

Retention of Inorganic Nitrogen by Epiphytic Bryophytes in a Tropical Montane Forest¹

Kenneth L. Clark²

Silas Little Experimental Forest, U.S. Forest Service, Northern Global Change Program, 501 Four Mile Road, New Lisbon, NJ 08064

Nalini M. Nadkarni

The Evergreen State University, Lab II 2259, Olympia, WA 98502

and

Henry L. Gholz

Division of Environmental Biology, National Science Foundation, 4201 Wilson Blvd., Arlington, VA 22230

ABSTRACT

We developed and evaluated a model of the canopy of a tropical montane forest at Monteverde, Costa Rica, to estimate inorganic nitrogen (N) retention by epiphytes from atmospheric deposition. We first estimated net retention of inorganic N by samples of epiphytic bryophytes, epiphyte assemblages, vascular epiphyte foliage, and host tree foliage that we exposed to cloud water and precipitation solutions. Results were then scaled up to the ecosystem level using a multilayered model of the canopy derived from measurements of forest structure and epiphyte mass. The model was driven with hourly meteorological and event-based atmospheric deposition data, and model predictions were evaluated against measurements of throughfall collected at the site. Model predictions were similar to field measurements for both event-based and annual hydrologic and inorganic N fluxes in throughfall. Simulation of individual events indicated that epiphytic bryophytes and epiphyte assemblages retained 33–67 percent of the inorganic N deposited in cloud water and precipitation. On an annual basis, the model predicted that epiphytic components retained 3.4 kg N ha/yr, equivalent to 50 percent of the inorganic N in atmospheric deposition (6.8 kg N ha/yr). 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_3^-) to less mobile (exchangeable NH_4^+) and recalcitrant forms in biomass and remaining litter and humus.

RESUMEN

En este estudio se desarrolló y se evaluó un modelo para estimar la retención de nitrógeno (N) inorgánico atmosférico en el dosel de un bosque tropical montano en Monteverde, Costa Rica. Primeramente, estimamos la retención de N inorgánico en muestras de briófitas, grupos de epífitas, hojas de epífitas, y hojas de árboles que fueron expuestas a agua de neblina y de lluvia. Basándose en medidas de estructura del bosque y la biomasa de epífitas se derivó un modelo multi nivel de dosel, estos resultados fueron aumentados a la escala de ecosistema. El modelo fue guiado por datos meteorológicos tomados a cada hora y datos de deposición atmosférica y las predicciones del modelo fueron evaluadas con medidas de la lluvia indirecta (throughfall) del sitio. Las predicciones del modelo fueron similares a los datos de campo para eventos individuales, el ciclo hidrológico anual y las fluctuaciones de N en la lluvia indirecta. La simulación de eventos individuales indicaron que las briófitas y grupos de epífitas retuvieron 33–67 por ciento de N inorgánico en agua de nubes y de lluvia. Predicciones anuales del modelo indican que los grupos de epífitas retienen 3.4 kg N ha/año, equivalente al 50 por ciento del N inorgánico en la deposición atmosférica (6.8 kg N ha/año). Nuestros resultados indican que las briófitas en el dosel desempeñan un papel muy importante en la retención y ciclaje de N inorgánico, porque transforman el N con alta movilidad en N de baja movilidad y a formas mas recalcitrantes en la biomasa, la hojarasca y el humus.

Key words: atmospheric deposition; Costa Rica; epiphytic bryophytes; nitrogen cycle; tropical montane forest.

FOREST CANOPIES RETAIN INORGANIC NITROGEN (N) from precipitation, dry deposition of gases, vapors and particles, and cloud water deposition (Lovett & Lindberg 1993, Asbury *et al.* 1994, Clark *et al.* 1998c, Friedland & Miller 1999). Process-level investigations have demonstrated the importance of solution residence times on canopy surfaces, and of cuticular resistances and diffusion gradients across canopy surfaces in controlling retention rates (Lovett *et al.* 1989, Schaefer & Reiners 1990, Wilson 1992, Lumme 1994). In tropical montane forests, epiphytic bryophytes (mosses and liverworts) form much of the surface area in the canopy (Hofstede *et al.* 1993, Nadkarni *et al.* 2000). Because of their large water storage capacity and their lack of a waxy cuticle, we hypothesized that epiphytic

bryophytes account for much of the inorganic N retained by the canopy from precipitation and cloud water deposition. Leaching and decomposition of bryophyte litter results in rapid release of only a small portion of the retained N (Coxson 1991, Clark *et al.* 1998a), thus much 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).

Because epiphytes can utilize atmospheric sources of nitrogen (Hietz *et al.* 2002), they may be susceptible to alterations to the N cycle in the tropics. 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 & Cowling 2002, van der Werf *et al.* 2004). Resultant concentrations of inorganic N in cloud water at some tropical sites can be as high as those at sites in

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² Corresponding author; e-mail: kennethclark@fs.fed.us

the northeastern United States that are affected by anthropogenic emissions (Clark *et al.* 1998b). 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. In this study, we developed and evaluated a hydrologic and inorganic N flux model for the canopy of a tropical montane forest at Monteverde, Costa Rica. We used the model to partition observed inorganic N retention among canopy components, and to explore some effects of increased N deposition to a tropical montane forest.

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 by 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 light precipitation; (b) wet season (May to October), characterized by convective precipitation with mean windspeed (u) < 2 m/sec; and (c) transition season (November to January), characterized by wind-driven precipitation with mean $u \geq 2$ m/sec. Mean annual precipitation measured at a site 3 km NW of the study site was 2519 mm (1959–1995), but cloud water and wind-driven precipitation inputs were not directly measured (Clark *et al.* 2000). Annual cloud water and precipitation input was 3547 mm at the site during the study period (1991–1992), 10 percent of which was deposited as cloud water (Clark *et al.* 1998c). Mean monthly temperatures ranged from 16 to 19°C at the site during our study (Clark *et al.* 2000).

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

MODEL DEVELOPMENT: RETENTION OF INORGANIC NITROGEN BY CANOPY COMPONENTS.—Samples of (a) epiphytic bryophytes; (b) epiphyte assemblages consisting of bryophytes, small vascular epiphytes, litter and humus; and (c) vascular epiphytes were collected at the field site and exposed to artificial cloud water and precipitation solutions in the laboratory (Appendix 1). Solution treatments were conducted *in situ* with the foliage of three common tree species in the canopy at the field site. Results from these experiments were used to estimate water-holding capacities and re-

tention rates of inorganic N for canopy components in the model (Appendix 1).

MODEL DEVELOPMENT: MODEL STRUCTURE.—We developed a multilayered canopy model using estimates of canopy structure and epiphyte mass to scale the results of the solution addition experiments to the ecosystem level (Appendix 2). Estimates of leaf area, projected epiphyte area, epiphyte biomass, and canopy litter and humus mass were derived from field measurements and destructive sampling at the field site (Nadkarni *et al.* 2000). The model is based on canopy water balance and Penman–Montieth equations. It simulates the effects of representative canopy components (epiphytic bryophytes, epiphyte assemblages, and foliage of vascular epiphytes and trees) on NO_3^- and NH_4^+ fluxes in cloud water and precipitation. The model was written in QuickBASIC, and was driven using hourly meteorological data (cloud water and precipitation inputs, air temperature, relative humidity, incident solar radiation, windspeed) and event-based cloud water and precipitation chemistry collected from a 30-m meteorological tower at the field site (Clark *et al.* 1998b,c; Appendix 2).

MODEL EVALUATION AND SIMULATIONS.—To evaluate model performance, the model was run using hourly meteorological data and concentrations of NH_4^+ and NO_3^- obtained during three events characterized by cloud water and light precipitation with mean windspeed (u) ≥ 2 m/sec, three events with relatively intense precipitation and mean $u \geq 2$ m/sec, and three events with convective precipitation and $u < 2$ m/sec. All events occurred following at least 48 hr without cloud water or precipitation inputs, and had complete precipitation and throughfall (TF) amounts and chemistry ($N = 20$ collectors within 150 m of the meteorological tower; Clark *et al.* 1998c). Correlation coefficients (Pearson's product-moment) were calculated for the relationship between measured versus predicted amounts and inorganic N flux in TF (SYSTAT 1992). To estimate the effects of epiphytic components versus vascular plant foliage on inorganic N fluxes from the atmosphere, inorganic N retention by each component was summed separately for the events described above and three additional cloud water events, and a Wilcoxon two-sample test was used to evaluate the differences among groups. On a longer time scale, annual hourly meteorological data and event-based deposition data were used to drive the model. Predicted inorganic N in TF was compared to field measurements using *t*-tests, and predicted retention was partitioned among components.

Reduced epiphyte mass was approximated by reducing solution storage capacities of epiphytic components. We explored the responses of canopy components to increased N deposition by increasing NH_4^+ and NO_3^- concentrations in cloud water and precipitation up to three times the ambient levels. Variation in the ability of epiphytic components to retain inorganic N was approximated by altering values of the resistance coefficient for NH_4^+ retention for all epiphytic components, and the value of the resistance coefficient for NO_3^- retention by epiphytic bryophytes in the upper canopy (Appendix 2).

RESULTS

MODEL EVALUATION AND SIMULATIONS.—The length of the events used for model evaluation ranged from 3 to 122 hr, 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 a wide range of precipitation intensities and inorganic N concentrations measured at the field site. Predicted TF amounts were within 1 SD of those measured in the field for all nine events simulated ($r = 0.98$; Fig. 1a). Predicted inorganic N flux in TF exceeded 1 SD of measured values during only one light precipitation event ($r = 0.91$; Fig. 1b).

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 1). Predicted retention by epiphytic bryophytes, litter and humus was equivalent to 33–67 percent of inorganic N deposition to the canopy, and 61–78 percent of the inorganic N

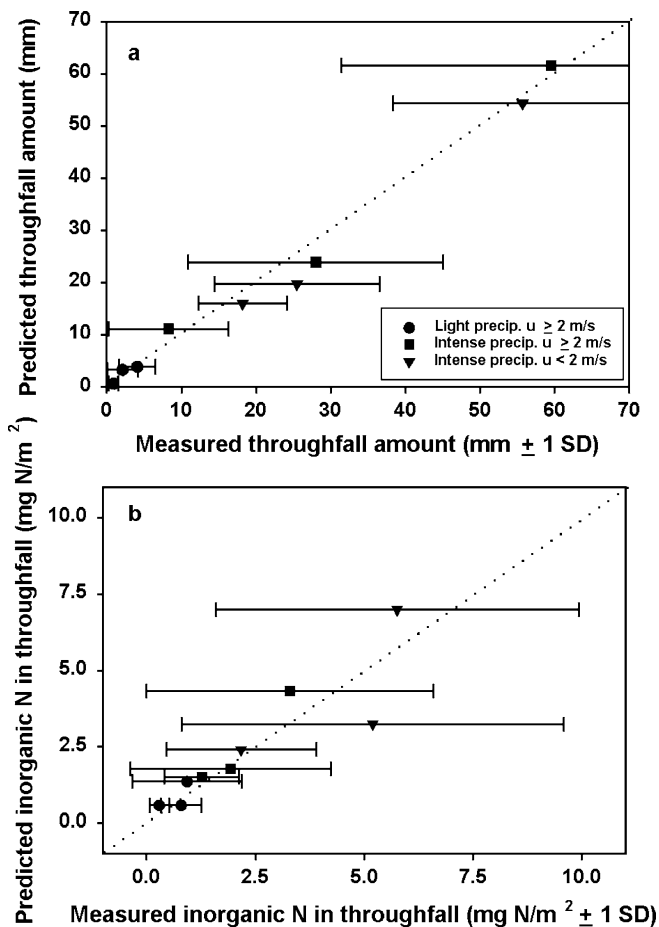


FIGURE 1. Comparison of (a) measured and predicted throughfall amounts (mean mm $\pm$ 1 SD, $N = 20$ collectors, correlation coefficient = 0.98), and (b) predicted inorganic N in throughfall (mean mg N/m² $\pm$ 1 SD, correlation coefficient = 0.91) for three categories of events.

TABLE 1. 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). Differences among groups are significant at $P < 0.01$.

Event type	Predicted net retention of inorganic N (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
Light precipitation	0.64 $\pm$ 0.53	5.43 $\pm$ 3.27
Intense precipitation ($u \geq 2$ /m ²)	0.26 $\pm$ 0.09	4.08 $\pm$ 1.71
Intense precipitation ($u < 2$ /m ²)	0.06 $\pm$ 0.05	1.50 $\pm$ 0.64

retained by the canopy. During simulated cloud water and light precipitation events, epiphytic bryophytes in the upper canopy layer retained greater amounts of N than epiphytic components lower in the canopy. This occurred because only small volumes of solution penetrated to lower canopy layers, and solutions that did reach these layers were already relatively depleted of inorganic N. During simulated events that were characterized by relatively high rates of precipitation, components in the upper canopy saturated rapidly and solution penetration to components lower in the canopy was greater, thus epiphytic components in the lower canopy became more important in retaining inorganic N.

Using hourly meteorological and event-based N deposition data for the 1991–1992 year to drive the model, we estimated that inorganic N in TF was 1.8 kg N ha/yr, *ca* 26 percent of annual N deposition (6.8 kg N ha/yr; Fig. 2), and similar to field measurements of inorganic N in TF (1.9 ± 0.3 kg N ha/yr (mean $\pm$ 1 SE) over the same period; Clark *et al.* 1998c). In the model, the canopy retained 82 percent of the NO_3^- and 61 percent of the NH_4^+ deposited in cloud water and precipitation, which also was similar to field measurements. Of the 5 kg N ha/yr retained by the canopy, we estimated that *ca.* 3.4 kg N ha/yr (68%) was retained by epiphytic bryophytes, litter and humus, and 1.4 kg N ha/yr was retained by the vascular plant foliage (Fig. 2). Overall, our model simulations suggest that nonvascular epiphytic components retained *ca* 50 percent of annual inorganic N deposition to this ecosystem.

Reduction of the mass of epiphytic components resulted in an increase in predicted TF depths for all simulated events. Inorganic N in TF increased in a curvilinear manner as the mass of epiphytes was reduced; up to a 4-fold increase in inorganic N flux to the forest floor resulted when epiphytic mass was reduced by 95 percent. An increase in NH_4^+ and NO_3^- concentrations from one to three times ambient levels in cloud water and light wind-driven precipitation resulted in a nearly linear increase in predicted amounts of inorganic N retained by the canopy, which averaged between 98 and 88 percent of deposition, respectively. Epiphytic bryophytes and vascular plant foliage in the upper canopy retained the greatest amounts of inorganic N during these simulations. Increasing the

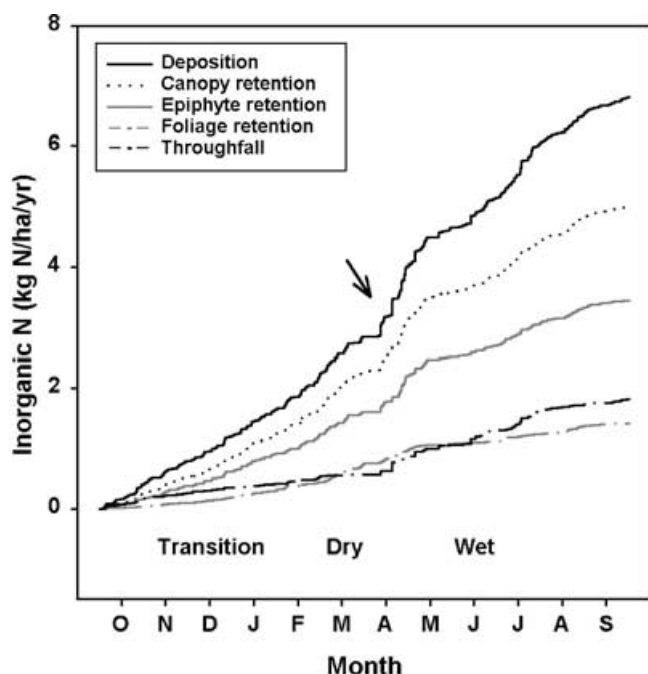


FIGURE 2. Annual atmospheric deposition of inorganic N, predicted net N retention by the canopy, net N retention by epiphytic components, net N retention by vascular plant foliage, and inorganic N in throughfall on the forest floor from October 1991 to September 1992. Inorganic N deposition was calculated using hourly cloud water and precipitation input, and event-based NH_4^+ and NO_3^- concentrations collected at the field site (Clark *et al.* 1998b). The arrow indicates the onset of the wet season.

value of the resistance coefficient for net retention of NH_4^+ by all epiphytic components increased inorganic N in TF during cloud water and advective precipitation events, but not during convective precipitation events. Negative values of $r_{\text{NH}_4^+}$ simulated the release of NH_4^+ from the canopy, even though vascular plant foliage in the lower canopy retained relatively larger amounts of NH_4^+ . Although this is only an approximation of net leaching of NH_4^+ from litter and humus in the canopy, release was observed only when relatively high concentrations of NH_4^+ occurred in solutions stored by epiphytic components. Nitrate flux to the forest floor doubled only when the value of the resistance coefficient for NO_3^- retention by epiphytic bryophytes in the upper canopy was increased 8-fold for cloud water events, and 5-fold for light precipitation events. During intense precipitation events, 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 NO_3^- from bryophytes in the upper canopy.

DISCUSSION

MODEL EVALUATION AND SIMULATIONS.—Our simulation of canopy water balance coupled with the Penman–Monteith equation at three levels appears to be a useful framework to model water storage

and evaporation from this canopy. Using a similar approach at a single level, Schellekens *et al.* (1999) reported that evaporation from the canopy of a lowland tropical rain forest in Puerto Rico was substantially underestimated, unless the evaporation rate from the wet canopy or canopy water storage capacity was increased substantially. In contrast to the forest studied by Schellekens *et al.* (1999), the canopy at Monteverde had a much smaller proportion of free throughfall (5% vs. 23%) and a much larger storage capacity (10.5 vs. 1.2 mm). Windspeed was typically greater at our site compared to the lowland forest site at Puerto Rico, which reduced aerodynamic resistance to evaporation in the model. In addition, our leeward cloud forest site was often at the trailing edge of the advective cloud cap over Monteverde, thus incident solar radiation was relatively high, even during measurable precipitation (Clark *et al.* 2000).

The relatively simple equations used to simulate retention from solutions stored by canopy components is also a useful approach to analyze inorganic N fluxes in complex canopies. Model predictions matched both individual events and annual fluxes measured at the field site well. Although NO_3^- is considered to be the more mobile form of inorganic N in forest ecosystems, >80 percent of the deposited NO_3^- was retained by the canopy. Less NH_4^+ was retained, which is consistent with the internal cycling of NH_4^+ in the canopy (Vance & Nadkarni 1990, Nadkarni *et al.* 2000, see below). Our model indicates that epiphytic components retained the majority of the N retained by the canopy, both on an event basis and on 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 light precipitation events, due to depletion of inorganic N in solutions by the upper canopy, and low rates of solution penetration to lower canopy layers. The depletion of deposited NH_4^+ by the upper canopy is consistent with results of Lovett *et al.* (1989) and Schaefer & Reiners (1990) in a *Abies balsamea* forest. Epiphytic components in the lower canopy were more important in retaining inorganic N when precipitation rates were higher, because components in the upper canopy saturated rapidly, and solution penetration to components lower in the canopy was greater. Concentrations of NO_3^- and NH_4^+ in cloud water increased 2- to 3-fold through the dry season at this site, due in part to biomass burning, and by 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). If retention coefficients are unaltered, increased N concentrations in cloud water and light precipitation will be retained primarily by epiphytic bryophytes in the upper canopy. However, the greatest rates of N loading occurred at the beginning of the wet season, when inorganic N concentrations were relatively high in intense precipitation, as evidenced by the slope of the deposition line during this time (arrow in Fig. 2). Thus, epiphytic components distributed throughout the canopy could potentially be exposed to increased N deposition from biomass burning.

In addition to atmospheric deposition and retention by canopy components, the internal cycling of inorganic N in litter and canopy soil potentially affects inorganic N fluxes in TF. Net N mineralization in the canopy was estimated at 11.0–14.2 kg N/ha/yr, and was dominated by NH_4^+ (Vance & Nadkarni 1990, Clark 1994, Clark *et al.* 1998a). Mineralization rates greatly exceeded the estimated amount of N retained by epiphytic bryophytes, litter and humus from atmospheric deposition (3.4 kg N/ha/yr). Ammonium in TF (1.3 ± 0.2 kg NH_4^+ N/ha/yr) represents <12 percent of the estimated inorganic N mineralized in the canopy. Episodes of NH_4^+ leaching from the canopy were detected only at the beginning of the wet season, and it is possible that high rates of NH_4^+ leaching and/or mineralization are decoupled from biotic demand in the canopy at this time. In the model, leaching occurred only when NH_4^+ pools in epiphytic components were relatively large.

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 & Cowling 2002). The effects of increased N deposition on the diverse epiphyte community are complex, but are likely to lead to an increase in the rate of N cycling in the canopy. Retention of inorganic N from the atmosphere can lead to higher tissue concentrations of N in epiphytic bryophytes (see Clark *et al.* 1998a), and 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 depress nitrate reductase activity of epiphytes, or 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 (*e.g.*, Berendse *et al.* 2001)? An understanding of these relationships is key to predicting the effects of increased N deposition to the diverse canopy biota in tropical montane forests. In contrast to temperate cloud forests, increased N inputs to tropical cloud forests 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 (Vance & 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 NO_3^- concentrations in stream water, calcium, and magnesium imbalances in foliage; Aber *et al.* 1998).

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APPENDIX 1

MODEL DEVELOPMENT: RETENTION OF INORGANIC NITROGEN BY CANOPY COMPONENTS.—Samples of (a) epiphytic bryophytes and (b) epiphyte assemblages consisting of epiphytic bryophytes, small vascular epiphytes, litter and humus were collected from the canopies of 10 trees and 14 recent treefalls (<2 weeks old) at the field site. Samples of bryophytes or epiphyte assemblages were placed in funnels attached to bottles so that shoot densities approximated those in the canopy. Analytical grade reagents and de-ionized water were used to prepare cloud water and precipitation solutions (Table A1). Cloud water and light precipitation solutions were applied with a manual pump sprayer, and relatively intense precipitation solutions were applied with a watering bottle. Concentrations of NO_3^- , NH_4^+ , and other major ions in artificial solutions and average application rates were within the range of those measured in cloud water and precipitation at the field site (Clark *et al.* 1998b,c). At the end of each treatment, leachates were measured for volume, filtered through Gelman 1.0 μ GF/A filters with a syringe, and stored at 4°C until analyzed (<1 week before analysis). Following each solution treatment, samples were weighed, dried at 60°C for 48 h, and weighed again.

Similar solution addition experiments were conducted with foliage and stems of intact samples (including roots and humus)

TABLE A1. Mean inorganic N concentrations, application rates, and experiment durations for artificial cloud water and precipitation solutions applied to (a) epiphytic bryophytes, (b) epiphyte assemblages, (c) vascular epiphyte foliage, and (d) host tree foliage.

Treatment	N concentrations		Rate (mm/h)	Duration (h)
	mg NO_3^- N/l	mg NH_4^+ N/l		
Cloud water	1.19	1.24	0.4	4–8
Precipitation 1	0.46	0.30	1.1	4–8
Precipitation 2	0.11	0.11	9.0	4
Precipitation 3	0.05	0.06	9.1	4
Precipitation 4	0.01	0.02	10.0	4

^aMean mass = 3.13 ± 0.97 g (mean $\pm$ 1 SD, $N = 100$).

^bMean mass = 8.81 ± 2.55 g ($N = 20$).

^cMean mass = 1.53 ± 0.55 g for *Disterigma* ($N = 10$), and 1.89 ± 0.35 g for *Pleurothallis* ($N = 10$).

^dMean leaf area = 2.4 ± 0.7 dm² for *Ocotea* ($N = 10$), 2.2 ± 0.4 dm² for *Ficus* ($N = 10$), and 2.3 ± 0.3 dm² for *Meliosma* ($N = 10$).

of two abundant vascular epiphytes (*Disterigma humboldtii* (Ericaceae) and *Pleurothallis ruscafolia* (Orchidaceae)). Samples were collected from three trees at the field site, and placed in plastic pots in the laboratory. Plastic trays with Parafilm sleeves fitted around the base of shoots were used to collect leachates from foliage and stem surfaces. Following treatments, foliage and stems were separated from roots and humus, dried at 60°C, and weighed. Solution treatments with foliage of three common tree species in the canopy (*Ocotea tonduzii* (Lauraceae), *Ficus tuerckheimii* (Moraceae), and *Meliosma ideopoda* (Sabiaceae)) were conducted *in situ* at the field site. Members of these families composed 34, 15, and 4 percent of the basal area of canopy trees > 30 cm dbh at this site (Nadkarni *et al.* 2000). Single rope techniques and the meteorological tower were used to gain access to foliage samples in mid-

canopy locations (16–23 m above the forest floor). Funnels and bottles suspended below the foliage samples were used to collect leachates.

Ammonium concentrations in solutions and leachates were determined using an indophenol blue colorimetric technique (Keeney & Nelson 1982). Nitrate + nitrite (NO_2^-) concentrations were determined colorimetrically following NO_3^- reduction in a copper–cadmium column (Keeney & Nelson 1982). All analyses were performed within 1 week of collection on a colorimeter (Sequoia Turner #340) equipped with a semi-automated flowcell assembly. A mass balance of inorganic N was calculated by subtracting $\text{NO}_3^- - \text{N} + \text{NH}_4^+ - \text{N}$ amounts in leachates collected beneath samples from those in the original cloud water and precipitation solution additions.

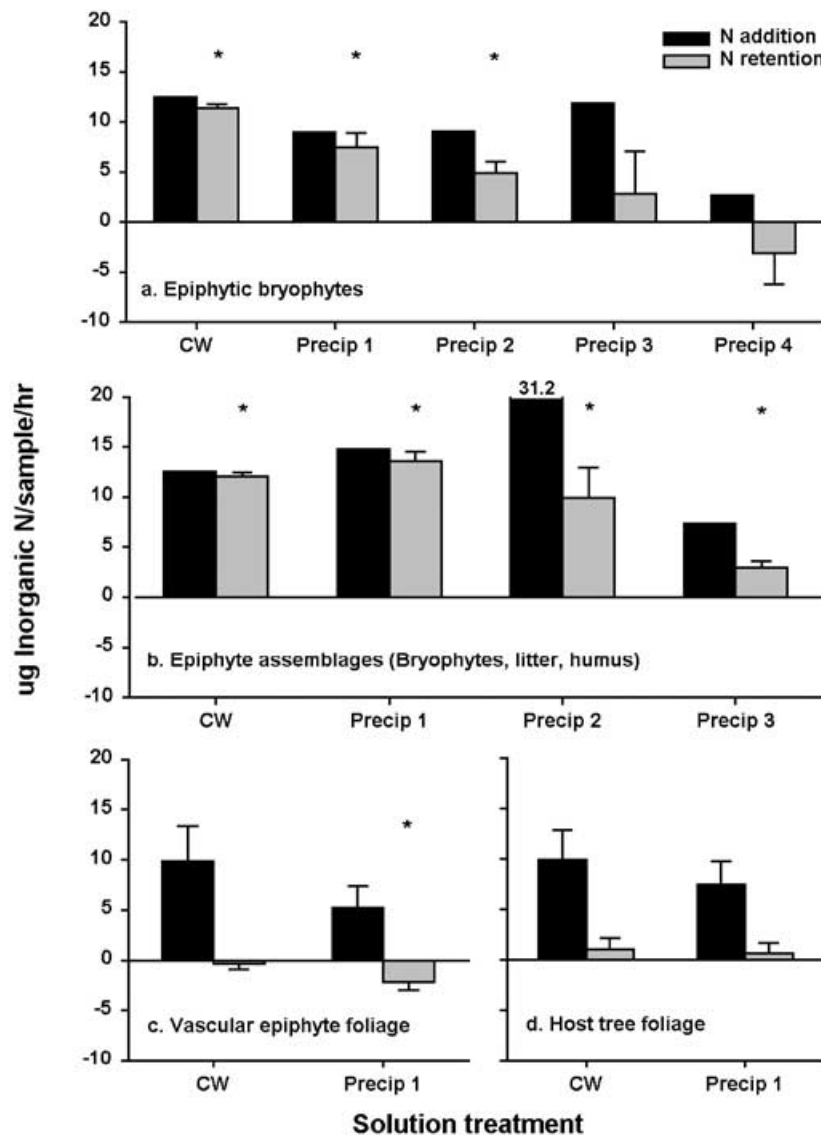


FIGURE A1. Inorganic nitrogen ($\text{NH}_4^+ \text{N} + \text{NO}_3^- \text{N}$) in solution additions and retained by (a) epiphytic bryophytes, (b) epiphyte assemblages, (c) vascular epiphyte foliage, and (d) host tree foliage during solution treatments. Retention values are means $\pm$ 1 SD, * = significant retention or leaching at $P < 0.05$.

Epiphytic bryophytes retained 59–93 percent of the inorganic N in cloud water and relatively concentrated precipitation solutions, but did not retain inorganic N from relatively dilute precipitation solutions (ANOVA, $P < 0.01$; Fig. A1a). Epiphyte assemblages retained 40–96 percent of the inorganic N in cloud water and precipitation solutions (ANOVA, $P < 0.01$; Fig. A1b). In contrast, samples of vascular epiphyte foliage and host tree foliage had only a minor effect on inorganic N in artificial cloud water and mist solutions (Fig. A1c, d).

APPENDIX 2

MODEL DEVELOPMENT: MODEL STRUCTURE.—The canopy is arrayed in three layers in the model, each composed of two components: (1) foliage of trees, and (2) epiphytic bryophytes (upper canopy layer), or (1) foliage of trees and vascular epiphytes, and (2) epiphyte assemblages (mid- and lower canopy layers) (Table A2). A running balance of solutions stored by each component is calculated as a function of inputs in cloud water, precipitation and drainage from other components, and outputs via evaporation and drainage (following 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

TABLE A2. Canopy structure and epiphyte mass used in the model. 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 on small branches and large branches and junctions with main stems, respectively.

Layer	Component	Surface area ^a (m ² /m ²)	Interception area (m ² /m ²)	Epiphyte mass ^b (g/m ²)	Solution storage ^c (l/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	1160	4.55
3	Foliage 3	1.0	0.393	—	0.1
	Epiphyte 3	0.1	0.1	1495	4.26

^aProjected LAI of vascular plant foliage was estimated at 6 m²/m², consistent with light attenuation measurements and litterfall collections at the field site (Nadkarni & Matelson 1991).

^bFrom Nadkarni *et al.* (2000).

^cSolution storage at saturation (epiphytic bryophytes = 5.41 ± 0.47 ml/g (mean ± 1 SD, $N = 60$), bryophytes, vascular epiphytes and humus = 4.59 ± 0.17 ml/g ($N = 18$), canopy humus and roots = 2.85 ± 0.11 ml/g ($N = 10$), and vascular plant foliage 1.00 ± 0.15 ml/m² ($N = 12$)) from Clark (1994) and Nadkarni *et al.* (2000).

were estimated from leaching experiments, and were similar to other studies (Table A2; Pocs 1982, Veneklaas *et al.* 1990). The 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 A2). The interception area for epiphytic bryophytes in the upper canopy was assumed to be 0.5 m²/m² for events characterized by vertically falling precipitation when $u < 2$ m/sec. At higher wind-speeds, tangential penetration of droplets into the canopy was simulated by increasing the interception area of epiphytic bryophytes to 0.9 m²/m² when $u > 2$ m/sec. Interception areas for epiphyte assemblages in the lower canopy were assumed to be 0.2 and 0.1 m²/m² ground area, respectively (Table A2). Alteration of the value of the interception area of epiphytic bryophytes in the upper canopy layer from 0.5 to 0.9 m²/m² ground area had relatively little effect on predicted TF amounts (<3% difference) or inorganic N in TF (<11% difference) for all simulated events used for model development and evaluation.

Potential rates of evaporation from each layer in the canopy were calculated using the Penman–Monteith equation (Monteith & 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. Vapor pressure deficit 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 was calculated for each component as a function of its surface area and a component-specific resistance term. Resistance terms were negligible when components were saturated, and calculated as a proportion of stored water when components were 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 were modeled as a “leaky cup” when they were wetting up (Massman 1983, De Ridder 2001). Approximately 5% of the drainage from each component was diverted to stems in the canopy (which resulted in lower values of stemflow at DBH), 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 TF. Altering the value of the stem drainage parameter from 0 to 0.1 around the estimated value of 0.05 (which simulated the diversion of 5% of the drainage from all components to stems) resulted in a ± 14 percent difference in TF amounts for all simulated events. Over this range of values of the stem drainage parameter, predicted amounts of inorganic N in TF varied between -8 and $+17$ percent for all simulated events.

Derivation of the inorganic N flux portion of the canopy model followed the model of K⁺ and NH₄⁺ exchange developed by Lovett *et al.* (1989) for an *Abies balsamea* forest. They recognized that the diffusion of NH₄⁺ into canopy components is a function of concentration gradients across canopy surfaces, and a surface

resistance to diffusion from external to internal pools (Schaefer & Reiners 1990, Wilson 1992):

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

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,

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

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.