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Atmospheric deposition and net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica

KENNETH L. CLARK*[1], NALINI M. NADKARNI†, DOUGLAS SCHAEFER‡, *and* HENRY L. GHOLZ*

**School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32605*
†The Evergreen State College, Olympia, WA 98505
‡University of Puerto Rico, San Juan, PR 00936
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ABSTRACT. Meteorological variables, bulk cloud water and precipitation (BCWP), and bulk precipitation (BP) were measured above the canopy, and throughfall (TF; n = 20) was collected beneath an epiphyte-laden canopy of a tropical montane forest (TMF) for 1 y at Monteverde, Costa Rica. Total deposition (cloud + wet + dry) of inorganic ions to the canopy was estimated using a sodium (Na^+) mass balance technique. Annual BCWP and BP depths were 2678 mm and 1792 mm for events where mean windspeeds (u) $\geq$ 2 m s^{-1}, and 4077 mm and 3191 mm for all events, respectively. Volume-weighted mean pH and concentrations of nitrate-N (NO_3^--N) and ammonium-N (NH_4^+-N) were 4.88, 0.09 and 0.09 mg l^{-1} in BCWP, and 5.00, 0.05 and 0.05 mg l^{-1} in BP, respectively. Cloud water and mist deposition to the canopy was estimated to be 356 mm. Estimated deposition of free acidity (H^+), NO_3^--N, and NH_4^+-N to the canopy was 0.49, 3.4 and 3.4 kg ha^{-1} y^{-1}, respectively. Mean TF depth was 1054 ± 83 mm (mean ± S.E.) for events where u $\geq$ 2 m s^{-1}, and 2068 ± 132 mm for all events. Volume-weighted mean pH and concentrations of NO_3^- -N and NH_4^+-N in TF were 5.72, 0.04 mg l^{-1}, and 0.07 mg l^{-1}, respectively. Mean fluxes of H^+, NO_3^- -N, and NH_4^+-N in TF were 0.04 ± 0.01, 0.6 ± 0.2 and 1.3 ± 0.2 kg ha^{-1} y^{-1}, and percent net retention of these ions by the canopy was 92 ± 2, 80 ± 6, and 61 ± 6%, respectively. Phosphate, potassium, calcium and magnesium were leached from the canopy. Seasonal data suggest that biomass burning increased concentrations of NO_3^- and NH_4^+ in cloud water and precipitation at the end of the dry season. Regardless, a large majority of the inorganic N in atmospheric deposition was retained by the canopy at this site.

KEY WORDS: atmospheric deposition; precipitation chemistry; interception loss; throughfall; nitrogen retention; cloud forest, tropics

[1] Author to whom correspondence should be addressed.

INTRODUCTION

Atmospheric deposition and net retention of ions by the forest canopy in temperate montane ecosystems have received considerable attention in the last two decades, in part because of the hypothesized roles of increased free acidity (H^+) and inorganic nitrogen (N) deposition in forest decline, acidification and N saturation of soils, and increased levels of H^+ and nitrate (NO_3^-) in surface waters (e.g., Aber 1992, Dise & Wright 1995, Draaijers *et al.* 1996, Johnson & Lindberg 1992, Schultze 1989). Cloud water often accounts for a significant portion of the total ion deposition to montane cloud forests because: (i) ion concentrations in cloud water are typically three to ten times greater than those in precipitation (Johnson & Lindberg 1992, Weathers *et al.* 1988), (ii) montane areas are frequently immersed in cloud (Bruijnzeel & Proctor 1995, Cavelier *et al.* 1996, Gordon *et al.* 1994, Vong *et al.* 1991), (iii) foliage, branches, and epiphytic vegetation are aerodynamically rough surfaces (Lovett & Reiners 1986, Monteith & Unsworth 1990, Nadkarni 1984), and (iv) canopy resistance to cloud water deposition via impaction is low when cloud immersion is coupled with the relatively high windspeeds that characterize many montane areas (Beswick *et al.* 1991, Gallagher *et al.* 1992, Lovett 1984). As a result, ion deposition is typically greater to montane cloud forests when compared to lower elevation forests which receive only wet and dry deposition (Fowler *et al.* 1988, Johnson & Lindberg 1992, Lovett & Kinsman 1990, Miller *et al.* 1993).

Net retention of ions by the canopy is typically estimated by comparing measured or modelled estimates of total deposition to fluxes in throughfall and stemflow (TF + ST). Numerous investigations in temperate forest ecosystems have indicated that the canopy-atmosphere interactions are complex, but clear patterns have emerged for individual ions. For example, many canopies retain H^+ and inorganic N from atmospheric deposition, and net retention rates are positively correlated with deposition rates. In contrast, potassium (K^+) is leached from most canopies (Johnson & Lindberg 1992, Parker 1983, Schaefer & Reiners 1990, Stevens *et al.* 1994, Van Ek & Draaijers 1994).

Considerably fewer estimates exist for atmospheric deposition and net retention of ions by the canopy in tropical montane forests (TMF) (Asbury *et al.* 1994, Steinhardt 1979, Steinhardt & Fassbender 1979, Veneklaas 1990). However, conversion of forest to pasture and croplands and the associated seasonal biomass burning activities, as well as other land use changes have generally increased rates of ion loading in the tropics (Crutzen & Andreae 1990, Galloway 1996, Galloway *et al.* 1994, Keller *et al.* 1991). These activities have contributed to concentrations of inorganic N in cloud water and precipitation that are as high as those at a number of North American sites (Clark *et al.* 1958). The canopy of TMFs are aerodynamically rough due to forest gaps, high leaf areas and abundant epiphytes, and therefore intercept substantial quantities of wind-driven cloud water and precipitation. Because many epiphytes are closely

linked to atmospheric sources of nutrients (Benzing 1990, Clark 1994, Nadkarni & Matelson 1991), estimates of atmospheric deposition and net retention of ions by the canopy are necessary to evaluate the potential effects of increased H^+ and N deposition to the diverse biota in the canopy, and to TMF ecosystems as a whole. The objectives of this study were to estimate (i) atmospheric deposition of selected ions to the canopy, and (ii) net retention of deposited ions by the canopy at a TMF site.

METHODS AND MATERIALS

Site description

Cloud water, precipitation, and throughfall samples were collected in the Research Area of the Monteverde Cloud Forest Reserve in the Cordillera de Tilarán, in west central Costa Rica (10°18′N, 84°48′W) from 30 September 1991 to 29 September 1992. Slopes and ridges in the Reserve are similar to those of other tradewind-dominated montane forests in terms of climate, forest physiognomy, and epiphyte mass and diversity (Ingram & Nadkarni 1993, Lawton & Dryer 1980, Nadkarni 1986). Three distinct seasons are differentiated primarily by the seasonal migration of the intertropical convergence zone: (i) a dry season (mid-January to April), characterized by moderate northeasterly tradewinds and wind-driven cloud and mist, (ii) a wet season (May to October), characterized by convective precipitation, and (iii) a transition season (November to mid-January), characterized by strong tradewinds and wind-driven precipitation and mist. Mean annual precipitation depth measured *c*. 3 km NW from the site between 1959 and 1994 was 2519 mm, but wind-driven cloud water and precipitation deposition was not measured (J. Campbell, *pers. comm*.). Mean monthly minimum and maximum temperatures ranged between 13.9 and 16.5 °C and between 17.6 and 21.1 °C, respectively, from 1 October 1991 to 30 September 1992.

The study site is in the tropical lower montane wet forest zone of Holdridge (1967), further classified as leeward cloud forest (Lawton & Dryer 1980). Elevation of the site ranges between 1480 and 1500 m. The soil is classified as a Typic Dystrandept, and has poorly differentiated horizons (Vance & Nadkarni 1990). Canopy height is 15 to 32 m, with a few emergents to 35 m, and stem density (30 cm dbh) is *c*. 160 stems ha^{-1}. Canopy species are primarily broad-leaved evergreens, and the five most frequently occurring plant families in the canopy are the Lauraceae, Moraceae, Leguminosae, Sabiaceae, and Meliaceae (Nadkarni *et al.* 1995). Total epiphyte mass is estimated at 3300 g m^{-2} (N. Nadkarni, unpubl. data), and includes diverse assemblages of bryophytes, vascular epiphytes, and accumulated litter and humus (Ingram & Nadkarni 1993; Vance & Nadkarni 1990, 1992).

Cloud water, precipitation, and throughfall sampling

Bulk cloud water and precipitation (BCWP) depth and ion concentrations were estimated using an Atmospheric Sciences Research Center-type passive

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cloud water collector (Falconer & Falconer 1980). The collector (30 cm tall, 10 cm diameter) consisted of an external ring of 100 Teflon monofilament lines (0.05 cm diameter) and an internal ring of eight acrylic plastic rods (1.0 cm diameter) mounted above a polypropylene funnel (16.3 cm diameter) and a 4-l bottle. The BCWP collector was located in a plastic basket at 17 m height on a 27 m meteorological tower located in a gap (*c*. 0.2 ha) in the forest, and was accessed using a rope and pulley system. Bulk precipitation (BP) was collected with a polypropylene funnel (16.3 cm diameter) and a 4-l bottle. The BCWP and BP collectors were positioned 30 cm apart in the plastic basket, and the BCWP collector was located downwind from the BP collector in the predominant wind direction to minimize interference. Samples were collected in clean (washed with 5% hydrochloric acid and rinsed five to ten times with deionized water) polypropylene bottles. Following sample collection, the BCWP collector, funnels and bottles were then brushed and rinsed with deionized water, or replaced. Hourly precipitation depth was measured with a tipping bucket rain gauge (Model No. 2501, Sierra-Misco Environmental Ltd. Victoria, B.C.) mounted on a boom at 12 m height on the tower. Windspeed (u) was measured at 27 m on the tower with a three-cup anemometer (Model No. 12-002, R. M. Young Co., Traverse City, Michigan). Instruments were connected to an automated data logger (Easy Logger Field Unit model EL824-GP, Omnidata International, Inc., Logan, Utah).

Throughfall (TF) was collected in 20 plots (25 m^2) distributed at random locations over 1 ha of primary forest adjacent to the meteorological tower. Plots were kept clear of all vegetation $\geq$ 30 cm tall and $\leq$ 5 cm stem diameter at the ground. At each plot, throughfall depth was measured with a sharp-rimmed rain gauge (5-cm diameter) mounted 1 m above the forest floor. Samples for ion chemistry were collected with a polypropylene funnel (12.5 or 19.5 cm diameter) attached to a 2-l polypropylene bottle mounted at 0.7 to 1 m above the forest floor and located within 1 m of the rain gauge. Funnel mouths were covered with polypropylene mesh (0.2 cm mesh size) to exclude litter and insects. Throughfall samples were collected at the same time as BCWP and BP samples, and subsamples were transferred to clean polypropylene bottles. Collectors were then brushed out and rinsed with deionized water, or replaced. Measurement of TF volumes in the polypropylene bottles for a subset of events indicated that there was little sampling bias when the standard rain gauges were used to estimate TF depths.

All BP, BCWP and TF samples were collected at 1–3-d periods depending on meteorological conditions. Samples were collected within 72 h of the onset of cloud immersion or precipitation. Events were delimited by periods of at least 12 h with no cloud water or precipitation as recorded by the tipping bucket rain gauge. Single tips (0.25 mm depth) that were recorded during apparently dry periods were discarded, and data from the tipping bucket rain gauge was corroborated by visual observations for a large sub-set of events.

Table 1. Analytical methods, detection limits, and precision for ion analyses.

Ion	Analytical method	Detection limit[1] (mg l^{-1})	Analytical precision[2] (%)	Reference
NO^{-}_{3}	Cadmium reduction column	0.02	4.3	Mackereth *et al*. 1978
NH^{+}_{4}	Indophenol blue	0.02	2.4	Harwood & Kuhn 1970
PO_4^{3-}	Molybdenum blue	0.01	2.7	Olsen & Sommers 1982
K^+	Flame emission	0.05	2.0	Instrument manual
Ca^{2+}	Atomic absorption	0.10	5.0	Instrument manual
Mg^{2+}	Atomic absorption	0.05	2.0	Instrument manual
Na^+	Flame emission	0.05	2.0	Instrument manual

[1] Detection limits are two times the SD of the mean of deionized water blanks analyzed throughout the study.
[2] Analytical precision is two times the SD of the mean/mean × 100 of medium concentration standards analyzed throughout the study.

Events were separated into two categories: (i) events where mean windspeeds (u) ≥ 2 m s^{-1}, and (ii) events where u < 2 m s^{-1}. Most (>90%) events where u ≥ 2 m s^{-1} were individual precipitation and/or cloud water events which originated from stratus or strato-cumulus clouds during the transition and dry seasons. Many of the precipitation events where u < 2 m s^{-1} originated from cumulus or cumulonimbus clouds in the afternoon or early evening during the wet season, and some samples integrated 2–3 d of convective precipitation activity (41% of the samples were single events).

Ion analyses

Within 24 h of collection, pH was determined on unfiltered subsamples using a Corning (model No. 120) pH meter calibrated with standard solutions (Fisher Scientific pH 4.01 and 7.01). Remaining subsamples were filtered through deionized water-rinsed Gelman AE 0.45 μm pore size filters using a polypropylene syringe and stored at 4°C. Nitrate, NH_4^+, and PO_4^{3-} analyses were performed at Monteverde on a Sequoia Turner 340 colorimeter equipped with a semi-automated flowcell assembly within 2 wk of collection for most (> 90%) samples (Table 1). Potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), and sodium (Na^+) concentrations were determined using standard procedures on a Perkin Elmer Model 603 atomic absorption spectrophotometer at the Analytical Research Laboratory, University of Florida. An air-acetylene flame was used for all analyses, and lanthanum additions (*c*. 500 mg l^{-1}) were used to reduce interferences during Ca^{2+} and Mg^{2+} analyses (Table 1).

Data analyses

Cloud water and precipitation depths were calculated by dividing volumes collected by funnel diameters for each event. Precipitation depth for events where u < 2 m s^{-1} was estimated from the BP collector data because slightly lower volumes in BCWP indicated that raindrops bounced off the top of this collector when windspeeds were low. Occasional data logger failure precluded an annual total from the standard rain gauge, but recorded precipitation depth

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corresponded closely to BP depth for events where $u < 2$ m s^{-1}, and the data were used to calculate event durations. Correlation coefficients (Pearson's product-moment using Bonferroni probabilities) were calculated for depths and ion concentrations in BCWP for events where $u \geq 2$ m s^{-1}, and in BP for events where $u < 2$ m s^{-1} following determination of normality of the data sets using SYSTAT statistical packages (SYSTAT 1992). Ion fluxes in BCWP and BP were calculated by multiplying depths collected by the appropriate ion concentrations, and then summing the products within each event category. Mean ion concentrations in cloud water and mist (CW) were calculated by subtracting ion fluxes in BP from those in BCWP, and then dividing by the difference in depth for each event where $u \geq 2$ m s^{-1}.

Throughfall depths for each collector were summed separately to estimate spatial variability over the 1-ha site. Interception loss by the canopy was estimated by subtracting mean TF depths from BP depths for events where $u < 2$ m s^{-1}, and from BP and BP + CW depths (see below) for all events. Correlation coefficients were calculated for depth and ion concentrations for both categories of events. Ion fluxes to each TF collector were also calculated separately. Although we measured ST on a subset of trees, accurately scaling these estimates up to the stand level is difficult. Therefore, we assumed that ion fluxes in ST were 5% of those in TF, and these values were added to mean ion fluxes in TF.

Total ion deposition (cloud + wet + dry) to the canopy was estimated using a mass balance for Na^+ (Ulrich 1983, Van Ek & Draaijers 1994, G. Lovett *pers. comm.*): We first subtracted the Na^+ flux in BP from that in TF + ST. The remaining Na^+ flux in TF + ST was assumed to be due to cloud water and mist deposition, and we divided this amount by the mean concentration of Na^+ in CW estimated above to calculate a mean depth of cloud water and mist deposition to the canopy. The mean depth of cloud water and mist was then multiplied by the appropriate ion concentrations to calculate fluxes, and these were added to fluxes in BP to estimate total deposition to the canopy.

RESULTS

Cloud water, precipitation and throughfall

Annual BCWP and BP depths were 4077 mm and 3191 mm, respectively (Table 2). Consistently greater depths were collected by the BCWP collector during events where $u \geq 2$ m s^{-1} when compared to the BP collector and the tipping bucket rain gauge, which indicated that the former was more effective at collecting wind-driven droplets. Volume-weighted mean ion concentrations were greater in both BCWP and BP from events where $u \geq 2$ m s^{-1} when compared to those in BP from events where $u < 2$ m s^{-1} (Table 3). Ion concentrations were greater in BCWP when compared to those in BP for most events where $u \geq 2$ m s^{-1}, suggesting that ion concentrations were relatively greater

Table 2. Mean event length (mean ± SE), mean bulk cloud water and precipitation (BCWP) or bulk precipitation (BP) intensity, total wet hours, and total depths of BCWP, BP, and throughfall (TF; mean ± SE, n = 20) by event category. a = precipitation depth estimated from BP.

Event category and number of collections	Mean length (h event^{-1})	Mean intensity (mm hr^{-1})		Total hours	Total depth (mm y^{-1})		
		BCWP	BP		BCWP	BP	TF
Windspeed ≥ 2 m s^{-1} (n = 65)	33.2 ± 3.4	1.24 ± 0.18	0.83 ± 0.13	1990	2678	1792	1054 ± 83
Windspeed < 2 m s^{-1} (n = 37)	6.6 ± 1.2	2.79 ± 0.58[a]	2.79 ± 0.58	442	1399[a]	1399	1014 ± 63
All events (n = 102)				2432	4077	3191	2068 ± 132

in wind-driven droplets, although dry deposition of these ions to the BCWP collector may also have been greater.

Depth was negatively correlated with some, but not all, ion concentrations in BCWP from events where u ≥ 2 m s^{-1}, but there was little relationship between depth and ion concentrations in BP from events where u < 2 m s^{-1} (Table 4). Interestingly, there were no correlations between H^+ and the other ion concentrations in either BCWP or BP. Nitrate and NH_4^+ concentrations were correlated in both BCWP and BP. Both NO_3^- and NH_4^+ concentrations were also correlated with metallic cation concentrations in BCWP, but they were correlated with only some cation concentrations in BP. Phosphate concentrations were only correlated with K^+ and Mg^{2+} in BP. All metallic cation concentration pairs were correlated in both BCWP and BP. Atmospheric deposition of all ions was 1.8 times (Ca^{2+}) to 3.0 times (Mg^{2+}) greater in BCWP when compared to BP from events where u ≥ 2 m s^{-1} (Table 5). Annual deposition in BCWP was estimated to be 0.53 kg H^+ ha^{-1} y^{-1} and 7.5 kg N ha^{-1} y^{-1}, 1.7 and 2.2 times the deposition of these ions in BP, respectively. The mean pH of cloud water and mist (CW) was 4.32, and mean ion concentrations were 0.47 ± 0.06 mg NO_3^-–N l^{-1} (mean ± SE, n = 65), 0.49 ± 0.07 mg NH_4^+–N l^{-1}, 0.003 ± 0.001 mg PO_4^{3-}–P l^{-1}, 0.62 ± 0.10 mg K^+ l^{-1}, 0.67 ± 0.10 mg Ca^{2+} l^{-1}, 0.89 ± 0.12 mg Mg^{2+} l^{-1}, and 6.42 ± 0.80 mg Na^+ l^{-1}.

Annual TF depth was 2068 ± 132 mm (mean ± SE, n = 20) (Table 2). Interception loss was estimated at 28% of precipitation for events where u < 2 m s^{-1},

Table 3. Volume weighted mean pH and ion concentrations (mg l^{-1}) in bulk cloud water and precipitation (BCWP), bulk precipitation (BP), and throughfall (TF) by event category.

Event category and number	pH collector	Volume weighted mean concentration (mg l^{-1})							
		NO_3^-–N	NH_4^+–N	PO_4^{3-}–P	K^+	Ca^{2+}	Mg^{2+}	Na^+	
Windspeed ≥ 2 m s^{-1} (n = 65)	BCWP	4.85	0.12	0.12	0.002	0.17	0.27	0.22	1.77
	BP	5.05	0.06	0.06	0.002	0.11	0.22	0.11	0.97
	TF	5.78	0.04	0.07	0.031	4.35	1.63	0.54	2.78
Windspeed < 2 m s^{-1} (n = 37)	BP	4.95	0.04	0.04	0.002	0.07	0.13	0.03	0.19
	TF	5.67	0.04	0.06	0.027	2.74	0.95	0.32	1.34
All events (n = 102)	BCWP	4.88	0.09	0.09	0.002	0.14	0.22	0.16	1.23
	BP	5.00	0.05	0.05	0.002	0.09	0.18	0.07	0.63
	TF	5.72	0.04	0.07	0.029	3.48	1.24	0.43	2.05

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Table 4. Correlation coefficients (Pearson product-momentum) for depth and ion concentrations in (i) bulk cloud water and precipitation (BCWP) from events where mean windspeed ≥ 2 m s^{-1} and bulk precipitation (BP) from events where mean windspeed < 2 m s^{-1}, and (ii) throughfall (TF) from events where mean windspeed ≥ 2 m s^{-1} and from events where $u < 2$ m s^{-1}.

(i) BCWP, windspeed ≥ 2 m s^{-1} (above) and BP, windspeed < 2 m s^{-1} s^{-1} (below).

	Depth	H^+	NO_3^-	NH_4^+	PO_4^{3-}	K^+	Ca^{2+}	Mg^{2+}	Na^+
Depth	–	–0.223	–0.419*	–0.428*	–0.193	–0.365	–0.405*	–0.427*	–0.446*
H^+	–0.246	–	0.249	0.323	–0.221	0.217	0.110	0.247	0.259
NO_3^-	–0.363	0.421	–	0.844**	0.184	0.747**	0.915**	0.897**	0.855**
NH_4^+	–0.269	0.407	0.949**	–	0.255	0.832**	0.869**	0.809**	–0.767**
PO_4^{3-}	–0.146	0.235	0.452	0.003	–	0.179	0.291	0.102	0.081
K^+	0.347	0.380	0.357	0.578**	0.802**	–	0.887**	0.823**	0.792**
Ca^{2+}	–0.489	0.323	0.571**	0.507*	–0.123	0.643**	–	0.938**	0.877**
Mg^{2+}	–0.484	0.209	0.648**	0.426	0.814**	0.699**	0.633**	–	0.978**
Na^+	–0.404	0.151	0.478	0.583**	0.274	0.921**	0.762**	0.734**	–

(ii) TF, windspeed ≥ 2 m s^{-1} (above), and TF, windspeed < 2 m s^{-1} (below).

	Depth	H^+	NO_3^-	NH_4^+	PO_4^{3-}	K^+	Ca^{2+}	Mg^{2+}	Na^+
Depth	–	0.381	–0.556	–0.529	–0.515	–0.546	–0.644	–0.591	–0.312
H^+	0.153	–	–0.176	–0.076	–0.215	–0.228	–0.166	–0.103	–0.277
NO_3^-	–0.120	–0.200	–	0.721*	0.944**	0.952**	0.855**	0.918**	0.375
NH_4^+	–0.315	0.232	0.769**	–	0.709*	0.609	0.577	0.669*	0.193
PO_4^{3-}	–0.332	–0.097	0.866**	0.683*	–	0.933**	0.809**	0.893**	0.484
K^+	0.319	0.121	0.871**	0.656	0.949**	–	0.857**	0.898**	0.377
Ca^{2+}	0.462	0.145	0.806**	0.659	0.847**	0.929**	–	0.966**	0.516
Mg^{2+}	–0.449	–0.024	0.828**	0.660	0.866**	0.939**	0.985**	–	0.501
Na^+	–0.229	–0.225	0.578	0.360	0.458	0.495	0.501	0.544	–

*, $P \leq 0.05$, **, $P \leq 0.01$.

35% of annual BP depth, and 42% of annual BP + CW depth. With the exception of H^+ and NO_3^-, volume-weighted mean ion concentrations were greater in TF from events where $u \geq 2$ m s^{-1} when compared to those from events where $u < 2$ m s^{-1} (Table 2). Free acidity and NO_3^- concentrations in TF were less than those in BCWP and BP from events where $u \geq 2$ m s^{-1}, NH_4^+ concentrations were intermediate between those in BCWP and BP, and PO_4^{3-}-P and cation concentrations were greatest in TF. Only H^+ concentrations in TF were less than those in BP from events where $u < 2$ m s^{-1}. There were no significant correlations between depth and ion concentrations, or between the concentrations of H^+ and the other ions in TF from either category of event (Table 3). Nitrate and NH_4^+ concentrations were correlated, and NO_3^- concentrations were correlated with the concentrations of all other ions except Na^+ in TF from both categories of events. In contrast, NH_4^+ concentrations were correlated only with PO_4^{3-} and Mg^{2+} concentrations in TF from events where $u \geq 2$ m^{-2}, and with PO_4^{3-} concentrations in TF from events where $u < 2$ m^{-2}. Potassium, Ca^{2+} and Mg^{2+} concentration pairs were correlated in TF from both categories of events. Free acidity and inorganic N fluxes in TF were 0.04 ± 0.01 g H^+ ha^{-1} y^{-1} and 1.9 ± 0.3 kg N ha^{-1} y^{-1} (mean $\pm$ SE, $n = 20$), respectively (Table 5). Nitrate-N accounted for only 22% of the inorganic N flux to the forest floor for events where $u \geq 2$ m s^{-1}, and 40% of the inorganic N flux for events where $u < 2$ m s^{-1}.

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Ion deposition and net retention by the canopy

Annual Na^+ flux in TF + ST was estimated to be 43.8 kg ha^{-1} y^{-1}. Sodium flux in BP was 20.5 kg ha^{-1} y^{-1}, and the deposition of Na^+ in cloud water and mist was assumed to be 23.3 kg ha^{-1} y^{-1}. Estimated total Na^+ deposition to the canopy represented 0.91 times the input to the BCWP collector and 2.14 times the input to the BP collector. Cloud water and mist depth calculated from the flux of Na^+ and the mean concentration of Na^+ in cloud water and mist was 356.3 mm y^{-1}. Total deposition of the other ions was calculated by multiplying the appropriate ion concentrations in cloud water and mist by this depth, and

Table 5. Ion deposition (kg ha^{-1} y^{-1}) in bulk cloud water and precipitation (BCWP) and bulk precipitation (BP), and ion fluxes in throughfall (TF). Standard errors for ion fluxes in TF are shown in parentheses (n = 20).

		Ion deposition or flux (kg ha^{-1} y^{-1})							
Event category	Collector	H^+	NO^-_3-N	NH^+_4-N	PO_4^{3-}-P	K^+	Ca^{2+}	Mg^{2+}	Na^+
Windspeed ≥ 2 m s^{-1}	BCWP	0.37	3.1	3.2	0.05	4.5	7.2	6.0	45.6
(n = 65)	BP	0.16	1.1	1.1	0.03	2.0	3.9	2.0	17.9
	TF	0.02	0.2	0.7	0.25	38.4	15.0	4.8	27.9
		(0.01)	(0.1)	(0.1)	(0.05)	(4.5)	(1.3)	(0.5)	(3.5)
Windspeed < 2 m s^{-1}	BP	0.16	0.6	0.6	0.02	1.0	1.9	0.4	2.6
(n = 37)	TF	0.02	0.4	0.6	0.23	25.2	8.7	2.9	13.4
		(0.01)	(0.1)	(0.1)	(0.06)	(4.7)	(1.2)	(0.5)	(1.7)
All events	BCWP	0.53	3.7	3.8	0.07	5.5	9.1	6.4	48.2
(n = 102)	BP	0.32	1.7	1.7	0.05	3.0	5.8	2.4	20.5
	TF	0.04	0.6	1.3	0.48	63.6	23.7	7.8	41.3
		(0.01)	(0.2)	(0.2)	(0.10)	(8.8)	(2.3)	(1.0)	(5.1)

adding input to the BP collector (Table 6). Calculated net retention of H^+ and inorganic N by the canopy represented 92 and 71% of total deposition, respectively (Table 5). Net retention of NO_3^- represented 91% of total deposition for events where u ≥ 2 m s^{-1}, and 38% of deposition for events where u < 2 m s^{-1}. Net leaching of PO_4^{3-} and metallic cations occurred from the canopy (Table 5).

DISCUSSION

Cloud water and precipitation

Wind-driven cloud water and precipitation depth, calculated for events where u ≥ 2 m s^{-1} from BCWP and BP data, was greater than horizontal precipitation depths (c.f. Bruijnzeel & Proctor 1995, Städtmuller 1987) reported from most of the other TMFs where similar collectors were used (Table 7). Although cloud water and precipitation depths are typically estimated with artificial surfaces, considerable uncertainties exist in using these estimates to calculate deposition to an aerodynamically rough forest canopy. Other methods to estimate cloud water and precipitation deposition to a forest canopy include the hydrologic balance technique (Juvik & Nullett 1995, Lovett 1988), the use of cloud water deposition models (Coe *et al.* 1991, Lovett 1984, Miller *et al.*

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Table 6. Ion deposition in BP, estimated ion deposition in cloud water and mist (CW) using Na^+ mass balance to calculate ion deposition to the canopy, the sum of BP and CW, ion fluxes in throughfall and stemflow (TF + ST), and percent net retention of ions by the canopy (mean ± SE).

Ion	Deposition ($kg\ ha^{-1}\ y^{-1}$)			TF + ST ($kg\ ha^{-1}\ y^{-1}$)	Percent net retention
	BP	CW	BP + CW		
H^+	0.32	0.17	0.49	0.04	92 ± 2
NO^-_3-N	1.7	1.7	3.4	0.6	82 ± 6
NH^+_4-N	1.7	1.7	3.4	1.4	61 ± 6
PO_4^{3-}-P	0.05	0.02	0.07	0.50	−614 ± 149
K^+	3.0	2.2	5.2	66.8	−1185 ± 169
Ca^{2+}	5.8	2.4	8.7	26.1	−200 ± 26
Mg^{2+}	2.4	3.2	5.6	8.6	−54 ± 18
Na^+	20.9	22.9	43.8	43.8	0 ± 12

1993), and micrometeorological techniques (Beswick *et al.* 1991, Gallagher *et al.* 1992, Vong & Kowalski 1995). All of these methods have limitations and typically require extensive hydrological and/or meteorological measurements. For example, an assumption implicit in the hydrologic balance method is that canopy surfaces are completely saturated, or that the amount of water stored by the canopy is in steady state. For a canopy with abundant epiphytes in a windy environment, water storage by the canopy is large and likely to be highly variable, potentially resulting in errors when this method is used to estimate cloud water and precipitation deposition. The hydrologic balance method also relies on accurate TF + ST estimates, which are difficult to obtain in structurally complex forests (Bruijnzeel 1990, Lloyd *et al.* 1988, Lovett 1988, Puckett 1991).

Modelling approaches have been used successfully to estimate cloud water deposition to the canopy at a number of temperate forest sites (Coe *et al.* 1991, Gallagher *et al.* 1992, Lovett 1984, Johnson & Lindberg 1992, Miller *et al.* 1993), but these models typically rely on accurate estimates of the liquid water content of cloud and other meteorological variables, which require relatively complex instrumentation. Micrometeorological techniques that calculate the covariance between wind components and liquid water content of cloud also require complex, fast-response meteorological instrumentation, including sonic anemometers which are prone to cloud water droplet coalescence and subsequent interferences (Beswick *et al.* 1991, Gallagher *et al.* 1992, Vong & Kowalski 1995). In addition, these latter methods were designed to estimate only cloud water deposition, and have not been used to estimate the deposition of wind-driven precipitation to a forest canopy. Wind-driven precipitation is an important hydrologic input to many TMFs, and obtaining accurate estimates at remote sites is a challenge for future research.

Volume-weighted mean pH in both BCWP and BP was intermediate when compared to values from other tropical premontane and TMF sites in Central and Northern South America (Table 8). Nitrate and NH_4^+ concentrations in BCWP and BP in Monteverde were greater when compared to those in wet

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Table 7. Precipitation depth collected with standard rain gauges, additional cloud water and precipitation depth collected with ASRC or Nagel-type collectors, and cloud water and precipitation as a percentage of precipitation at selected TMF sites.

Location	Precipitation depth (mm)	Cloud water and precipitation depth (mm)	Percent
Pu'u La'au, Hawaii[a]	257	98	38
Jalapa, Mexico[b]	597	125	21
Altotonga, Mexico[b]	746	166	22
Serranía de Macuira, Colombia[c]	853	796	93
Teziutlan, Mexico[b]	942	159	17
Tortutla, Mexico[b]	1082	339	31
Cordillera Central, Panamá[d]	1495	2295	154
Santa Ana, Venezuela[c]	1630	522	32
Monteverde, Costa Rica[e]	3191	886	28
Cordillera Central, Panamá[d]	3630	1130	31
Cerro Copey, Venezuela[c]	4461	458	10
Cordillera Central, Panamá[d]	5696	448	8

[a] Juvik & Nullet (1995).
[b] Vogelmann (1973).
[c] Cavelier & Goldstein (1989).
[d] Cavelier *et al.* (1996).
[e] This study.

deposition in El Verde, Puerto Rico and BP in Turrialba, Costa Rica, but NH_4^+ concentrations were much greater in BP in Santa Rosa de Cabal, Colombia. Phosphate concentrations in BCWP and BP in Monteverde were at the low end of the range of concentrations from the other premontane and TMF sites. Metallic cation concentrations in BCWP and BP in Monteverde were intermediate when compared to the other premontane and TMF sites. Both estimated rates of ion deposition to the canopy and in BP in Monteverde were generally within the range of deposition rates in BP reported from other tropical premontane and TMF sites, although NH_4^+-N deposition was much greater in Colombia (Table 9).

Table 8. Volume weighted mean pH and ion concentrations in bulk precipitation (BP) at tropical pre-montane and TMF sites in central and northern South America. n.d = not determined.

		Ion concentration (mg l^{-1})						
Location	pH	NO^-_3-N	NH^+_4-N	PO_4^{3-}-P	K^+	Ca^{2+}	Mg^{2+}	Na^+
Santa Rosa de Cabal, Columbia[a]	4.40	n.d.	0.86	0.034	0.38	0.48	0.15	1.14
	4.39	n.d.	0.77	0.033	0.48	0.51	0.17	1.10
San Eusebio, Venezuela[b]	4.55	n.d.	n.d.	n.d.	0.17	0.36	0.33	0.21
Monteverde, Costa Rica[c]	4.88	0.09	0.09	0.002	0.14	0.22	0.16	1.23
	5.00	0.05	0.05	0.002	0.09	0.18	0.07	0.63
El Verde, Puerto Rico[d]	5.14	0.04	0.02	0.001	0.09	0.34	0.22	1.63
Turrialba, Costa Rica[e]	5.34	0.02	0.05	0.004	0.11	0.06	0.04	0.25

[a] Veneklaas (1990): sites at 2550 and 3370 m elevation.
[b] Steinhardt & Fassbender (1979): 2300 m elevation.
[c] This study: 1480 m elevation, values for BCWP and BP.
[d] McDowell *et al.* (1990): 400 m elevation, NO^-_3-N and NH^+_4-N for wet-only deposition.
[e] Hendry *et al.* (1984): 650 m elevation.

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Throughfall

Interception loss by the canopy calculated for events where $u < 2$ m s^{-1} was at the high end of the range of interception estimates from other TMFs, and interception loss calculated from annual BP and BP + CW depths exceeded this

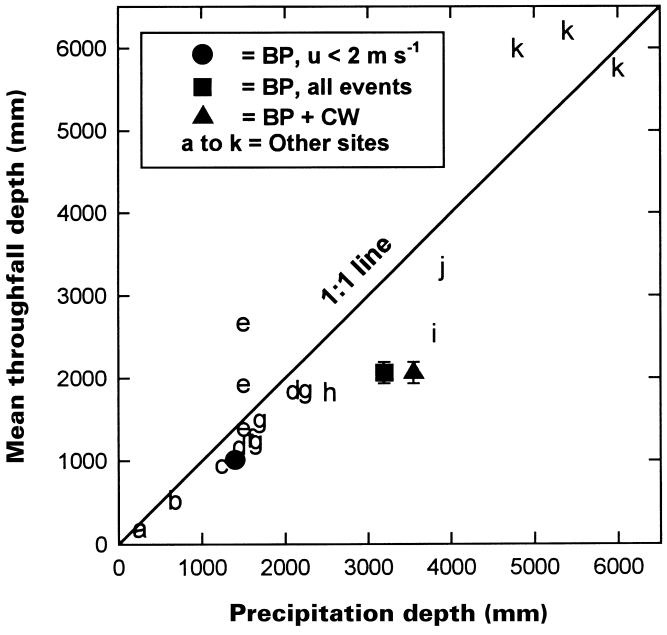

Figure 1. Annual precipitation depth (mm) versus mean throughfall depth (mm) at selected premontane and TMF sites. Symbols represent TF depth (mean ± SE, mm) at Monteverde, letters are other sites; a = Juvic & Nullet (1995), b = Cavelier & Goldstein (1989), c = Lundgren & Lundgren (1979), d = Veneklaas & Van Ek (1990), e = Stadtmuller & Aguedelo (1990), f = Steinhardt (1979), g = Vis (1986), h = Clements & Colon (1975), i = Edwards (1982), j = Mamanteo & Veracion (1985), k = Weaver (1972).

range (Figure 1). Three factors may have contributed to the relatively high interception loss at this site: (i) rates of evaporation from the canopy on leeward slopes may be large when compared to those from windward or ridge top forests, (ii) hydrologic flux to stems may have been relatively large, and (iii) TF sampling may have been biased and underestimated hydrologic flux to the forest floor. Because the site is located to the lee of the continental divide and is often behind the trailing edge of the hill cap cloud, frequent but intermittent cloud water and precipitation events were interspersed with periods of relatively greater shortwave radiation flux and atmospheric vapour pressure deficit. Coupled with the large water storage capacity of epiphytes in the canopy (calculated at *c*. 8 mm precipitation; Clark 1994), and their relatively low resistance to water vapour loss when at or near saturation, these factors may have resulted in high rates of evaporation from the canopy (Gallagher & Choularton 1989). Transpiration from abundant vascular epiphytes and hemi-epiphytes, many of which have access to water stored in the large accumulations of litter and humus on stems and branches, may also have contributed to the apparently

high rates of evaporation and hence precipitation interception at this site. It is also possible that the movement of relatively warm, dry air masses from the lowlands over the site contributed energy to evaporation process (Calder 1990).

Estimated interception loss at this site may also have been confounded by the diversion of water from branches to stems via conduction through continuous mats of epiphytes. Although a considerable amount of precipitation fell before stemflow was generated when the canopy was initially dry (K. Clark, *pers. obs.*), this pathway may represent a significant flux of water to the forest floor when continuous mats of epiphytes are saturated for long periods of time. A number of TMF sites which receive over 2500 mm of precipitation have relatively high values for precipitation interception, suggesting that hydrologic flux along stems may also be substantial in these other forests (Figure 1). Relatively large stemflow fluxes have been reported from elfin forest sites with a high density of stems (Weaver 1972), but information for other TMF sites is limited.

Hydrologic flux in TF is highly variable in structurally complex forests, thus it is difficult to sample accurately (Bruijnzeel 1990, Lloyd *et al.* 1988, Puckett 1991). However, when 26 to 40 throughfall collectors were used to sample TF events at this site from 15 April to 20 June, 1988, mean interception loss represented 32% of incident precipitation (K. Clark, unpubl. data), similar to the results obtained in the October 1991 to September 1992 sampling period reported here. Therefore, it is unlikely that our sampling underestimated TF amounts.

Ion deposition and net retention by the canopy

Because of the difficulties involved in the estimation of wind-driven cloud water and precipitation deposition, the Na^+ mass balance used here is a valuable method to estimate total deposition to some TMFs. However, this method likely applies only to relatively wet, tradewind-dominated sites because (i) rates of Na^+ deposition are relatively high (Table 9), (ii) Na^+ and other ion concentrations in cloud water and precipitation are significantly correlated (McDowell *et al.* 1990, Table 4), and (iii) precipitation interception and subsequent evaporation is a relatively large portion of the latent heat flux so that rates of transpiration and associated Na^+ uptake from soil solutions may be relatively low (Bruijnzeel & Proctor 1995, Grubb 1977).

Few other estimates exist for the net retention of ions by the canopy in TMFs. The canopy at Monteverde retained a greater proportion of H^+, a similar proportion of NO_3^--N, and a lower proportion of NH_4^+-N from atmospheric deposition when compared to proportions of these ions retained by the canopy from cloud water during 12 events without precipitation at Pico del Este, Puerto Rico (74, 75 and 79%, respectively; Asbury *et al.* 1994). The canopy in Monteverde retained a greater proportion of the NH_4^+-N in atmospheric deposition when compared to that retained by the canopy in Santa Rosa de Cabal, Colombia (Table 10). The proportions of PO_4^{3-} -P and Ca^{2+} removed from the canopy in Monteverde were greater, and the proportions of K^+ and Mg^{2+} were

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Table 9. Ion deposition in bulk precipitation (BP) at tropical premontane and TMF sites in Central and Northern South America. n.d. = not determined.

Location	Ion deposition (kg ha^{-1} y^{-1})							
	H^+	NO^-_3-N	NH^+_4-N	PO_4^{3-}-P	K^+	Ca^{2+}	Mg^{2+}	Na^+
Siguartepeque, Honduras[a]	n.d.	0.4	n.d.	0.10	3.0	18.3	18.5	4.4
Turrialba, Costa Rica[b]	0.09	0.5	1.2	0.09	2.5	1.4	1.1	5.9
El Verde, Puerto Rico[c]	0.25	2.0	1.5	n.d.	3.3	11.4	7.7	55.4
Pico del Este, Puerto Rico[d]	0.32	5.3	6.9	n.d.	27	47	30	247
Monteverde, Costa Rica[e]	0.49	3.4	3.4	0.06	5.2	8.7	5.6	43.8
	0.32	1.6	1.6	0.04	3.0	5.8	2.4	19.5
San Eusebio, Venezuela[f]	0.81	n.d.	n.d.	n.d.	2.6	5.6	5.2	3.3
Santa Rosa de Cabal, Colombia[g]	0.84	n.d.	11.2	0.72	7.9	10.1	3.2	24.1
	0.59	n.d.	18.3	0.48	6.9	7.3	2.5	15.9

[a] Kellman *et al.* (1982).
[b] Hendry *et al.* (1984).
[c] McDowell *et al.* (1990); NO^-_3-N and NH^+_4-N for wet-only deposition.
[d] Asbury *et al.* (1994).
[e] This study; estimates for deposition to the canopy and BP.
[f] Steinhardt & Fassbender (1979).
[g] Veneklaas (1990); sites at 3370 and 2550 m elevation.

Table 10. Estimated ion deposition to the canopy using a sodium mass balance (D), ion fluxes in throughfall (TF), and percent net retention (%NR) of ions by the canopy. n.d. = not determined.

Location		Ion deposition or flux (kg ha^{-1} y^{-1})							
		H^+	NO^-_3-N	NH^+_4-N	PO_4^{3-}-P	K^+	Ca^{2+}	Mg^{2+}	Na^+
San Eusebio, Venezuela[a]	D	n.d.	n.d.	n.d.	1.96	3.5	7.5	6.9	4.4
	TF	n.d.	n.d.	n.d.	1.38	69.7	6.9	3.3	4.4
	%NR	–	–	–	30	−1891	8	52	0
Santa Rosa de Cabal, Colombia[b]	D	n.d.	n.d.	22.8	0.80	8.8	11.3	3.6	26.9
	TF	n.d.	n.d.	21.5	1.67	95.2	27.1	10.7	26.9
	%NR	–	–	6	−109	−982	−140	−197	0
	D	n.d.	n.d.	11.2	0.48	6.9	7.3	2.5	15.9
	TF	n.d.	n.d.	11.6	0.40	33.0	18.8	7.0	14.4
	%NR	–	–	−3	17	−378	−158	−180	9
Monteverde, Costa Rica[c]	D	0.49	3.4	3.4	0.06	5.2	8.7	5.6	43.8
	TF	0.04	0.6	1.4	0.50	66.8	26.1	8.6	43.8
	%NR	92	82	61	−614	−1185	−200	−54	0

[a] Steinhardt (1979).
[b] Veneklaas (1990); sites at 2550 and 3370 m elevation.
[c] This study.

intermediate when compared to values calculated for Santa Rosa de Cabal, Colombia, and San Eusebio, Venezuela.

A more complete data set for ion deposition and net retention by the canopy exists for temperate sites in North America as part of the Integrated Forest

Study (IFS; Lindberg & Johnson 1992). Estimated H^+ and inorganic N deposition to the canopy at Monteverde was at the low end of the range of deposition estimates of 0.25 to 2.00 kg H^+ ha^{-1} y^{-1}, and 4.8 to 27 kg N ha^{-1} y^{-1} reported from IFS sites. This reflects the facts that no major urban areas or point sources of H^+, NO_x, or NH_3 exist in the vicinity, and that cloud immersion was estimated to occur only *c*. 7% of the time at this site. In addition, dry deposition of HNO_3 and NH_3 may have been underestimated by the BCWP and BP collectors used at this site. Although only two relatively long dry periods occurred during the sampling period (148 and 170 h), they occurred at the end of the dry season when biomass burning activities in the region were greatest and atmospheric concentrations of HNO_3, NH_3, and other gases and particles containing inorganic N were likely to be high.

Net retention of H^+ and inorganic N by the canopy at Monteverde was within the range of –0.2 to 0.5 kg H^+ ha^{-1} y^{-1} and 1 to 12 kg N ha^{-1} y^{-1} reported from the 12 sites in the IFS (Johnson & Lindberg 1992). Percent net retention of inorganic N by the canopy was greater at Monteverde when compared to most IFS sites (71 vs. 49 ± 21% (mean ± SD), range of 11 to 82%), but was closer to the values reported from the four sites where canopies had a substantial coverage of non-vascular epiphytes (62 ± 14% (mean ± SD); Great Smokey Mountains, Tennessee; Whiteface Mountain, New York; and two sites in Thompson Forest, Washington) (Friedland *et al.* 1991, Johnson *et al.* 1991, Lovett & Lindberg 1993). Net retention of NO_3^--N by the canopy was greater than that of NH_4^+-N at this site (80 vs. 61%), and NO_3^--N flux in TF was only 46% of the NH_4^+-N flux. The lower net retention rate of NH_4^+-N may have been partially due to the leaching of NH_4^+-N mineralized from litter and humus in the canopy (Clark 1994, Coxson 1991, Vance & Nadkarni 1990). Net retention of NO_3^--N was approximately equal to that for NH_4^+-N at the IFS sites. However, NO_3^--N fluxes in TF + ST were 1.5 to 6 times greater than those of NH_4^+-N, which reflect the relatively large dry deposition rates of HNO_3 and particles containing NO_3^- to a number of temperate forests in North America. Net retention of NO_3^--N averaged 57% of NO_3^--N deposition for the four canopies in the IFS which had a substantial coverage of epiphytic vegetation (Lovett & Lindberg 1993).

Although biomass burning may have increased inorganic N concentrations in cloud water and precipitation in Monteverde at the end of the dry season, deposition of inorganic N was intermediate when compared to other premontane and TMF sites, and relatively low when compared to deposition estimates from the IFS sites. The majority of the H^+ and inorganic N in atmospheric deposition was retained by the canopy. Results from a canopy hydrology and inorganic N flux model suggest that epiphytic bryophytes (mosses and liverworts) and assemblages of epiphytic bryophytes, vascular epiphytes, litter and humus accounted for *c*. 80% of the inorganic N retained by the canopy (Clark 1994). These abundant epiphytes may initially retain inorganic N as a

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function of N deposition from the atmosphere, and may buffer 'pulses' of inorganic N before they reach the forest floor. Retained N is apparently added to the relatively large pools of N in epiphytic biomass, litter and humus in the canopy (Vance & Nadkarni 1990, 1992), and eventually to the very large pool of N in soil organic matter (Bruijnzeel & Proctor 1995, Edwards & Grubb 1977, Grieve *et al.* 1990). For example, epiphytic bryophytes were only moderately productive, but bryophyte-derived litter decomposed very slowly, and net N accumulation was estimated at 8 to 13 kg ha^{-1} y^{-1} (Clark *et al.* 1997). Unfortunately, there is little information on leaching of NO_3^- from TMFs, but evidence suggests that forest growth may be N limited (Grubb 1977; Tanner *et al.* 1990, 1992). Therefore, it is possible that TMFs are more resistant to increases in N deposition than many temperate montane forests, because increased N inputs may initially stimulate the production of both epiphytes and their host trees, and are then stored in highly recalcitrant canopy and soil organic matter. However, the effects of increased, long-term N deposition to TMFs, particularly to those on windward slopes and ridges which receive greater cloud water inputs, are unknown and await further investigation.

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LITERATURE CITED

ABER, J. D. 1992. Nitrogen cycling and nitrogen saturation in temperate forest ecosystems. *Trends in Ecology and Evolution* 7:220–223.

ASBURY, C. E., MCDOWELL, W. H., TRINIDAD-PIZARRO, R. & BERRIOS, S. 1994. Solute deposition from cloud water to the canopy of a Puerto Rican montane forest. *Atmospheric Environment* 28:1773–1780.

BENZING, D. H. 1990. *Vascular epiphytes: general biology and related biota*. Cambridge University Press, Cambridge, England. 354 pp.

BESWICK, K. M., HARGREAVES, K., GALLAGHER, M. W., CHOULARTON, T. W. & FOWLER, D. 1991. Size resolved measurements of cloud droplet deposition velocity to a forest canopy using an eddy correlation technique. *Quarterly Journal of the Royal Meteorological Society* 117:623–645.

BRUIJNZEEL, L. A. 1990. *Hydrology of moist tropical forests and effects of conversion: a state of knowledge review*. IHP-UNESCO Humid Tropical Programme, Paris. 224 pp.

BRUIJNZEEL, L. A. & PROCTOR, J. 1995. Hydrology and biogeochemistry of tropical montane cloud forests: what do we really know? Pp. 25–46 in L. S. Hamilton, J. O. Juvik & F. N. Scatena (eds), *Tropical montane cloud forests*. Springer-Verlag, New York.

CALDER, I. R. 1990. *Evaporation in the uplands*. J. Wiley & Sons, New York. 148 pp.

CAVELIER, J. & GOLDSTEIN, G. 1989. Mist and fog interception in elfin cloud forests in Colombia and Venezuela. *Journal of Tropical Ecology* 5:309–322.
CAVELIER, J., SOLIS, D. & JARAMILLO, M. A. 1996. Fog interception in montane forests across the Central Cordillera of Panamá. *Journal of Tropical Ecology* 12:357–369.
CLARK, K. L. 1994. *The role of epiphytic bryophytes in the net accumulation and cycling of nitrogen in a tropical montane cloud forest.* Ph.D. dissertation, University of Florida, Gainesville, Florida. 271 pp.
CLARK, K. L., NADKARNI, N. M. & GHOLZ, H. L. 1997. Growth, net production, litter decomposition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest. *Biotropica*, in press.
CLARK, K. L., NADKARNI, N. M., SCHAEFER, D. & GHOLZ, H. L. 1998. Cloud water and precipitation chemistry in a tropical montane forest, Monteverde, Costa Rica. *Atmospheric Environment*, in press.
CLEMENTS, R. G. & COLON, J. A. 1975. The rainfall interception process and mineral cycling in a montane rain forest in eastern Puerto Rico. Pp. 813–823 in Howell, F. G., Gentry, J. B. & Smith, M. H. (eds), *Mineral cycling in southeastern ecosystems*. Technical Information Center, Energy Research Development and Administration, Washington, D.C.
COE, H., CHOULARTON, T. W., CARRUTHERS, D. J., GALLAGHER, M. W. & BOWER, K. N. 1991. A model of occult deposition applicable to complex terrain. *Quarterly Journal of the Royal Meteorological Society* 117:803–823.
COXSON, D. S. 1991. Nutrient release from epiphytic bryophytes in tropical montane rain forest (Guadeloupe). *Canadian Journal of Botany* 69:2122–2129.
CRUTZEN, P. J. & ANDREAE, M. O. 1990. Biomass burning in the tropics: impacts on atmospheric chemistry and biogeochemical cycles. *Science* 250:1669–1678.
DISE, N. B. & WRIGHT, R. F. 1995. Nitrogen leaching from European forests in relation to nitrogen deposition. *Forest Ecology and Management* 71:153–161.
DRAAIJERS, G. P. J., ERISMAN, J. W., SPRANGER, T. & WYERS, G. P. 1996. The application of throughfall measurements for atmospheric deposition monitoring. *Atmospheric Environment* 30:3349–3361.
EDWARDS, P. J. 1982. Studies of mineral cycling in a montane rain forest in New Guinea. V. Rates of cycling in throughfall and litter fall. *Journal of Ecology* 70:807–827.
EDWARDS, P. J. & GRUBB, P. 1977. Studies of mineral cycling in a montane rain forest in New Guinea. I. The distribution of organic matter in the vegetation and soil. *Journal of Ecology* 65:943–969.
FALCONER, R. E. & FALCONER, P. D. 1980. Determination of cloud water acidity at a mountain observatory in the Adirondack Mountains of New York State. *Journal of Geophysical Research* 85:7465–7470.
FOWLER, D., CAPE, J. N., LEITH, I. D., CHOULARTON, T. W., GAY, M. J. & JONES, A. 1988. The influence of altitude on rainfall composition at Great Dun Fell. *Atmospheric Environment* 22:1355–1362.
FRIEDLAND, A. J., MILLER, E. K., BATTLES, J. J. & THORNE, J. F. 1991. Nitrogen deposition, distribution, and cycling in a subalpine spruce-fir forest in the Adirondacks, New York, U.S.A. *Biogeochemistry* 14:31–55.
GALLAGHER, M. W., BESWICK, K., CHOULARTON, T. W., COE, H., FOWLER, D. & HARGREAVES, K. 1992. Measurements and modelling of cloudwater deposition to moorland and forests. *Environmental Pollution* 75:97–107.
GALLAGHER, M. W. & CHOULARTON, T. W. 1989. The effect of solar radiation on occult deposition over hills. *Quartarly Journal of the Royal Meteorological Society* 115:701–708
GALLOWAY, J. N. 1996. Anthropogenic mobilization of sulphur and nitrogen: immediate and delayed consequences. *Annual Review of Energy and the Environment* 21:261–92.
GALLOWAY, J. N., LEVY II, H. & KASIBHATLA, P. S. 1994. Year 2020: consequences of population growth and development on deposition of oxidized nitrogen. *Ambio* 3:120–123.
GORDON, C. A., HERRERA, R. & HUTCHINSON, T. C. 1994. Studies of fog events at two cloud forests near Caracas, Venezuela-I. Frequency and duration of fog. *Atmospheric Environment* 28:317–322.
GRIEVE, T. G. A., PROCTOR, J. & COUSINS, S. A. 1990. Soil variation with altitude on Volcan Barva, Costa Rica. *Catena* 17:525–543
GRUBB, P. J. 1977. Control of forest growth and distribution on wet tropical mountains; with special reference to mineral nutrition. *Annual Review of Ecology and Systematics* 8:83–107.
HARWOOD, J. E. & KUHN, A. L. 1970. A colorimetric method for ammonia in natural waters. *Water Resources Research* 4:805–811.
HENDRY, C. D., BARRISH, C. W. & EDGERTON, E. S. 1984. Precipitation chemistry at Turrialba, Costa Rica. *Water Resources Research* 20:1677–1684.
HOLDRIDGE, L. R. 1967. *Life zone ecology.* Tropical Science Center, San José, Costa Rica. 67 pp.
INGRAM, S. W. & NADKARNI, N. M. 1993. Composition and distribution of epiphytic organic matter in a neotropical cloud forest, Costa Rica. *Biotropica* 25:370–383.

JOHNSON, D. W. & LINDBERG, S. E. 1992. *Atmospheric deposition and nutrient cycling in forest ecosystems*. Springer-Verlag, New York. 707 pp.

JOHNSON, D. W., VAN MIEGROET, H., LINDBERG, S.E., HARRISON, R. B. & TODD, D. E. 1991. Nutrient cycling in red spruce forests of the Great Smoky Mountains. *Canadian Journal of Forest Research* 21:769–787.

JUVIK, J. O. & NULLET, D. 1995. Relationships between rainfall, cloud-water interception, and canopy throughfall in a Hawaiian montane forest. Pp. 102–114 in Hamilton, L. S., Juvik, J. O. & Scatena, F. S. (eds). *Tropical montane cloud forests*. Springer-Verlag, New York. 264 pp.

KELLER, M., JACOB, D. J., WOFSY, S. C. & HARRISS, R. C. 1991. Effects of tropical deforestation on global and regional atmospheric chemistry. *Climatic Change* 19:139–158.

KELLMAN, M., HUDSON, J. & SANMUGADAS, K. 1982. Temporal variability in atmospheric nutrient influx to a tropical ecosystem. *Biotropica* 14:1–9.

LAWTON, R. O. & DRYER, V. 1980. The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia* 18:101–116.

LLOYD, C. R., GASH, J. H. C., SHUTTLEWORTH, W. J. & DE O. MARQUES-FILHO, A. 1988. The measurement and modelling of rainfall interception by Amazonian rainforest. *Forest and Agricultural Meteorology* 43:277–294.

LOVETT, G. M. 1984. Rates and mechanisms of cloud water deposition to a subalpine coniferous forest. *Atmospheric Environment* 18:361–371.

LOVETT, G. M. 1988. A comparison of methods for estimating cloud water deposition to a New Hampshire, USA subalpine forest. Pp. 309–320 in Unsworth, M. H. & Fowler, D. (eds). *Acid deposition at high elevation sites*. Kluwer, Dordrecht, The Netherlands.

LOVETT, G. M. & KINSMAN, J. D. 1990. Atmospheric pollutant deposition to high-elevation ecosystems. *Atmospheric Environment* 24A:2767–2786.

LOVETT, G. M. & LINDBERG, S. E. 1993. Atmospheric deposition and canopy interactions of nitrogen in forests. *Canadian Journal of Forest Research* 23:1603–1616.

LOVETT, G. M. & REINERS, W. A. 1986. Canopy structure and cloud water deposition in subalpine coniferous forests. *Tellus* 38B:319–327.

LUNDGREN, L. & LUNDGREN, B. 1979. Rainfall interception and evaporation in the Mazumbai forest reserve, West Usambara Mountains, Tanzania. *Geografiska Annaler* 61A:157–177.

MACKERETH, F. J. H., HERON, J. & TALLING, J. F. 1978. *Water analysis*. Scientific Publications Freshwater Biological Association No. 36. pp.

MAMANTEO, B. P. & VERACION, V. P. 1985. Measurements of fogdrip, throughfall and stemflow in the mossy and Benguet pine (*Pinus kesiya* Royal ex. Gordon) forests in the upper Agno river basin. *Sylvatrop, the Philippines Forest Research Journal* 10:271–282.

MCDOWELL, W. H., SANCHEZ, C. G., ASBURY, C. E. & RAMOS PEREZ, C. R. 1990. Influence of sea salt aerosols and long range transport on precipitation chemistry at El Verde, Puerto Rico. *Atmospheric Environment* 24A:2813–2821.

MILLER, E. K., FRIEDLAND, A. J., ARONS, E. A., MOHNEN, V. A., BATTLES, J. J., PANEK, J. A., KADLECEK, J. & JOHNSON, A. H. 1993. Atmospheric deposition to forests along an elevational gradient at Whiteface Mountain, NY, U.S.A. *Atmospheric Environment* 27A:2121–2136.

MONTEITH, J. L. & UNSWORTH, M. H. 1990. *Principles of environmental physics, (2nd Edition)*. Edward Arnold, London. 291 pp.

NADKARNI, N. M. 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. *Biotropica* 16:249–256.

NADKARNI, N. M. 1986. An ecological overview and checklist of vascular epiphytes in the Monteverde Cloud Forest Reserve, Costa Rica. *Brenesia* 10:35–39.

NADKARNI, N. M. & MATELSON, T. J. 1991. Dynamics of fine litterfall within the canopy of a tropical cloud forest, Monteverde. *Ecology* 72:2071–2082.

NADKARNI, N. M., MATELSON, T. J. & HABER, W. A. 1995. Structural characteristics and floristic composition of a neotropical cloud forest, Monteverde, Costa Rica. *Journal of Tropical Ecology* 11; 481–495.

OLSEN, S. R. & SOMMERS, L. E. 1982. Phosphorus. Pp. 403–430 in Page, A. L., Miller, R. H. & Keeney, D. R. (eds). *Methods of soil analysis. Part 2: Chemical and microbial properties*. American Society of Agronomy and the Soil Science Society of Amarilo, Madison, Wisconsin. 1159 pp.

PARKER, G. G. 1983. Throughfall and stemflow in the forest nutrient cycle. *Advances in Ecological Research* 13:57–133.

PUCKETT, L. J. 1991. Spatial variability and collector requirements for sampling throughfall volume and chemistry under mixed-hardwood canopy. *Canadian Journal of Forest Resources* 21:1581–1588.

SCHAEFER, D. A. & REINERS, W. A. 1990. Throughfall chemistry and canopy processing mechanisms. Pp. 241–284 in Lindberg, S. E., Page, L. A. & Norton, S. A. (eds). *Acid precipitation: Volume 3. Sources, deposition and canopy interactions*. Springer-Verlag, Berlin, New York.

SCHULZE, E. -D. 1989. Air pollution and forest decline in a spruce (*Picea abies*) forest. *Science* 244:776–783.

STÄDTMULLER, T. 1987. *Cloud forests in the humid tropics: a bibliographic review*. Centro Agronomico Tropical de Investigacion y Ensenanza, Turrialba, Costa Rica. 81 pp.

STÄDTMULLER, T. & AGUDELO, N. 1990. Amount and variability of cloud moisture input in a tropical cloud forest. *International Association of Hydrological Sciences Publication* 193:25–32.

STEINHARDT, U. 1979. Untersuchungen über den Wasser- und Nährstoffhaushalt eines andienen Wolkenwaldes in Venezuela. *Göttinger Bodenkundliche Berichte* 56: 1–185.

STEINHARDT, U. & FASSBENDER, H. W. 1979. Caracteristicas y composición quimica de las lluvias del los Andes occidentales de Venezuela. *Turrialba* 29:175–182.

STEVENS, P. A., NORRIS, D. A., SPARKS T. H. & HODGSON, A. L. 1994. The impacts of atmospheric nitrogen inputs on throughfall, soil and stream water interactions for different aged forest and moorland catchments in Wales. *Water, Air, and Soil Pollution* 73:297–317.

SYSTAT, 1992. *SYSTAT: The system for statistics*. Systat, Inc., Evanston, Illinois. 257 pp.

TANNER, E. V. J., KAPOS, V. & FRANCO, W. 1992. Nitrogen and phosphorus fertilization effects of Venezuelan montane forest trunk growth and litterfall. *Ecology* 73:78–86.

TANNER, E. V. J., KAPOS, V., FRESKOS, S., HEALY, J. R. & THEOBALD, A. M. 1990. Nitrogen and phosphorus fertilization of Jamaican montane forest trees. *Journal of Tropical Ecology* 6:231–238.

ULRICH, B. 1983. Interaction of forest canopies with atmospheric constituents: SO_2, alkali and earth alkali cations and chloride. Pp. 33–45 in Ulrich, B. & Pankrath, J. (eds). *Effects of accumulation of air pollutants in forest ecosystems*. D. Reidel, Dordrecht, The Netherlands.

VANCE, E. D. & NADKARNI, N. M. 1990. Microbial biomass and activity in canopy organic matter and the forest floor of a tropical cloud forest. *Soil Biology and Biochemistry* 22:677–684.

VANCE, E. D. & NADKARNI. N. M. 1992. Root biomass distribution in a moist tropical montane forest. *Plant and Soil* 142:31–39.

VAN EK, R. AND DRAAIJERS, G. P. J. 1994. Estimates of atmospheric deposition and canopy exchange for three common tree species in the Netherlands. *Water, Air, and Soil Pollution* 73:61–82.

VENEKLAAS, E. V. 1990. *Rainfall interception and aboveground nutrient fluxes in Colombian montane tropical rain forest*. Ph.D. thesis, University of Utrecht, Utrecht, The Netherlands.

VENEKLAAS, E. V. & VAN EK, R. 1990. Rainfall interception in two tropical montane rain forests, Colombia. *Hydrological Processes* 4:311–326.

VIS, M. 1986. Interception, drop size distributions and rainfall kinetic energy in four Colombian forest ecosystems. *Earth Surface Processes and Landforms* 11:591–603.

VOGELMANN, H. W. 1973. Fog interception in the cloud forest of eastern Mexico. *Bioscience* 23:96–100.

VONG, R. J. & KOWALSKI, A. S. 1995. Eddy correlation measurements of size-dependent cloud droplet turbulent fluxes to complex terrain. *Tellus* 47B:331–352.

VONG, R. J., SIGMON, J. T. & MUELLER, S. F. 1991. Cloud water deposition to Appalachian forests. *Environmental Science and Technology*. 25:1014–1021.

WEATHERS, K. C., LIKENS, G. E., BORMANN, F. H., BICKNELL, S. H., BORMANN, H. T., DAUBE, B. C., EATON, J. S., GALLOWAY, J. N., KEENE, W. C., KIMBALL, K. D., MCDOWELL, W. H., SICCAMA, T. G., SMILEY, D & TARRANT, R. A. 1988. Cloud water chemistry from ten sites in North America. *Environmental Science and Technology* 22:1018–1026.

WEAVER, P. L. 1972. Cloud moisture interception in the Luquillo Mountains in Puerto Rico. *Caribbean Journal of Science* 12:129–144.