

**Retention and Release of Inorganic Nitrogen by Epiphytic Bryophytes in a Tropical Montane Forest<sup>1</sup>**

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**ABSTRACT**

We investigated the role of epiphytic bryophytes in the nitrogen (N) cycle of a tropical montane forest in Monteverde, Costa Rica. We used a mass balance approach to calculate net retention of inorganic N by (a) epiphytic bryophytes, (b) epiphyte assemblages, (c) host tree foliage, and (d) vascular epiphyte foliage that we exposed to cloud water and precipitation solutions. Results were scaled up to the ecosystem level using a multi-layered model of the canopy that was driven by meteorological and atmospheric deposition data. Model predictions were evaluated against measurements of throughfall at the site. We used ion exchange resin cores to estimate net N mineralization in bryophyte litter and humus in the canopy. Results showed that epiphytic bryophytes and epiphyte assemblages retained 40-96% of the inorganic N additions in cloud water, mist, and concentrated precipitation solutions. In contrast, retention by foliage of host trees and vascular epiphytes from solutions was insignificant. Our model estimated that epiphytic components retained 3.4 kg N ha<sup>-1</sup> yr<sup>-1</sup>, which is equivalent to 50% of the inorganic N in atmospheric deposition (6.8 kg N ha<sup>-1</sup> yr<sup>-1</sup>). Annual net N mineralization in bryophyte litter was 5-8 kg N ha<sup>-1</sup> yr<sup>-1</sup>, which is equivalent to 39-51% of total annual net N mineralization in the canopy (13-16 kg N ha<sup>-1</sup> yr<sup>-1</sup>). Our results indicate that epiphytic bryophytes play a major role in N retention and cycling in this canopy by transforming highly mobile inorganic N (ca. 50% of atmospheric deposition is NO<sub>3</sub><sup>-</sup>N) to less mobile (exchangeable NH<sub>4</sub><sup>+</sup>) and recalcitrant forms in biomass and remaining litter.

*Key words: Epiphytic bryophytes; nitrogen cycle; atmospheric deposition; nitrogen mineralization; tropical montane forest; Costa Rica.*

Forest canopies alter fluxes of energy, water and nutrients in predictable manners. A mechanistic understanding of a number of processes has been limited by our knowledge of the canopy's structural and biological complexity. For example, tropical montane forests support a great diversity of epiphytes, many of which have evolved efficient strategies for acquiring water and nutrients (Benzing 1990), but we know little about their effects on hydrologic and nutrient fluxes at the ecosystem level.

Because many epiphytes are closely linked to atmospheric sources of nutrients (Hietz et al. 2002), they also may be susceptible to alterations to nutrient cycles in the tropics, particularly increased nitrogen (N) deposition. Increased N deposition has had significant negative effects on community composition and ecosystem processes in a number of temperate ecosystems (e.g., Aber et al. 1998, Berendse et al. 2001). Thus, determining the role of epiphytes in N cycling is important in understanding the implications of N loading in tropical montane forests. Recently, changes in land use, including the conversion of forest to agricultural lands and the associated seasonal biomass burning, have increased N emissions to the atmosphere at tropical latitudes (Vitousek et al. 1997, Galloway and Cowling 2002). The concentrations of nitrate ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ) in cloud water at some tropical sites are as high as those at sites in the northeastern United States that are affected by anthropogenic emissions (Clark et al. 1998b). Nitrate and  $\text{NH}_4^+$  ions are deposited on the canopy by wet deposition of precipitation, dry deposition of gases, vapors, and particles, and cloud water deposition (Lovett and Lindberg 1993, Asbury et al. 1994, Clark et al. 1998c). The net effect of a forest canopy on deposition from the atmosphere is typically calculated by comparing measured or modeled estimates of total deposition (wet + dry + cloud) to N fluxes in throughfall (TF) and stemflow. Using this approach, ecosystem-level investigations in temperate forests have shown that most forest canopies retain inorganic N from atmospheric deposition, and that N retention is strongly related to N deposition. Highest rates of deposition and retention have been reported from montane forest sites that are exposed to cloud water in addition to wet and dry deposition (Lovett and Lindberg 1993, Friedland and Miller 1999).

Process-level investigations in temperate forests have elucidated mechanisms of canopy uptake and leaching of inorganic N, and have demonstrated the importance of solution residence times, cuticular resistances, and diffusion gradients across canopy surfaces to control rates of inorganic N retention (Lovett et al. 1989, Schaefer and Reiners 1990, Wilson 1992). Foliage of both coniferous and broad-leaved species retain some  $\text{NH}_4^+$  but little  $\text{NO}_3^-$  from cloud water and precipitation (Reiners and Olson 1984, Garten and Hanson 1990, Wilson 1992, Lumme 1994). Epiphytic lichens on twig and branch surfaces retain both  $\text{NH}_4^+$  and  $\text{NO}_3^-$  from atmospheric deposition (Reiners and Olson 1984). Parallel research in tropical montane forests have been fewer. Epiphyte-laden canopies exhibit large evaporative losses of cloudwater and precipitation (Bruijnzeel and Proctor 1995, Clark et al. 1998c, Ataroff and Rada 2000), and retain much of the inorganic N in atmospheric deposition (Asbury et al. 1994, Clark et al. 1998c). However, the importance of epiphytic vegetation in regulating inorganic N fluxes from the atmosphere has not been evaluated.

A large portion of the epiphytic biomass in tropical montane forests is composed of epiphytic bryophytes (mosses and liverworts). Because of their lack of a waxy cuticle and their large water storage capacities, we hypothesized that epiphytic bryophytes act as

capacitors, buffering inputs of inorganic N in wet and cloud water deposition to the canopy. Leaching and decomposition of bryophyte litter results in a rapid release of a small portion of the retained N (Coxson 1991, Clark et al. 1998a), and most of this N is stored as recalcitrant litter and humus in the canopy (Hofstede et al. 1993, Clark et al. 1998a, Nadkarni et al. 2000).

Therefore, by converting pulsed, highly mobile forms of N into less mobile forms, epiphytic bryophytes could strongly regulate N fluxes from the atmosphere and N release during decomposition. Because vascular epiphyte roots are associated with bryophyte litter throughout the canopy (Vance and Nadkarni 1992, Hofstede et al. 1993, Ingram and Nadkarni 1993), epiphytic bryophytes may play a pivotal role in the supply of N to vascular epiphytes.

In this study, we explored the effects of epiphytes on N flux in a tropical montane forest in three ways. First, we exposed samples of (a) epiphytic bryophytes, (b) “epiphyte assemblages” (composed of bryophytes, vascular epiphytes, and humus), (c) foliage of host trees, and (d) foliage of vascular epiphytes to artificial cloud water, mist and precipitation to determine their effects on inorganic N fluxes in these solutions. Second, we developed and evaluated a hydrologic and inorganic N flux model for the canopy by integrating these data in a multi-layered representation of canopy structure to scale experiments to the ecosystem level. We used the model to partition observed inorganic N retention by the canopy among canopy components, and to explore the effects of increased N deposition to a tropical montane forest. Third, we measured net N mineralization rates in epiphytic bryophyte litter and humus to estimate annual amounts of N cycled internally in the canopy.

## **MATERIALS AND METHODS**

**STUDY SITE.**--- Research was conducted within a 4-ha plot of primary forest in the Monteverde Cloud Forest Reserve in the Cordillera de Tilarán, in west central Costa Rica (10° 18' N, 84° 48' W), described in Nadkarni and Wheelwright (2000). The three seasons are differentiated by the migration of the intertropical convergence zone: (a) dry season (February to April), characterized by wind-driven cloud and mist; (b) wet season (May to October), characterized by convective precipitation with mean windspeed ( $u$ ) < 2 m s<sup>-1</sup>; and (c) transition season (November to January), characterized by wind-driven mist and precipitation with mean  $u$  ≥ 2 m s<sup>-1</sup>. Mean annual precipitation measured at a site 3 km NW of the study site (1959-1995) was 2519 mm, but note that wind-driven cloud water and mist inputs were not directly measured (Clark et al. 2000). Annual cloud water and precipitation depth at the site during the study was 3547 mm, 10% of which was deposited as cloud water and mist (Clark et al. 1998c). Mean monthly minimum and maximum temperatures at the site during this period ranged between 13.9 and 16.5 °C and between 17.6 and 21.1 °C, respectively (Clark et al. 2000).

The study site is in the tropical lower montane wet forest zone of Holdridge (1967), further classified by Lawton and Dryer (1980) as leeward cloud forest. Canopy height is 15 to 32 m with a few emergents to 35 m, and stem density (>30 cm dbh) is ca. 160 stems ha<sup>-1</sup>. Total epiphyte and live bryophyte masses are estimated at 33.1 t ha<sup>-1</sup> and 4.0 t ha<sup>-1</sup>, respectively (Nadkarni et al. 2000). Upper portions of the canopy have a substantial coverage of epiphytic bryophytes. Assemblages of bryophytes, vascular epiphytes, and canopy humus

are abundant on large branches and stems lower in the canopy. Litter accumulates beneath most bryophytes, and roots of vascular epiphytes and host trees are associated with litter and humus throughout the canopy (Vance and Nadkarni 1992, Ingram and Nadkarni 1993, Nadkarni et al. 2000).

RETENTION OF INORGANIC NITROGEN BY CANOPY COMPONENTS. --- Samples of (a) epiphytic bryophytes, and (b) epiphyte assemblages were collected from the canopies of 10 trees and 14 recent treefalls (<2 weeks old) at the field site. In the laboratory, live, green shoots of epiphytic bryophytes were sorted into four groups that typically co-occurred in the canopy: pendants, fans + tails, mats + wefts, and turfs + cushions (life-form terminology *sensu* Düring 1992). Samples of live bryophytes or epiphyte assemblages were placed in funnels attached to bottles. Shoot densities in the funnels closely approximated those that occur in the canopy. To estimate the release of inorganic N from senescent bryophyte shoots, samples consisting of brown shoots with > 90% intact foliage were placed in a third set of funnels so that shoot densities approximated those that occur beneath live bryophytes in the field.

Analytical grade reagents and de-ionized water were used to prepare cloud water, mist, and precipitation solutions (Table 1a,b). Cloud water and mist solutions were applied with a manual pump sprayer, and precipitation solutions were applied with a watering bottle. Average application rates and concentrations of  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ , and other major ions in artificial solutions were within the range of those measured in cloud water, mist, and precipitation at the field site (Clark et al. 1998b,c). Ambient air temperatures ranged between 17 °C and 21 °C, and ambient light intensity and relative humidity levels were not controlled but were similar for all treatments. At the end of each treatment, leachates were measured for volume, filtered through Gelman 1.0  $\mu$  GF/A filters with a syringe, and stored at 4 °C until analyzed (< 1 week). A mass balance of inorganic N was calculated by subtracting  $\text{NO}_3^-$ -N +  $\text{NH}_4^+$ -N amounts in leachates collected beneath samples from those in the original cloud water and precipitation solution additions. Following each solution treatment, samples were dried at 60 °C for 48 hours and weighed.

Solution treatments were also conducted *in situ* with foliage of three common tree species in the canopy at the field site (*Ocotea tonduzii* (Lauraceae), *Ficus tuerckheimii* (Moraceae), and *Meliosma ideopoda* (Sabiaceae); Table 1c). Members of these families composed 34, 15 and 4 % of the basal area of canopy trees > 30 cm dbh (Nadkarni et al. 2000). Single rope techniques and a meteorological tower were used to gain access to foliage samples in mid-canopy locations (16-23 m above the forest floor). Solutions were applied as described above (Table 1), and leachates were collected with funnels and bottles suspended below the samples. Similar solution treatments were conducted with two abundant vascular epiphytes (*Disterigma humboldtii* (Ericaceae), and *Pleurothallis ruscafolia* (Orchidaceae)) in the laboratory (Table 1d). Intact samples (including roots and humus) were collected from three trees at the field site. Samples were placed in plastic pots, and plastic trays with Parafilm sleeves were fitted around the base of shoots to collect leachates from foliage and stem surfaces. Following each treatment, foliage and stems were separated from roots and humus, dried at 60 °C, and weighed.

MODEL DEVELOPMENT. --- We developed a multi-layered canopy model using estimates of leaf area, projected epiphyte area, epiphyte biomass, and canopy humus mass that were assessed at the field site to scale up the results of the solution addition experiments to the ecosystem level. Estimates of canopy structure and epiphyte mass were made from field measurements and destructive sampling at the field site (Nadkarni et al. 2000; Table 2).

The model is based on the Rutter and Penman-Monteith equations. It simulates the effects of representative canopy components (tree and vascular epiphyte foliage, epiphytic bryophytes, and epiphyte assemblages) on  $\text{NO}_3^-$  and  $\text{NH}_4^+$  fluxes in cloud water and precipitation (Table 2). The model was written in QuickBASIC, and was driven by hourly meteorological data (cloud water and precipitation inputs, air temperature, relative humidity, incident solar radiation, windspeed) and event-based cloud water and precipitation chemistry (ARSC-type passive cloud water collector, bulk precipitation collector) collected at the field site (Clark et al. 1998b,c). Do we need to say something about the tower from which the data were collected – from a small gap adjacent to the field site, 27 m tall....

In the model, the canopy is arrayed in three layers, each composed of either (1) foliage of trees, and (2) epiphytic bryophytes (upper canopy), or (1) foliage of trees and vascular epiphytes, and (2) epiphyte assemblages, and humus (mid- and lower canopy) (Table 2). A running balance of solutions stored by each component was calculated as a function of inputs in cloud water, precipitation and drainage from other components, and outputs via evaporation and drainage (Rutter et al. 1971):

$$dS_i/dt = P_i + D_{i-1} - E_i - D_i \quad (1)$$

where,  $S_i$  is the water stored by canopy component  $i$ ,  $P_i$  is the interception rate of cloud water and precipitation,  $D_{i-1}$  is the drainage rate from components above  $i$ ,  $E_i$  is the evaporation rate from  $i$ , and  $D_i$  is the rate of drainage from  $i$ . Solution storage capacities were estimated from field and laboratory leaching experiments, and were similar to other studies (Table 2; Pocs 1982, Veneklaas et al. 1990).

Precipitation input to each component was calculated as a function of its interception area. Interception areas for vascular plant foliage were approximated as a negative exponential function of leaf area (Table 2). Interception area for epiphytic bryophytes in the upper canopy was estimated to range between 0.5 to 0.9  $\text{m}^2 \text{m}^{-2}$  ground area, and was modeled as a function of mean windspeed. Interception area was assumed to be 0.5  $\text{m}^2 \text{m}^{-2}$  for events characterized by vertically falling precipitation when  $u < 2 \text{ m s}^{-1}$ . At higher windspeeds, tangential penetration of droplets into the canopy was simulated by increasing the interception area up to a maximum of 0.9  $\text{m}^2 \text{m}^{-2}$ . Interception areas for epiphyte assemblages in the lower canopy were assumed to be 0.2 and 0.1  $\text{m}^2 \text{m}^{-2}$  ground area (Table 2).

Potential rates of evaporation from each layer in the canopy were calculated using the Penman-Monteith equation (Monteith and Unsworth 1990). Net radiation at each layer was estimated as a negative exponential function of incident shortwave radiation, assuming an albedo of 0.15, and the projected surface area of each layer. Mean windspeed at each canopy layer was approximated as an exponential decay function of windspeed measured above the canopy. VPD above and within the canopy was estimated from relative humidity (RH) measurements at the top of the canopy and empirical RH profiles through the canopy (Clark 1994). An actual rate of evaporation is calculated for each component as a function of its surface area and a component-

specific resistance term. Resistance terms are negligible when components were saturated, and were calculated as a proportion of stored water when components are unsaturated (Rutter et al. 1971, Gash et al. 1979).

Drainage from each component was calculated as a function of its surface area, and drainage rates are modeled as a 'leaky cup' when they are wetting up (Massman 1983, De Ridder 2001). Approximately 5% of the drainage from each component is diverted to stems, but hydrologic and inorganic N fluxes in stemflow were not simulated in this version of the model. Solution drainage from components and non-intercepted cloud water and precipitation were summed at each time-step to calculate hydrologic flux to the forest floor in throughfall.

Derivation of the inorganic N flux portion of the canopy model followed the model of  $K^+$  and  $NH_4^+$  exchange developed by Lovett et al. (1989) for an *Abies balsamea* forest. They recognized that the diffusion of  $NH_4^+$  into canopy components is a function of concentration gradients across canopy surfaces, and a surface resistance to diffusion from external to internal pools (Schaefer and Reiners 1990, Wilson 1992):

$$F_N = ([N_{int}] - [N_{ext}]) / r_N \quad (2)$$

where  $F_N$  is the flux of  $NH_4^+$  or  $NO_3^-$  across the component surface,  $N_{int}$  and  $N_{ext}$  are the internal and external concentrations, respectively, and  $r_N$  is the resistance to diffusion from external to internal pools.  $N_{int}$  is assumed to be minimal due to assimilation by living cells, and  $N_{ext}$  is expressed as the amount of inorganic N stored in solutions on canopy surfaces:

$$F_N = -[N_{ext}] / S_i * r_N \quad (3)$$

Resistance coefficients for each component were derived from the results of solution treatments. We assumed that cloud water and precipitation inputs mixed completely with solutions already stored by components, and that components retained  $NH_4^+$  and  $NO_3^-$  only from stored solutions. We calculated the value of  $r_N$  by solving equation (3) using the empirical value of  $F_N$  for each solution treatment. We obtained mean values of  $r_N$  for each component by averaging results from all of the solution treatments using that component.

MODEL EVALUATION, SENSITIVITY ANALYSES, AND SIMULATIONS. --- To evaluate model performance, the model was run using meteorological variables and concentrations of  $NH_4^+$  and  $NO_3^-$  obtained during nine events. Three events were characterized by mist-only, three events by advective precipitation with mean  $u \geq 2 \text{ m}^{-2}$ , and three events by convective precipitation with mean  $u < 2 \text{ m}^{-2}$ . All occurred following at least 48 hr without cloud water or precipitation inputs, and had complete precipitation and TF depths and chemistry ( $n = 20$  collectors within 1 ha; Clark et al. 1998b). Model sensitivity analyses were performed on 1) the interception area of epiphytic bryophytes in the upper canopy, 2) the resistance coefficients for net  $NH_4^+$  retention for all epiphytic components, and 3) the stemflow drainage parameter for all components.

To estimate the effects of epiphytic components vs. vascular plant foliage on inorganic N fluxes from the atmosphere, inorganic N retention by each component was summed separately during event simulations. A Wilcoxon two-sample test was used to evaluate differences in the amount of inorganic N retained among groups. Reduced epiphyte mass was approximated by simultaneously reducing solution storage capacities of epiphytic components. We explored the responses of canopy components to increased N deposition by

increasing  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations in cloud water and precipitation up to three times ambient levels. We approximated variation in the ability of epiphytic components to retain inorganic N by altering values of the resistance coefficient for  $\text{NH}_4^+$  retention for all epiphytic components simultaneously, and the value of the resistance coefficient for  $\text{NO}_3^-$  retention by epiphytic bryophytes in the upper canopy. On a longer time scale, annual meteorological and deposition data were used to drive the model. Predicted inorganic N in TF was compared to field measurements, and predicted retention was partitioned among components.

NET NITROGEN MINERALIZATION FROM LITTER AND HUMUS. --- Plastic tubes containing litter or humus and ion exchange resins enclosed in mesh rings were used to estimate rates of net N mineralization from bryophyte litter and canopy humus. Samples were collected and separated following the protocol above. Using paired subsamples, one subsample (equivalent to ca. 1.0 g dry weight for recently dead bryophyte shoots or 4.0 g dry weight for humus) was placed on top of a pair of mesh-covered rings (0.5 cm tall, 7 cm diameter) containing 5 g of anion exchange resin (Ionac NA-38, 16-50 mesh size beads) or cation exchange resin (Dowex 50W-X8, 20-50 mesh size beads) in an open-ended PVC plastic tube (12 cm tall, 7 cm inner diameter) (DiStefano and Gholz 1986). A second pair of cation and anion resin rings was placed above the sample in the tube to absorb ions entering in throughfall. The other subsample was extracted in 100 ml of 2 M KCl for 24 hours, dried for 48 hr at 60 °C, and weighed. Additional litter and humus samples were also extracted in 100 ml deionized water or 2 M KCl.

Litter and humus cores were placed in mid-canopy locations of three trees at the field site in the transition season (November 1992) and the wet season (August 1993). A third set of litter cores was stored in the dark in the laboratory at 17 to 21 °C, and leached with deionized water every 2 days (equivalent to 1.0 cm day<sup>-1</sup>). All cores were harvested after 21 days. Litter and humus samples were extracted in 100 ml 2 M KCl, dried and weighed. Anion and cation resin rings were extracted separately in 100 ml of 2 M KCl. Net  $\text{NH}_4^+$  and  $\text{NO}_3^-$  mineralization was calculated as  $[(\mu\text{g } \text{NH}_4^+ \text{-N or } \text{NO}_3^- \text{-N extracted from resin rings} + \mu\text{g } \text{NH}_4^+ \text{-N or } \text{NO}_3^- \text{-N extracted from samples in cylinders after 21 days}) \text{ g dry wt}^{-1}] - ((\mu\text{g } \text{NH}_4^+ \text{-N or } \text{NO}_3^- \text{-N}) \text{ g dry wt}^{-1})$  extracted from subsamples at the beginning of the experiment (DiStefano and Gholz 1986).

CHEMICAL ANALYSES. ---Ammonium concentrations in solutions, leachates, and KCl extractions were determined using an indophenol blue colorimetric technique (Harwood and Kuhn 1970, Keeney and Nelson 1982). Nitrate + nitrite ( $\text{NO}_2^-$ ) concentrations were determined colorimetrically following  $\text{NO}_3^-$  reduction in a copper-cadmium column (Mackereth et al. 1978, Keeney and Nelson 1982). All analyses were performed within one week of collection on a colorimeter (Sequoia Turner #340) equipped with a semi-automated flowcell assembly.

DATA ANALYSES. ---One-way ANOVAs and Tukey's HSD multiple comparisons or t-tests were used where appropriate following determination of homogeneity of group variances

(Bartlett's test; data were log-transformed and retested where necessary). Correlation coefficients (Pearson's product-moment) were calculated for the relationship between measured vs. predicted depths and inorganic N in TF. SYSTAT statistical packages were used for all analyses (SYSTAT 1992).

## RESULTS

**NET RETENTION OF INORGANIC NITROGEN BY CANOPY COMPONENTS.** --- Epiphytic bryophytes retained 59-93% of the inorganic N in cloud water, mist, and relatively concentrated precipitation solutions, but did not retain inorganic N from relatively dilute precipitation solutions (ANOVA,  $P < 0.01$ ; Fig. 1a). Similar proportions of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were retained from cloud water and mist solutions, and a greater proportion of  $\text{NH}_4^+$  was retained from precipitation solutions (paired sample t-tests,  $P < 0.05$ ; Table 3).

The four life-form groups of epiphytic bryophytes retained similar amounts of inorganic N on a per-sample basis. However, pendants and fans + tails retained greater amounts of inorganic N than mats + wefts and turfs + cushions on a mass basis (ANOVA,  $P < 0.05$ ).

A greater proportion of  $\text{NH}_4^+$  than  $\text{NO}_3^-$  was leached from senescent shoots of epiphytic bryophytes treated with mist and precipitation solutions (Table 3).

Epiphyte assemblages retained 40-96 % of the inorganic N in cloud water, mist, and precipitation solutions (ANOVA,  $P < 0.01$ ; Fig. 1b). In contrast, samples of host tree foliage and vascular epiphyte foliage had only a minor effect on inorganic N in artificial cloud water and mist solutions (Fig. 1c, d).

**MODEL EVALUATION, SENSITIVITY ANALYSES, AND SIMULATIONS.** --- The length of events used for model evaluation ranged from 3 to 122 hours, and with the exception of events characterized by only cloud water deposition (which produced insufficient TF to analyze and use for model evaluation), these spanned the range of precipitation intensities and N concentrations measured at the field site. Predicted TF depths were within 1 SD of those measured in the field ( $r = 0.98$ ; Fig. 2). Predicted inorganic N flux in TF exceeded measured values during only one mist event, and this by  $0.3 \text{ mg N m}^{-2}$ , representing 9% of atmospheric deposition for that event ( $r = 0.91$ ; Fig. 3). Altering the value of the interception area of epiphytic bryophytes in the upper canopy layer from  $0.5$  to  $0.9 \text{ m}^2 \text{ m}^{-2}$  ground area had relatively little effect on predicted TF depths ( $< 3\%$  difference) or inorganic N in TF ( $< 11\%$  difference) for all simulated events. Increasing the value of the resistance coefficient for net retention of  $\text{NH}_4^+$  by all epiphytic components from 1.25 to 20 increased inorganic N in TF by 80 to 109% for cloud water, mist and precipitation events with  $u > 2 \text{ m s}^{-1}$ , but only by 10% for convective precipitation (Fig. 4).

Negative values of  $r_{\text{NH}_4^+}$  simulated net release of  $\text{NH}_4^+$  from the canopy, even though vascular plant foliage in the lower canopy retained relatively greater amounts of  $\text{NH}_4^+$ . Although this is only an approximation of net leaching of  $\text{NH}_4^+$  from litter and humus in the canopy, release was observed only when relatively large pools of  $\text{NH}_4^+$  occurred in solutions stored by epiphytic components. Altering the value of the stem drainage parameter from 0 to 0.1 around the estimated value of 0.05 (which simulated 5% of drainage from all components to

stems) resulted in a  $\pm 14\%$  difference in TF depths for all simulated events. Over this range of values of the stem drainage parameter, predicted amounts of inorganic N in TF varied between  $-8\%$  to  $+17\%$  for all simulated events.

Predicted retention of inorganic N by epiphytic components was greater than that for vascular plant foliage for all simulated events during model evaluation (Wilcoxon two-sample test,  $P < 0.01$ , Table 4). This was equivalent to 33-67% of inorganic N deposition to the canopy, and 61-78 % of the inorganic N retained by the canopy. During simulated cloud water and mist events, epiphytic bryophytes in the upper canopy layer retained greater amounts of N than epiphytic components lower in the canopy, because only small volumes of solution penetrated to lower canopy layers, and solutions that did reach these layers were relatively depleted in inorganic N. During simulated precipitation events that were characterized by relatively high rates of solution input to the canopy, components in the upper canopy saturated rapidly, and solution penetration to components lower in the canopy was greater. Epiphytic components in the lower canopy thus became more important in retaining inorganic N when precipitation rates were higher.

Reduction of the mass of epiphytic components to 5% of mass values estimated from field measurements resulted in an increase in predicted TF depths of 30-116% for all simulated events. Mass reduction of epiphytes increased inorganic N in TF in a non-linear manner. A reduction to 5% of initial values resulted a 3- to 4-fold increase in inorganic N flux to forest floor for cloud water, mist, and advective precipitation events, but only a 2-fold increase for intense convective precipitation (Fig. 5). An increase in  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations from 1 to 3 times ambient levels in cloud water or mist resulted in a nearly linear increase in predicted amounts of inorganic N retained by the canopy, which averaged 98% and 88% of deposition, respectively. Epiphytic bryophytes and vascular plant foliage in the upper canopy retained the greatest amounts of inorganic N during these events. Nitrate flux to the forest floor doubled when the value of the resistance coefficient for  $\text{NO}_3^-$  retention by epiphytic bryophytes in the upper canopy was increased 8-fold (1.01 to 8.0) for cloud water events, and 5-fold (1.01 to 5.0) for mist events. During precipitation events characterized by high rates of solution input to the canopy,  $\text{NO}_3^-$  flux to the forest floor was not doubled until small negative values of  $r_{\text{NO}_3^-}$  were used, which simulated net leaching of  $\text{NO}_3^-$  from bryophytes in the upper canopy.

Using the 1991-1992 annual meteorological and N deposition data to drive the model, we estimated that N in TF was  $1.8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , ca. 26% of annual N deposition ( $6.8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ) (Fig. 6). Predicted inorganic N in TF were similar to field measurements. Inorganic N in TF was  $1.9 \pm 0.3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (mean  $\pm 1$  SE) over the same period (Clark et al. 1998b). In the model, the canopy retained ca. 82% of the  $\text{NO}_3^-$  and 61% of the  $\text{NH}_4^+$  deposited in cloud water, mist and precipitation. Of the  $5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  retained by the canopy, ca.  $3.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (68%) was retained by epiphytic bryophytes, litter and humus, and  $1.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  was retained by vascular plant foliage. Overall, our model simulations suggest that non-vascular epiphytic components retained ca. 50% of annual inorganic N deposition to this ecosystem (Fig. 6).

NET N MINERALIZATION IN LITTER AND HUMUS. --- Exchangeable inorganic N in recently formed bryophyte litter and canopy humus was dominated by  $\text{NH}_4^+$  (> 86%; T-test,  $P < 0.05$ ; Table 5). Greater amounts of  $\text{NH}_4^+$  were extracted with 2 M KCl than with de-ionized water, indicating the presence of a large pool of exchangeable  $\text{NH}_4^+$  in litter. Net  $\text{NH}_4^+$  mineralization in bryophyte litter was greater than net nitrification during all three experiments, and represented > 72% of net N mineralized (T-tests,  $P < 0.001$ ; Table 6). Net N mineralization from bryophyte litter was significantly greater than that from canopy humus (ANOVA,  $P < 0.05$ ; Table 6).

## DISCUSSION

NET RETENTION OF INORGANIC NITROGEN BY CANOPY COMPONENTS. --- High concentrations of inorganic N in cloud water, mist, and relatively concentrated precipitation solutions lead to the development of relatively steep concentration gradients at cell walls and membranes, which facilitates ion exchange and assimilation by epiphytic bryophytes (Schaefer and Reiners 1990, Bates 1992). Nitrate assimilation by *Sphagnum* spp. is apparently due to the activity of noninducible carriers (Diesing and Rudolph 1987). Species of *Sphagnum* and several taxa of epiphytic bryophytes show inducible as well as constitutive nitrate reductase activity when exposed to  $\text{NO}_3^-$  in solution (Woodin et al. 1985, Diesing and Rudolph 1988, Rudolph et al. 1993, K. Clark, unpub. data). The  $\text{NH}_4^+$  assimilating enzymes glutamine synthetase and glutamate synthase have been detected in some bryophytes (Meade 1984).

The lack of inorganic N retention by epiphytic bryophytes from relatively dilute precipitation solutions contrasts with results reported for terrestrial bryophytes from cool temperate and boreal ecosystems (e.g., Woodin and Lee 1987, Bowden 1991). For example, *Sphagnum fuscum* from a subarctic bog retained >95% of the  $\text{NO}_3^-$  in bulk precipitation in the field, and 55-90% of the  $\text{NO}_3^-$  loadings during laboratory leaching experiments (Woodin and Lee 1987). The lack of retention of  $\text{NO}_3^-$  and an insignificant trend towards the retention of  $\text{NH}_4^+$  by vascular plant foliage, which has relatively thick, waxy cuticles, is consistent with results reported for leaching experiments obtained with temperate species (Garten and Hanson 1990, Wilson 1992, Lumme 1994)

MODEL EVALUATION, SENSITIVITY ANALYSES, AND SIMULATIONS. --- The relatively simple equations used to simulate inorganic N retention from solutions stored by canopy components, and our approximation of canopy structure appears to be a useful framework to analyze inorganic N fluxes in this complex canopy. Model predictions matched both individual events and annual fluxes measured at the field site. Although  $\text{NO}_3^-$  is considered to be the more mobile form of inorganic N in forest ecosystems, nearly all of the deposited  $\text{NO}_3^-$  was retained by the canopy. Less  $\text{NH}_4^+$  was retained by the canopy, which is consistent with the internal cycling of  $\text{NH}_4^+$  in the canopy (see below).

Our model indicated that epiphytic components retained a majority of the N retained by the canopy, both on an event basis and at an annual time scale. Model results further indicated that a relatively small biomass of epiphytes had a large effect on inorganic N retention by the canopy, if they are distributed throughout the canopy. Epiphytic bryophytes in the upper canopy layer retained greater amounts of N than epiphytic components lower in the canopy during simulated cloud water and mist events, due to low rates of solution penetration to lower canopy layers, and depletion of inorganic N in the upper canopy. The depletion of deposited  $\text{NH}_4^+$  by the upper canopy during these events is consistent with results of Lovett et al. (1989) in a *Abies balsamea* forest. Epiphytic components in the lower canopy were more important in retaining inorganic N when precipitation rates were higher. This is probably because components in the upper canopy saturated rapidly, and solution penetration to components lower in the canopy was greater.

If retention coefficients are unaltered, increased N concentrations in cloud water and mist would be retained primarily by epiphytic bryophytes in the upper canopy. Seasonal biomass burning resulted in 2- to 3-fold increase in the concentrations of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  in cloud water through the dry season at this site, and concentrations in the late dry season were as high as those at a number of sites in the northeastern United States that are affected by anthropogenic emissions (Clark et al. 1998b). However, the greatest rates of N loading occurred at the beginning of the wet season, when inorganic N concentrations were relatively high in precipitation, as evidenced by the slope of the deposition line during this time (Fig. 6). These results suggest that epiphytic components throughout the canopy could potentially be exposed to increased N deposition from biomass burning.

NET NITROGEN MINERALIZATION IN LITTER AND HUMUS. --- Leaching of inorganic N from recently dead bryophyte shoots and extractable inorganic N in recently formed litter was dominated by  $\text{NH}_4^+$ , which is similar to terrestrial bryophyte litter (Urban and Eisenreich 1988, Verhoeven et al. 1990) and canopy humus (Vance and Nadkarni 1990, Hofstede et al. 1993). Differences in the amount of inorganic N extracted with water vs. KCl indicate the importance of cation exchange sites on cell walls in mediating the storage and leaching of  $\text{NH}_4^+$  from litter (Clymo and Hayward 1982, Richter and Dainty 1989a, Bates 1992). In contrast, relatively smaller pools of KCl-extractable  $\text{NO}_3^-$  in litter are likely a result of fewer anion exchange sites on cell walls (Richter and Dainty 1989b), but are also a function of the relatively small populations of nitrifying bacteria in the canopy at this site (Vance and Nadkarni 1990).

Net N mineralization from recently formed litter of epiphytic bryophytes was greater than rates from canopy humus reported here or previously reported for this site ( $-1.1 \pm 1.6$  to  $3.6 \pm 2.4 \mu\text{g N g}^{-1} \text{ day}^{-1}$ ; Vance and Nadkarni 1990). Relatively high rates of N leaching and net N mineralization have also been reported for litter of terrestrial bryophytes when compared to more highly decomposed peat (e.g., Verhoeven et al. 1990). Initial high rates of inorganic N release from litter are a result of leaching of labile N pools and mineralization by microbial populations, coupled with apparently low rates of N immobilization. The availability of labile C may limit microbial communities in *Sphagnum* litter, which subsequently limits N immobilization (Verhoeven et al. 1990). Vance and Nadkarni (1990) reported a significant increase in  $\text{CO}_2$  evolution and a decrease in levels of extractable inorganic N following the addition of labile C (as glucose) to canopy humus, which is consistent with the hypothesis of Verhoeven et al. (1990).

As decomposition progresses and labile N pools in litter are depleted, rates of leaching and mineralization are presumably reduced and approach the relatively low rates that characterize canopy humus. Canopy litterbag data suggested that labile N pools in recently formed litter of epiphytic bryophytes are depleted relatively rapidly; N mass declined to ca. 70% of initial N mass within six months in the canopy and remained at this level over the second year monitored (Clark et al. 1998a).

Assuming that epiphytic bryophyte biomass is in steady state, we estimated that  $0.8\text{--}1.6 \text{ t ha}^{-1} \text{ yr}^{-1}$  of new bryophyte litter accumulates in the canopy annually (annual production =  $1.2\text{--}2.0 \text{ t ha}^{-1} \text{ yr}^{-1}$  minus litterfall to the forest floor;  $0.4 \text{ t ha}^{-1} \text{ yr}^{-1}$ ; Clark et al. 1998a,

Nadkarni and Matelson 1992). Humus mass in the canopy at this site (approx. 20.8 t ha<sup>-1</sup>; Nadkarni et al. 2000) and mean rates of net N mineralization from litter and humus reported here and by Vance and Nadkarni (1990) were used to calculate annual net N mineralization in the canopy. We assumed that mean rates were representative of net N mineralization in the canopy during the wet and transition seasons (9 months), and that rates were minimal during the dry season (3 months), when litter and humus in the canopy had the lowest water contents (Bohlman et al. 1995). Net N mineralization in recently formed litter was estimated at 4.9 to 8.2 kg N ha<sup>-1</sup> yr<sup>-1</sup>, and accounted for approximately 63% of the annual N loss from recently dead shoots in litterbags in the canopy (7.9-13.1 kg N ha<sup>-1</sup> yr<sup>-1</sup>; Clark et al. 1998a). Net N mineralization in canopy humus was estimated at 7.8 kg N ha<sup>-1</sup> yr<sup>-1</sup>. Although the estimated mass of recently formed litter is only 6-10% of the mass of humus in the canopy, net N mineralization from litter was 39-51% of the N mineralized in the canopy annually.

Ammonium in TF ( $1.3 \pm 0.2$  kg NH<sub>4</sub><sup>+</sup>-N ha<sup>-1</sup> yr<sup>-1</sup>) represented < 8% of the estimated inorganic N mineralized in the canopy. Little of the mineralized NH<sub>4</sub><sup>+</sup> was leached from the canopy, probably because of the high density of cation exchange sites on bryophytes, litter and humus, and because of biotic demand. It is likely that mineralized N was redistributed to new, actively-growing bryophyte shoots, as has been reported for terrestrial bryophytes (e.g., Bates 1992, Rudolph et al. 1993). Mineralized N was also likely taken up by vascular epiphytes, hemi-epiphytes, and host trees, because root biomass is relatively large in the canopy (5.2 t ha<sup>-1</sup>; Vance and Nadkarni 1992, Nadkarni et al. 2000), and fine root ingrowth was detected in canopy litterbags (ca. 0.03 t (t litter)<sup>-1</sup> yr<sup>-1</sup>; Clark 1994) at this site.

Episodes of NH<sub>4</sub><sup>+</sup> leaching from the canopy were detected only at the beginning of the wet season. Flushes of N mineralization following rewetting have been noted in a range of soils (e.g., Cabrera 1993), and it is possible that initial high rates of NH<sub>4</sub><sup>+</sup> leaching and/or mineralization in the canopy are decoupled from biotic demand at the onset of the wet season. Although we have little information on the kinetics of N mineralization rates from recently dead shoots and humus, biotic demand likely increased as the wet season progressed, and resulted in reduced leaching losses from the canopy. Therefore, the relative importance of N sources for epiphytes may be strongly seasonal. Internal cycling of N is probably more important in the wet and transition seasons when N concentrations in precipitation are low and net N mineralization rates are relatively high. Overall, the internal cycling of N in recently formed litter and humus (15.7 to 20.9 kg N ha<sup>-1</sup> yr<sup>-1</sup>) greatly exceeded the amount of N retained by epiphytic bryophytes, litter and humus from atmospheric deposition (3.4 kg N ha<sup>-1</sup> yr<sup>-1</sup>).

Nitrogen emissions are projected to increase at tropical latitudes, and will increase concentrations of N in cloud water and precipitation in tropical montane forests (Vitousek et al. 1997, Clark et al. 1998b, Galloway and Cowling 2002). Both leaching experiments and model simulations indicate that a large portion of the deposited NO<sub>3</sub><sup>-</sup> was retained by epiphytic bryophytes. Because NO<sub>3</sub><sup>-</sup> reduction is energetically expensive, it is possible that inducible nitrate reductase activity in bryophytes is reduced when N is more abundant. This assay could serve as an early indicator of increased N deposition in these ecosystems.

The effects of increased N deposition to the diverse epiphyte community are complex, but are likely to lead to an increase in the rate of N cycling in the canopy. At other sites, retention of inorganic N from the atmosphere has led to higher tissue concentrations of N in terrestrial and epiphytic bryophytes (Ferguson et al. 1984, Farmer et al. 1991, Aerts et al. 1992, Baddeley et al. 1994). Higher tissue N concentrations will likely result in greater rates of N mineralization from bryophyte litter in the canopy.

Questions that should be addressed in future research include: (1) at what level of inorganic N deposition do epiphytic bryophytes become "N saturated" (sensu Aber et al. 1998)? (2) Do negative feedbacks on the rates of N cycling exist in the canopy, i.e., does increased N deposition reduce N fixation by cyanobacteria? (3) At what point will increased N deposition and rates of N cycling in the canopy lead to significant changes in competitive interactions and community composition in the canopy of tropical montane forests (Baddeley et al. 1994, Berendse et al. 2001). (4) What are the ecosystem implications of greater epiphyte productivity on overall forest dynamics? An understanding of these relationships is key to predicting the effects of increased atmospheric deposition of N to the diverse canopy biota in tropical montane forests.

In contrast to temperate cloud forests, increased N inputs may stimulate the production of both epiphytes and host trees, and are then stored as highly recalcitrant pools in the canopy and soil organic matter (Grieve et al. 1990, Vance and Nadkarni 1990, Nadkarni et al. 2000). Therefore, significant changes in canopy biota could occur before the more "typical" symptoms of N saturation are detected (e.g., enhanced  $\text{NO}_3^-$  concentrations in stream water, calcium and magnesium imbalances in foliage; Aber et al. 1998).

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Table 1. Inorganic N concentrations, application rates, and experiment duration for the artificial cloud water, mist, and precipitation solutions applied to (a) epiphytic bryophytes, (b) assemblages of epiphytic bryophytes, vascular epiphytes, and humus, (c) host tree foliage, and (d) vascular epiphyte foliage.

Treatment	N concentrations		Rate mm hr <sup>-1</sup>	Duration hr
	mg NO <sub>3</sub> <sup>-</sup> N l <sup>-1</sup>	mg NH <sub>4</sub> <sup>+</sup> N l <sup>-1</sup>		
a. Epiphytic bryophytes <sup>1</sup>				
Cloud water	1.16	1.35	0.5	8
Mist	0.45	0.41	1.0	8
Precipitation 1	0.10	0.09	5.0	4
Precipitation 2	0.06	0.06	10.0	4
Precipitation 3	0.01	0.02	10.0	4
b. Epiphyte assemblages (bryophytes, small vascular epiphytes, and humus) <sup>2</sup>				
Cloud water	1.15	1.36	0.5	8
Mist	0.62	0.12	1.8	4
Precipitation 1	0.12	0.12	13.0	4
Precipitation 2	0.04	0.05	8.2	4
c. Host tree foliage <sup>3</sup>				
Cloud water	1.14	1.44	0.38 ± 0.11	4
Mist	0.46	0.39	0.87 ± 0.27	4
d. Vascular epiphyte foliage <sup>4</sup>				
Cloud water	1.32	0.81	0.23 ± 0.08	8
Mist	0.32	0.28	0.88 ± 0.36	4

<sup>1</sup>Mean mass was 2.41 ± 0.39 g (mean ± 1 SD, n = 25) for pendants, 2.41 ± 0.62 g for fans and tails, 3.26 ± 0.59 for mats and wefts, and 4.45 ± 0.53 g for turfs and cushions.

<sup>2</sup>Mean mass was 8.81 ± 2.55 g (n = 20)

<sup>3</sup>Mean leaf area was 2.4 ± 0.7 dm<sup>2</sup> (n = 10) for *Ocotea*, 2.2 ± 0.4 dm<sup>2</sup> for *Ficus*, and 2.3 ± 0.3 dm<sup>2</sup> for *Meliosma*.

<sup>4</sup>Mean mass was 1.53 ± 0.55 g (n = 10) for *Disterigma*, and 1.89 ± 0.35 g for *Pleurothallis*.

Table 2. Canopy structure and epiphyte mass used in the model. Projected LAI of vascular plant foliage was estimated at  $6 \text{ m}^2 \text{ m}^{-2}$ , consistent with light attenuation measurements and litterfall collections at the field site (Nadkarni and Matelson 1991). Epiphyte 1 is intended to simulate (a) epiphytic bryophytes in the upper portions of the canopy, and Epiphyte 2 and 3 are intended to simulate (b) epiphyte assemblages composed of epiphytic bryophytes, vascular epiphytes, and humus on small branches and large branches and junctions with main stems, respectively.

Layer	Component	Surface area $\text{m}^2/\text{m}^2$	Interception area ( $\text{m}^2/\text{m}^2$ )	Epiphyte mass <sup>1</sup> ( $\text{g}/\text{m}^2$ )	Solution Storage <sup>2</sup> ( $\text{l}/\text{m}^2$ )
1	Foliage 1	3.0	0.778	----	0.3
	Epiphyte 1	0.5 - 0.9	0.5 - 0.9	340	1.70
2	Foliage 2	2.0	0.632	----	0.2
	Epiphyte 2	0.2	0.2	1,160	4.55
3	Foliage 3	1.0	0.393	----	0.1
	Epiphyte 3	0.1	0.1	1,495	4.26

<sup>1</sup>from Nadkarni et al. 2000

<sup>2</sup>Solution storage at saturation (epiphytic bryophytes  $541 \pm 47 \text{ ml g}^{-1}$  (mean  $\pm 1 \text{ SD}$ ,  $n = 60$ ), bryophytes, vascular epiphytes, and litter  $459 \pm 17 \text{ ml g}^{-1}$  ( $n = 18$ ), canopy humus and roots  $285 \pm 11 \text{ ml g}^{-1}$  ( $n = 10$ ), and vascular plant foliage  $100 \pm 15 \text{ ml m}^2$  ( $n = 12$ )) from Clark et al. 1994 and Nadkarni et al. 2000

Table 3. Percent net retention of  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N additions by live shoots or recently formed litter of epiphytic bryophytes from artificial cloud water, mist and precipitation solutions. Values with different superscripts are significantly different (Paired-sample T-tests,  $P < 0.05$ ).

Sample	Treatment	% net retention (+) or release (-) $\pm$ 1 SD	
		$\text{NO}_3^-$ -N	$\text{NH}_4^+$ -N
Epiphytic bryophytes (n = 20 for each treatment)			
	Cloud water	92.0 $\pm$ 5.5	94.9 $\pm$ 3.4
	Mist	84.5 $\pm$ 10.6	81.3 $\pm$ 25.5
	Precipitation 1	49.2 $\pm$ 14.4 <sup>a</sup>	68.3 $\pm$ 12.4 <sup>b</sup>
	Precipitation 2	34.4 $\pm$ 16.8	14.3 $\pm$ 68.1
	Precipitation 3	-10.6 $\pm$ 56.9 <sup>a</sup>	-211.7 $\pm$ 204.1 <sup>b</sup>
Epiphytic bryophyte litter (n = 5)			
	Mist	24.2 $\pm$ 12.3 <sup>a</sup>	-239.3 $\pm$ 165.2 <sup>b</sup>
	Precipitation 2	-19.8 $\pm$ 50.7 <sup>a</sup>	-462.7 $\pm$ 376.2 <sup>b</sup>

Table 4. Predicted net retention of inorganic N by vascular plant foliage and epiphytic bryophytes, litter and humus from cloud water, mist, and precipitation events (n = 3 for each type of event)

Event type	Predicted net retention of inorganic N ( $\text{mg N m}^{-2} \pm 1$ SD)	
	Vascular plant foliage	Bryophytes, litter, humus
Cloud water	1.09 $\pm$ 0.76	7.97 $\pm$ 2.99
Mist	0.64 $\pm$ 0.53	5.43 $\pm$ 3.27
Precipitation ( $u \geq 2 \text{ m}^{-2}$ )	0.26 $\pm$ 0.09	4.08 $\pm$ 1.71
Precipitation ( $u < 2 \text{ m}^{-2}$ )	0.06 $\pm$ 0.05	1.50 $\pm$ 0.64

Table 5. Exchangeable inorganic nitrogen in recently formed litter of epiphytic bryophytes (n = 10) and canopy humus (n = 5). Significant differences among sample types are indicated with different letters (ANOVA,  $P < 0.05$ ), all differences among  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N are significant (T-tests,  $P < 0.05$ ).

Sample type	Extractant	Exchangeable inorganic N (mean $\mu\text{g N g}^{-1} \pm 1 \text{ SD}$ )		
		$\text{NO}_3^-$ -N	$\text{NH}_4^+$ -N	$\text{N}_{\text{inorg}}$
Epiphytic bryophytes	DI $\text{H}_2\text{O}$	$2.2 \pm 0.1$	$48.7 \pm 5.6^{\text{a}}$	$50.9 \pm 6.0^{\text{a}}$
Epiphytic bryophytes	2M KCl	$15.4 \pm 23.7$	$96.2 \pm 14.9^{\text{b}}$	$111.6 \pm 34.8^{\text{b}}$
Canopy humus	2M KCl	$0.4 \pm 0.1$	$73.2 \pm 6.6^{\text{b}}$	$73.5 \pm 6.7^{\text{b}}$

Table 6. Net nitrogen mineralization from recently dead shoots of epiphytic bryophytes and canopy humus measured in ion exchange resin cores. Significant differences among sample types, date, and location are indicated with different letters (ANOVA,  $P < 0.05$ ), significant differences among  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N are indicated with different numbers (T-tests,  $P < 0.05$ ). bdl = below detection limits.

Sample type Location/season	Net N mineralization (mean $\mu\text{g N g}^{-1} \text{ day}^{-1} \pm 1 \text{ s.d.}$ )		
	$\text{NO}_3^-$ -N	$\text{NH}_4^+$ -N	$\text{NO}_3^-$ -N + $\text{NH}_4^+$ -N
Bryophyte litter			
November (trans.)	$4.6 \pm 1.9^{\text{a1}}$	$11.8 \pm 1.4^{\text{a2}}$	$16.3 \pm 1.7^{\text{a}}$
August (wet)	$0.7 \pm 0.6^{\text{b1}}$	$9.5 \pm 1.5^{\text{a2}}$	$10.2 \pm 1.2^{\text{b}}$
Laboratory	$0.5 \pm 0.4^{\text{b1}}$	$16.9 \pm 4.6^{\text{a2}}$	$17.3 \pm 5.0^{\text{a}}$
Canopy humus			
August (wet)	bdl	$0.9 \pm 0.3^{\text{b}}$	$0.9 \pm 0.3^{\text{c}}$

## Figure captions

Figure 1. Inorganic nitrogen ( $\text{NH}_4^+ + \text{NO}_3^-$ ) in solution additions and retained by (a) epiphytic bryophytes, (b) assemblages of epiphytic bryophytes, vascular epiphytes, litter and humus, (c) host tree foliage, and (d) vascular epiphyte foliage during solution treatments. Retention values are means  $\pm$  1 SD, \* = significant retention or leaching at  $P < 0.05$ .

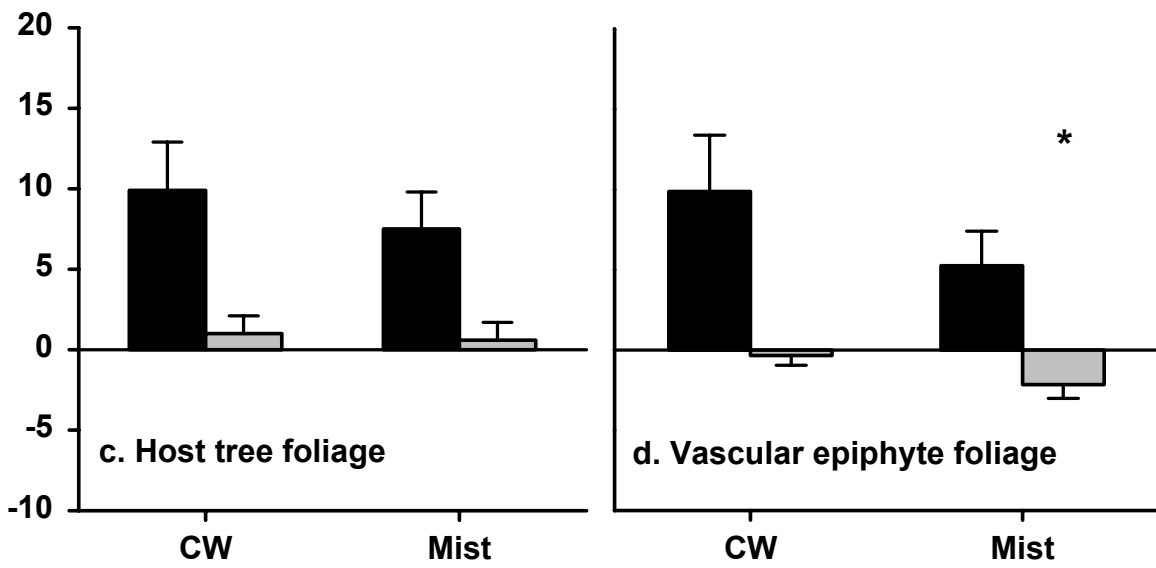
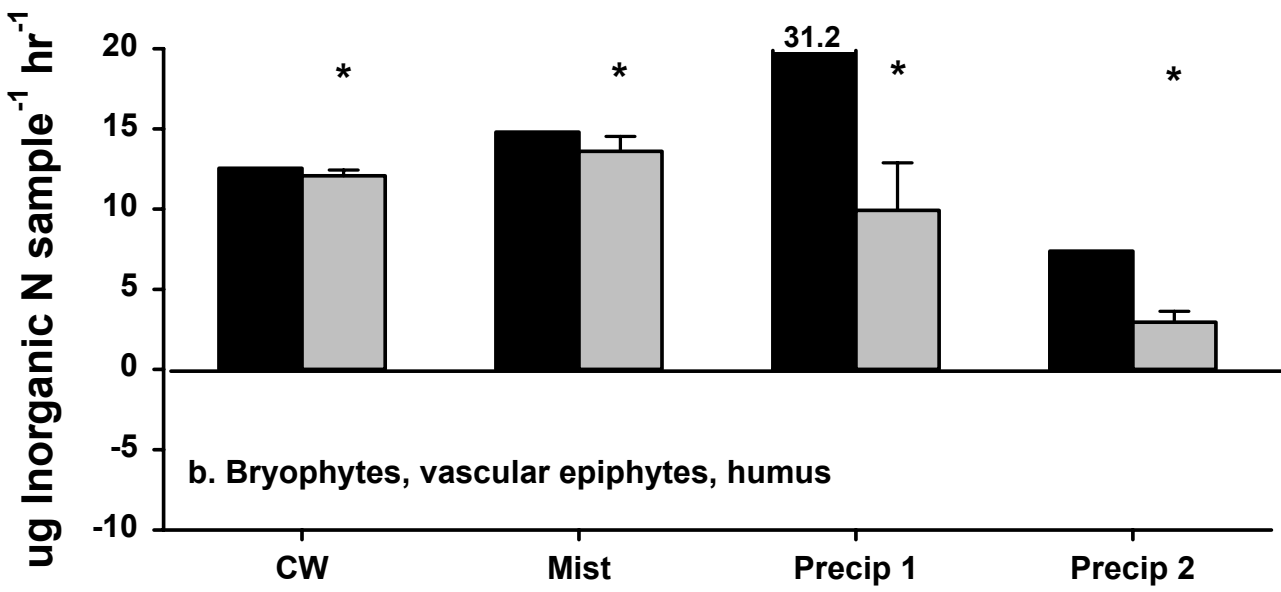
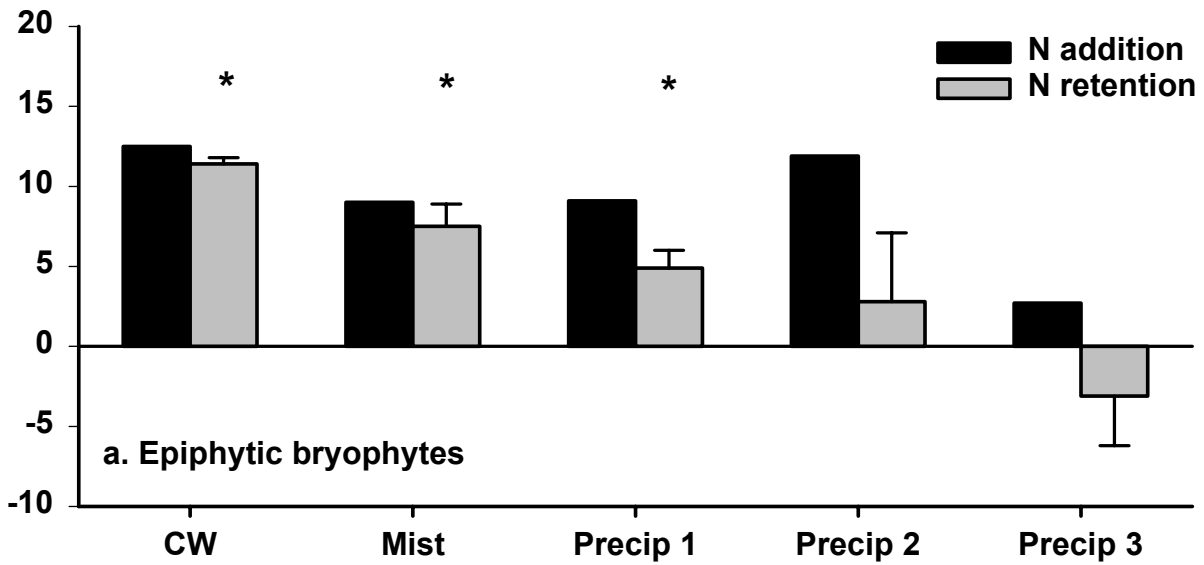
Figure 2. Comparison of measured (mean mm  $\pm$  1 SD, n = 20 collectors) and predicted throughfall depths on the forest floor for three categories of events. Correlation coefficient = 0.98.

Figure 3. Comparison of measured (mean mg N m<sup>-2</sup>  $\pm$  1 SD, n = 20 collectors) and predicted inorganic N in TF on the forest floor for three categories of events. Correlation coefficient = 0.91.

Figure 4. Effect of epiphyte biomass on inorganic N in TF on the forest floor during cloud water and precipitation events with mean deposition rates and inorganic N chemistry.

Figure 5. Effect of the value of the coefficient for  $\text{NH}_4^+$  retention by epiphytic components on inorganic N in TF on the forest floor during cloud water or precipitation events with mean deposition rates and inorganic N chemistry. Deposition of inorganic N for each event is indicated with an arrow for each event.

Figure 6. Annual atmospheric deposition of inorganic N, predicted N net retention by the canopy, net N retention by epiphytic components, net N retention by vascular plant foliage, and inorganic N in TF on the forest floor. Inorganic N deposition was calculated using cloud water and precipitation depths, and event-based  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations collected at the field site in 1991-92 (Clark et al. 1998b).



**Solution treatment**

