent palms had particularly high concentrations for Cl^-, NO_3^- and H^+, which exceeded the concentrations of all other tree and palm classes (Table 3).

3.2. Solute fluxes

Fluxes of all solutes except Na^+ increased during the passage through the canopy (Table 4). Potassium and NO_3^- had the greatest flux increases from rainfall to throughfall plus stemflow (13-fold), followed by Mg^{2+} (4-fold), H^+ (3-fold), and Cl^- (double). It varied between solutes whether throughfall or stemflow dominated nutrient fluxes (Table 4). While H^+ flux in stemflow was 3-fold that in throughfall, similar fluxes by stemflow and throughfall were found for NO_3^- (Table 4). For the remaining solutes, we found higher fluxes in throughfall than in stemflow. Enrichment ratios per basal area, however, highlight the localized input of solutes by stemflow that exceeded the respective rainfall flux more than 2000-fold for NO_3^- and 1000-fold for K^+, but only 35-fold for Na^+ (Table 4).

The comparison of total solute fluxes of all nine events between broadleaf tree classes and the mature arborescent palm class revealed that more than 90% of Cl^-, NO_3^-, and H^+ fluxes in stemflow of this open tropical forest were attributed to mature palms (Fig. 2). Stemflow of these palms was also between 46% and 68% of total stemflow fluxes for all solutes. Differences between broadleaf tree classes were much less pronounced. The maximal flux differences between small and large broadleaf trees were for K^+ (6-fold) and Ca^{2+} (5-fold).

Table 2
Mean solute concentrations in rainfall, throughfall and stemflow of the nine analyzed events. Mean concentrations were calculated form solute rainfall concentrations and volume-weighted means of throughfall ($VWM_{TF,E}$) and stemflow ($VWM_{SF,E}$) per event for the entire tree population.

	Solute concentration [μmol L^{-1}]		
	Rainfall	Throughfall	Stemflow
Na^+	7.57[a]	7.35[a]	9.89[a]
NH_4^+	3.74[a]	4.82[ab]	7.53[b]
K^+	5.96[a]	65.07[b]	274.78[c]
Mg^{2+}	2.20[a]	8.72[b]	23.12[c]
Ca^{2+}	17.10[a]	17.74[a]	43.53[b]
Cl^-	12.48[a]	20.85[b]	149.42[c]
SO_4^{2-}	0.63[a]	1.63[b]	3.48[b]
NO_3^-	0.60[a]	4.24[b]	48.97[c]
H^+	0.81[a]	0.66[a]	23.88[b]
	(pH = 6.1)	(pH = 6.2)	(pH = 4.6)

Significantly differing mean concentrations between rainfall, throughfall and stemflow are indicated by different letters (Mann–Whitney U-test, $p < 0.05$).

4. Discussion

4.1. Solute concentration

4.1.1. Throughfall and stemflow enrichments

Enrichment of solute concentrations in throughfall and stemflow compared to rainfall has been widely reported from tropical forests. In general, enrichment ratios depend on the distance of the research site to nutrient sources (e.g., distance to the sea or industrial areas), tree species and size (including differences in tree architecture and phenology), and meteorological parameters (e.g., event size and intensity) (Levia and Frost, 2003). While the geographic stetting influences the concentration of nutrient inputs by rainfall, tree characteristics and meteorological settings influence the potential for nutrient concentration increase of throughfall and stemflow. Both, input and output concentrations are highly influenced by seasonal effects (Germer et al., 2007).

Throughfall enrichment ratios of K^+ greater than 10, as found in this study, are common in tropical forests in Brazil, Cameroon and Venezuela (Chuyong et al., 2004; Dezzeo and Chacon, 2006; Filoso et al., 1999; Forti and Moreira-Nordemann, 1991), secondary tropical forests in Brazil and Nigeria (Hölscher et al., 1998; Muoghalu, 2003), montane evergreen forest in China (Liu et al., 2002), as well as in forests in Japan and Spain (Bellot and Escarre, 1991; Chiwa et al., 2010; Rodrigo et al., 2003). Stemflow enrichment ratios of K^+ exceeding 40 as we found are less common, but were found in a lowland Amazon forest (Dezzeo and Chacon, 2006), a montane evergreen forest in the Chinese Ailao Mountains (Liu et al., 2002), a mixed oak–beech forest in the Belgian Ardennes (André et al., 2008a), and a Douglas–fir plantation in the French Beaujolais Mountains (Marques and Ranger, 1997). The enrichment of K^+ concentration results mainly from plant nutrient leaching, which is particularly high during flowering, leaf emergence, leaf senescence, and if leaves are damaged by insects (Parker, 1983; Staelens et al., 2007; Tukey, 1970).

Table 1
Percentage of broadleaf tree in different DBH size classes of 5–10 cm (T_{5-10}), 10–20 cm (T_{10-20}), and >20 cm ($T_{>20}$) and mature arborescent palm (PA) stems, basal area, basal area as a fraction of total plot area, and stemflow.

DBH	Stem number [%]	Basal area [%]	Basal area as fraction of plot area [%]	Proportion of stemflow [%]
T_{5-10}	36	4	0.01	18
T_{10-20}	37	16	0.05	9
$T_{>20}$	23	70	0.21	16
PA	4	10	0.03	57

Table 3
Mean solute concentration in stemflow per tree and palm class of the nine analyzed events. Mean concentrations were calculated from volume-weighted means of stemflow per tree and palm class ($VWM_{SF,E,c}$) per event.

	Solute concentration [μmol L^{-1}]					
	T$_{5-10}$	T$_{10-20}$	T$_{>20}$	P$_{3-6}$	P$_{>6}$	P$_A$
Na$^+$	13.01[a]	10.70[a]	10.92[a]	10.80[a]	7.64[a]	8.49[a]
NH$_4^+$	6.03[a]	13.19[bc]	11.25[b]	7.47[acd]	16.52[bd]	6.07[ad]
K$^+$	74.68[a]	203.70[b]	514.70[c]	86.40[a]	150.82[b]	281.85[d]
Mg^{2+}	11.59[a]	26.90[b]	28.52[b]	8.05[a]	12.97[a]	24.64[b]
Ca^{2+}	14.68[a]	39.32[b]	87.37[c]	8.22[d]	14.69[a]	40.99[b]
Cl$^-$	17.03[a]	38.73[b]	46.95[bc]	30.54[b]	78.52[c]	237.47[d]
SO$_4^{2-}$	1.33[a]	4.79[b]	2.84[cd]	1.42[a]	3.20[bd]	4.13[b]
NO$_3^-$	3.21[ac]	13.83[b]	10.10[b]	2.01[a]	5.41[cd]	79.88[d]
H$^+$	0.82[a]	1.30[b]	0.62[a]	3.27[bc]	7.85[c]	41.26[d]
	(pH = 6.1)	(pH = 5.9)	(pH = 6.2)	(pH = 5.5)	(pH = 5.1)	(pH = 4.4)

Significantly differing mean concentrations between classes are indicated by different letters (Mann–Whitney U-test, $p < 0.05$).

Table 4
Solute inputs by rainfall, throughfall and stemflow for each millimeter of rainfall and the stemflow enrichment ratio per trunk basal area. The enrichment ratio for water is Herwitz (1986a) funneling ratio.

	Flux per mm of rainfall [g ha^{-1}]			Stemflow enrichment ratio
	Rainfall	Throughfall	Stemflow	
Na$^+$	1.74	1.50	0.18	35
NH$_4^+$	0.67	0.77	0.11	54
K$^+$	2.33	22.65	8.60	1230
Mg^{2+}	0.53	1.89	0.45	281
Ca^{2+}	6.85	6.33	1.40	68
Cl$^-$	4.42	6.58	4.24	319
SO$_4^{2-}$	0.61	1.39	0.27	147
NO$_3^-$	0.37	2.34	2.43	2161
H$^+$	0.81	0.60	1.93	791
Water	–	–	–	27

While stemflow enrichment ratios >40 for K$^+$ were reported from different types of forests, we found little evidence in the literature for similar concentration increases from rainfall to stemflow, as documented above, for NO$_3^-$ (81-fold), H$^+$ (30-fold), and Cl$^-$ (12-fold). An exception was the high NO$_3^-$ enrichment (79-fold) reported by Raich (1983b) for the understory palm *Asterogyne martiana* in an lowland rainforest of Costa Rica. Our high enrich-

ment ratios more likely resulted from comparatively lower concentrations in rainfall than from higher stemflow concentrations compared with other studies. Even though our rainfall K$^+$ concentrations fell within the reported range of comparable studies, our NO$_3^-$, H$^+$, and Cl$^-$ rainfall concentrations were lower (Abas et al., 1992; Chiwa et al., 2010; Chuyong et al., 2004; Laclau et al., 2003; Liu et al., 2003; Muoghalu, 2003; Olsen et al., 1981; Rodrigo et al., 2003; Tobón et al., 2004; Whitford et al., 1997). The dry season NO$_3^-$ rainfall concentrations at our site (Germer et al., 2007), however, were similar to annual values reported by Tobón et al. (2004). Germer et al. (2007) found no seasonal differences in H$^+$ and Cl$^-$ concentrations in rainfall. Likely reasons for low solute concentrations in rainfall include seasonal and regional influences, as for example (for NO$_3^-$), low aerosol concentrations in the wet season compared to the dry season (Germer et al., 2007) as well as the distance to industrial pollution emission sources (Levia et al., 2011a) and (for Cl$^-$), the great distance to the Atlantic and hence low influence by maritime air masses (Germer et al., 2007). Our stemflow concentrations of K$^+$, NO$_3^-$, H$^+$, and Cl$^-$ fell within the range of reported values (Abas et al., 1992; Chiwa et al., 2010; Chuyong et al., 2004; Laclau et al., 2003; Liu et al., 2003; Muoghalu, 2003; Olsen et al., 1981; Rodrigo et al., 2003; Tobón et al., 2004; Whitford et al., 1997).

Even though this study was based on just nine events, the results are broadly representative for the wet season, because no
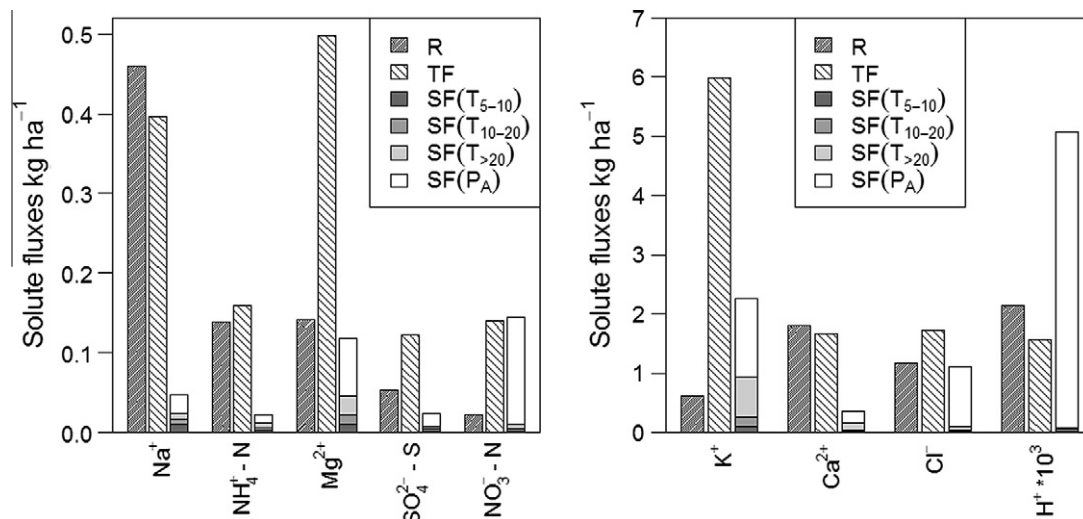

Fig. 2. Total rainfall, throughfall, and stemflow solute fluxes of the nine analyzed events. Stemflow fluxes are plotted separately for the tree classes and mature arborescent babassu palms.

differences were found in rainfall and throughfall solute concentrations between this study and respective wet season solute concentrations found in a previous study of rainfall and throughfall chemistry at this site based on 22 events that included the nine events from this study (Fig. 1) (Germer et al., 2007). We expect, however, enrichment ratios from rainfall to stemflow to be lower during the transition from dry to wet season compared to the wet season as it is the case for throughfall (Germer et al., 2007).

4.1.2. Stemflow solute concentrations of trees and palms

Most solutes had increasing stemflow concentrations with increasing tree and palm size class. This was similar to increasing K^+ stemflow concentrations for larger trees found in a Malaysian rainforest (Turner et al., 2007) and with increasing NO_3^-, Cl^-, Ca^{2+}, and H^+ concentrations, but not with decreasing K^+ stemflow concentration in a Douglas–fir plantation in France (Marques and Ranger, 1997). They attributed higher concentrations in stemflow of large trees to the longer distance water flows over branches and the trunk, which could favor ionic exchange or increased capture of dry deposition. Others have emphasized the role of rough and thick bark of larger trees in increasing the residence time of the water on the trunk surface (André et al., 2008a). It is probably the combination of both effects that was responsible for concentration increases in stemflow from young trees with smooth bark to older ones with rougher bark at our site. This suggests that mature forest might have higher stemflow concentrations and, hence, higher solute concentration enrichment ratios than young forests.

We found that particularly high enrichment ratios from rainfall to stemflow concentrations were caused by the presence of mature babassu palms that displayed disproportionately high Cl^-, NO_3^- and H^+ stemflow concentrations (Table 3). While K^+ is typically rapidly leached from canopy leaves and stems, NO_3^- is more slowly released by coupled litter decomposition and nitrification, or in some cases, even absorbed by tree canopies (Bellot and Escarre, 1991; Cornejo et al., 1994; Lisanework and Michelsen, 1994; Parker, 1983). NO_3^- reduction from rainfall to throughfall and stemflow can result from sequestration by lichens and epiphytes that are established within the canopy (Levia, 2002; Umana and Wanek, 2010). High H^+ concentrations in throughfall or stemflow are often attributed to dry deposition of organic acids (HouBao et al., 1999). Dry deposition is a major influence on throughfall Cl^- concentrations, though this is most important for maritime sites (Bellot and Escarre, 1991; Parker, 1983).

We suspect that the relatively high H^+ and NO_3^- concentrations in stemflow originate from the decomposition of organic material that typically accumulates in the crown of babassu palms. Concentration increases due to a long residence time of water on the palm trunk, in contrast, seem to be less likely because full-grown babassu palms have a smooth bark. Similar observations of organic material accumulation within the canopy have been made by Raich (1983b) for the understory palm *A. martiana*.

In addition, the presence of arbuscular mycorrhiza fungi might increase *N* uptake of the babassu palms and increase litter nitrogen content. Experiments with pairs of plants with and without arbuscular mycorrhiza fungi showed that the fungus increased plant grows and *N* content (Hodge and Fitter, 2010). A study of babassu palm roots revealed root diameters in excess of 2 mm, which indicates abundance of mycorrhiza, and another study found a characteristic arbuscalar mycorrhizal species composition under babassu dominated sites (unpublished data, Christoph Gehring). Dry deposition was not a likely source of NO_3^- in palm stemflow because we sampled in the middle of the wet season when there is little evidence for significant dry deposition (Germer et al., 2007). The decomposition of babassu fruits may have contributed to high H^+ in stemflow. Babassu fruits are very rich in organic acids, especially lauric acid (Janick and Paull, 2008). The source of high Cl^- in palm stemflow is not known. The long distance from the Atlantic and short time between rains makes elevated wet and dry Cl^- deposition unlikely. Because the Cl^- concentration in stemflow of young palms (frond flow) was still twice that of medium and large trees, and because young palms did not have accumulated organic matter, leaching of Cl^- from babassu palm fronds is the most likely source of elevated Cl^- in babassu palm stemflow. Although Cl^- is often assumed to be an inert tracer suitable for dry deposition estimation (Ulrich, 1983), our results indicate that Cl^- is leached from palm fronds and, hence, it can not be used for dry deposition estimation in these forests. If the arboreal accumulation of organic matter and the funneling of water by babassu palms is the primary mechanism that enriches stemflow, we would expect this effect to be greater during the wet season when rainfall solute concentrations are low compared with the dry season or early wet season when rainfall solute fluxes and fluxes originating from dry deposition are higher (Germer et al., 2007).

Slash-and-burn systems that include babassu palms are widespread in northeastern Brazil (Gehring et al., 2011; May et al., 1985). Recent research focuses on agroforestry with permanent vegetation cover including babassu palms as an alternative for slash-and-burn (Moura et al., 2009). From the management perspective such systems might profit from high NO_3^- enrichment ratios but might suffer from acidic and Cl^--rich input by stemflow. While a low soil pH might decrease root uptake of major ions and induce toxicities (e.g., Al, Mn) (Brady and Weil, 1999; Schubert et al., 1990), high soil Cl^- concentrations can reduce water uptake and hence decrease crop yield (Dang et al., 2008).

4.2. Stemflow solute fluxes

4.2.1. Contribution of stemflow solute flux to the total solute flux

Studies that estimate nutrient fluxes in forests do not routinely consider stemflow. Solute fluxes in stemflow, however, can reach or even exceed those in throughfall. Neglecting stemflow solute fluxes in our study would have considerably underestimated total fluxes to the forest floor. This is particularly true for H^+, NO_3^-, Cl^- and K^+, for which stemflow fluxes amounted to 76%, 51%, 39% and 28% of the total solute flux (throughfall + stemflow), respectively (Table 5). These numbers clearly exceeded the stemflow fraction of 8% on the total water flux, which indicates that the stemflow solute fluxes at our site resulted from high solute concentrations in stemflow and not only from large quantities of stemflow water. Similar observations were reported for a beech tree where the H^+ flux in stemflow amounted to 40% of the total flux compared to 11% of water flux by stemflow (Staelens et al., 2007). Other comparable studies also found large contributions of stemflow solute fluxes to the total solute flux. Crockford et al. (1996), for instance, detected particularly high contributions of stemflow fluxes in an Eucalyptus forest (Table 5) where stemflow solute flux of several cations (Na^+, NH_4^+, Ca^{2+}) and nitrate amounted to more than 40% of the overall solute flux (throughfall + stemflow). These large contributions were partly related to Eucalyptus species with smooth-barked branches and trunks with flakey, detaching bark which efficiently channeled water to the trunk where stemflow readily leached the inner bark zone (Crockford et al., 1996).

Our comparison (Table 5) indicates that large contributions of stemflow solute fluxes are probably not an exceptional phenomenon: five of the 13 study sites (Table 5) show stemflow solute fluxes exceeding 10% of the total flux for the majority of the investigated solutes. Moreover, even in forests where the majority of solutes contribute little, the stemflow flux of single solutes can still comprise a considerable share on their overall flux (e.g., K^+ in Neary and Gizyn, 1994). These findings imply that stemflow should

Table 5
Percentage of solute and water fluxes by throughfall (TF) and stemflow (SF) relative to the total flux (TF + SF = 100%) for different forests worldwide.

Site	Period	Vegetation	Flowpath	Fluxes [%]									
				Na^+	NH_4^+	K^+	Mg^{2+}	Ca^{2+}	Cl^-	SO_4^{2-}	NO_3^-	H^+	Water
Brazil[a]	Wet season	Open tropical rainforest	TF	89.3	87.7	72.5	80.8	81.9	60.8	83.6	49.1	23.7	91.8
Brazil[a]	Wet season	Open tropical rainforest	SF	10.7	12.3	27.5	19.2	18.1	39.2	16.4	50.9	76.3	8.2
Cameroon[b]	1 year	Tropical rainforest, low ectomycorrhizal abundance	TF			98.2	97.9	97.5					98.5
Cameroon[b]	1 year	Tropical rainforest, low ectomycorrhizal abundance	SF			1.8	2.1	2.5					1.5
Cameroon[b]	1 year	Tropical rainforest, high ectomycorrhizal abundance	TF			97.3	97.9	97.2					97.6
Cameroon[b]	1 year	Tropical rainforest, high ectomycorrhizal abundance	SF			2.7	2.1	2.8					2.4
Canada[c]	2 years	Deciduous forest	TF	94.9	98.7	84.7	90.6	88.6	93.2	90.5	96.6	97.6	96.3
Canada[c]	2 years	Deciduous forest	SF	5.1	1.3	15.3	9.4	11.4	6.8	9.5	3.4	2.4	3.7
Canada[c]	2 years	Coniferous forest	TF	97.0	99.6	91.9	94.8	92.2	95.0	92.2	99.0	94.9	97.5
Canada[c]	2 years	Coniferous forest	SF	3.0	0.4	8.1	5.2	7.8	5.0	7.8	1.0	5.1	2.5
Nigeria[d]	Wet season	Secondary lowland rainforest	TF	93.2	93.7	91.1	91.8	90.1			93.0		93.8
Nigeria[d]	Wet season	Secondary lowland rainforest	SF	6.8	6.3	8.9	8.2	9.9			7.0		6.2
SE Australia[e]	5 years	Eucalypts	TF	56.1	56.0	78.4	68.6	55.4			53.3		
SE Australia[e]	5 years	Eucalypts	SF	43.9	44.0	21.6	31.4	44.6			46.7		
SE Australia[e]	5 years	Pines	TF	60.1	71.3	74.6	74.5	56.0			69.5		
SE Australia[e]	5 years	Pines	SF	39.9	28.7	25.4	25.5	44.0			30.5		
Spain[f]	3 years	Holm oak forest	TF	88.3		79.9	85.1	84.7	83.8	82.5	89.0	87.8	84.1
Spain[f]	3 years	Holm oak forest	SF	11.7		20.1	14.9	15.3	16.2	17.5	11.0	12.2	15.9
Spain[g]	1 year	Holm oak forest (sheltered from pollution)	TF	97.6	97.8	96.7	97.6	99.7	97.3	97.4	98.3	97.6	96.6
Spain[g]	1 year	Holm oak forest (sheltered from pollution)	SF	2.4	2.2	3.3	2.4	0.3	2.7	2.6	1.7	2.4	3.4
Spain[g]	1 year	Holm oak forest (exposed to pollution)	TF	93.2	94.7	93.9	93.1	92.5	93.1	93.0	93.8	91.4	93.1
Spain[g]	1 year	Holm oak forest (exposed to pollution)	SF	6.8	5.3	6.1	6.9	7.5	6.9	7.0	6.2	8.6	6.9
Chile[h]	17 months	Southern beech forest (Nothofagus betuloides)	TF	98.6	100.0	98.4	97.6	97.3			96.3		98.5
Chile[h]	17 months	Southern beech forest (Nothofagus betuloides)	SF	1.4	0.0	1.6	2.4	2.7			3.7		1.5
Belgium[i]	1 year	Beech tree (Fagus sylvatica)	TF	81.0	85.5	90.7	88.6	89.9	81.0	87.6	90.4	60.0	88.8
Belgium[i]	1 year	Beech tree (Fagus sylvatica)	SF	19.0	14.5	9.3	11.4	10.1	19.0	12.4	9.6	40.0	11.2

[a] This study.
[b] Chuyong et al. (2004).
[c] Neary and Gizyn (1994).
[d] Muoghalu (2003).
[e] Crockford et al. (1996).
[f] Bellot and Escarre (1991).
[g] Rodrigo et al. (2003).
[h] Oyarzun et al. (2004).
[i] Staelens et al. (2007).

be generally considered as an important pathway of solutes to the forest floor unless evidence suggests otherwise.

4.2.2. The importance of large trees and palms

At our site, large broadleaf trees contributed a large share of the K^+ and Ca^{2+} stemflow solute fluxes (Fig. 2). Although small trees contributed as much as big trees to total stemflow water flux per hectare (Table 1), their contribution to the stemflow solute flux was less for all solutes except Na^+ and H^+ (Fig. 2). But because small trees still contribute more to the Na^+ and H^+ flux and half of the NH_4^+, Cl^-, SO_4^{2-}, and NO_3^- flux compared to big trees on a per hectare basis, they should not be ignored in stemflow flux studies. The distribution of stemflow solute fluxes among tree size classes has received scant consideration in the literature. To our knowledge, only André et al. (2008a,b) provided evidence of increasing solute fluxes with increasing size of trees. Our data corroborate these findings.

Although broadleaf trees contributed half of total stemflow solute flux for Na^+, NH_4^+, and Ca^{2+}, full-grown aborescent babassu palms clearly dominated stemflow solute fluxes (Fig. 2). Particularly for H^+, NO_3^-, and Cl^-, high concentrations in the stemflow of mature babassu palms (Table 3) plus a share of 57% of total stemflow water generated by these palms (Table 1) resulted in solute fluxes that can be ascribed almost exclusively to mature babassu palms (>90% of total stemflow flux) (Fig. 2). Schroth et al. (2001) reported similar observations for peach palms. These palms also showed very high stemflow volumes and solute concentrations, which increased fluxes of P, K, Ca and Mg in the vicinity of their stems by a factor of 7–13 compared to the plot-average wet deposition (Schroth et al., 2001).

The findings have implications for sampling strategies of studies concerned with stemflow solute fluxes. First, the sampling should include as many species as possible over a wide range of trunk diameters to increase the probability of detecting species that contribute large stemflow solute fluxes. Second, if previous knowledge exists regarding "high stemflow" species, the sampling strategy should accommodate these species. Third, investigations of stemflow solute fluxes generally should estimate the distribution of stems and record the abundance of key species (such as palms) to allow for accurate, weighted estimates of stemflow solute fluxes.

4.2.3. Stemflow and its relevance for persistent chemical hotspots

On the plot scale, total solute input to the soil surface by stemflow for our nine sampled events exceeded by far that from rainfall on an area of equivalent size (0.3% of the plot area). The combination of water funneling by the canopy and concentration increases from rainfall to stemflow led to enrichment ratios per basal area of, e.g., 1000 for K^+ and up to 2000 for NO_3^-. We are unaware of comparable studies on a plot scale. Data of two other studies, which are based on measurements on a single pignut hickory (Carya glabra Mill.) tree (Levia and Herwitz, 2000), a small group of two American beech (Fagus grandifolia Ehrh.), and three yellow poplar (Liriodendron tulipifera L.) trees (Levia et al., 2011b) indicate that the enrichment ratios at our study site indeed define the higher end of range: Levia and Herwitz (2000) reported mean K^+ enrichment ratios of 580, whereas Levia et al. (2011b) found median enrichment ratios that were much lower for most solutes (K^+:88 and 17, NO_3^-:23 and >1, respectively). The comparability to our data, however, is limited because Levia et al. (2011b) used the median as a measure of central tendency, and because both studies (Levia and Herwitz, 2000; Levia et al., 2011b) worked on an event basis and not with flux totals per sampling period as in this study. Nevertheless, the results of these studies indicate that enrichment ratios of individual events vary widely; for instance, K^+ shows,

depending on meteorological conditions, event-based enrichment ratios as high as 1700 (Levia and Herwitz, 2000).

In view of the particularly large solute fluxes from mature babassu palms and considering that these palms occupy only 0.03% of the study area, the forest floor around babassu stems is likely a microsite with soil properties distinct from the bulk soil. Studies from a wide range of forest types provide evidence that sites that receive considerable amounts of stemflow tend to show a relatively low pH and high element turnover rates (Chang and Matzner, 2000a; Falkengren-Grerup and Björk, 1991). There is evidence from Rondônia forests that combination of higher soil moisture and high NO_3^- availability could create hotspots for denitrification and N_2O emission (Garcia-Montiel et al., 2003, 2001). These stemflow-induced microsites are important features in forest ecosystems not only because of their large ion fluxes (Chang and Matzner, 2000a), but also because of the temporal stability of these fluxes. Throughfall solute deposition patterns, for instance, show a temporal stability at scales of weeks to several months (Raat et al., 2002; Staelens et al., 2006; Zimmermann et al., 2008, 2007). Stemflow-induced microsites, in contrast, persist for decades or even longer depending on the lifespan of the tree (Chang and Matzner, 2000a; Falkengren-Grerup and Björk, 1991). Because babassu palms have an average lifespan of 150–180 years (Pinheiro, 2004) the stemflow-induced microhabitat around these palms exists for more than a century. The persistently high stemflow solute fluxes may become particularly important during times of low nutrient availability. During the end of the rainy season, for instance, the limited amount of leaf litter on the forest floor allows only limited nutrient release (Chuyong et al., 2002), which may result in an even larger contrast between stemflow- induced solute input hotspots and the surrounding environment.

5. Conclusions

High stemflow concentrations can lead to stemflow solute fluxes that equal or exceed those by throughfall. We found that most solutes had higher concentrations in stemflow than in throughfall. Even though throughfall water fluxes per hectare exceeded that of stemflow by a factor of 10, stemflow fluxes of H^+ exceeded and NO_3^- were similar to fluxes in throughfall.

In addition, stemflow concentrations and fluxes depended on tree species and tree trunk diameter. Even though stemflow had higher concentrations and flux for larger trees, smaller trees still contributed a significant share to total stemflow flux per plot and should not be excluded from nutrient cycling studies. A single size category of one species, mature babassu palms, occupied only 0.03% of total plot area but contributed 57% of stemflow water fluxes and nearly all stemflow flux of Cl^-, NO_3^-, and H^+. Studies of solute fluxes in forest ecosystems should ideally identify beforehand whether species with high stemflow water funneling or with great influence on stemflow chemistry exist in the respective forest and include stemflow sampling of these species. In particular, babassu palms are very abundant in Amazonian open tropical forests and pastures and they are the dominant species in secondary forests in some regions in the Amazon such as Maranhão (Pinheiro, 2004). The high stemflow nutrient fluxes associated with babassu palms as well as the spatial focusing of canopy water fluxes by babassu may make this palm species an important and under-recognized regulator of biogeochemical function over wide areas of tropical forest.

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