Inorganic nitrogen and phosphorus in stemflow of the palm Astrocaryum mexicanum Liebm. located in Los Tuxtlas, Mexico

JAVIER ÁLVAREZ-SÁNCHE \mathbf{Z}^{1*} , GUADALUPE BARAJAS-GUZMÁN 1 , JULIO CAMPO 2 & RICARDO LEÓN 1,3

¹Facultad de Ciencias, Universidad Nacional Autónoma de México, Circuito Exterior Ciudad Universitaria 04510 Mexico, D.F., Mexico

²Instituto de Ecología, Universidad Nacional Autónoma de México, AP 70-275, Mexico D.F., Mexico

³Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Carretera Pachuca-Tulancingo s/n km. 4.5, Mineral de La Reforma, 42001 Pachuca, Hidalgo, Mexico

Abstract: Stemflow was studied for *Astrocaryum mexicanum*, a palm that acts like a natural litter trap in the tropical rainforest at Los Tuxtlas in eastern Mexico. We quantified the concentration of inorganic N (NH₄⁺ and NO₃⁻) and P (PO₄) in the rainfall, stemflow, and throughfall in this tropical rainforest during the driest (March) and the wettest (September) months of the year, over two years. Ammonium concentrations were higher than NO₃⁻ in rainfall, while concentrations of NO₃⁻ and PO₄ in stemflow were higher than those of NH₄⁺. A significant year-pathway interaction was detected for NH₄⁺ and PO₄ concentrations, and the interaction of nutrient pathway, month and year was significant for NO₃⁻ and PO₄. The concentration of all nutrients in rainfall, stemflow and throughfall was generally greater in the wet than in the dry season. The fit of the pairwise model was significant for rainfall-stemflow and rainfall-throughfall for all nutrient-pathway combinations. This allows us to suggest that stemflow from palm cover is an important path of N and P inputs to the soil in this rainforest.

Resumen: Se estudió el flujo caulinar en *Astrocaryum mexicanum*, una palma que funciona como trampa natural de hojarasca en el bosque tropical lluvioso en Los Tuxtlas, oriente de México. Cuantificamos la concentración de N (NH₄+and NO₃·) y de P (PO₄) inorgánicos en la precipitación, el flujo caulinar y la precipitación a través del follaje en este bosque tropical durante el mes más seco (marzo) y el más húmedo (septiembre) del año, en dos años. Las concentraciones de amonio fueron mayores que el NO₃· en la lluvia, mientras que las concentraciones de NO₃· y PO₄ en el flujo caulinar fueron mayores que las de NH₄+. Se detectó una interacción significativa año-ruta para las concentraciones de NH₄+ y PO₄, y la interacción de la ruta de nutrientes, mes y año fue significativa para el NO₃· y el PO₄. La concentración de todos los nutrientes en la lluvia, el flujo caulinar y la precipitación a través del follaje fue por lo general mayor en la época lluviosa que en la seca. El ajuste del modelo pareado fue significativo para lluvia-flujo caulinar y lluvia-precipitación a través del follaje para todas las combinaciones de nutrientes-ruta. Esto nos permite sugerir que el flujo caulinar proveniente de la cobertura de las palmas es una ruta importante de entradas de N y P hacia el suelo en este bosque lluvioso.

Resumo: O escoamento pelo tronco foi estudado para a *Astrocaryum mexicanum*, uma palmeira que age como uma armadilha natural de folhada na floresta tropical em Los Tuxtlas, no leste do México. Foram quantificadas a concentração de N inorgânico (NH₄⁺ e NO₃⁻) e P (PO₄) na precipitação, escorrimento pelo tronco, e através do copado nesta floresta tropical durante o mês

^{*}Corresponding Author; e-mail: javier.alvarez@ciencias.unam.mx

mais seco (março) e o mais húmido (setembro) do ano, durante mais de dois anos. As concentrações de amónio foram superiores ao NO₃· na precipitação, enquanto que as concentrações de NO₃· e PO₄ em escoamento pelo tronco foram maiores do que as de NH₄+. Uma interação anual significativa foi detectado para as concentrações de NH₄+ e PO₄, e a interação das vias de nutrientes, mensais e anuais foi significativa para NO₃· e PO₄. A concentração de todos os nutrientes na precipitação, escorrimento pelos troncos e a não intersetada pelo copado foi em geral maior na estação chuvosa do que na estação seca. O ajuste do modelo de pares foi significativo para precipitação-escorrimento pelo tronco e precipitação-não interceptada pelo copado para todas as combinações de vias de nutrientes. Isto permite-nos sugerir que escorrimento pelo tronco da cobertura de palmeira é uma importante via de suprimento de N e P ao solo nesta floresta de chuvas.

Key words: Nitrogen, palm, phosphorus, throughfall, tropical rainforest.

Handling Editor: Cristina Martinez-Garza

Introduction

In tropical rainforest (TRF) the coexistence of many growth forms like vines, palms, and trees in both the understory and the canopy affects the nutrient flux by throughfall and stemflow to the forest floor (André et al. 2008; Staelens et al. 2008). A significant proportion of incident rainfall may reach the soil as throughfall and stemflow in tropical forest biomes (Campo et al. 2001; Levia & Frost 2003). For example, throughfall in TRF has been estimated at 77 % to 91 % of the total rainfall (Chuyong et al. 2004; Dietz et al. 2006; Holwerda et al. 2006; Manfroi et al. 2004; McJannet et al. 2007), whereas 2 % to 10 % of the total rainfall arrives at the soil as stemflow (Dezzeo & Chacón 2006; Park & Cameron 2008). The amount of stemflow is influenced by biological factors such as stem density, crown structure, and species composition (Hölscher et al. 2005; Staelens et al. 2008), as well as by meteorological factors such as rainfall volume and intensity, wind speed, and evaporation rate (Levia & Frost 2003). Understory trees in TRF can also play an important role in the stemflow pathway, accounting for 77 % to 90 % of the total volume of forest stemflow (Manfroi et al. 2004).

Because of their architecture, understory palms act as a natural trap for decaying leaves. Senescent leaf interception has been observed in several TRFs for several species of Arecaceae family: Barro Colorado Island, Panama (Foster & Brokaw 1985), Malaysia (Rickson & Rickson 1986), Costa Rica (Raich 1983), the Brazilian Amazon (Campbell et al. 1986), the equatorial Amazon (Balslev et al. 1987) and Los Tuxtlas, Veracruz, Mexico (Álvarez-Sánchez & Guevara 1993). Litterfall intercepted by the leaves of Astrocaryum mexicanum Liebm.

(Arecaceae) in Los Tuxtlas was 4.4 to 27.1 Mg ha⁻¹ year⁻¹ (Álvarez-Sánchez & Guevara 1999). The decomposing leaves caught on the palms release nutrients that are transported by stemflow and concentrate soil nutrient inputs into a smaller area than throughfall (Martínez-Meza & Whitford 1996); this has been shown to persist for decades (Johnson & Lehmann 2006). Architecture of understory palms could define the patterns of stemflow for nitrogen (N) and phosphorus (P) flux in water in this ecosystem.

Although litterfall is the main pathway for internal nutrient cycling in tropical forests (Campo et al. 2000, 2001), stemflow may transport large quantities of nutrients to the ground near the base of trees (Levia & Herwitz 2000). For example, in an oak forest nutrient addition via stemflow was the main reason for higher pH and calcium content (Andersson 1991). In fact, the composition of stemflow water from the woody surfaces of canopy trees has a higher nutrient concentration than that of throughfall water from foliar surfaces (Levia & Herwitz 2000). In the rainforest of Los Tuxtlas, the presence of A. mexicanum palms in the understory appears to dominate stemflow volume and nutrient flux in the system as a result of the architecture of this species and the capture of decaying leaves in its canopy. Our hypothesis is that stemflow will have greater nutrient concentrations than throughfall. The mass of decaying leaves intercepted by A. mexicanum in the dry season (0.5 g m⁻² day⁻¹), when overall litterfall was at its maximum, was the double of that intercepted in the wet season (0.25 g m⁻² day⁻¹) (Álvarez-Sánchez & Guevara 1999). Even when this forest is considered a tropical moist forest, there is seasonality in the rain (see Methods section). Therefore, we propose that the nutrient concen-

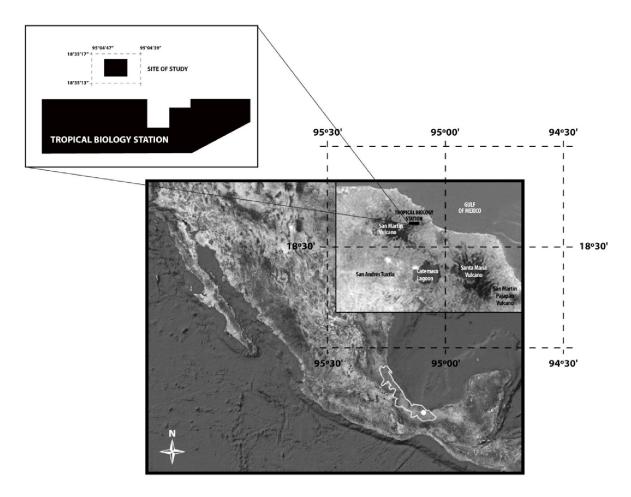


Fig. 1. Location of the Los Tuxtlas Tropical Biology Station, Veracruz, Mexico, and the study site.

tration would increase during the wet season at Los Tuxtlas.

Despite the potential effects of stemflow on the hydrology and intrasystem cycling of nutrients in these forests, nutrient flux by understory vegetation stemflow compared to throughfall particularly that of Astrocaryum palms, has not yet been well documented in tropical rainforest. Thus, the objective of the present study was to assess the N and P concentrations in the stemflow of A. mexicanum in a primary TRF in the state of Veracruz, Mexico. To this end, stemflow was sampled during the wet and dry seasons over two years. For comparison, we simultaneously measured inorganic N and P concentrations in throughfall under the cover of the palms in the same sites and in rainfall in nearby gaps. In an ecosystem with a complex structure like Los Tuxtlas rainforest, one would expect a higher stemflow by the influence of canopy architecture and there should be a relationship throughfallstemflow, considering the relationship between throughfall and stemflow volumes and chemistry with rainfall amounts (Waring & Running 2007).

Materials and methods

Study site

The study was carried out in the Los Tuxtlas Tropical Biology Station (LTBS), an experimental station located just north of the town Catemaco, in eastern Veracruz, Mexico (94° 42' to 95° 27' W and 18° 10' to 18° 45' N), in a highly diverse primary forest (Fig. 1). The study site is < 5 km from the Gulf of Mexico, and has a mean annual temperature of ~25 °C that varies by 6 °C annually. The short but marked dry season typically occurs between March and May of each year, when monthly precipitation averages < 100 mm (García 2004). The mean annual precipitation during the study period (September 1997 to March 1999) was 5058 ± 611 mm, with a clear peak in September (Soto & Gama 1997).

Table 1. Soil characteristics (mean \pm SE) in the Los Tuxtlas Tropical Biological Station, Mexico (data from Tobón *et al.* 2011).

Forest floor	
Litter dry mass (Mg ha ⁻¹)	1.53 ± 0.15
N (kg N ha ⁻¹)	2.68 ± 0.26
P (kg P ha ⁻¹)	0.56 ± 0.06
N:P ratio	4.8 ± 0.03
Mineral soil (0-5 cm in depth)	
Bulk density (Mg m ⁻³)	0.49 ± 0.08
Texture (Clays: Silt: Sand %)	15:22:63
pH (H ₂ O)	5.9 ± 0.1
Organic C (Mg C ha ⁻¹)	56.6 ± 6.2
Total N (Mg N ha ⁻¹)	3.17 ± 0.33
C:N ratio	18 ± 3
NO ₃ - (kg N ha ⁻¹)	4.45 ± 0.29
NH ₄ ⁺ (kg N ha ⁻¹)	6.25 ± 1.12
NO ₃ -: NH ₄ + ratio	0.7 ± 0.2
Total P (kg P ha ⁻¹)	148 ± 34
Extractable P (kg P ha ⁻¹)	4.00 ± 0.53

The study area lies on the mountain massif of Los Tuxtlas (200 to 500 m a.s.l.), created by volcanic eruptions and which is 80 km long. The volcanism occurred during the Oligocene, and eruptions were of the effusive-fissural type; the pyroclastic material, ash and lava define the geomorphology of the area (Lugo & Córdoba 1992). Soils in the area are 60 % sand-dominated Entisols, from typical ustorthents to lithic ustorthents, and are rich in organic material (Table 1; Tobón *et al.* 2011).

The vegetation in the area is typical of TRF (Miranda & Hernández 1963). Mean canopy height is 30 - 35 m and tree (DBH ≥1.0 cm) density is 2976 stems per ha (Bongers et al. 1988). At the LTBS there are 940 species belonging to 129 Angiosperm families in an area of 640 ha (Ibarra-Manríquez et al. 1997). In the canopy the most important species are Nectandra ambigens Blake C. K. Allen, Pseudolmedia oxyphyllaria Donn.Sm., Ficus yoponensis Desv., and Guarea glabra Vahl. (Bongers et al. 1988). Palms comprised 2.7 % of all species and 48.1 % of all stems with DBH \geq 1 cm (Bongers et al. 1988). The most abundant species in the understory is A. mexicanum, which usually grows to a maximum height of 7 m and accounts for 85 % of the total understory stems (6840 m² ha⁻¹) (Popma et al. 1988).

Study species

Astrocaryum mexicanum is a monopodial plant that grows according to an aerial version of Corner's pleonantic model (Martínez-Ramos 1997), with a height between 1 and 8 m (Popma et al. 1988). Individuals of this species are very resistant to physical damage by tree and branch fall. They have flexible stems and the capacity to form adventitious roots that permit continued growth after being crushed by tree fall, beginning in the top meristem (Martínez-Ramos 1997).

Collection of rainfall, throughfall and stemflow samples

In the same forest area sampled by Bongers et al. (1988) in the LTBS, 8 individuals of A. mexicanum were selected at random at the beginning of December 1996. The crown cover of the palms was calculated using the formula for the area of an ellipse: $C = D_1 \times D_2 \times \pi/4$ (Park & Cameron 2008) and the number of individuals from Bongers et al. (1988) was used to estimate the total basal area. The mean height of the A. mexicanum palms in our plots at the study site was 3.83 ± 0.50 m (mean \pm SE), mean crown cover was 9.41 ± 1.27 m² and the total cover provided by its stems was 301.16 m², with a total basal area of 2.21 m² ha-1.

Rainfall, throughfall and stemflow samples were collected for nutrient analysis in September (the wettest month) 1997, March (the driest month) 1998, September 1998 and March 1999; the most representative months of the wet and dry seasons at the LTBS (Fig. 2). Stemflow was collected from the selected palms (\geq 3 cm DBH), throughfall was collected 1 m away from palm cover, and rainfall was collected in two treefall gaps, each > 200 m² nearest to sites where palms were located; these are considered large gaps (Martínez-Ramos 1997) (*i.e.*, 8 replicates per pathway).

Rainfall, throughfall and stemflow were collected with 18-cm diameter funnels connected to polyethylene dark bottles (4 L capacity). All collection bottles, tubes and funnels were washed three times with $1.0\ N$ HCl and rinsed three times in distilled water prior to installation. For stemflow collection, the palms were fitted with clear vinyl tubing (internal diameter 20 mm) cut lengthwise, fastened around the entire stem with nails and then sealed to the bark with silicone; this tube was connected to polyethylene bottles and

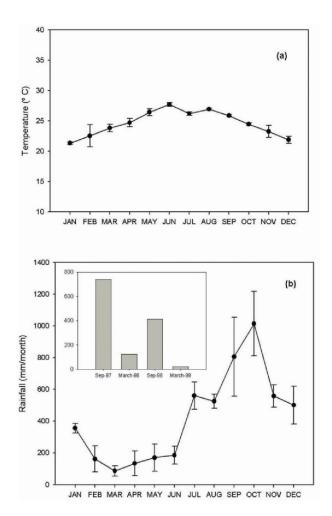


Fig. 2. Monthly rainfall during the study period (1997 - 1999) (a) and long term monthly rainfall (\pm SE) (b) at the Los Tuxtlas Tropical Biology Station (94°42' to 95°27' W and 18°10' to 18°45' N; 150 m a.s.l.). In the left histogram total rainfall is given for the specific survey dates.

sealed with silicone (McJannet *et al.* 2007). A polyethylene net (2.5 mm mesh opening) was placed in the funnels to prevent contamination by decaying leaves and insects (Dezzeo & Chacón 2006). The amount of water in the bottles was measured every week.

The samples were filtered and preserved with 2 mL of H₂SO₄ (pH < 2.0). Subsamples for chemical analysis were stored in clean 125 mL polyethylene bottles (American Public Health Association *et al.* 2012). The samples were then transported in cold containers (one day after sampling) to the *Instituto Mexicano de Tecnología del Agua* (Mexican Institute of Water Technology), according to the procedures set out in the standard norm (NOM) NMX-AA-029-SCFI-2001 in Mexico for P and N

water analysis (Ministry of the Economy 2001, 2010), and stored (48 h prior to analyses for NO_{3} and NH_{4} and 72 h for PO_{4}) at 4 °C for further nutrient analysis.

Nutrient analysis

NO₃ was determined using the Brucine Method by colorimetry spectrophotometry (Ministry of the Economy 2010); NH₄⁺ was measured by using photometry according to the Standard Method for the Examination of Water and Wastewater (Franson 1995); and PO₄ was determined by a colorimetric method following digestion with ammonium persulfate (Franson 1995).

Data analysis

Differences between year, season and water pathway (rainfall, stemflow and throughfall) for each nutrient concentration were evaluated with three-way Analysis of Variance (ANOVA) (Zar 1984). When analyses indicated significant differences, the Tukey Honest Difference Test was applied *a posteriori*. All statistical analyses were performed at the 95 % confidence level.

In order to explore the relationship in concentrations of NH_4 ⁺, NO_3 ⁻ and PO_4 among the three water pathways, adjustments were made to the best pairwise model for each nutrient pathway using the Table Curve program (2D Windows v 3.0). Means and standard error are showed in results.

Results

The concentration of NO3- and PO4 increased as rainfall moved through the canopy as stemflow (Tables 2 & 3). NO₃ and PO₄ concentrations in throughfall had intermediate values relative to stemflow and rainfall, and were not statistically different that rainfall (P > 0.05). In contrast, NH₄+ concentration decreased significantly because rainfall had higher values than stemflow and (Table 3). Overall 2-y average throughfall concentrations were 1.46 ± 0.71 for NH₄+, $0.32 \pm$ 0.12 for NO₃, and 0.48 ± 0.30 mg L-1 for PO₄ in rainfall; 1.02 ± 0.50 for NH_4^+ , 0.77 ± 0.30 for NO_3^- , and 0.62 ± 0.28 mg L-1 for PO₄ in stemflow, and 0.90 ± 0.30 for NH₄+, 0.40 ± 0.12 for NO₃, and 0.55 ± 0.24 mg L-1 for PO₄ in throughfall. The concentration of nutrients in different pathways was generally greater in the wet than in the dry season.

 PO_4

Pathway								
	Rainfall		Stemflow		Throughfall			
	Dwy accom	Wet season	Dry	Wet season	Dry	Wet season		
	Dry season	wet season	season		season			
Year 1								
$\mathrm{NH_{4}^{+}}$	0.67 ± 0.01	3.24 ± 0.20	0.30 ± 0.01	0.92 ± 0.06	0.34 ± 0.02	1.22 ± 0.21		
NO_{3}	0.19 ± 0.01	0.58 ± 0.03	0.42 ± 0.05	1.16 ± 0.09	0.29 ± 0.01	0.70 ± 0.10		
PO_4	0.16 ± 0.01	1.20 ± 0.08	0.26 ± 0.05	0.79 ± 0.16	0.27 ± 0.06	0.85 ± 0.07		
Year 2								
$\mathrm{NH_{4}^{+}}$	0.58 ± 0.02	1.36 ± 0.09	2.25 ± 0.23	0.61 ± 0.03	1.44 ± 0.17	0.59 ± 0.05		
NO_3	0.13 ± 0.01	0.37 ± 0.01	1.29 ± 0.23	0.23 ± 0.02	0.32 ± 0.05	0.30 ± 0.06		

Table 2. Mean nutrient concentration (mg L^{-1}) (\pm SE) in rainfall, stemflow and throughfall in the Los Tuxtlas tropical rainforest.

Table 3. Results of the ANOVA for NH₄⁺, NO₃⁻, and PO₄ concentrations in the rainfall, stemflow and throughfall pathways in the Los Tuxtlas tropical rainforest.

 1.22 ± 0.05

 0.20 ± 0.02

Factor	NH ₄ +		NO ₃ -		PO_4	
	F	P	F	P	F	P
Year	0.12	N.S.	5.54	0.021	3.96	N.S.
Season	30.9	< 0.001	6.67	0.011	7.19	0.02
Pathway	23.6	< 0.001	35.3	< 0.001	4.16	0.01
Year-season	186	< 0.001	71.3	< 0.001	252	< 0.001
Year-pathway	56.2	< 0.001	0.74	N.S.	20.1	< 0.001
Season-pathway	87.3	< 0.001	9.29	< 0.001	57.7	< 0.001
Year-season-pathway	1.42	N.S.	27.5	< 0.001	11.3	< 0.001

First degree interactions were significant (except year-pathway for NO₃); for the year-pathway interaction, NH₄+ concentration was higher for the second year, whereas for PO₄, only stemflow concentrations were different between years according to Tukey's test (P < 0.05) (Table 3). The second degree interaction was significant for NO₃- and PO₄: Year 2-dry-stemflow had the higher values, and year 2-dry-rainfall the lowest: Many interactions including throughfall had lower values than the ones including other pathways (Table 3).

 0.12 ± 0.01

 0.44 ± 0.04

The fit of the pairwise model was significant for rainfall-stemflow and rainfall-throughfall for all nutrient-pathway combinations (Figs. 3 & 4). As the concentrations of NO₃, NH₄⁺ and PO₄ increase in rainfall, they held constant in the stemflow but not at lower concentrations (Fig. 3); for the rainfall-throughfall pairwise model we observed this pattern only for PO₄ (Fig. 4).

Discussion

Changes in the rainfall nutrient concentration as the canopy partitions rainfall into throughfall and stemflow have been studied for TRF (Chuyong et al. 2004; Goller et al. 2006; Tobón et al. 2004). These changes have been associated with the exchange of nutrients by the forest canopy through leaching and absorption, and with dry deposition being washed off the leaves (Potter et al. 1991). This process is accentuated by the abundance of palms in the forest understory that account for about 66 % of the stemflow (Holwerda et al. 2006). This seems to occur in the rainforest of los Tuxtlas where the total cover of A. mexicanum is high (7 %; Popma et al. 1988). In our study, NO₃: and PO₄ concentrations were higher in stemflow than in rainfall.

 0.96 ± 0.06

 0.13 ± 0.02

The pairwise model results suggest that as the concentrations of NH_4 ⁺, NO_3 ⁻ and PO_4 in rainfall increase, their concentration in the stemflow was low (Fig. 3). This pattern is supported by the season-pathway interaction that was significant for all nutrients. However, we did find significant differences for NH_4 ⁺ throughfall enrichment in the wet season, and for the wet season-rainfall interaction which was highest for this nutrient. NH_4 ⁺ is a highly soluble ion; and when NH_4 ⁺ concentration increases in rainfall, in the other two pathways its concentrations are consistently lower

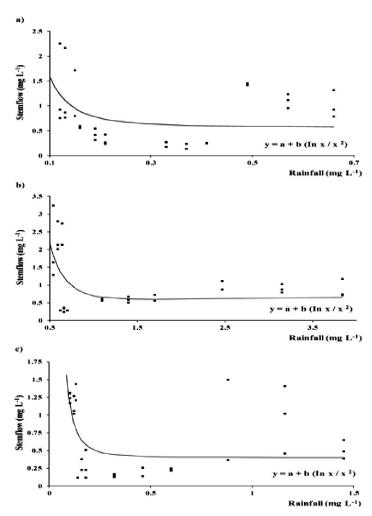


Fig. 3. Rainfall-stemflow model adjustments for NO₃· ($r^2 = 0.15$, F = 5.37) (top), for NH₄ ($r^2 = 0.28$, F = 11.8), and for PO₄ ($r^2 = 0.28$, F = 11.4) (bottom) (P < 0.05 for all cases). Rainfall is in mg L⁻¹.

regardless of season (Tables 2 & 3). This suggests that there might be a threshold of N mineralization in the understory because we observed significantly higher NO₃ concentrations in palm stemflow. These results are consistent with our statement that stemflow is the most important pathway for N. These N dynamics in the forest understory seem to be related to the decomposing leaves that get caught on the palms (Alvarez-Sánchez & Guevara 1999). According to Piirainen et al. (1998), this could indicate that NO₃ ion exchange processes occurring in the canopy and stemflow input may transfer nutrients from the canopy to the forest floor (Dezzeo & Chacón 2006; Tobón et al. 2004). In addition to dry fall, an increase in NO₃ in stemflow may be due to the biological activity of the microbiota of the leaves and bark in the canopy (Whitford et al. 1997). In our study, NO₃ concentration was significantly higher in stemflow than in throughfall or rainfall. Stemflow of NO₃ has been reported higher for

species with greater stemflow partitioning (regardless of climate type), because plant canopy morphology appears to be strongly related to the stemflow flux of mobile nutrients in the ecosystem (Johnson & Lehmann 2006). This claim is consistent with the shape of the palm's crown and NO₃ flux in the Los Tuxtlas rainforest. Preliminary data shows that mean water flux in stemflow in the Los Tuxtlas rain forest is 0.78 (L m⁻² day⁻¹), four times greater than that of rainfall (Álvarez-Sánchez et al. unpublished data). Our first hypothesis stated that the nutrients concentration should be highest in stemflow, which is supported for the nitrate and phosphate, not for ammonium which was highest in the rainfall. Our results support that stemflow had the highest values of nutrients (see Table 3).

According to our second hypothesis, the pairwise models show that as N increases in rainfall, there was an increase in throughfall too (Fig. 4). Staelens *et al.* (2008) report a throughfall enrichment of NO₃-

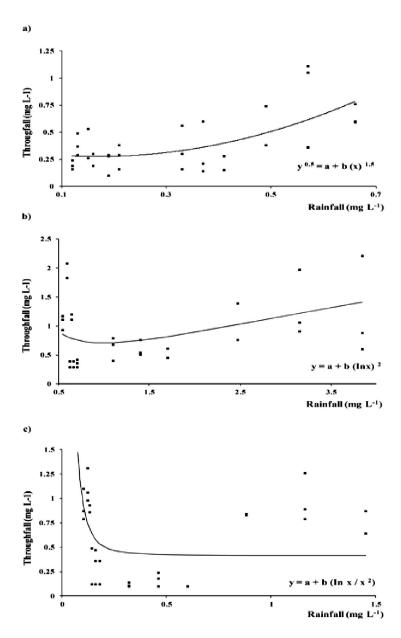


Fig. 4. Rainfall-throughfall model adjustments for NO₃ ($r^2 = 0.34$, F = 15.5) (top), for NH₄+ ($r^2 = 0.14$, F = 5.02), and for PO₄ ($r^2 = 0.18$, F = 6.80) (bottom) (p < 0.05 for all cases). Rainfall is in mg L⁻¹.

that is significantly higher in the wet season than in the leafless dry season. Contrary to our hypothesis, concentrations were not higher in the dry season. In this case, the effect of climatic season is not clear, although in our study period, the amount of rain was clearly higher in the rainy season than in the dry season (see Table 3). We do not think that palm cover alters the concentration on the pathway, suggesting that NO₃ leaching and mineralization are occurring in the canopy. Litter accumulation occurs on *A. mexicanum*, so mineralization could be occurring because NO₃ was

greater than NH₄⁺ al least in year 1 for both seasons; however, this was not observed for year 2. The increase in the NO₃- concentration in stemflow and its stabilization in the throughfall suggests that NH₄⁺ was mineralized. This confirms that stemflow is a very important pathway of NO₃- inputs for the forest soil. Parker (1983) showed that NO₃- and NH₄⁺ move similarly in throughfall, and can either be lixiviated or retained by the forest canopy, depending on the concentration gradient between the canopy and rainfall. Tobón *et al.* (2004) suggested that during rainfall events

 NH_{4}^{+} is taken up by the foliage and nitrified at the leaf surfaces.

It is very interesting to note that PO₄ concentrations were higher in rainfall than in stemflow and throughfall (wet season, first year). The regressions were significant, showing that PO₄ concentration increase in rainfall but did not change in stemflow or throughfall amounts. Given the complexity of the P-cycle, we believe in the Los Tuxtlas region the cut-slash and burn system is still being used for agricultural purposes, which is causing P release into the atmosphere (Giardina *et al.* 2000).

The range of our data is higher compared to other studies from tropical forests. In the case of NH₄+, in Ecuador Goller *et al.* (2006) reported 0.11 (mg L-1) in rainfall (RF), 0.21 - 0.32 for throughfall (TF) and 0.26 - 0.33 for stemflow (SF), while in Costa Rica and Colombia, Clark et al. (1998) and Veneklaas (1990) determined 0.86 and 0.05 RF, 0.07 and 1.16 TF, respectively. For NO₃-, Goller et al. (2006) reported 0.10 (mg L-1) in RF, 0.22 to 0.61 TF (only these values are higher than the one of our study) and 0.21 to 0.63 in SF, while in Costa Rica and Puerto Rico, Clark et al. (1998) and Asbury $et\ al.\ (1994)$ reported 0.05 and 0.11 RF, and 0.20 TF, respectively. For PO₄ was found < 0.005 RF, from 0.004 to 0.73 TF (Asbury et al. 1994, Clark et al. 1998, Goller et al. 2006), and 0.15 to 0.97 SF (Goller et al. 2006). From an ecosystem perspective, the effect of the stemflow in the Los Tuxtlas rainforest would be greater as our selected individuals represent only 5 % of the total cover of this palm in the forest (6840 m², Bongers et al. 1988); besides, our results belonging only to one species; the other studies report for all forest cover. This allows us to suggest that stemflow from palm cover is an important path of N and P inputs to the soil. However, the mechanisms underlying this palm effect could be more complex than a simple increase in N and P return to soil.

Acknowledgments

Lucio Sinaca, Ramiro Gómez, Oswaldo Núñez and Juan Carlos Cruz assisted with data collection; Irene Sánchez-Gallen helped collect and analyze the data. This research was supported by a grant from CONACYT (1038 PN 9507). We are grateful for the critical and insightful comments of the editor and two anonymous reviewers, which helped us to improve the manuscript considerably for publication.

References

- Álvarez-Sánchez, J. & S. Guevara. 1993. Litter fall dynamics in a Mexican lowland tropical rain forest. *Tropical Ecology* **34**: 127-142.
- Álvarez-Sánchez, J. & S. Guevara. 1999. Litter interception on *Astrocaryum mexicanum* Liebm. (Palmae) in a tropical rain forest. *Biotropica* 31: 89-92.
- American Public Health Association (APHA), American Water Works Association (AWWA) & the Water Environment Federation (WEF). 2012. Standard Methods for the Examination of Water and Wastewater. E. W. Rice, R. B. Baird, A. D. Eaton & L. S. Clesceri (eds.) Port City Press, Baltimore.
- Andersson, T. 1991. Influence of stemflow and throughfall from common oak (*Quercus robur*) on soil chemistry and vegetation patterns. *Canadian Journal of Forest Research* 21: 917-924.
- André F., M. Jonard & Q. Ponette. 2008. Influence of species and rain event characteristics on stemflow volume in a temperate mixed oak-beech stand. *Hydrological Processes* 22: 4455-4466.
- Asbury, C. E., W. H. McDowell, R. Trinidad-Pizarro & S. Berrios. 1994. Solute deposition from cloud water to the canopy of a Puerto Rican montane forest. *Atmospheric Environment* **28**: 1773-1780.
- Balslev, H., J. Luteyn, B. Ollgaard & L. B. Holm-Nielsen. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Botanica* **92**: 37-57.
- Bongers, F., J. Pompa, J. Meave & J. Carabias. 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* 74: 55-80.
- Campbell, D., D. Daly, G. Prance & U. Maciel. 1986. Quantitative ecological inventory of terra firme and varzea tropical forest on the Rio Xingu, Brazilian Amazon. *Brittonia* **38**: 369-393.
- Campo, J., J. M. Maass, V. J. Jaramillo & A. Martínez-Yrízar. 2000. Calcium, potassium, and magnesium cycling in a Mexican tropical dry forest ecosystem. *Biogeochemistry* 49: 21-36.
- Campo, J., M. Maass, V. J. Jaramillo, A. Martínez-Yrízar & J. Sarukhán. 2001. Phosphorus cycling in a Mexican tropical dry forest ecosystem. *Biogeo*chemistry 53: 161-179.
- Chuyong, G. B., D. M. Newbery & N. C. Songwe. 2004. Rainfall input, throughfall and stemflow of nutrients in a central African rain forests dominated by ectomycorrhizal trees. *Biogeochemistry* 67: 73.91.
- Clark, K. L., N. M. Nadkarni, D. Schaefer & H. L. Gholz. 1998. Atmospheric deposition and net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica. *Journal of Tropical Ecology*

- **14**: 27-45.
- Dezzeo, N. & N. Chacón. 2006. Nutrient fluxes in incident rainfall, throughfall, and stemflow in adjacent primary and secondary forests of the Gran Sabana, southern Venezuela. Forest Ecology and Management 234: 218-226.
- Dietz, J., D. Hölscher & C. Leuschner. 2006. Rainfall partitioning in relation to forest structure in differently managed montane forest stands in Central Sulawesi, Indonesia. Forest Ecology and Management 237: 170-178.
- Foster, R. & N. Brokaw. 1985. Structure and history of the vegetation of Barro Colorado Island. pp. 67-81.
 In: E. G. Leigh & D. M. Windsor (eds.) The Ecology of a Tropical Forest. Smithsonian Institution Press, Washington D.C.
- Franson, M. 1995. Standard Methods for the Examination of Water and Wastewater. American Public Health Association, American Water Works Association and Water Environment Federation, Washington.
- García, E. 2004. Modificaciones al Sistema de Clasificación climática de Kôppen. Instituto de Geografía, Universidad Nacional Autónoma de México, México D F
- Giardina, C. P., R. L. Sanford Jr., I. C. Døckersmith & V. J. Jaramillo. 2000. The effects of slash burning on ecosystem nutrients during the land preparation phase of shifting cultivation. *Plant and Soil* 220: 247-260.
- Goller, R., W. Wilcke, K. Fleischbein, C. Valarezo & W. Zech. 2006. Dissolved nitrogen, phosphorus, and sulfur forms in the ecosystem fluxes of a montane forest in Ecuador. *Biogeochemistry* 77: 57-89.
- Hölscher, D., J. Mackensen & J. M. Roberts. 2005. Forest recovery in the humid tropics: changes in vegetation structure, nutrient pools and the hydrological cycle.
 pp. 598-621. In: M. Bonnell & L. A. Bruijnzeel (eds.) Forests, Water and People in the Humid Tropics. Cambridge University Press, New York.
- Holwerda, F., F. N. Scatena & L. A. Bruijnzeel. 2006. Throughfall in a Puerto Rican lower montane rain forest: A comparison of sampling strategies. *Journal* of Hydrology 327: 592-602.
- Ibarra-Manríquez, G., M. Martínez-Ramos, R. Dirzo & J. Núñez-Farfán. 1997. La vegetación. pp. 61.85. In: E. González-Soriano, R. Dirzo & R. Vogt (eds.) Historia Natural de Los Tuxtlas. CONABIO, Instituto de Biología, Instituto de Ecología, Universidad Nacional Autónoma de México, México D.F.
- Johnson, M. S. & J. Lehmann. 2006. Double-funneling of trees: Stemflow and root-induced preferential flow. *Ecoscience* 13: 324-333.
- Levia, D. & S. Herwitz. 2000. Physical properties of

- water in relation to stemflow leachate dynamics: implications for nutrient cycling. *Canadian Journal of Forest Research* **30**: 662-666.
- Levia, D. & E. Frost. 2003. A review and evaluation of stemflow literature in the hydrologic and biogeochemical cycles of forested and agricultural ecosystems. *Journal of Hydrology* **274**: 1-29.
- Lugo, H. J. & F. C. Córdoba. 1992. Regionalización geomorfológica de la República Mexicana. *Investigaciones Geográficas* **25**: 25-63.
- Manfroi, O., K. Koichiro, T. Nobuaki, S. Masakazu, M. Nakagawa, T. Nakashizuka & L. Chong. 2004. The stemflow of trees in a Bornean lowland tropical forest. *Hydrological Processes* 18: 2455-2474.
- Martínez-Meza, E. & W. Whitford. 1996. Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. *Journal of Arid Environments* 32: 271-287.
- Martínez-Ramos, M. 1997. Astrocaryum mexicanum (Chocho, Chichón). pp. 92-97. In: E. González-Soriano, R. Dirzo & R. Vogt (eds.) Historia Natural de Los Tuxtlas. CONABIO, Instituto de Biología, Instituto de Ecología, Universidad Nacional Autónoma de México, México D.F.
- McJannet, D., J. Wallace & P. Reddell. 2007. Precipitation interception in Australian tropical rainforests: II. Altitudinal gradients of cloud interception, stemflow, throughfall and interception. *Hydrological Processes* 21: 1703-1718.
- Martínez-Ramos, M. 1994. Regeneración natural y diversidad de especies arbóreas en selvas húmedas. Boletin De La Sociedad Botanica De Mexico 54: 179-224.
- Ministry of the Economy. 2001. Análisis de Aguas. Determinación de Fósforo Total en Aguas naturales, Residuales y Residuales Tratadas. Método de Prueba. México, D.F.
- Ministry of the Economy. 2010. Norma Mexicana. Análisis de Agua. Medición de Nitrógeno Total Kjeldahl en Aguas Naturales, Residuales y Residuales Tratadas. Método de Prueba. México, D.F.
- Miranda, F. & E. Hernández. 1963. Los tipos de vegetación de México y su descripción. Boletín de la Sociedad Botánica de México 28: 29-178.
- Park, A. & J. L. Cameron. 2008. The influence of canopy traits on throughfall and stemflow in five tropical trees growing in a Panamanian plantation. Forest Ecology and Management 255: 1915-1925.
- Parker, G. G. 1983. Throughfall and stemflow in the forest nutrient cycle. Advances in Ecological Research 13: 57-132.
- Piirainen, S., L. Finér & M. Starr. 1998. Canopy and soil retention of nitrogen deposition in a mixed boreal forest in eastern Finland. Water Air and Soil

- Pollution 105: 165-174.
- Popma, J., F. Bongers & J. Meave. 1988. Patterns in the vertical structure of the tropical lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* 74: 81-91.
- Potter, C. S., H. L. Ragsdale & W. T. Swank. 1991. Atmospheric deposition and foliar leaching in a regenerating southern Appalachian forest canopy. *Journal of Ecology* **79**: 97-115.
- Raich, J. W. 1983. Understory palms as nutrient traps: a hypothesis. *Brenesia* **21**: 119-129.
- Rickson, F. R. & M. M. Rickson. 1986. Nutrient acquisition facilitated by decaying leaves collection and ant colonies on two Malaysian palms. *Biotropica* 18: 337-343.
- Soto, M. & L. Gama. 1997. Climas. pp. 7-24. In: E. González-Soriano, R. Dirzo & R. Vogt (eds.) Historia Natural de Los Tuxtlas. CONABIO, Instituto de Biología, Instituto de Ecología, Universidad Nacional Autónoma de México, México D.F.
- Staelens, J., A. Schrijver, K. Verheyen & N. E. Verhoest. 2008. Rainfall partitioning into throughfall, stemflow, and interception within a single beech (*Fagus sylvatica* L.) canopy: influence of foliation, rain

- event characteristics, and meteorology. *Hydrological Processes* **22**: 33-45.
- Tobón, C., J. Sevink & J. M. Verstraten. 2004. Solute fluxes in throughfall and stemflow in four forest ecosystems in northwest Amazonia. *Biogeochemistry* **70**: 1-25.
- Tobón, W., C. Martínez-Garza & J. Campo. 2011. Soil responses to restoration of a tropical pasture in Veracruz, south-eastern Mexico. *Journal of Tropical Forest Science* 23: 338-344.
- Veneklaas, E. J. 1990. Nutrient fluxes in bulk precipitation and throughfall in two montane tropical rain forests, Colombia. *Journal of Ecology* 78: 974.992.
- Waring, R. H. & S. W. Running. 2007. Forest Ecosystems Analysis at Multiple Scales. 3rd edn. Elsevier Academic Press, Burlington.
- Whitford, W., J. Anderson & P. Rice. 1997. Stemflow contribution to the 'fertile island' effect in creosotebush, *Larrea tridenta*. *Journal of Arid Environments* **35**: 451-457.
- Zar, J. H. 1984. *Biostatistical Analysis*. Prentice Hall, New Jersey.

(Received on 25.06.2013 and accepted after revisions, on 31.03.2014)