

## Growth, Net Production, Litter Decomposition, and Net Nitrogen Accumulation by Epiphytic Bryophytes in a Tropical Montane Forest<sup>1</sup>

Kenneth L. Clark<sup>2</sup>

School of Forest Resources and Conservation, University of Florida, Gainesville, Florida 32611, U.S.A.

Nalini M. Nadkarni

The Evergreen State College, Olympia, Washington 98505, U.S.A.

and

Henry L. Gholz

School of Forest Resources and Conservation, University of Florida, Gainesville, Florida 32611, U.S.A.

### ABSTRACT

To understand the ecological roles of epiphytic bryophytes in the carbon (C) and nitrogen (N) cycles of a tropical montane forest, we used samples in enclosures to estimate rates of growth, net production, and N accumulation by shoots in the canopy, and litterbags, to estimate rates of decomposition and N dynamics of epiphytic bryophyte litter in the canopy and on the forest floor in Monteverde, Costa Rica. Growth of epiphytic bryophytes was estimated at 30.0–49.9 percent/yr, net production at 122–203 g/m<sup>2</sup>/yr, and N accumulation at 1.8–3.0 g N/m<sup>2</sup>/yr. Cumulative mass loss from litterbags after one and two years in the canopy was 17 ± 2 and 19 ± 2 percent (mean ± 1 SE) of initial sample mass, respectively, and mass loss from litter and green shoots in litterbags after one year on the forest floor was 29 ± 2 and 45 ± 3 percent, respectively. Approximately 30 percent of the initial N mass was released rapidly from litter in both locations. Nitrogen loss from green shoots on the forest floor was greater; about 47 percent of the initial N mass was lost within the first three months. There was no evidence for net N immobilization by litter or green shoots, but the remaining N in litter was apparently recalcitrant. Annual net accumulation of C and N by epiphytic bryophytes was estimated at 37–64 g C/m<sup>2</sup>/yr and 0.8–1.3 g N/m<sup>2</sup>/yr, respectively. Previous research at this site indicated that epiphytic bryophytes retain inorganic N from atmospheric deposition to the canopy. Therefore, they play a major role in transforming N from mobile to highly recalcitrant forms in this ecosystem.

**Keywords:** annual production; carbon cycle; epiphytic bryophytes; litter decomposition; litter nitrogen dynamics; Monteverde, Costa Rica; nitrogen cycle.

EPIPHYTES AND THEIR ACCUMULATED dead organic matter (DOM) are conspicuous features of the canopy in many tropical montane forests (TMFs). Epiphytes and DOM are important in the carbon (C) and nitrogen (N) cycles of these forests because (i) they intercept and retain N from atmospheric deposition (Nadkarni 1986a, Lugo & Scatena 1992, Clark 1994), (ii) rates of N<sub>2</sub> fixation by blue-green bacteria associated with epiphytes and DOM have been estimated at up to 1.6 g N/m<sup>2</sup>/yr (Forman 1975, Bentley & Carpenter 1984, D. Schaefer, pers. comm.), (iii) epiphytes and DOM store up to 1750 g C and 44 g N/m<sup>2</sup> ground area, often greater than the C and N mass in tree foliage (Tanner 1980a, Grubb & Edwards 1982, Nadkarni 1984, Hofstede *et al.* 1993), (iv) leaching of C and N from epiphytes has been estimated at up to 12

g C and 1.2 g N/m<sup>2</sup>/yr (Coxson *et al.* 1992, Coxson 1991), and (v) they contribute up to 20 g C and 0.7 g N/m<sup>2</sup>/yr in litterfall, representing up to 6 percent of the total C and 8 percent of the total N in fine litterfall inputs to the forest floor (Tanner 1980b, Veneklaas 1990, Nadkarni & Matelson 1992a).

Although high species diversity characterizes the epiphyte community in TMFs (Kress 1986, Benzing 1990, Ingram & Nadkarni 1993), epiphytic bryophytes (mosses and liverworts) and their accumulated DOM typically dominate in terms of C and N mass in the canopy, and in the fluxes of epiphyte litterfall to the forest floor. These nonvascular epiphytes likely play an important role in the accumulation of C and N in TMFs because these ecosystems are characterized by high humidity levels, frequent cloud cover and precipitation, and moderate temperatures which favor the growth of bryophytes (Richards 1984, Frahm 1990). Growth drives the uptake of N from a variety of sources,

including atmospheric deposition (Grubb *et al.* 1969, Nadkarni & Matelson 1991, Clark 1994), N leached from other canopy components (Coxson 1991), animal inputs, and N mineralized from DOM in the canopy (Vance & Nadkarni 1990). Because litter derived from epiphytic bryophytes may be characterized by relatively low rates of decomposition (Berg 1984, Van Toreen 1988, Rochefort *et al.* 1990, Longron 1992), they may also be important in the net accumulation of C and N. However, quantitative information is lacking on the roles of epiphytic bryophytes and DOM in the C and N cycles of TMFs. The objectives of this study were to: (i) measure mass accumulation by epiphytic bryophyte samples and estimate their annual growth, net production, and rate of N accumulation; (ii) estimate the decomposition rates and N dynamics of epiphytic bryophyte litter in the canopy and on the forest floor; and (iii) estimate the net accumulation of C and N by epiphytic bryophytes in a TMF.

### MATERIALS AND METHODS

**STUDY SITE.**—Investigations were conducted in a 4 ha plot of primary forest in the research area of the Monteverde Cloud Forest Reserve (MVCFR) in the Cordillera de Tilarán, in west-central Costa Rica (10°18'N, 84°48'W). Slopes and ridges in the MVCFR are similar to other tradewind-dominated lower montane forests in terms of climate, forest physiognomy, and epiphyte mass and diversity (Lawton & Dryer 1980, Nadkarni 1986b, Ingram & Nadkarni 1993). Mean annual precipitation measured at a site approximately 3 km NW and 100 m downslope from the study site between 1959 and 1993 was 2519 mm, but advective cloud water and mist inputs were underestimated (J. Campbell, pers. comm.). Annual precipitation at the study site was 3191 mm between October 1991 and September 1992, 60 percent of which fell during the wet season. An additional 800 mm was deposited as wind-driven cloud water and precipitation (Clark 1994). Mean monthly minimum and maximum temperatures ranged between 13.9–16.5°C and between 17.6–21.1°C, respectively, during the same period.

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. Elevation of the site is between 1480 and 1520 m. Canopy height is 15 to 32 m with a few emergents to 35 m, and stem density is about 160 stems ha<sup>-1</sup> (>30 cm DBH). 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<sup>2</sup>, and live bryophyte biomass is estimated at 406 g/m<sup>2</sup> (Nadkarni *et al.*, unpub. data). Upper and outer portions of the canopy have a substantial coverage of pendant, fan-, and tail-forming bryophytes (life-form terminology *sensu* Mägdefrau 1982, During 1992). Fan-, tail-, weft-, and mat-forming bryophytes are abundant lower in the canopy, and turf- and cushion-forming bryophytes occur on large branches and stems. Accumulations of DOM occur beneath most bryophyte life-forms, and vascular epiphytes are associated with DOM throughout the canopy (Vance & Nadkarni 1990, 1992, Ingram & Nadkarni 1993).

**GROWTH, NET PRODUCTION, AND NITROGEN ACCUMULATION BY SHOOTS.**—Epiphytic bryophyte samples in enclosures (mesh cylinders or cups with mesh bases, depending upon bryophyte life-form) were used to estimate rates of growth, net production, and N accumulation by shoots in the canopy over six-month periods (Russel 1988). Epiphytic bryophyte samples were collected from the canopy and from recent treefalls (<2 weeks old) at the field site and transported to the laboratory. Samples were pooled into two groups: (i) pendant-, fan-, and tail-forming bryophytes, and (ii) mat-, weft-, and turf-forming bryophytes. These groupings were consistent with their co-occurrence on twigs and small branches, and large branches and trunks, respectively. Litter and brown shoots were removed so that samples consisted primarily of live, green shoots.

Samples of pendant-, fan-, and tail-forming bryophytes were separated into sets consisting of two subsamples each (2–5 g fresh weight). Within sets, one subsample was weighed and then loosely packed into a nylon mesh cylinder (1 cm mesh size, 10–12 cm long, 5–7 cm dia., with an open top and a 0.2 cm mesh size base) so that the density of shoots in the mesh cylinders approximated those on twigs and small branches. The other subsample was weighed immediately, dried at 60°C for 48 h, then weighed again to calculate the initial water content and dry mass of the subsample in the mesh cylinder. Twelve trees (> 50 cm dbh) were selected at the field site to represent the most frequently occurring genera in the canopy (Table 1). Nylon lines were placed over small branches in the upper canopy using a modified slingshot connected to a

<sup>1</sup> Received 30 January 1996; revision accepted 28 August 1996.

<sup>2</sup> Author to whom correspondence should be addressed.

TABLE 1. Trees used to monitor (i) mass accumulation by pendant-, fan-, and tail-forming epiphytic bryophytes in mesh cylinders, (ii) mass accumulation by mat-, weft-, and turf-forming epiphytic bryophytes in cups, and (iii) mass loss from epiphytic bryophyte litter in litterbags. Total numbers of mesh cylinders, cups, or litterbags are in parentheses.

Species	(i) Number of trees with mesh cylinders	(ii) Number of trees with cups	(iii) Number of trees with litterbags
<i>Ocotea tonduzii</i>	5 (45)	2 (8)	3 (48)
<i>Meliosma ideopoda</i>	2 (21)	1 (8)	2 (39)
<i>Ficus tuerckheimii</i>	2 (17)	1 (5)	3 (21)
<i>Pouteria viride</i>	1 (13)	1 (4)	1 (24)
<i>Inga tonduzii</i>	1 (7)	—	—
Unknown sp.	1 (3)	—	—
Total	12 (106)	5 (25)	8 (132)

fishing reel. Three to six mesh cylinders containing samples were tied to these lines and positioned next to twigs and small branches in the upper and middle canopy of each tree. Samples were placed in the canopy over four six-month periods: June–December 1990, January–June 1991, August 1991–March 1992, and April–September 1992. Immediately after retrieval, new shoots that had emerged from the mesh cylinders were removed with scissors, samples were removed from the mesh cylinders, and all shoots were dried at 60°C for 48 h and weighed.

Samples of mat-, weft-, and turf-forming bryophytes were separated into sets consisting of two subsamples (5–10 g fresh weight). Within sets, one subsample was weighed and placed in a polypropylene cup (7.5 cm diameter, 5 cm tall, with an open top and a 0.2 cm mesh size base to facilitate drainage). The other subsample was weighed immediately, dried at 60°C for 48 h, and weighed again. Five trees (> 50 cm dbh) were climbed using modified rock-climbing techniques (Table 1). Ten locations along medium and large branches in the mid-canopy were selected in each tree, and two to five of these were chosen randomly for sample placement. Samples were placed in the canopy for two 6-month periods: August 1991–March 1992 and April–September 1992. After retrieval, extraneous material was removed from samples, and they were dried at 60°C for 48 h and then weighed.

DECOMPOSITION AND NITROGEN DYNAMICS OF LITTER.—Decomposition and N dynamics of litter de-

rived from epiphytic bryophytes were estimated using litterbags in the canopy and on the forest floor. Litterbags containing green shoots were also placed on the forest floor. Samples of epiphytic bryophytes (pendant-, fan-, tail-, mat-, weft-, turf-, and cushion-forms) were collected from the canopy and recent treefalls at the site in July and August 1991. For the litter samples, brown, apparently dead shoots with >90 percent of the leaves intact were separated by removing green shoots and more highly decomposed DOM and then pooled to produce a homogeneous mixture. Litterbags (about 10 by 15 cm, with a 0.2 cm mesh size;  $N = 180$ ) were weighed and a subsample (about 8–12 g fresh weight) of litter was loosely packed into each litterbag. Litterbags were dried at 60°C for 48–72 h to prevent the growth of any live shoots, and then weighed again (Berg 1984, Van Toren 1988, Rochefort *et al.* 1990). An additional 50 litterbags containing green shoots were prepared in a similar manner, dried at 60°C for 48–72 h, and then weighed again.

Eight dominant trees with moderate to heavy epiphyte loads were selected for placement of litterbags in the canopy (Table 1). Litterbags were placed on branches of various sizes and inclinations beneath: (i) actively-growing bryophyte shoots, (ii) accumulated bryophyte litter, and (iii) vascular epiphytes but above more highly decomposed DOM. Twelve to 24 litterbags were placed in each tree. Two or three litterbags were collected from each tree after 3, 6, 9, 12, 15, and 24 months. Litterbags were air-dried immediately following harvest. Extraneous material was removed, and samples were dried at 60°C for 48 h and then weighed. Subsamples of litter from each litterbag were stored in clean glass vials. Five 100 m<sup>2</sup> plots were located randomly within the field site for placement of litterbags containing litter or green shoots on the forest floor, and ten litterbags of each type were placed at random locations within each plot. Two litterbags of each type were collected from each plot after 3, 6, 9, 12, and 15 months.

NITROGEN CONCENTRATIONS OF NEW SHOOTS AND LITTER.—Nitrogen concentrations of new shoots in the mesh cylinders and cups were estimated from tissue N concentrations of young, green shoots collected from the canopy of eight trees. Epiphytic bryophyte samples were sorted into the same two life-form groups as above, and green, actively growing shoots were separated with scissors. Samples were dried at 60°C for 48 h and stored in clean

polypropylene vials. Dried subsamples (about 0.1 g) of green shoots, litter from litterbags, or pine foliage standards (Forest Response Program quality assurance samples #02 and #31) were digested in concentrated sulfuric acid with dropwise additions of hydrogen peroxide on a Technicon BD-40 block digester at 340°C (Thomas *et al.* 1967). Diluted ammonium standards (0.1 M NH<sub>4</sub>Cl; Orion #951006) or sulfuric acid blanks were also digested. Nitrogen concentrations in digests were analyzed as ammonium (NH<sub>4</sub><sup>+</sup>) N using an indophenol blue colorimetric technique (Scheiner 1976, Keeney & Nelson 1982), following neutralization with low N NaOH. Colorimetric analyses were performed on a Sequoia Turner 340 colorimeter with a semiautomated flowcell assembly. Percent recovery of N from the pine foliage standards ranged from 93–105 percent of the mean concentration determined with mass spectrometry.

DATA ANALYSES.—Mass accumulation or loss by epiphytic bryophyte samples in the mesh cylinders and cups was calculated as a percentage change from initial sample mass. Two values for mean mass accumulation by each life-form group were calculated from these data for each sampling period. One mean mass accumulation value was calculated by comparing the percent mass accumulation or loss by samples to the initial 6-month percent cumulative mass loss from litterbags in the canopy (see below); samples that exceeded this percentage loss rate were assumed to have lost mass due to disturbance and were excluded from the data sets. A second mean mass accumulation value was calculated by further excluding all samples that lost mass. Normality of all data sets was established. Homogeneity of group variances was determined with Bartlett's test, and data were log-transformed and retested where necessary. For pendant-, fan-, and tail-forming bryophytes, one-way ANOVAs were used to detect differences in mean mass accumulation values among sampling periods. T-tests were used to detect differences in mean mass accumulation values among the two sampling periods for mat-, weft-, and turf-forming bryophytes. T-tests were also used to detect differences in mean mass accumulation values among life-form groups averaged over all sampling periods, and to detect differences in N concentrations among life-form groups. SYSTAT statistical packages (SYSTAT 1992) were used for all analyses. Annual growth rates for epiphytic bryophyte samples were calculated by multiplying overall mean mass accumulation values for the 6-month sampling periods by

two. Net production by epiphytic bryophytes was estimated by multiplying these annual percent growth rates by the estimate of epiphytic bryophyte biomass at the site (406 g/m<sup>2</sup>). Accumulation of N by epiphytic bryophytes was estimated by multiplying the two net production estimates by the mean N concentration of green shoots, assuming there were no seasonal changes in N concentration.

Cumulative mass loss from litter and green shoots in litterbags was calculated as a percent of initial sample mass. Percent change in the N mass of litter and green shoots in litterbags was calculated as:  $100 \times (\text{mass at harvest time } (t_h) \times N \text{ concentration at } t_h) / (\text{initial mass} \times \text{initial N concentration})$ . Net accumulation of C and N by epiphytic bryophytes in the canopy was estimated by subtracting mass and N fluxes in epiphytic bryophyte litterfall to the forest floor (35 g mass and 0.5 g N/m<sup>2</sup>/yr; Nadkarni & Matelson 1992a) from the net production estimates, and then subtracting first year mass and N losses calculated for litterbags in the canopy. Net accumulation of C and N by epiphytic bryophytes on the forest floor was estimated by subtracting first year mass and N losses calculated for litterbags containing green shoots on the forest floor from the amount of epiphytic bryophyte litterfall to the forest floor. Mass estimates were then converted to C mass by multiplying by 0.4 g C (g/mass).

## RESULTS

GROWTH, NET PRODUCTION, AND NITROGEN ACCUMULATION BY SHOOTS.—Mean mass accumulation values for pendant-, fan-, and tail-forming bryophytes in mesh cylinders were similar among sampling periods, so values were pooled (Table 2). Emergent shoot mass contributed 39 and 30 percent to the two mean mass accumulation values ( $6.9 \pm 0.8$  and  $8.0 \pm 1.0$  percent mass accumulation for 6 months; mean  $\pm 1$  SE), respectively. Mean mass accumulation values for mat-, weft-, and turf-forming bryophytes in cups were also similar among sampling periods (Table 2). Pooled mean mass accumulation values were similar among life-form groups, and the overall mean mass accumulation values were  $15.5 \pm 2.4$  and  $24.9 \pm 2.7$  percent (mean  $\pm 1$  SE). Annual percentage growth rates of epiphytic bryophytes calculated from the two overall mean mass accumulation values were  $30.0 \pm 4.8$  percent/yr and  $49.9 \pm 5.4$  percent/yr, and annual net production of epiphytic bryophytes was estimated at  $122 \pm 19$  and  $203 \pm 22$  g/m<sup>2</sup>/yr (mean  $\pm 1$  SE), respectively. Mean N

TABLE 2. Mean mass accumulation (as % change of initial mass over six months) by pendant-, fan-, and tail-forming epiphytic bryophytes in mesh cylinders, and mat-, weft-, and turf-forming epiphytic bryophytes in cups. Sample sizes are in parentheses.

Time period	Mass accumulation (mean % $\pm$ 1 SE)			
	Pendant-, fan-, and tail-forming bryophytes in mesh cylinders		Mat-, weft-, and turf-forming bryophytes in cups	
	Samples $\leq$ 14.3 percent mass loss	Samples $\leq$ 0.0 percent mass loss	Samples $\leq$ 14.3 percent mass loss	Samples $\leq$ 0.0 percent mass loss
June–Dec. 1990	12.9 $\pm$ 7.7 (10)	32.7 $\pm$ 8.1 (5)	—	—
Jan.–June 1991	14.6 $\pm$ 3.6 (14)	19.7 $\pm$ 2.9 (11)	—	—
Aug. 1991–Mar. 1992	22.4 $\pm$ 5.0 (32)	28.4 $\pm$ 5.2 (27)	7.6 $\pm$ 5.2 (14)	16.6 $\pm$ 6.2 (9)
Apr.–Sept. 1992	15.7 $\pm$ 5.3 (28)	27.1 $\pm$ 6.3 (19)	1.1 $\pm$ 4.8 (9)	14.9 $\pm$ 4.5 (4)
Mean of time periods	17.7 $\pm$ 2.8 (84)	26.8 $\pm$ 3.1 (62)	5.0 $\pm$ 3.7 (23)	16.1 $\pm$ 4.4 (13)

concentrations of green shoots were similar among the two life-form groups (Table 3). Accumulation of N by epiphytic bryophytes, calculated as the product of the two net production estimates and mean N concentration of new shoots, was estimated at  $1.8 \pm 0.3$  and  $3.0 \pm 0.3$  g N/m<sup>2</sup>/yr (mean  $\pm$  1 SE).

DECOMPOSITION AND NITROGEN DYNAMICS OF LITTER.—Cumulative mass loss from epiphytic bryophyte litterbags in the canopy was  $17.3 \pm 1.5$  percent (mean  $\pm$  1 SE,  $N = 17$ ) after one year and  $19.3 \pm 2.3$  percent ( $N = 17$ ) after two years (Fig. 1). Cumulative mass loss was  $29.1 \pm 2.2$  percent ( $N = 7$ ) from litter on the forest floor, and  $44.9 \pm 2.7$  percent ( $N = 7$ ) from green shoots on the forest floor after one year (Fig. 1). The initial N

TABLE 3. Mean nitrogen concentration of green shoots of pendant-, fan-, and tail-forming epiphytic bryophytes, and mat-, weft-, and turf-forming epiphytic bryophytes.

Life-form group	Sample size	Nitrogen concentration (mg N/g)	
		Mean	SE
Pendant-, fan-, and tail-forming bryophytes	34	14.1	0.6
Mat-, weft-, and turf-forming bryophytes	25	15.6	0.5
Mean of groups	59	14.7	0.4

concentration of litter was  $12.3 \pm 0.3$  mg N/g (mean  $\pm$  1 SE,  $N = 6$ ). Nitrogen mass remaining in litter was about 67 percent of the initial N mass after one year in both locations (Fig. 2). Nitrogen mass remaining in green shoots after one year was slightly less at 57 percent of the initial N mass. There was no evidence for net N immobilization by litter or green shoots, but the remaining N in litter was apparently recalcitrant during the study (Fig. 2).

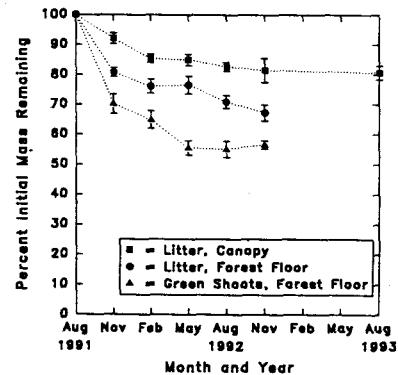


FIGURE 1. Percent of initial mass remaining (mean  $\pm$  1 SE) in litterbags containing epiphytic bryophyte litter or green shoots in the canopy and on the forest floor from August 1991 to August 1993.

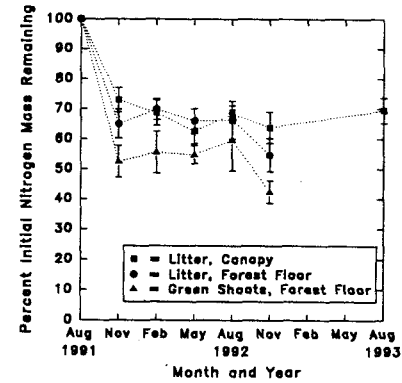


FIGURE 2. Percent of initial nitrogen mass remaining (mean  $\pm$  1 SE) in litterbags containing epiphytic bryophyte litter or green shoots in the canopy and on the forest floor from August 1991 to August 1993.

NET ACCUMULATION OF CARBON AND NITROGEN.—Net accumulation of C and N by epiphytic bryophytes in the canopy was estimated at 29 and 56 g C/m<sup>2</sup>/yr, and 0.6 and 1.2 g N/m<sup>2</sup>/yr, respectively, and net accumulation on the forest floor was estimated at 8 g C/m<sup>2</sup>/yr and 0.2 g N/m<sup>2</sup>/yr. Overall net accumulation of C and N by epiphytic bryophytes was estimated at 37 and 64 g C/m<sup>2</sup>/yr, and 0.8 and 1.3 g N/m<sup>2</sup>/yr, respectively.

## DISCUSSION

GROWTH, NET PRODUCTION, AND NITROGEN ACCUMULATION BY SHOOTS.—When individual mass accumulation or loss values for epiphytic bryophyte samples in mesh cylinders or cups were compared to the initial 6-month mean mass loss rate from litterbags in the canopy (14.6% mass loss), mass loss from 18 percent of the samples exceeded this rate. An additional 24 percent of all samples lost some mass. This "excessive" mass loss from samples could have been due to four factors: (i) loss of shoots when samples were placed in or removed from the canopy; (ii) natural disturbances due to wind or arboreal animal activity; (iii) leaching of shoots and particulates by precipitation; and (iv) measurement errors associated with the initial mass estimates. Mass loss due to herbivory was probably minimal (e.g., Gerson 1982, Longton 1992). Despite these methodological limitations, annual percent growth rates calculated for epiphytic bryophytes at Monteverde are within the range of those

of terrestrial bryophytes in north temperate ecosystems (17–70%/yr; Reiley *et al.* 1979, Binkley & Graham 1981, Oechel & Van Cleve 1986, Lindholm & Vasander 1990, Bowden 1991). They exceed the only other annual growth estimate for epiphytic bryophytes (8.2%/yr for epiphytic bryophytes on the lowest 2 m of stems over a 3-year period in the Transvaal; Jacobson 1978).

Net production estimates for epiphytic bryophytes at Monteverde are lower than many production estimates for terrestrial bryophytes in a number of ecosystems where bryophytes are relatively abundant (40–790 g/m<sup>2</sup>/yr; Reiley *et al.* 1978, Binkley & Graham 1981, Wieder & Lang 1983, Grigal 1985, Russel 1985, Oechel & Van Cleve 1986, Lindholm & Vasander 1990, Rochefort *et al.* 1990). High net production estimates for terrestrial bryophytes, particularly for *Sphagnum* and *Polytrichum*, are frequently a result of high cover values (80–135%) and large biomass values (2500–4500 g/m<sup>2</sup>), rather than high rates of growth (Russel 1985, Wallen *et al.* 1988, Bowden 1991, Malmer & Wallen 1993).

Nitrogen concentrations of epiphytic bryophytes at Monteverde are greater than those reported for epiphytic bryophytes at other sites (Table 4), and are also greater than those of most terrestrial bryophytes (with the exception of *Sphagnum* from regions with high rates of N deposition from the atmosphere; Ferguson *et al.* 1984, Malmer 1988, Aerts *et al.* 1992). Although net production of epiphytic bryophytes at Monteverde is relatively low when compared to other ecosystems, estimated N accumulation by epiphytic bryophytes at Monteverde is at the high end of the range of estimates reported for terrestrial bryophytes in a number of ecosystems, primarily because of the relatively high tissue N concentrations at Monteverde (Table 6).

Annual net production of epiphytic bryophytes represented 15–25 percent of annual foliage production at this site as estimated from litterfall (about 800 g/m<sup>2</sup>/yr; Nadkarni & Matelson 1992b). Accumulation of N by epiphytic bryophytes is equivalent to 11–19 percent of the estimated annual net uptake of N by foliage. In contrast to vascular plant foliage, a relatively large portion of the N requirement of epiphytic bryophytes may be met by inorganic N inputs from the atmosphere (Clark 1994). Therefore, epiphytic bryophytes are apparently important in transforming N from highly mobile forms in atmospheric deposition to recalcitrant forms in biomass, litter, and humus.

TABLE 4. Nitrogen concentration of mature shoots of: (i) epiphytic bryophytes in tropical montane forests, (ii) terrestrial bryophytes other than Sphagnum, and (iii) Sphagnum (mean  $\pm$  1 SE, where reported). Regions of high N deposition are indicated with an "a".

Location	N concentration (mg N/g)	Reference
<b>Epiphytic bryophytes</b>		
Santa Rosa de Cabal, Colombia	7.1	Hofstede <i>et al.</i> 1993
Marafunga, New Guinea	12.7	Grubb & Edwards 1982
Monteverde, Costa Rica	14.7 $\pm$ 0.5	This study
Monteverde, Costa Rica	16.4 $\pm$ 0.7	Nadkarni 1984
<b>Terrestrial bryophytes</b>		
A. J. Andrews, Oregon	9.0 to 11.0	Binkley & Graham 1981
Luquillo Forest, Puerto Rico	9.1	Frangi & Lugo 1992
Wylrer Akkers, The Netherlands	11.3 <sup>a</sup>	Van Tooren <i>et al.</i> 1987
<b>Sphagnum</b>		
Andoya, Scandinavia	6.4 $\pm$ 1.0	Malmer 1988
Stordalen Mire, N. Sweden	7.0 $\pm$ 0.4	Aerts <i>et al.</i> 1992
Moor House, United Kingdom	8.6 $\pm$ 0.3	Heal & Smith 1978
Various, S. Sweden	11.5 $\pm$ 1.4 <sup>a</sup>	Malmer 1988
Akhult Mire, S. Sweden	13.5 $\pm$ 0.8 <sup>a</sup>	Aerts <i>et al.</i> 1992
Holm Moss, United Kingdom	to 33.5 <sup>a</sup>	Ferguson <i>et al.</i> 1984

DECOMPOSITION AND NITROGEN DYNAMICS OF LITTER.—Mass loss from litter is an integration of litter comminution, leaching of soluble compounds and particles, and gaseous losses of CO<sub>2</sub> and H<sub>2</sub>O due to microbial respiration. Mesh size of litterbags can potentially influence mass loss due to exclusion of macrofauna and the leaching of particles, but has little effect on microbial populations. The mesh size of our litterbags was larger than those used in other terrestrial bryophyte litterbag studies (0.2 cm mesh size vs. 0.02–0.1 cm mesh size; Rosswall *et al.* 1975, Berg 1984, Van Toren 1988, Rochefort *et al.* 1990, Johnson & Damman 1991), which may have affected the loss of particles. However, litterbags in the canopy were placed below live epiphytes and accumulated litter at the beginning of the experiment, and litterbags on the forest floor were incorporated into the litter layer relatively rapidly, which would presumably reduce such losses.

First-year mass loss values from litter in the canopy and on the forest floor are within and slightly greater than the range of first-year mass loss values reported for terrestrial bryophyte litterbags in other studies (4–28%; Table 5). Mass loss from canopy litterbags decreased to about 2 percent during the second year, which is also within the reported range of second-year mass loss values (1–5%). First-year mass loss from green shoots in litterbags on the forest floor exceeded first-year mass losses from terrestrial bryophytes. The initially high rates of mass loss from litter and green shoots are

typically a result of the utilization of more labile C fractions (e.g., soluble cellular constituents and cellulose) by microbial populations. Lower rates of mass loss as decomposition progressed indicate that the remaining litter was composed of more recalcitrant C fractions (Berg & Staff 1981, Melillo *et al.* 1982, Berg 1984, Melillo *et al.* 1989). Concomitant with the decomposition of bryophyte litter was a compaction of the litter structure, resulting in an increase in bulk density (Johnson *et al.* 1990, Malmer & Wallen 1993). The amorphous humified material on remaining leaf and stem tissue in litterbags in the canopy was identical in appearance to canopy humus, suggesting that epiphytic bryophytes are a major contributor to the accumulations of DOM in the canopy (Edwards & Grubb 1977, Nadkarni 1984, Vance & Nadkarni 1990).

First-year mass loss from epiphytic bryophyte litterbags in the canopy was less when compared to mass loss from vascular plant litter in the canopy (30% mass loss; Nadkarni & Matelson 1991). First-year mass loss from both types of litterbags on the forest floor was also less when compared to the estimated mass loss from fine vascular plant litter on the forest floor (about 60% mass loss; Nadkarni & Matelson 1992b). These relatively low rates of decomposition of epiphytic bryophyte litter indicate that litter quality exerts a major effect on the decomposition process. Terrestrial bryophyte litter contains relatively high concentrations of lignin-like compounds (Berg 1984, Chapin *et al.*

TABLE 5. Cumulative mass loss from bryophyte litter in litterbags. Values for Sphagnum are from acrotelm (aerobic) sites only. Ranges are given for mean mass loss of different species of Sphagnum (where reported).

Location	Genus	Cumulative mass loss (% of initial mass)		
		1st year	2nd year	3rd year
Palsa Mire, N. Sweden <sup>a</sup>	<i>Sphagnum</i>	4 to 7	8 to 19	—
Ontario, Canada <sup>b</sup>	<i>Sphagnum</i>	5 to 27	16 to 24	14 to 27
Moor House, United Kingdom	<i>Sphagnum</i>	6 to 18	—	—
Akhult Mire, S. Sweden <sup>d</sup>	<i>Sphagnum</i>	11 to 22	13 to 28	—
Scots Pine forest, Sweden <sup>c</sup>	<i>Dicranum</i>	15	26	34
<b>Monteverde, Costa Rica<sup>f</sup></b>				
Canopy	Mixed	17	19	—
Forest floor	Mixed	29	—	—
South Limburg, the Netherlands <sup>g</sup>	<i>Calliergonella</i>	18 to 28	18 to 40	—
Scots Pine forest, Sweden <sup>e</sup>	<i>Sphagnum</i>	27	33	—

<sup>a</sup> Rosswall *et al.* 1975.

<sup>b</sup> Rochefort *et al.* 1990; after 14, 26, and 38 months.

<sup>c</sup> Clymo 1965.

<sup>d</sup> Johnson & Damman 1991; after 10 and 22 months.

<sup>e</sup> Berg 1984.

<sup>f</sup> This study.

<sup>g</sup> Van Tooren 1988, values reported from 2 sites.

1987) and polymerized aliphatic compounds (Kälviäinen *et al.* 1985), which are recalcitrant with respect to microbial degradation (Melillo *et al.* 1982, Longton 1992).

Nitrogen dynamics during the decomposition of vascular plant litter have been characterized as a three-phase process: (i) initial N leaching, (ii) net N immobilization by microbial populations, and (iii) final net N release (Berg & Staff 1981, Melillo *et al.* 1982, Blair *et al.* 1990). In contrast, the mean N mass of epiphytic bryophyte litter in the canopy decreased to about 70 percent of initial N mass after one year and remained at about 70 percent after two years. These results suggest that labile C and N fractions were utilized or leached rapidly, and that net N immobilization by microbial populations was minimal. The remaining N mass in litter was apparently recalcitrant, and was likely associated with structural C fractions (Brock & Bregman 1989). These results are consistent with the patterns of N dynamics reported for terrestrial bryophyte litter (Berg 1984, Van Toren 1988, Brock & Bregman 1989).

NET ACCUMULATION OF CARBON AND NITROGEN.—Results from this study indicate that epiphytic bryophytes are disproportionately important in the net accumulation of C and N in the canopy and on the forest floor when compared to vascular plant litter at this site. Although estimates of N leaching

from the soil are lacking for this site, accumulation of N in bryophyte biomass and DOM presumably reduces overall losses. In this context, the functioning of epiphytic bryophytes in the net accumulation of C and N in this ecosystem is similar to that of terrestrial bryophytes in other ecosystems where they are abundant (Oechel & Van Cleve 1986, Urban & Eisenreich 1988, Longton 1992, Malmer & Wallen 1993; Table 6).

There is little information on the effects of N availability on growth, net production, and N concentrations of epiphytic bryophytes in TMFs, but increased N deposition due to current land use practices and biomass burning in tropical regions (Crutzen & Andreae 1990, Keller *et al.* 1991, Galloway *et al.* 1994) may affect epiphytic bryophytes in various ways. Increased N supply to terrestrial bryophytes has stimulated net production in some cases (Rochefort *et al.* 1990, Aerts *et al.* 1992), and caused declines in others (Press *et al.* 1986, Rudolf *et al.* 1986, Jauhiainen *et al.* 1994). The direction and magnitude of these effects are apparently a function of deposition rates, although the effects of pollutants other than sulfur dioxide have not been evaluated in field studies. Where increased N deposition is not associated with appreciable increases in acidity, ozone, and other pollutants (Warneck 1988, Crutzen & Andreae 1990, Johnson & Lindberg 1992), a "fertilizer effect" is likely to occur and may initially stimulate net production of epi-

TABLE 6. Nitrogen content in live bryophyte biomass. N accumulation in net production, and net N accumulation in selected ecosystems where bryophytes are abundant (mean  $\pm$  1 SE, where reported).  $\alpha$  = net ecosystem N accumulation calculated from input-output budget,  $\beta$  = net ecosystem N accumulation calculated from peat accumulation, n.d. = not determined.

Ecosystem	N in biomass (g/m <sup>2</sup> )	N accumulation (g/m <sup>2</sup> /yr)	Net N accumulation (g/m <sup>2</sup> /yr)
<i>Pendulostegia</i> forest, Oregon <sup>a</sup>	0.9	0.4	n.d.
<i>Polypodium</i> , successional, New Hampshire <sup>b</sup>	3.3 $\pm$ 0.4	1.2 $\pm$ 0.2	0.6 <sup>c</sup> , 1.0 <sup>d</sup>
Ombrotrophic mire, Sweden <sup>e</sup>	4.4	0.4	0.4 <sup>e</sup> , 0.9 <sup>f</sup>
<i>Sphagnum</i> bog, Minnesota <sup>g</sup>	5.4 $\pm$ 0.2	4.0 $\pm$ 0.2	0.7 <sup>h</sup> , 1.2 <sup>i</sup>
Tropical Montane Forest, Costa Rica <sup>j</sup>	5.9	1.8 $\pm$ 0.3	0.8,
		3.0 $\pm$ 0.3	1.3
Taiga forest, Alaska <sup>k</sup>	7.2	1.3	n.d.

<sup>a</sup> Bindley & Graham 1981.  
<sup>b</sup> Bowden 1991.  
<sup>c</sup> Rosswall & Granhall 1980.  
<sup>d</sup> Urban & Eisenreich 1988.  
<sup>e</sup> This study.  
<sup>f</sup> Oechel & Van Cleve 1986.

phytic bryophytes. Interactions among increased N deposition, increased phosphorus (P) deposition due to biomass burning (Lewis 1981, K Clark unpub. data) and gradual increases in atmospheric CO<sub>2</sub> levels may further stimulate net production of epiphytic bryophytes (Proctor 1982, Sveinbjornsson & Oechel 1992, Jaubianen *et al.* 1994). However, long-term increased N deposition has apparently caused a substantial decline in net production and biomass of *Sphagnum* and *Racomitrium* in some regions of Europe (Tallis 1964, Press *et al.* 1986, Baddley *et al.* 1994).

Increased N deposition has also led to an increase in N concentrations of both epiphytic and terrestrial bryophytes at temperate and boreal sites (Ferguson *et al.* 1984, Malmer 1988, Farmer *et al.* 1991, Aerts *et al.* 1992, Baddley *et al.* 1994). Where net production is stimulated by increased N deposition, subsequent control over net production may be exerted by limitations of other nutrients, particularly P (Aerts *et al.* 1992). Although N concentrations of epiphytic bryophytes at Montevide were greater than those in epiphytic bryophytes from other TMF sites, N to P ratios are currently within the range of ratios reported for bryophytes from sites characterized by low rates of N deposition from the atmosphere (Nadkarni 1984, Malmer 1988, Aerts *et al.* 1992, Holstede *et al.* 1993).

Increased N deposition and N availability have also caused significant changes in competitive interactions and community composition in a range of ecosystems characterized by low nutrient status (Vethösten & Schmitz 1991, Bowman *et al.* 1993, Marrs 1993, Baddley *et al.* 1994). Higher N concentrations in epiphytic bryophyte litter may accelerate rates of N leaching and decomposition (e.g., Clymo & Hayward 1982, Longton 1992, Hogg *et al.* 1994), potentially leading to increased N supply in the canopy (Vance & Nadkarni 1990, Clark 1994). Because a number of vascular epiphytes are characterized by a relatively low capacity for ion uptake (e.g., Orchidaceae; Benzing 1989, 1990; Hew *et al.* 1993) and relatively low growth rates, increased N deposition and relatively rapid rates of N cycling in the canopy could favor species as a result of changes in N availability. The effects of increased N deposition on the net production and N concentrations of epiphytic bryophytes, rates of N cycling in the canopy, and structure of diverse epiphyte communities in TMFs await further investigation.

ACKNOWLEDGMENTS

We thank the Tropical Science Center and the Montevide Cloud Forest Reserve for access to the field site and logistical support. R. Solano and N. Barbour assisted with fieldwork. This research was partially supported by NSF (BSR 86-14935 and 90-18006), the Whittaker Foundation, and the National Geographic Society Committee for Research and Exploration. We thank S. Brown and two anonymous reviewers for helpful comments on an earlier draft of this manuscript.

LITERATURE CITED

AERTS, R., B. WALLEIN, AND N. MALMER. 1992. Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *J. Ecol.* 80: 131-140.

BADDELEY, J. A. D., B. A. THOMSON, AND J. A. LEE. 1994. Regional and historical variation in the nitrogen content of *Racomitrium lanuginosum* in Britain in relation to atmospheric nitrogen deposition. *Environmental Pollution* 84: 189-196.

BENTLEY, B. L., AND E. J. CAREY. 1984. Direct transfer of newly-fixed nitrogen from free-living epiphyllous microorganisms to their host plant. *Oecologia* 63: 52-56.

BENZING, D. H. 1989. The mineral nutrition of epiphytes. *In* U. Lüttge (Ed.), *Vascular plants as epiphytes: evolution and ecophysiology*. Ecological studies 76, pp. 167-199. Springer-Verlag, Berlin, New York.

\_\_\_\_\_. 1990. Vascular epiphytes: general biology and related biota. Cambridge University Press, Cambridge, England.

BENG, B. 1984. Decomposition of moss litter in a mature Scots pine forest. *Redobiologia* 26: 301-308.

\_\_\_\_\_, AND H. STRÅVE. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. *In* E. E. Clark and T. Rosswall (Eds.), *Terrestrial nitrogen cycles*, pp. 163-178. *Swed. Nat. Sci. Res. Council*, Stockholm, Sweden.

BINKLEY, D., AND R. L. GRAHAM. 1981. Biomass, production, and nutrient cycling of mosses in an old-growth Douglas-fir forest. *Ecology* 62: 1387-1389.

BLAIR, J. M., R. M. PASZKULEK, AND M. H. BEARE. 1990. Decay rates, nitrogen fluxes, and decomposer communities of single- and mixed-species foliar litter. *Ecology* 71: 1976-1985.

BOWDEN, R. D. 1991. Input, output, and accumulation of nitrogen in an early successional moss (*Polypodium*) ecosystem. *Ecol. Mono.* 61: 207-223.

BOWMAN, W. D., T. A. THEODORE, J. A. SCHAFER, AND R. T. CONNOR. 1993. Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology* 74: 2085-2097.

BROCK, T. C. M., AND R. BEGGMAN. 1989. Periodicity in growth, productivity, nutrient content and decomposition of *Sphagnum retrovum* var. *macrocarpum* in a fen woodland. *Oecologia* 80: 44-52.

CHARRIN, F. S., W. C. OECHEL, K. VAN CLEVE, AND W. LAWRENCE. 1987. The role of mosses in the phosphorus cycling of an Alaskan black spruce forest. *Oecologia* 74: 310-315.

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.

CLIMO, R. S. 1965. Experiments on the breakdown of *Sphagnum* in two bogs. *J. Ecol.* 53: 747-758.

\_\_\_\_\_, AND P. M. HAYWARD. 1982. The Ecology of *Sphagnum*. *In* A. J. E. Smith (Ed.), *Bryophyte ecology*, pp. 229-269. Chapman and Hall, London, England.

COXSON, D. S. 1991. Nutrient release from epiphytic bryophytes in tropical montane rain forest (Guadeloupe). *Can. J. Bot.* 69: 2122-2129.

\_\_\_\_\_, D. D. McINTYRE, AND H. J. VOGL. 1992. Pulse release of sugars and polyols from canopy bryophytes in tropical montane rain forest (Guadeloupe, French West Indies). *Biotropica* 24: 121-133.

CRUTZEN, P. J., AND M. O. ANDERSON. 1990. Biomass burning in the tropics: impacts on atmospheric chemistry and biogeochemical cycles. *Science* 250: 1669-1678.

DUNING, H. J. 1992. Ecological classifications of bryophytes and lichens. *In* J. W. Bates and A. M. Farmer (Eds.), *Bryophytes and lichens in a changing environment*, pp. 1-31. Clarendon Press, Oxford, England.

EDWARDS, P. J., AND P. J. GRANA. 1977. Studies of mineral cycling in a montane rain forest in New Guinea. 1. The distribution of organic matter in the vegetation and soil. *J. Ecol.* 65: 943-969.

FARMER, A. M., J. W. BATES, AND J. N. B. BELL. 1991. Seasonal variations in acidic pollutant inputs and their effects on the chemistry of stemflow, bark and epiphyte tissues in three oak woodlands in NW Britain. *New Phytol.* 118: 441-451.

FERGUSON, P., R. N. ROBINSON, M. C. PRESS, AND J. A. LEE. 1984. Element concentrations in five *Sphagnum* species in the southern Pennines. *J. Bryol.* 112: 579-583.

FRAMAN, R. T. T. 1975. Canopy lichens with blue-green algae: a nitrogen source in a Colombian rainforest. *Ecology* 56: 1176-1184.

FURUKAWA, J. P. 1990. The effect of light and temperature on the growth of the bryophytes of tropical rain forests. *Nova Hedwigia* 51: 151-164.

FRANZ, J. L., AND A. E. LUCCI. 1992. Biomass and nutrient accumulation in ten year old bryophyte communities inside a flood plain in the Llanquile Experimental Forest, Puerto Rico. *Biotropica* 24: 106-112.

GALLOWAY, J. N., H. LEVY II, AND R. S. KASIBATTA. 1994. Year 2020: Consequences of population growth and development on deposition of oxidized nitrogen. *Ambio* 23: 120-123.

GARSON, U. J. 1982. Bryophytes and invertebrates. *In* A. J. E. Smith (Ed.), *Bryophyte ecology*, pp. 291-332. Chapman and Hall, London, England.

GARCIA, D. F. 1985. *Sphagnum* production in forested bogs of northern Minnesota. *Can. J. Bot.* 1204-1207.

GRUBIS, P. J., O. B. FURR, AND S. C. GREGORY. 1969. Preliminary observations on the mineral nutrition of epiphytic mosses. *Trans. Br. Bryol. Soc.* 5: 802-817.

\_\_\_\_\_, AND E. J. EDWARDS. 1982. Studies of mineral cycling in a montane rain forest in New Guinea. 3. The distribution of mineral elements in the above-ground material. *J. Ecol.* 70: 623-648.

- HEAL, O. W., AND R. A. H. SMITH. 1978. Introduction and site description. In O. W. Heal and D. F. Perkins (Eds.), *Production ecology of british moors and montane grasslands*, pp. 3-16. Ecol. Stud. 27. Springer-Verlag, Berlin, New York.
- HEW, C. S., L. Y. LIM, AND C. M. LOW. 1993. Nitrogen uptake by tropical orchids. *Environ. Exp. Bot.* 33: 273-281.
- HOFSTEDE, R. G. M., J. D. H. WOLF, AND D. H. BENZING. 1993. Epiphytic biomass and nutrient status of a Colombian upper montane rain forest. *Selbyana* 14: 37-45.
- HOGG, E. H., N. MALMER, AND B. WALLEN. 1994. Microsite and regional variation in the potential decay rate of *Sphagnum magellanicum* in south Swedish raised bogs. *Ecography* 17: 50-59.
- HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.
- INGRAM, S. W., AND N. M. NADKARNI. 1993. Composition and distribution of epiphytic organic matter in a neotropical cloud forest, Costa Rica. *Biotropica* 25: 370-383.
- JACOBSEN, N. H. G. 1978. An investigation into the ecology and productivity of epiphytic mosses. *J. S. Afr. Bot.* 44: 297-312.
- JAUHAINEN, J., H. VASANDER, AND J. SILVOLA. 1994. Response of *Sphagnum fuscum* to N deposition and increased CO<sub>2</sub>. *J. Bryol.* 18: 83-96.
- JOHNSON, D. W., AND S. E. LINDBERG. 1992. Atmospheric deposition and nutrient cycling in forest ecosystems. Springer-Verlag, Berlin, New York.
- JOHNSON, L. C., AND A. W. H. DAMMAN. 1991. Species-controlled *Sphagnum* decay on a south Swedish raised bog. *Oikos* 61: 234-242.
- , A. W. H. DAMMAN, AND N. MALMER. 1990. *Sphagnum* macrostructure as an indicator of decay and compaction in peat cores from an ombrotrophic south Swedish peat-bog. *J. Ecol.* 78: 633-647.
- KALVIANINEN, E., P. KARUNEN, AND R. EKMAN. 1985. Age-related contents of polymerized lipids in the ectohydric forest mosses *Pleurozium schreberi* and *Hylacomium splendens*. *Physiol. Plant.* 65: 269-274.
- KEENEY, D. R., AND D. W. NELSON. 1982. Nitrogen-inorganic forms. In A. L. Page, R. H. Miller, and D. R. Keeney (Eds.), *Methods of soil analysis, part 2: chemical and microbial properties*, pp. 643-698. Am. Soc. of Agron. and Soil Sci. Soc. Am., Madison, Wisconsin.
- KELLER, M., D. J. JACOB, S. C. WOFSEY, AND R. C. HARRISS. 1991. Effects of tropical deforestation on global and national atmospheric chemistry. *Climatic Change* 19: 139-158.
- KRESS, J. W. 1986. The systematic distribution of vascular epiphytes: an update. *Selbyana* 9: 2-22.
- LAWTON, R. O., AND V. DRYER. 1980. The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia* 18: 101-116.
- LEWIS, W. M. 1981. Precipitation chemistry and nutrient loading by precipitation in a tropical watershed. *Water Resour. Res.* 17: 169-181.
- LINDHOLM, T., AND H. VASANDER. 1990. Production of eight species of *Sphagnum* at Suurisuo mire, southern Finland. *Ann. Bot. Fennici* 27: 145-157.
- LONGTON, R. E. 1992. The role of bryophytes and lichens in terrestrial ecosystems. In J. W. Bates and A. M. Farmer (Eds.), *Bryophytes and Lichens in a Changing Environment*, pp. 32-76. Clarendon Press, Oxford.
- LUGO, A. E. AND F. N. SCATENA. 1992. Epiphytes and climate change research in the Caribbean: a proposal. *Selbyana* 13: 123-130.
- MAGDEFRAU, K. 1982. Life-forms of bryophytes. In A. J. E. Smith (Ed.), *Bryophyte ecology*, pp. 45-58. Chapman and Hall, London, England.
- MALMER, N. 1988. Patterns in the growth and accumulation of inorganic constituents in the *Sphagnum* cover on ombrotrophic bogs in Scandinavia. *Oikos* 53: 105-120.
- , AND B. WALLEN. 1993. Accumulation and release of organic matter in ombrotrophic bog hummocks-processes and regional variation. *Ecography* 16: 193-211.
- MARRS, R. H. 1993. Soil fertility and nature conservation in Europe: theoretical considerations and practical management solutions. *Adv. Ecol. Res.* 24: 241-300.
- MELILLO, J. M., J. D. ABER, AND A. M. MURATORE. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecol.* 63: 621-626.
- , J. D. ABER, AND A. E. LINKINS. 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. *Plant and Soil* 115: 189-198.
- NADKARNI, N. M. 1984. Epiphyte biomass and nutrient capital of a neo-tropical elfin forest. *Biotropica* 16: 249-256.
- . 1986a. The nutritional effects of epiphytes on host trees with special reference to alteration of precipitation chemistry. *Selbyana* 9: 45-51.
- . 1986b. An ecological overview and checklist of vascular epiphytes in the Monteverde Cloud Forest Reserve, Costa Rica. *Brenesia* 10: 35-39.
- , AND T. J. MATELSON. 1991. Dynamics of fine litterfall within the canopy of a tropical cloud forest, Monteverde. *Ecology* 72: 2071-2082.
- , AND ———. 1992a. Biomass and nutrient dynamics of epiphytic litterfall in a neotropical cloud forest, Monteverde, Costa Rica. *Biotropica* 24: 24-30.
- , AND ———. 1992b. Biomass and nutrient dynamics of fine litter of terrestrially rooted material in a neotropical montane forest, Costa Rica. *Biotropica* 24: 113-120.
- , AND W. A. HABER. 1995. Structural characteristics and floristic composition of a neotropical cloud forest, Monteverde, Costa Rica. *J. Trop. Ecol.* 11: 485-495.
- OECHEL, W. C., AND K. VAN CLEVE. 1986. The role of bryophytes in nutrient cycling in the taiga: a synthesis of structure and function. In K. Van Cleve, F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness (Eds.), *Forest ecosystems in the alaskan taiga*, pp. 121-137. Ecol. Stud. 57. Springer-Verlag, Berlin, New York.
- PRESS, M. C., S. J. WOODIN, AND J. A. LEE. 1986. The potential importance of an increased atmospheric nitrogen supply to the growth of ombrotrophic *Sphagnum* species. *New Phytol.* 103: 45-55.
- PROCTOR, M. C. F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In A. J. E. Smith (Ed.), *Bryophyte Ecology*, pp. 333-382. Chapman and Hall, London, England.
- RICHARDS, P. W. 1984. The ecology of tropical forest bryophytes. In R. M. Schuster (Ed.), *New manual of bryology*, Vol. 2, pp. 1233-1270. Hattori Botanical Laboratory, Nichinan, Japan.
- RIELEY, J. O., P. W. RICHARDS, AND A. D. L. BEBBINGTON. 1979. The ecological role of bryophytes in a North Wales woodland. *J. Ecol.* 67: 497-527.
- ROCHFERT, L., D. H. VITT, AND S. E. BAYLEY. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *Ecology* 71: 1986-2000.
- ROSSWALL, T., AND U. GRANHALL. 1980. Nitrogen cycling in a subarctic ombrotrophic mire. In M. Sonnesson (Ed.), *Ecology of a Subarctic Mire*, pp. 209-234. Ecological Bulletins No. 30. Swedish Natural Science Research Council.
- , A. VEUM, AND L. KARENLAMPI. 1975. Plant litter decomposition at Fennoscandian tundra sites. In F. E. Wiegolowski (Ed.), *Fennoscandian Tundra Ecosystems. 1. Plants and Microorganisms*, pp. 268-277. Springer-Verlag, Berlin, New York.
- RUDOLF, H., AND J. U. VOIGT. 1986. Effects of NH<sub>4</sub>-N and NO<sub>3</sub>-N on growth and metabolism of *Sphagnum magellanicum*. *Physiol. Plant.* 66: 339-343.
- RUSSEL, S. 1985. Bryophyte production at Marion Island. In W. R. Siegfried, P. R. Condy and R. M. Laws (Eds.), *Antarctic Nutrient Cycles and Food Webs*, pp. 200-203. Springer-Verlag, Berlin, New York.
- . 1988. Measurement of bryophyte growth. 1. Biomass (harvest) techniques. In J. M. Glimme (Ed.), *Methods in Bryology*, pp. 249-257. Hattori Botanical Laboratory, Nichinan, Japan.
- SCHNEIDER, D. 1976. Determination of ammonia in Kjeldahl nitrogen by the indophenol method. *Water Resour. Res.* 10: 31-36.
- SVEINBJORNSSON, B., AND W. C. OECHEL. 1992. Controls on growth and productivity of bryophytes: environmental limitations under current and anticipated conditions. In J. W. Bates and A. M. Farmer (Eds.), *Bryophytes and lichens in a changing environment*, pp. 77-102. Clarendon Press, Oxford, England.
- SYSTAT. 1992. SYSTAT: the system for statistics. Systat, Inc., Evanston, IL.
- TALLIS, J. H. 1964. Studies on southern Pennine peats. 3. The behaviour of *Sphagnum*. *J. Ecol.* 52: 345-353.
- TANNER, E. V. J. 1980a. Studies on the biomass and productivity in a series on montane rain forests in Jamaica. *J. Ecol.* 68: 573-588.
- . 1980b. Litterfall in montane rain forests of Jamaica and its relation to climate. *J. Ecol.* 68: 833-848.
- THOMAS, R. L., R. W. SHEARD AND J. R. MOYER. 1967. Comparison of conventional and automated procedures for nitrogen, phosphorus, and potassium analyses of plant material using a single digestion. *Agronomy Journal* 59: 240-243.
- URBAN, N. R., AND S. J. EISENREICH. 1988. Nitrogen cycling in a forested Minnesota bog. *Can. J. Bot.* 66: 435-449.
- VAN TOOREN, B. F. 1988. Decomposition of bryophyte material in two Dutch chalk grasslands. *J. Bryol.* 15: 343-352.
- , J. DEN HERTOEG, AND J. VERHAAR. 1987. The role of bryophytes in a chalk grassland ecosystem. *Symposia Biologica Hungarica* 35: 665-675.
- VANCE, E. D., AND N. M. NADKARNI. 1990. Microbial biomass and activity in canopy organic matter and the forest floor of a tropical cloud forest. *Soil Biol. Biochem.* 22: 677-684.
- , AND ———. 1992. Root biomass distribution in a moist tropical montane forest. *Plant and Soil* 142: 31-39.
- VENEKLAAS, E. V. 1990. Rainfall interception and aboveground nutrient fluxes in a Colombian montane tropical rain forest. Ph. D. thesis, University of Utrecht, Netherlands.
- VERHOEVEN, J. T. A., AND M. B. SCHMITZ. 1991. Control of plant growth by nitrogen and phosphorus in mesotrophic fens. *Biogeochem.* 12: 135-148.
- WALLEN, B., U. FALENGREN-GREERUP, AND N. MALMER. 1988. Biomass, productivity, and relative rate of photosynthesis of *Sphagnum* and different water levels on a south Swedish peat bog. *Hol. Ecol.* 11: 70-76.
- WARNECK, P. 1988. Chemistry of the natural atmosphere. *Int. Geophys. Ser.*, Vol. 41. Academic Press, San Diego, California.
- WIEDER, R. K., AND G. E. LANG. 1983. Net primary production of the dominant bryophytes in a *Sphagnum*-dominated wetland in West Virginia. *Bryologist* 86: 280-286.