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Canopy interactions of rainfall in an off-shore mangrove ecosystem dominated by *Rhizophora mangle* (Belize)

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Summary Bulk precipitation, throughfall and stemflow were collected to study anthropogenic effects on above-ground nutrient cycling in an off-shore mangrove forest (*Rhizophora mangle* L.) on Twin Cays, Belize. Samples were collected in a nitrogen limited fringe and phosphorus limited dwarf zone, and from an adjacent nitrogen fertilized fringe and a phosphorus fertilized dwarf zone. Inorganic cations and anions, dissolved organic carbon (DOC) and nitrogen (DON) were analysed. Throughfall represented 84% of precipitation volume. Sea salt ions (Cl^- , Na^+ , SO_4^{2-} and Mg^{2+}) and DOC accounted for the highest proportion of solutes in rainwater, throughfall and stemflow in *R. mangle* stands. Non-marine sources dominated the flux of DON, DOC, NO_3^- , NH_4^+ , and inorganic P (P_i) in bulk precipitation and throughfall and partially contributed to Ca^{2+} and K^+ . Deposition ratios (throughfall deposition:bulk deposition) showed that inorganic NH_4^+ , and less so P_i were retained in the canopy of *R. mangle* from throughfall while all other solutes increased. Canopy leaching contributed in increasing order to net throughfall of Ca^{2+} , Cl^- , $\text{SO}_4^{2-}/\text{K}^+$, Mg^{2+} and Na^+ but dry deposition dominated the net throughfall flux during the investigated period. Fertilizer treatment and zone did only slightly affect solute concentrations of hot-water extracts of leaves, of throughfall and stemflow in stands of similar stature. While litterfall and primary production have previously been shown to increase substantially upon nutrient enrichment of mangroves we therefore conclude that fertilization, as a surrogate of anthropogenic eutrophication, may not increase nutrient leaching from mangrove canopies, and thus may only have a minor effect on soluble organic matter cycling and inputs into mangrove food webs.

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Introduction

Due to their position at the ecotone between terrestrial and marine systems, mangrove forests play an important ecological role as they stabilize shorelines, support adjacent marine ecosystems and protect inshore areas (e.g., Odum and Heald, 1975). Mangrove forests represent nursery sites and are a major source of organic matter input into coastal and estuarine food webs (Lee, 1999). Litterfall, throughfall and stemflow are important internal pathways in the nutrient cycle of tropical forests by which above-ground organic matter (litter and leachates) reaches the soil surface and nutrients are released by litter decomposition and mineralization (Whitmore, 1998). Their relative importance for nutrient transfer to the forest soil depends on the mobility of solutes or ions and on the nutrient status of the ecosystem, but also on plant species, tree architecture, season, vicinity of the sea, and herbivory (Parker, 1983).

Mangrove soils are often high in organic matter. Frequent inundation by seawater leads to slow decomposition of litter and soil organic matter resulting in peat accumulation, low rates of inorganic nitrogen and phosphorus release for growth, high sulphide concentrations in soil solution and high salinity (e.g. Feller et al., 2002). Mangroves therefore frequently represent oligotrophic coastal wetland ecosystems with a flora adapted to low-nutrient conditions, as a result of the combination of the physico-chemical factors of sheltered tropical shores, (Lugo and Snedaker, 1974; Boto and Wellington, 1984; Koch, 1997; Feller et al., 2002; McKee et al., 2002). While most solutes increase in concentration in throughfall in temperate and tropical forest ecosystems (i.e., net leaching), in some oligotrophic ecosystems tree canopies can scavenge nutrients from precipitation e.g. inorganic N and P (Jordan et al., 1980; Veneklaas, 1990; Lovett and Lindberg, 1993). The major limiting nutrients in remote mangrove forests are N and P (Feller et al., 1999; Feller et al., 2002; McKee et al., 2002), and nutrient enrichment caused enhanced mangrove growth (Feller, 1995; McKee et al., 2002). Onuf et al. (1977) also found significantly higher N concentrations in senescent and new leaves on a mangrove island which was naturally fertilised by bird guano, compared to one without birds present. Since worldwide mangrove ecosystems are endangered by anthropogenic disturbance and increased anthropogenic input of nutrients (Ellison and Farnsworth, 1996; Gibson et al., 1998), eutrophication could trigger important effects on nutrient cycling, i.e. leachate composition and concentration and litterfall.

In several temperate throughfall studies nutrient addition enhanced throughfall deposition as the foliar pools of leachable nutrients increased (Parker, 1983). Therefore, increased nutrient input may markedly increase the availability of nutrients to mangrove trees, alter the natural cycling of nutrients in mangrove ecosystems and thereby impair mangrove ecosystem functioning and organic matter provision to the mangrove food web. Previous studies demonstrated that soil nutrient enrichment caused enhanced mangrove growth e.g. twig length, leaf number and leaf area increased (Feller, 1995; McKee et al., 2002), but also markedly affected nutrient resorption efficiency and increased nutrient concentrations in litter (Feller et al., 2002) in the same pristine off-shore mangrove forest in

Belize that was studied here. However, so far no data are available on solute concentrations and the importance of throughfall and stemflow as a nutrient return vector in mangrove ecosystems.

This investigation was therefore conducted to test the following research questions: (i) What are the main atmospheric sources of nutrients deposited to a pristine mangrove forest? (ii) How does the mangrove forest canopy alter solute patterns in throughfall and stemflow compared to rainfall? (iii) Does the alleviation of nutrient limitation of mangroves through N or P fertilization increase nutrient leaching from mangrove canopies?

The data presented in this study are the first reported on solute concentrations and fluxes in throughfall and stemflow in mangrove ecosystems. However, this study represents a preliminary assessment of changes of solute concentrations in rainwater during its passage through red mangrove canopies and of the effect of topography and nutrient enrichment on solute cycling since the study was confined to the wet season. Nonetheless, the data allow first conclusions on above-ground solute fluxes as related to the impact of fertiliser and site, and enable to estimate the contribution of different solute sources to bulk deposition and to net throughfall in this strongly marine influenced ecosystem.

Materials and methods

Study site

The study was carried out during August and September 2001 on Twin Cays, a peat based mangrove island belonging to the barrier reef of central Belize (Feller, 1995). Peat deposits developed to 7–10 m thickness, and have formed primarily through deposition and slow turnover of mangrove roots and partly from shoot material (Middleton and McKee, 2001). These peat soils are high in sulphide but low in phosphate, nitrate and ammonium (Feller et al., 2002). The long-term mean annual precipitation at the cays is about 930 mm, with a maximum during June–October (Koltes et al., 1998). The investigated mangrove forest can be divided into three zones: close to the main channel that separates the two large islands is a fringe zone of 3–7 m high *Rhizophora mangle* L. (red mangrove) trees. Dwarf *R. mangle* trees of 1–2 m height cover the interior of the island (dwarf zone). The transition zone between these two zones is comprised of *R. mangle* interspersed by *Avicennia germinans* L. (black mangrove) and *Luncularia racemosa* (L.) Gaertn.f. (white mangrove).

Experimental design

The islands were chosen due to the availability of previously established fertilised plots (Feller, 1995; Feller et al., 2002) that revealed N limitation of fringe and P limitation of dwarf trees. Three transects 25–50 m long and 10 m apart were selected oriented perpendicular to the shoreline at each of three sites, and transects were subdivided into fringe, transition and dwarf zones based on tree height. To minimize disturbance of the system, individual trees of *R. mangle* (three replicates each) rather than plots were treated by direct fertilizer application to the root zone of the target

trees. Three nutrient treatments (300-g doses) were established: N fertilizer as urea, P fertilizer as triple superphosphate (P_2O_5), and control (no nutrient enrichment). Fertiliser was enclosed in dialysis tubing in 150-g doses, and placed in two holes (7 cm diameter \times 30 cm deep) in the peat substrate on opposing sides of each tree, beneath the outermost margin of the canopy and approximately 30 cm from a grounded prop root from the target tree. For control trees, holes were cored and sealed but no fertilizer was added. Trees were fertilized twice a year at 6-mo intervals from January 1995 through January 1997. Experiments in this study were conducted in the fringe as well as the dwarf zone. To assess the effect of nutrient limitation on solute release we selected each three unfertilized trees in both zones as well as three N fertilised trees in the N limited fringe zone, and three P fertilised trees in the P limited dwarf zone for throughfall and stemflow collection. Distance between trees was \sim 4 m within treatments and $>$ 10 m between fertilized and control trials. Photographs were taken with a wide-angle lens (28 mm) from the openings of the throughfall samplers towards the sky to estimate canopy closure. The pictures were scanned and the sky was differentiated from the canopy using contrast differences and the histogram function by Adobe Photoshop 6 (Adobe Systems). Canopy closure was calculated as percentage of total picture area covered by leaves, twigs and stems.

Foliar concentrations of hot-water extractable solutes

Five young, fully expanded and senescent leaves of *R. manglie* were collected from the three trees within each zone and treatment that have been selected for throughfall and stemflow collection. Leaves were washed superficially and after treatment in a microwave oven (three-times 30 s at full power) were immediately oven-dried at 60 °C for three days at the field station at Carrie Bow Cays and thereafter transported to the Department of Chemical Ecology and Ecosystem Research, University of Vienna, Austria, for chemical analysis. Leaf material was homogenised in a ball mill (Retsch MM2000). Hot-water extracts were prepared by extracting aliquots of 40 mg leaf powder with 1 mL deionised water at 95 °C for 60 min, and solute concentrations were analysed by ion chromatography and elemental analysis (see below).

Throughfall and stemflow collection

For throughfall collection, high-density polyethylene buckets (5-L volume, diameter 25.7 cm) were used which were covered with fine-mesh nylon cloth to prevent debris from entering. Each one collector was mounted at a fixed position on the tree above the prop roots but below the lowest twigs and branches. On each trees' stem an appropriate piece of flexible hosepipe that was cut longitudinally was stapled to the tree trunk in an upward spiral and sealed with sanitary silicone for stemflow collection (Herwitz, 1986). After installation the stemflow collectors were rinsed with deionised water and 5 L high-density polyethylene bottles were attached to the lower end of the tubing. Rainfall was collected

using three rainfall collectors made of high-density polyethylene funnels (diameter 25.7 cm) attached to high-density polyethylene bottles (5 L) at the nearby station island, Carrie Bow Cay. Rainwater samplers were mounted at 1.5 m height above-ground, well distanced from each other and from surrounding trees, houses and the sea. Rainfall, throughfall and stemflow solutions were collected on an event basis and were brought to the laboratory the day after each rain event. In the case of strong storms some rain and throughfall collectors were overloaded or became temporarily inoperable reducing the number of parallel samples available for replication. Furthermore, water samples with inorganic phosphorus (P_i) concentration $>$ 50 μ M were omitted from statistical analysis as an indicator of presence of bird droppings. The collected water samples were immediately sterile filtered (Whatman GF/F, nominal pore size 0.6 μ m) and mercury acetate was added to a final concentration of 10 μ mol L⁻¹ to inhibit microbial growth. After transport to Vienna, the samples were stored frozen until analysis.

Chemical analysis

Anion concentrations were analysed by anion chromatography using a high performance liquid chromatography system (DX 500, Dionex). Anions were separated on an AS11 column (250 \times 4 mm i.d., Dionex) by NaOH gradient elution from 0.05 to 37.5 mM. Flow rate was 2 mL at 32 °C and total run time was 25 min. Cations were quantified by cation chromatography (DX 500, Dionex) using a cation exchange column (CS16, 250 \times 4 mm i.d., Dionex) and 48 mM methyl sulfonate as isocratic eluent. Cations were separated at 40 °C and a flow rate of 1 ml min⁻¹ and total run time was 15 min.

Dissolved organic nitrogen (DON) was estimated from two rain events after alkaline persulphate digestion (Cabrera and Beare, 1993). Briefly, sample aliquots (10 mL) were mixed with 3.5 mL 0.148 M $K_2S_2O_8$ and 0.175 mL 3 M NaOH in digestion flasks and sealed immediately thereafter. The flasks were autoclaved for 30 min at 121 °C and 0.12 MPa. By this method, total dissolved N (TDN) is oxidized to NO_3^- that was analysed by anion chromatography as mentioned above. DON was calculated by subtracting the concentration of dissolved inorganic N ($DIN = NH_4^+ + NO_3^-$) from TDN.

Dissolved organic C (DOC) was analysed from the same rain events as DON using a TOC analyzer (Shimadzu TOC-5000). Before analysis, the samples were flushed with CO_2 -free air. Potassium hydrogen phthalate was used as an external standard. As water samples contained mercury acetate as an additive background DOC levels were measured in blanks (deionised water, containing the additive at the respective concentration) and were subtracted from DOC concentrations of the samples.

Calculations and statistical analysis

Volume-weighted mean (VWM) concentrations of solutes in throughfall and rainwater were calculated as follows:

$$VWM = \frac{\sum_{i=1}^n (C_i * V_i)}{\sum_{i=1}^n (V_i)} \quad (1)$$

Where, C_i is the concentration of a species in sample i , V_i is the volume of precipitation or throughfall of event i , and n

is the number of samples for which measurements were made. VWM and non-VWM solute concentrations did not differ significantly (VWM:non-VWM = 0.96 ± 0.07 , mean \pm 1SE for all solutes; one-way ANOVA, $P > 0.1$). As throughfall and particularly stemflow volumes were not available for all collectors and all rain events, results are presented based on non-VWM solute concentrations.

The contribution of non-sea water sources (non-SWC) to solute concentrations in bulk precipitation was calculated using a dilution factor (f_{dil}). f_{dil} is here defined as the concentration ratio between seawater and bulk precipitation and was calculated for Cl^- , SO_4^{2-} , Na^+ and Mg^{2+} , ions which are thought to be most closely linked to marine aerosols and therefore reflect marine origin. Using the average f_{dil} of these ions non-SWC of other solutes was calculated as follows:

$$\text{Non-SWC (\%)} = 100 * (C_{\text{BP}} - C_{\text{SW}}/f_{\text{dil}})/C_{\text{BP}}, \quad (2)$$

where C_{BP} and C_{SW} are the solute concentrations in bulk precipitation and seawater, respectively.

Net throughfall (NTF) was calculated on an event basis as the difference between bulk deposition flux (Flux_{BD}) and throughfall flux (Flux_{TF}), the flux being calculated as the product of solute concentration in rain water times rainfall volume (V_{BP}) or as the product of solute concentration in throughfall times throughfall volume (V_{TF}):

$$\text{NTF} = \text{Flux}_{\text{TF}} - \text{Flux}_{\text{BD}} \quad (3)$$

Deposition ratios were calculated on an event basis as the ratio between throughfall deposition (Flux_{TF}) and bulk deposition (Flux_{BD}).

The multiple regression approach was used to estimate the contribution of dry deposition and canopy exchange to net throughfall (Lovett and Lindberg, 1984). Multiple regressions were calculated by StatGraphics 5.0 using event NTF of a solute as the dependent variable and the antecedent dry period (ADP, in days) and precipitation volume (P, in mm) as independent variables:

$$\text{NTF} = b_1 * \text{ADP} + b_2 * \text{P} + a \quad (4)$$

The regression coefficients obtained represent the mean dry deposition rate (b_1 , $\text{mmol m}^{-2} \text{d}^{-1}$), the canopy exchange rate (b_2 , $\text{mmol m}^{-2} \text{mm}^{-1}$ rainfall) and an y-axis intercept (a), respectively. Using data on duration of dry periods and rainfall volume dry deposition and canopy exchange amount can be calculated for a given observation period. The canopy budget model as suggested by Ulrich (1983) and reviewed by Draaijers and Erisman (1995) could not be used as it is based on the assumption that Na^+ behaves conservatively and in throughfall is only affected by dry deposition but not by canopy leaching. However, due to the high foliar concentration of Na^+ we cannot assume that canopy leaching of Na^+ is zero (pers. observ., J Hofmann; Tobon et al., 2004).

Significant differences between treatments and zones were assessed by one-way ANOVA (analysis of variance), followed by a post-hoc test (multiple range test using Scheffé-test). Regression analysis was performed using the Spearman correlation matrix. Statistical analysis was carried out with StatGraphics Plus 5.0 software (Statistical Graphics Inc.).

Results and discussion

Extractable solutes in leaves

In general, foliar concentrations of *R. mangle* declined in the order DOC , Cl^- , Na^+ , Mg^{2+} , SO_4^{2-} , Ca^{2+} , K^+ and DON in hot-water extracts (Table 1). Foliar NO_3^- , P_i and NH_4^+ concentrations were lowest throughout. Zone and fertilisation did not affect DOC , Cl^- , Na^+ , Mg^{2+} , SO_4^{2-} , Ca^{2+} , and NO_3^- concentration (Table 1). Significant differences in solute concentrations between zones and treatments were only apparent for foliar P_i , NH_4^+ , K^+ and DON . Phosphorus fertilisation increased extractable leaf P_i of trees in the dwarf zone (Table 1). Soluble N concentrations were similar in all treatments and zones compared to increased total N concentrations of living and senescent leaves of N fertilised trees at Twin Cays. Hot-water extractable P_i of leaves increased in response to P fertilisation in accordance to total leaf P (Feller et al., 2002). Considering the increased productivity of fertilised *R. mangle* trees (Feller et al., 2002), inorganic N and P has clearly been taken up from the fertilizer. However, considering the low foliar concentrations of inorganic N and P throughout all treatments the nutrients supplied by the fertilisation treatment have been assimilated into high-molecular weight organic compounds in leaves of *R. mangle* that are less mobile and therefore less prone to foliar leaching.

Rainfall interception and canopy structure

The rain events sampled between August and September 2001 ranged from 2 to 155 mm ($n = 6$) and represented 27% of the average annual rainfall. Throughfall volume (V_{TF}) comprised $84.5 \pm 9.7\%$ (mean \pm SE) of incident rainfall, close to data reported for coastal mangroves in Florida, where precipitation inputs to the forest floor were 75% by throughfall (Twilley and Chen, 1998). Throughfall volume showed a highly significant relationship with rainfall volume (V_{BP} ; $V_{\text{TF}} = 0.698 * V_{\text{BP}} + 9.2$; $P < 0.001$, $R^2 = 0.792$). Although there was a trend towards higher throughfall volume generation under unfertilised dwarf and N fertilised fringe trees this was not significant ($P = 0.332$, one-way ANOVA). Moreover, throughfall volume was not related to the percentage of canopy closure which for unfertilised dwarf trees was dramatically lower (39%) compared to all other trees (76–84%). Twilley and Chen (1998) found that 19% of bulk precipitation was diverted to the forest floor by stemflow which is among the highest values recorded (Supplementary Table 1) and possibly is related to the architecture of red mangrove trees, funnelling rainfall towards the stem and thereby generating large stemflow fluxes. Though stemflow volume was not quantified in this study, stemflow likely contributed <10% to overall canopy hydrological fluxes due to a higher throughfall proportion in this study and some rainfall loss by canopy interception and evaporation.

Solute sources in bulk precipitation

The prevalent solutes in bulk precipitation samples were Cl^- (631 μM), DOC (595 μM), and Na^+ (474 μM), followed by DON (76.1 μM), Mg^{2+} (53.9 μM), SO_4^{2-} (38.8 μM), Ca^{2+} (33.9 μM), K^+

(16.7 μM), NO_3^- (13.1 μM), NH_4^+ (6.5 μM) and inorganic P (1.0 μM) (Table 2). There were striking similarities between the proportional composition of sea water and precipitation, particularly for Na^+ , Cl^- , Mg^{2+} and SO_4^{2-} . Concentration

ratios between seawater and bulk precipitation (dilution factor, f_{dil}) for these ions averaged 957 ± 70 (mean \pm SE, $n = 4$ ions). Using the average dilution factor we calculated the non-seawater contribution (non-SWC) to solute concen-

Table 1 Concentrations of hot-water extractable solutes ($\mu\text{mol g}^{-1}$ DW) from leaves of *Rhizophora mangle* in Twin Cays, Belize

Solute	Fringe zone		Dwarf zone		ANOVA
	Control	N fertilised	Control	P fertilised	P
Cl^-	888 \pm 89.7	718 \pm 40.5	890 \pm 60.8	909 \pm 39.6 n.s.	0.106
SO_4^{2-}	212 \pm 57.6	306 \pm 67.0	194 \pm 41.5	178 \pm 34.5 n.s.	0.310
NO_3^-	1.49 \pm 0.43	0.82 \pm 0.22	1.37 \pm 0.32	1.60 \pm 0.27 n.s.	0.334
P_i	2.73 \pm 0.38 a	3.00 \pm 0.40 a	3.43 \pm 0.55 ab	4.47 \pm 0.46 b	0.045
Na^+	597 \pm 59.9	568 \pm 46.5	592 \pm 40.1	537 \pm 28.6 n.s.	0.783
NH_4^+	4.89 \pm 0.38 b	3.67 \pm 0.16 a	4.83 \pm 0.23 b	3.34 \pm 0.26 a	<0.001
Mg^{2+}	281 \pm 28.3	276 \pm 21.8	289 \pm 21.4	284 \pm 33.6 n.s.	0.989
K^+	108 \pm 13.2 a	126 \pm 8.0 a	295 \pm 29.3 b	113 \pm 13.4 a	<0.001
Ca^{2+}	137 \pm 30.9	151 \pm 23.5	139 \pm 22.3	180 \pm 29.6 n.s.	0.654
Sol. org. C	8001 \pm 595	7771 \pm 584	7509 \pm 625	8771 \pm 662 n.s.	0.514
Sol. org. N	28.6 \pm 1.6 a	28.2 \pm 2.2 a	38.7 \pm 3.0 b	38.0 \pm 3.3 b	0.007

Leaves (young, mature and senescent) were sampled from each three trees per zone and fertiliser treatment. Data given represent means \pm SE of all leaf ages ($n = 15$; sol. org. N and C, $n = 9$). Means followed by different letters signify significant differences between groups (multiple range test, LSD test, $P < 0.05$). P -Values are given from one-way ANOVA.

Table 2 Comparison of solute concentrations in rainfall and throughfall (A) and rainfall and stemflow (B) of different *Rhizophora mangle* stands

Solute	Rain	Fringe zone		Dwarf zone		ANOVA
		Control	N fertilised	Control	P fertilised	P
(A)	<i>Rain</i>	<i>Throughfall</i>				
Cl^-	631 \pm 212 a	1830 \pm 821 a	1347 \pm 218 a	6057 \pm 1574 b	2196 \pm 387 a	0.0002
SO_4^{2-}	38.8 \pm 12.2 a	99.9 \pm 40.5 a	80.5 \pm 12.7 a	302.7 \pm 75.7 b	118.6 \pm 17.8 ab	0.0002
NO_3^-	13.1 \pm 3.86	23.2 \pm 13.0	13.5 \pm 4.9	12.9 \pm 3.0	11.8 \pm 4.4 n.s.	0.763
P_i	0.98 \pm 0.56	0.10 \pm 0	0.26 \pm 0.16	0.39 \pm 0.16	0.24 \pm 0.14 n.s.	0.215
Na^+	474 \pm 199 a	761 \pm 198 ab	956 \pm 165 ab	3214 \pm 650 c	1958 \pm 369 bc	<0.0001
NH_4^+	6.52 \pm 1.60 b	1.39 \pm 0.55 a	2.88 \pm 0.87 ab	3.38 \pm 1.34 ab	2.52 \pm 0.95 ab	0.018
Mg^{2+}	53.9 \pm 22.4 a	80.0 \pm 22.1 ab	109.0 \pm 21.0 ab	374 \pm 76.8 c	243 \pm 44.5 bc	<0.0001
K^+	16.7 \pm 6.6 a	31.3 \pm 6.0 ab	40.5 \pm 7.3 ab	94.5 \pm 19.4 c	64.0 \pm 10.0 bc	<0.0001
Ca^{2+}	33.9 \pm 10.3 a	39.7 \pm 6.0 a	51.4 \pm 8.3 a	121.8 \pm 23.0 b	81.5 \pm 12.2 ab	<0.0001
DOC	595 \pm 26.0	899 \pm 109	912 \pm 213	463 \pm 53.3	913 \pm 237 n.s.	0.037
DON	76.1 \pm 32.8	378 \pm 199	228 \pm 132	821 \pm 335	134 \pm 35.7 n.s.	0.116
(B)	<i>Rain</i>	<i>Stemflow</i>				
Cl^-	631 \pm 212 a	2411 \pm 904 a	1994 \pm 504 a	7334 \pm 1263 b	1046 \pm 271 a	<0.0001
SO_4^{2-}	38.8 \pm 12.2 a	127.5 \pm 49.0 ab	89.2 \pm 23.4 ab	383.3 \pm 56.1 b	185.6 \pm 135 ab	0.013
NO_3^-	13.1 \pm 3.86	27.2 \pm 18.4	3.1 \pm 0.7	11.1 \pm 2.0	6.0 \pm 1.3 n.s.	0.305
P_i	0.98 \pm 0.56	0.38 \pm 0.19	0.10 \pm 0	0.26 \pm 0.16	0.10 \pm 0 n.s.	0.193
Na^+	474 \pm 199 a	830 \pm 240 a	1395 \pm 256 ab	3005 \pm 1039 b	1192 \pm 386 ab	0.004
NH_4^+	6.52 \pm 1.60	5.06 \pm 2.82	3.72 \pm 3.22	2.63 \pm 2.12	17.0 \pm 11.3 n.s.	0.498
Mg^{2+}	53.9 \pm 22.4 a	81.8 \pm 25.0 ab	104.9 \pm 25.0 ab	269.0 \pm 111.9 b	134.2 \pm 43.4 ab	0.030
K^+	16.7 \pm 6.6 a	33.8 \pm 7.9 ab	39.3 \pm 8.3 ab	94.6 \pm 35.1 b	46.2 \pm 11.4 ab	0.006
Ca^{2+}	33.9 \pm 10.3 a	43.1 \pm 10.2 a	47.1 \pm 9.3 ab	127.0 \pm 46.3 b	53.2 \pm 13.6 ab	0.013
DOC	595 \pm 26.0	1325 \pm 327	1263 \pm 236	980 \pm 318	725 \pm 166 n.s.	0.054
DON	76.1 \pm 32.8 a	486 \pm 221 a	216 \pm 94.6 a	1433 \pm 258 b	170 \pm 70.3 a	<0.0001

Data presented are means \pm 1SE ($n = 14$ –15; except DOC and DON, $n = 5$ –8). P -values are given from one-way ANOVA. Means followed by different letters signify significant differences between groups (multiple range test, Scheffé post-hoc test, $P < 0.05$).

trations in bulk precipitation. Non-SWC was undetectable for Na^+ and Mg^{2+} and increased from 7% (SO_4^{2-}) to 14% (Cl^-), 47% (K^+), 63% (Ca^{2+}) and 100% (NO_3^- , NH_4^+ , P_i , DOC, DON). This result was further corroborated by principal component analysis of bulk precipitation composition (Table 4). PCA axis 1, explaining 74% of data variability, shows that K^+ , Ca^{2+} , Mg^{2+} , Na^+ , and Cl^- and SO_4^{2-} were strongly related, indicating a common source of these ions, i.e. marine aerosols. Marine aerosols are commonly the dominant source of Na^+ , Mg^{2+} , SO_4^{2-} and Cl^- in bulk precipitation at sites in close proximity to the ocean (McDowell et al., 1990). This was also found for Puerto Morelos, Yucatan

(Bravo et al., 2000), a site only 400 km distant to the Great Barrier Reef off-shore Belize.

In contrast, marine aerosols constituted no significant source of NO_3^- , NH_4^+ , P_i , DOC and DON. Though NH_4^+ was also strongly related to the marine component (PCA 1), it constitutes a minor component of sea water and probably also of marine aerosols. NH_4^+ may, however, be released by agriculture and burning which is indicated by negative and positive relations to P_i in PCA 3 and PCA 4, which explain 7.1% and 1.3% of data variability. Both, NO_3^- and P_i exhibited high component weights on PCA axis 2 (17.2%), clearly indicating a non-marine source of both anions, while DON and DOC

Table 3 Event-based regression analysis between solute concentrations in bulk precipitation ($\mu\text{mol L}^{-1}$, y-axis) and rainfall volume (mm, x-axis)

Solute	Equation	R^2	P	df
Cl^-	$y = -635 \ln(x) + 2872$	0.576	0.001	13
SO_4^{2-}	$y = -36.5 \ln(x) + 168$	0.578	0.001	13
NO_3^-	$y = -8.91 \ln(x) + 44.7$	0.347	0.021	13
P_i	Nd	0.003	0.833	13
Na^+	$y = -474 \ln(x) + 2153$	0.493	0.008	11
NH_4^+	$y = -3.25 \ln(x) + 17.9$	0.348	0.034	11
Mg^{2+}	$y = -51.8 \ln(x) + 237$	0.462	0.011	11
K^+	$y = -14.0 \ln(x) + 66.3$	0.386	0.024	11
Ca^{2+}	$y = -21.1 \ln(x) + 109$	0.308	0.029	11

Logarithmic regression curves were fitted, and coefficient of determination (R^2), probability values (P) and df are given for each solute.

Table 4 Results of principle component analysis of solute concentrations (excl. DON and DOC), combined for all sites and calculated for bulk precipitation and throughfall separately

Solute	PCA 1 (% , r)	PCA 2 (% , r)	PCA 3 (% , r)	PCA 4 (% , r)
<i>Bulk precipitation (12 complete cases)</i>				
	(73.9%)	(17.2%)	(7.1%)	(1.3%)
Cl^-	0.379	0.080	0.212	-0.111
SO_4^{2-}	0.378	0.075	0.231	-0.088
NO_3^-	0.074	0.705	0.535	0.251
P_i	-0.022	0.681	-0.647	-0.308
Na^+	0.386	-0.008	0.057	-0.134
NH_4^+	0.351	0.006	-0.387	0.846
Mg^{2+}	0.386	-0.051	0.005	-0.197
K^+	0.383	-0.049	-0.120	-0.158
Ca^{2+}	0.373	-0.151	-0.171	-0.157
<i>Throughfall (90 complete cases)</i>				
	(51.0%)	(15.6%)	(11.4%)	(10.7%)
Cl^-	0.354	0.431	0.008	0.023
SO_4^{2-}	0.248	0.376	0.047	0.064
NO_3^-	0.082	0.724	0.022	0.167
P_i	0.003	-0.058	-0.830	0.578
Na^+	0.447	-0.141	0.010	-0.080
NH_4^+	0.060	-0.190	0.547	0.807
Mg^{2+}	0.451	-0.152	-0.019	-0.074
K^+	0.449	-0.184	0.000	0.019
Ca^{2+}	0.445	-0.179	-0.095	-0.060

Component weights >0.3 and <-0.3 are presented in bold.

were not analyzed by PCA due to the small data set (seven complete cases).

NO_3^- , NH_4^+ , P_i , DOC and DON showed comparatively high concentrations in bulk precipitation. Opposed to the remoteness of this site, the high solute concentrations in rainwater at Twin Cays and peak concentrations found at other sites (Supplementary Table) are generally associated with biomass burning, fossil fuel burning and dust deposition. Though we can not dissect the importance of different sources of nutrient input into this mangrove ecosystem, frequent nearby fires at the Yucatan peninsula (Ceron et al., 2002) and long-distance transport and deposition of Saharan dust (Reid et al., 2003) probably are major contributors to ecosystem inputs of Ca^{2+} and K^+ , NO_3^- , NH_4^+ , P_i , DOC and DON via bulk precipitation. The significance of biogenic sources was also indicated by the decrease of VWM concentrations at the Yucatan peninsula during the dry-to-wet season transition when fire frequency and release of biogenic NO_x , NH_3 , K^+ and P_i decrease (Supplementary Table 1; Ceron et al., 2002).

The large fraction of total N being present in organic forms (>80%) at Twin Cays was also found for a Australian mangrove ecosystem on Hinchinbrook Island (Robertson and Alongi, 1992). However, DOC and DON concentrations in bulk precipitation were not correlated indicating that the processes controlling the DOC and DON in bulk precipitation were partially independent (Cornell et al., 2003).

In comparison in bulk precipitation most solutes were higher in concentration at Twin Cays than at other lowland and montane tropical rainforest sites (Supplementary Table 1). Only during the dry season similar or higher solute concentrations were encountered e.g. in Congo (Laclau et al., 2003) and in the Rio Negro basin (Filoso et al., 1999). During the dry season prolonged rain-free periods, lower rain intensities and increased fire frequency result in elevated concentrations of aerosols as well as of solutes in rain water due to washout. The significance of dry deposition and aerosol mass was also apparent considering the logarithmic relationship between solute concentrations in bulk precipitation and rainfall volume on an event basis ($P < 0.05$, R^2 between 0.31 and 0.58; Table 3).

Throughfall and stemflow chemistry

Similar to bulk deposition, the prevalent solutes in throughfall were Cl^- (1347–6057 μM), DOC (463–913 μM), and Na^+ (761–3214 μM) (Table 2). Inorganic N, i.e. NH_4^+ (1.4–3.4 μM) and NO_3^- (12–23 μM), and P_i concentrations (0.1–0.39 μM) were lowest in throughfall. Passage of rainwater through the mangrove canopy resulted in large increases in solute concentrations in throughfall, which, due to the high data variability, were only significant for Cl^- , SO_4^{2-} , Na^+ , Mg^{2+} , K^+ , and Ca^{2+} in control trees and to a lesser degree in fertilised trees of the dwarf zone. No significant changes were evident for DON, DOC, NO_3^- and P_i . NH_4^+ and P_i concentrations decreased from bulk precipitation to throughfall, though significantly only for NH_4^+ in control trees of the fringe zone (Table 2). This solute-specific trend was also mirrored in the deposition ratio for the solutes. Deposition ratios, calculated on an event basis, differed significantly between sites and treatments for Na^+ (dwarf

control, 22.2, compared to others, 3.9–6.6; $P = 0.048$, one-way ANOVA), but not for the other solutes (data not shown). Deposition ratios were therefore pooled for site and treatment, and ranged from 0.6 (NH_4^+) to 1.4–1.7 (P_i , NO_3^- , DOC), 4.0–4.9 (Ca^{2+} , DON), 6.3–7.5 (K^+ , Na^+ , Mg^{2+}) and 8.2–9.7 (SO_4^{2-} , Cl^-) (Fig. 2).

Similar to bulk precipitation, concentrations of various solutes in throughfall and stemflow were higher compared to other study sites in the humid tropics (Supplementary Table 1), demonstrating greater wet season inputs by dry deposition and canopy leaching at Twin Cays.

Generally, stemflow is more enriched in solutes compared to throughfall (Levia and Frost, 2003). However, in this study the pattern of solute enrichment or depletion was very similar for throughfall and stemflow of the different treatments and zones (Table 2). Two-way ANOVA for the factors site/treatment and flow path showed no significant difference in solute concentrations between throughfall and stemflow (data not shown). On average, solute concentrations were slightly higher in throughfall than in stemflow, the reverse trend was only found for NH_4^+ (Table 2, Fig. 1). The general similarity in solute concentrations between throughfall and stemflow at Twin Cays (Fig. 1) points to similar sources of solutes and mechanisms of solute enrichment/depletion along the rainwater flow path which are discussed below for throughfall only.

Principle component analysis of throughfall chemistry demonstrates the large influence of solutes of marine origin on throughfall chemistry, as shown via the component loads of Cl^- , Na^+ , Mg^{2+} , Ca^{2+} , and K^+ on PCA 1 which explains 51% of the data variability (Table 5). Interestingly, in contrast to the PCA analysis of bulk precipitation NO_3^- was related to Cl^- and SO_4^{2-} in throughfall (PCA 2, 15.6%) while NH_4^+ and P_i determined PCA 3 (11.4%) and PCA 4 (10.7%). These data clearly point to an increasing influence of processes apart from bulk deposition or sea water deposition on throughfall chemistry (Table 5).

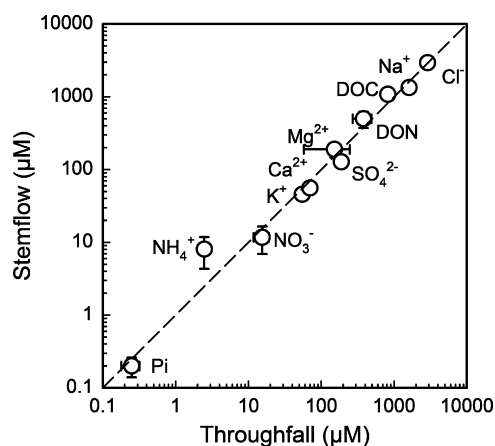


Figure 1 Relationship between solute concentrations in throughfall and stemflow in a *Rhizophora mangle* ecosystem, Carrie Bow Cays, Belize. The dashed lines represent the 1:1 relationship between the respective solute concentrations in throughfall and stemflow. Data represent means \pm 1SE of all sites and treatments combined ($n = 19$ –58 for throughfall and stemflow).

Table 5 Dry deposition and canopy exchange (mmol m^{-2}) of *Rhizophora mangle* for the observation period 1 August to 22 September 2001 at Twin Cays, Belize

Solute	Dry deposition	Canopy exchange	Rel. DD	P_{model}	Adj. R^2 by df
Cl^-	907 \pm 480	257 \pm 183	70	0.018	0.104
SO_4^{2-}	36.8 \pm 24.3	16.9 \pm 9.2	69	0.017	0.107
NO_3^-	-4.53 \pm 1.55	0.10 \pm 0.06	0	0.013	0.116
P_i	-0.65 \pm 0.15	0.08 \pm 0.05	0	0.0002	0.243
Na^+	477 \pm 492	417 \pm 135	53	0.0005	0.224
NH_4^+	-2.35 \pm 0.75	0.02 \pm 0.20	0	0.004	0.163
Mg^{2+}	65.8 \pm 56.5	40.9 \pm 15.9	62	0.002	0.192
K^+	17.3 \pm 12.1	7.67 \pm 3.09	69	0.002	0.179
Ca^{2+}	20.5 \pm 14.4	7.66 \pm 4.09	73	0.006	0.146

Multiple regression analysis of net throughfall (combined data) with length of antecedent dry period (days) and precipitation amount (mm) was carried out to calculate dry deposition and canopy exchange coefficients according to Lovett and Lindberg (1984), based on six rainfall events. Dry deposition was calculated by multiplying the dry deposition coefficient with number of dry days (23) and canopy exchange by multiplying the canopy exchange coefficient with precipitation volume during the observation period (511 mm). Rel. DD represents dry deposition flux as percentage of net throughfall flux. P values (P_{model}) and coefficients of determination (R^2) adjusted for degrees of freedom (df) are given for each model.

Mechanisms of solute enrichment and depletion in throughfall

Multiple regression analysis was performed to calculate the contributions of dry deposition and canopy exchange to net throughfall on an event basis (Table 5). The regression models were highly significant for all solutes ($P_{\text{model}} < 0.05$, Table 5) but coefficients of determination were generally low (adjusted R^2 between 0.11 and 0.24). Therefore, the results have to be taken cautiously, even more so since the model calculations are based on six rain events only. Due to lack of sufficient event data the multiple regression approach was not applied to net throughfall of DOC and DON.

Using the above model and the number of dry days and precipitation volumes we calculated the dry deposition and canopy exchange flux for the period August to September 2001 (Table 5). Dry deposition comprised 53% (Na^+), 62% (Mg^{2+}), 69–70% (K^+ , Ca^{2+} , SO_4^{2-}) and 73% (Cl^-) of the net throughfall flux (Table 5). Canopy exchange controlled the fluxes of NO_3^- , P_i and NH_4^+ .

Dry deposition

Cl^- and Na^+ enrichment in throughfall samples (Fig. 1) is explained by the vicinity of the sea and its effect on dry deposition of sea salts (Table 1). In line, Parker (1983) summarized several throughfall studies and reported a clear oceanic effect on concentrations of Na^+ , Cl^- , Mg^{2+} and SO_4^{2-} in precipitation and throughfall. However, comparing all zones and fertiliser treatments the concentrations of marine ions (Na^+ , Cl^- , Mg^{2+} and SO_4^{2-}) and also of K^+ and Ca^{2+} and DON were highest in throughfall and stemflow of the unfertilised dwarf trees (Table 2). N fertilisation had no effect on solute concentrations in throughfall and stemflow in the fringe zone but P fertilisation markedly reduced solute concentrations in the dwarf zone. In general, exposed leaf area and canopy closure are major factors that positively affect dry deposition and throughfall fluxes (e.g. Filoso et al., 1999). In the present study, canopy closure appears to play a minor role for throughfall fluxes as in the dwarf control

treatment, with its low canopy closure, the highest throughfall solute concentrations were recorded. These trees are different from the other trees by their low stature (<1.5 m), resulting in direct droplet deposition of sea water, particularly during strong winds and heavy rainfalls. The tree height effect cancelled out for P fertilised trees in the dwarf zone as they assumed normal growth and thereby reached greater canopy heights and canopy closures. Fertilisation and zone therefore had rather an indirect effect on dry deposition via changes in mangrove growth and architecture than direct effects such as on foliar levels of leachable solutes.

Canopy leaching and uptake

Between 27% and 47% of net throughfall of major inorganic cations (Na^+ , K^+ , Mg^{2+} , Ca^{2+}) and anions (Cl^- , SO_4^{2-}) were explained by canopy leaching while canopy exchange processes dominated the net throughfall flux of NO_3^- , NH_4^+ and P_i (Table 5). We are only aware of two studies of net throughfall in tropical forests where the multiple regression approach was applied (Filoso et al., 1999; Tobon et al., 2004). Filoso et al. (1999) reported that canopy exchange was the dominant source of base cations and P_i to net throughfall while net throughfall of Cl^- and SO_4^{2-} was dominated by dry deposition. Nitrate and NH_4^+ were retained within the canopy during the wet season but enriched in throughfall by dry deposition during the dry season (Filoso et al., 1999). Moreover, canopy exchange exerted a major control on net throughfall chemistry, explaining 52% of throughfall composition in four different forest ecosystems in Amazonia (Tobon et al., 2004).

There is strong evidence that non-essential ions or such that are in ample or excessive supply like Na^+ , Cl^- , Mg^{2+} and SO_4^{2-} undergo net leaching from mangrove canopies (Fig. 3, Table 5). This is particularly interesting as so far Na^+ has been assumed to behave conservatively in plant canopies and is therefore considered to show no detectable leaching from foliage (see also Tobon et al., 2004, for discussion). Therefore, Na^+ leaching of red mangrove leaves

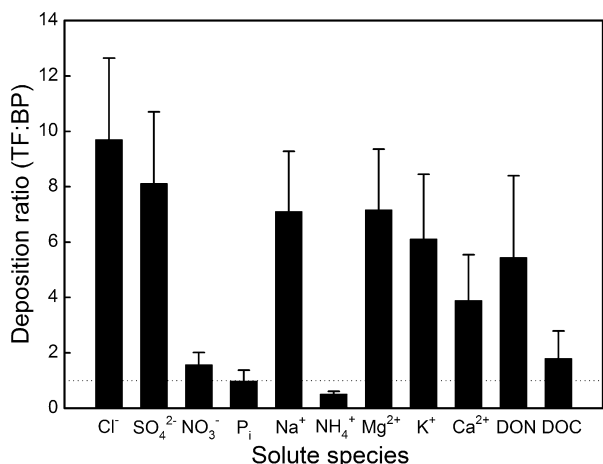


Figure 2 Ratio of throughfall deposition to bulk deposition calculated on an event basis (mmol m^{-2}) for a *Rhizophora mangle* ecosystem, Carrie Bow Cay, Belize. Data represent means \pm 1SE of six events, combined for sites and treatments ($n = 19\text{--}58$).

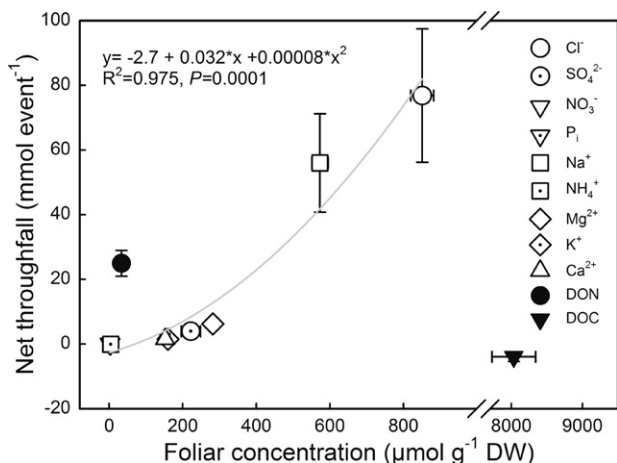


Figure 3 Relationship between solute concentrations in *Rhizophora mangle* leaves and average net throughfall ($\text{mmol event}^{-1} \text{m}^{-2}$) in a mangrove ecosystem, Carrie Bow Cays, Belize. A curvilinear regression model was fitted to the ionic solutes excluding the DOC and DON data. Data represent means \pm 1SE ($n = 9\text{--}15$ for foliar concentrations, $n = 19\text{--}58$ for net throughfall).

violated the major assumption of the canopy budget model (Ulrich, 1983) and hindered the application of this model to our data set.

Leaching of internal plant pools and ion-exchange processes occurring in the tree canopies contribute to solute enrichment in throughfall (Scherbatskoy and Tyree, 1990; Hambuckers and Remacle, 1993), however, the controls of foliar leaching are still not fully understood. Parker (1983) suggested that fertilisation affects throughfall concentrations by raising the foliar pools of leachable nutrients which has been demonstrated for temperate forest ecosystems (e.g. Mahendrappa and Ogden, 1973). We found no relationship between the concentration of specific foliar solutes

e.g. K^+ in mangrove leaves of the different zones and treatments and the respective net throughfall fluxes (one-way ANOVA, $P > 0.1$). In contrast, a curvilinear relationship was apparent when plotting the concentration of foliar solutes in *R. mangle* against their net throughfall flux (Fig. 3). The curvilinearity of this relationship points to preferential leaching of the most abundant foliar ions, Na^+ and Cl^- . The striking deviation of DON and DOC from the common solute behaviour may be explained by DON release from epicaulous and epiphyllous N_2 fixers (e.g. Sheridan, 1992) and by underestimation of throughfall enrichment of DOC due to rapid microbial degradation by leaf surface microflora (e.g. Lee and Hyde, 2002).

On the other hand we found canopy uptake of P_i and NH_4^+ from precipitation (Table 2, Fig. 2). This may supplement nutrients which limit plant growth in oligotrophic mangroves (Feller, 1995; Feller et al., 2002; McKee et al., 2002) or in other nutrient-poor forest ecosystems (Lovett and Lindberg, 1993).

Fertiliser effects and conclusions

N and P fertilization of mangroves at Twin Cays significantly decreased resorption efficiencies for N and P, respectively, and therefore reduced the conservation of essential nutrients while markedly enhancing growth in dwarf red mangroves (Feller et al., 1999; Feller et al., 2002). Besides increases in growth, tree height and canopy closure of dwarf red mangrove by P fertilisation, fertilisation had a negligible direct effect on concentrations of hot-water extractable solutes of leaves and on throughfall N and P concentrations in this study. Fertilisation did also not directly affect DOC and DON concentrations in throughfall (Table 2). We therefore suggest that in mangroves anthropogenic inputs, i.e. fertilizer as surrogate for increasing N deposition or eutrophication may have only a minor effect on nutrient return via throughfall, as far as specific limits of N and P input are not exceeded. Compared to net throughfall, litterfall returns a greater fraction of nutrients from the tree canopy to the soil, i.e. 100% P, 99% C and 43% N (pers. comm., J. Hofmann, I. Feller). Since fertilisation at Twin Cays greatly increased leaf production, growth and nutrient concentrations in leaf litter (Feller et al., 2002), eutrophication may markedly accelerate nutrient cycling via litterfall and decomposition in these ecosystems and enhance organic matter provisioning to mangrove food webs.

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Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jhydrol.2007.07.012.

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