Nitrogen deposition, distribution and cycling in a subalpine spruce-fir forest in the Adirondacks, New York, USA

ANDREW J. FRIEDLAND[1], ERIC K. MILLER[2],
JOHN J. BATTLES[3] & JAMES F. THORNE[4]

[1] *Environmental Studies Program, Dartmouth College, Hanover, NH 03755, USA;* [2] *Dept. of Earth Science, Dartmouth College, Hanover, NH 03755, USA;* [3] *Dept. of Natural Resources, Cornell University, Ithaca, NY 14853, USA;* [4] *Dept. of Landscape Architecture and Regional Planning, University of Pennsylvania, Philadelphia, PA 19104, USA*

Abstract. Nitrogen inputs, fluxes, internal generation and consumption, and outputs were monitored in a subalpine spruce-fir forest at approximately 1000-m elevation on Whiteface Mountain in the Adirondacks of New York, USA. Nitrogen in precipitation, cloudwater and dry deposition was collected on an event basis and quantified as an input. Throughfall, stemflow, litterfall and soil water were measured to determine fluxes within the forest. Nitrogen mineralization in the forest floor was estimated to determine internal sources of available N. Lower mineral horizon soil water was used to estimate output from the ecosystem. Vegetation and soil N pools were determined.

During four years of continuous monitoring, an average of 16 kg N ha^{-1} yr^{-1} was delivered to the forest canopy as precipitation, cloudwater and dry deposition from the atmosphere. Approximately 30% of the input was retained by the canopy. Canopy retention is likely the result of both foliar uptake and immobilization by bark, foliage and micro-organisms. Approximately 40 kg of N was made available within the forest floor from mineralization of organic matter. Virtually all the available ammonium (mineralized plus input from throughfall) is utilized in the forest floor, either by microorganisms or through uptake by vegetation. The most abundant N component of soil water solutions leaving the system was nitrate. Net ecosystem fluxes indicate accumulation of both ammonium and nitrate. There is a small net loss of organic N from the ecosystem. Some nitrate leaves the bottom of the B horizon throughout the year. Comparisons with other temperate coniferous sites and examination of the ecosystem N mass balance indicate that N use efficiency is less at our site, which suggests that the site is not severely limited by N.

Introduction

Comprehensive ecosystem studies of N deposition and cycling have been conducted in the low-elevation forests of the northeastern United States (Likens et al. 1977), but only portions of the process have been studied

at higher elevations — e.g. deposition (Lovett et al. 1982; Mohnen & Kadlecek 1989); throughfall and stemflow (Olson et al. 1981); soil solution chemistry (Cronan 1980); N mineralization (Olson & Reiners 1983); and N losses from ecosystems (Vitousek et al. 1982). Nitrogen cycling in high-elevation forests in the Northeast is of interest for a number of reasons including: (1) the greater deposition of water and N that occurs at high elevations as compared to low elevations (Lovett et al. 1982); (2) the greater presence of natural stresses at high elevations as compared to low-elevation forests at the same latitude (Tranquillini 1979; DeLucia & Berlyn 1984; Marchand 1987); and (3) the decline of red spruce that has been observed in the northern Appalachians and Adirondacks (Siccama et al. 1982; Scott et al. 1984; Johnson & Siccama 1983) and the possible role of atmospheric N deposition in that decline.

Nitrogen is generally considered to be the limiting nutrient in many forested ecosystems including spruce forests (Lea et al. 1979; Vitousek et al. 1982) and periodic decreases in N availability have been hypothesized as a possible non-anthropogenic factor in red spruce decline (Pastor et al. 1987). Others have suggested that excess or untimely anthropogenic N deposition could contribute to forest tree decline (e.g. Nihlgård 1985; Waring 1987; Schulze 1989) and to red spruce decline in particular (Friedland et al. 1984). Previous work less than one km from the present study site (at 1200-m elevation) determined that total ecosystem N is high relative to other forests and the author suggested that this finding may be the result of high N inputs (Sprugel 1984). The primary objectives of this study were to (1) measure N input, uptake, internal generation and export; (2) quantify N pools in biomass and soils in a high-elevation forest in the Adirondacks of New York; and (3) assess the relative importance of atmospheric deposition of N compounds in N cycling processes. A secondary objective was to evaluate some of the proposed hypotheses about the role of N in red spruce decline in relation to our study site.

Materials and methods

Site description

Whiteface Mountain (elevation 1483 m) is located in Wilmington, New York near the northeastern boundary of the Adirondack Mountains (44°22′N, 73°54′W). The study area is a narrow west-northwest trending basin on the flank of Esther Mountain (elevation 1292 m), the eastern peak of the Whiteface massif. A restricted access road to the summit of Whiteface cuts north-south across the basin approximately 60 m from the study area at 960 m elevation. Sampling and monitoring for this study

occurred between 970 and 1100 m elevation on a north-facing slope of the drainage basin.

Mean annual temperature at the study site is approximately 2 °C. Mean annual precipitation is 130 cm, 30% of which falls as snow. The growing season spans from June through September. Snow cover normally persists from November through April; soil frost to the depth of the forest floor is common. The bedrock on Esther Mountain is primarily a Precambrian anorthosite. Soils are Typic Cryohumods or Typic Cryorthods developed on anorthosite colluvium and basal till of local origin. Average depth to till is 64 cm; average depth to bedrock is approximately 1 m. The study site is in the middle of the spruce-fir zone (Bormann et al. 1970) and the canopy trees are *Abies balsamea* (L.) Mill (balsam fir), *Betula papyrifera* var. *cordifolia* Reg. (paper birch) and *Picea rubens* Sarg. (red spruce). Understory vegetation consists primarily of saplings of overstory species and is a small fraction of forest biomass ($< 1\%$). Whereas certain areas of Whiteface Mountain have been logged or burned, the study area has not been logged or burned during the last century or more (J.J. Battles, unpublished data).

Permanent vegetation plots

Four 0.1-ha permanent vegetation plots were established at 1020, 1060, 1070 and 1090 m elevation in July 1985 and remeasured in July 1988. All plots are within 250-m ground distance of each other. Plots were chosen to represent the major types of forest cover in the subalpine spruce-fir zone: two are closed-canopy, mature stands; two are open-canopy stands. One open-canopy stand is an old-growth spruce-dominated area; the other stand is one where some old-growth spruce have recently fallen and fir regeneration has begun in a few areas. Measurements of diameter-at-breast-height (dbh), 1.37 m above the ground, were made for each tree greater than 2 cm dbh. Plots were clearly marked and there was no disturbance of the plots between 1985 and 1988, when the plots were remeasured.

Biomass estimates for each tree species and for tree parts (branch, bole, foliage, roots, wood and root increment) were made with the method described by Whittaker et al. (1974).* Height as a function of dbh was determined at our site in 1985. These regression curves were used to determine parabolic volume from individual tree dbh. The parabolic volume was then used as the independent variable in the Whittaker et al.

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* One error in the original equation was corrected (T. G. Siccama, Yale Univ., pers. comm.).

(1974) allometric equations to estimate biomass for each sample tree. These estimates were summed for each plot and a total live biomass was computed. Our error in predicting parabolic volume from dbh was < 3% (data not shown). We recognize that Whittaker et al. (1974) determined the allometric equations on trees that were younger, growing at slightly lower elevations and at a different site in the northeastern United States, which may contribute to slightly different biomass allocations among tree parts.

Nutrient cycling plots

Four plots were established adjacent to the four permanent vegetation plots. Water collectors have been monitored from September 1985 through the present time. In this paper, data summaries from four 'water years' (June of one year through May of the following year) from June 1986 through May 1990 are presented.

Nitrogen pool sampling

Foliage, bark, bole wood and root wood were sampled from the three dominant tree species in September 1985 except birch foliage which was collected in July 1986. Only one root size class was collected (> 2mm).

Organic and mineral soil samples were collected in 1985 and 1987 using a quantitative 0.707 × 0.707-m pit, modified after Hamburg (1984). The forest floor was collected as one unit whereas the mineral soil was collected by major horizon (ABhs and Bs) and by fixed intervals (0—10, 10—20, 20+ cm). Mineral soil was sieved to pass a 2-mm sieve and both fractions were weighed. Forest floor was sieved to pass a 1-cm sieve and both fractions were weighed. All chemical analyses and mass calculations were done on the sieved fractions. Field-moist soil mass was converted to oven-dry mass based on the wet and dry mass of subsamples.

Nitrogen flux monitoring

Precipitation. Event samples were collected from June 1986 through May 1990 at three locations (one location during winter) near the study site. We were unable to sample 25% of the events in 1986; precipitation chemistry data for these events were taken from a MAP3S (Multistate Atmospheric Power Production Pollution Study) collection station at 600-m elevation, approximately 3 km from the study site. Precipitation amounts at the study site for the events missed in 1986 were estimated using a regression established from individual storm events measured at

the two locations during 1987. During winter, a 0.5-m diameter plastic container placed in a clearing was used to collect snow on an event basis.

Cloudwater and dry deposition. A teflon-strand collector (Mohnen & Kadlecek 1989) was raised above the canopy on a tower during cloud events and multiple samples were taken during each event. Dry deposition, including nitric acid vapor deposition, was estimated from surrogate surfaces and air filters (Lindberg et al. 1989). Chemical determinations of cloudwater and dry deposition samples were made by SUNY-Albany and methods relating to these data are similar to Lindberg et al. (1986). Deposition velocities for cloudwater, particles and nitric acid vapor were estimated using multiple resistance models (Lovett 1984; Hicks et al. 1987).

Throughfall. Five polyethylene buckets (National Atmospheric Deposition Program-type), 30-cm diameter, were randomly placed throughout each instrument plot. Throughfall was collected weekly and pooled monthly for chemical analysis during the summer of 1986 and was collected and analyzed on an event basis from fall 1986 onwards. During winter, throughfall and precipitation are predominantly in the form of snow. Since snow at this site has minimal chemical interaction with the forest canopy, throughfall during winter months was assumed equal to incident snowfall plus cloudwater deposition.

Stemflow. Three randomly located trees of the three major tree species at each plot were fitted with spiral collars of plastic tubing. Stemflow was collected weekly and pooled monthly for chemical analysis in 1986 only.

Litterfall. Litterfall was collected in 0.25 m² collectors placed at ground level. Five litterfall collectors were randomly placed in each instrument plot. Litterfall was collected twice per year, ground in a Wiley Mill and analyzed. The two collections were made in late spring and late fall, which coincided with the major periods of litterfall accumulation (Rustad & Cronan 1989).

Soil water. Sixty-mm diameter fritted glass lysimeters (Corning, VF) were placed under a continuous 10 kPa vacuum from 1 m hanging-drop water columns. At each plot, three replicates were placed in each of three horizons: immediately under the Oa horizon of the forest floor, approximately 12—15 cm depth below the surface; in the ABhs, approximately 30 cm depth below the surface; and as low as possible in the B, usually 45 to 60 cm depth below the surface. This horizon was usually a Bs horizon.

Mineralization estimates

Buried 0.05 mm polyethylene bags with soil in them, and equal amounts of soil brought to the laboratory at the beginning of each month, were used to determine monthly ammonification and nitrification rates (Nadelhoffer et al. 1983) in the forest floor and mineral soil. Twenty bags were placed in three 10 × 10 m plots in close proximity to the nutrient cycling plots. Ammonium and nitrate were determined from bagged forest floor samples at the beginning and end of each monthly period from October, 1985, through September, 1987. Fewer plots with only 10 incubations each (to lower trampling impact) were used in the second year of study. Ammonification and nitrification were determined in mineral soil samples from October 1986 through September 1987 by carrying out 2 incubations at each of 4 equal depth increments in the B horizon of 2 excavated pits each month. Further details are given in Thorne & Miller (1991).

Water budgets

Water flux was determined by direct measurements of precipitation and throughfall and by estimates of cloudwater deposition and soil water movement. Cloudwater input was estimated by micrometeorological methods (Lovett 1984). Modelled cloudwater fluxes agreed well with water balance calculations during test periods (data not shown). Soil water flux was estimated by apportioning a fraction of total Thornthwaite evapotranspiration adjusted for cold climates (Hamon 1963) to each soil horizon, with greatest evapotranspiration and root uptake occurring in the zone with highest root density (the forest floor) (after Friedland & Johnson 1985).

Chemical analyses

Tissue and soil samples were dried at 30 °C and digested at the Oak Ridge National Laboratory (ORNL) for total N using a block digester and Auto-Analyzer analysis for ammonium. Detailed descriptions of all analysis protocols are given in Lindberg et al. (1989). Average recovery was 95% for NBS Pine Needles SRM #1574. Solutions were analyzed for ammonium and nitrate by ion chromatograph, and for total N by block digestion and subsequent analysis for ammonium. Throughfall samples were filtered before analysis. Water analyses were conducted at ORNL, the Atmospheric Sciences Research Center (SUNY), Wilmington, NY and at Dartmouth College. Repeated cross-comparisons among the three laboratories showed that there were no systematic differences among sites.

Samples were kept at 4°C or colder throughout storage and shipping until analysis. Determinations of ammonium and nitrate on forest floor and mineral soil mineralization extracts were performed using an Auto-Analyzer at the University of Pennsylvania.

Results and discussion

Stand composition

Live stand density and live basal area in the study area were 2243 stems ha^{-1} and 28.1 m^2 ha^{-1} in 1985 (Table 1). Total live density in the four plots ranged from 1650—2540 stems ha^{-1} while live basal area in the four plots ranged from 24.8—30.9 m^2 ha^{-1} (data not shown). Because the four study plots were not chosen to be replicates but rather were chosen to attempt to represent the range of spruce-fir plots on Whiteface Mountain, we have not presented statistics on variation among plots. The mean values for density and basal area are comparable to other old-growth red spruce stands (e.g. Foster & Reiners 1983) and to a larger study of the entire Whiteface Mountain massif (Battles et al. 1991). The high proportion of red spruce at our site reflects our deliberate selection of a site with abundant red spruce. Results from the present study are from a high-elevation, old-growth, spruce-fir forest. Therefore, inferences about nitrogen cycling based on our findings applied to younger sites, lower elevation sites or sites with a history of disturbance should be made with caution.

The percentage of standing dead red spruce at our site (53% dead by

Table 1. Density and basal area of major tree species at 1000-m elevation on Whiteface Mountain, NY in July 1985.

	Live density	Total density	Live basal area	Total basal area
	(stems ha^{-1})		(m^2 ha^{-1})	
Picea rubens	87.5	160	7.5	15.8
Abies balsamea	2060	2505	16.2	22.5
Betula papayrifera	67.5	72.5	4.1	4.4
Sorbus americana	27.5	30	0.3	0.3
Unknown[a]	0	2.5	0	0.03
Total	2243	2770	28.1	43.0

Values were determined from four 0.1 ha permanent plots.
[a] Dead trees that have decayed to the point where identification by species is not possible.

basal area; 45% standing dead by density) (determined from Table 1) is similar to other reports of standing dead red spruce in the Adirondacks (Johnson & Siccama 1983; Scott et al. 1984; Craig & Friedland 1991; Battles et al. 1991). Estimated biomass for the study site was 145 ($\pm$ 12.5, s.d.) tons ha^{-1} (112 tons ha^{-1} not including roots), which is greater than at least one estimate of boreal coniferous forests but is less than most temperate forest estimates (Cole & Rapp 1981). Sprugel (1984) reported that estimated biomass for subalpine fir forests on Whiteface (approximately 200 m in elevation above our site) was 118 tons ha^{-1}, not including roots.

Tissue and soil nitrogen concentrations

Average total N concentrations for vegetation and soils (Table 2) are within the ranges reported for many other sites. Nitrogen concentrations for spruce foliage of 10.0 g kg^{-1} (1.0%) are similar to values reported for other spruce stands in eastern North America (Friedland et al. 1988; Robarge et al. 1989; Fernandez et al. 1990). Bark, twigs and root N concentrations for spruce, fir and birch are not substantially different than values reported in other studies (Likens & Bormann 1970; Sprugel 1984; Lang et al. 1982). Fir foliage N concentrations (14.0 g kg^{-1}) are in the same range as samples collected on the same mountain (Sprugel 1984) but

Table 2. Mean concentrations (and standard errors in parentheses) of total nitrogen in vegetation by species and part and in soils by horizon from 1000-m elevation at Whiteface Mountain. Soil horizon mass and percent organic matter are also presented. $n = 5$ for each species and part except *Sorbus americana*, $n = 1$. Soil horizon sample sizes are listed below.

	Foliage	Twigs	Bark	Bole	Root
Tree species			g N kg^{-1}		
Picea rubens	10.2 (0.22)	6.18 (0.20)	3.18 (0.09)	0.53 (0.01)	4.44 (0.26)
Abies balsamea	13.9 (0.43)	6.48 (0.17)	4.82 (0.22)	0.75 (0.03)	5.64 (0.29)
Betula papyrifera	23.1 (0.48)	9.67 (0.20)	4.72 (0.27)	1.12 (0.02)	5.60 (0.30)
Sorbus americana	16.6	10.4	8.0	1.0	7.5

Soil horizon	n	Tons ha^{-1}	g N kg^{-1}	% O.M.
O (Forest floor)	8	141	16.9 (0.08)	86.4 (1.6)
ABhs	13	1060	4.8 (0.04)	21.5 (1.8)
Bs	10	1980	2.4 (0.03)	12.1 (1.6)
BC	1	n.d.	2.0	8.0

are lower than values reported by Lang et al. (1982) from the White Mountains. Experiments with seedlings grown in sand cultures suggest that N levels in red spruce below 13.0 g N kg⁻¹ N are deficient (Swan 1971). However, most natural-grown red spruce do not grow in sand and average around 10 g N kg⁻¹ (Friedland et al. 1988; Fernandez et al. 1990). Thus, all naturally growing red spruce are N deficient or sand culture experiments on seedlings are not representative of critical N levels for forest canopy red spruce trees. Alternatively, foliar nutrient levels of mature trees may not be a good indicator of nutritional status (Waring & Schlesinger 1985).

Nitrogen concentrations in the organic horizon of soil (16.9 g kg⁻¹) (Table 2) are within the ranges reported for other spruce-fir and fir forests (Lang et al. 1981; Olson & Reiners 1983; Federer 1983). Nitrogen concentrations in the mineral soil are high (ABhs: 4.8 g kg⁻¹; Bs: 2.0 g kg⁻¹) (Table 2) compared to lowland, hardwood forests but are similar to values reported for montane (Olson & Reiners 1983) and low-elevation (Federer 1983) coniferous forests. At our site, the relatively high N concentrations in the mineral soil are probably a result of the relatively large concentration of organic material in the mineral soil (Table 2), which may be due to mechanical mixing from windthrows and to eluviation of organic matter from the overlying organic horizon. This may also be a result of the absence of logging or fire history at the site in recent centuries, which has allowed a greater accumulation of organic matter.

Solution nitrogen concentrations

The solution nitrogen concentrations reported in this study are derived from more than 500 samples for each above-ground measurement (precipitation, cloudwater, throughfall) and at least 175 samples for each below-ground level (O, ABhs, Bs). Coefficients of variation were greater than 100% for each level and N compound (data not shown). Similar variability in soil solutions has been reported previously (e.g. Shepard et al. 1990) and can be attributed to spatial variability in soils as well as temporal variability in soil solution chemistry. Ammonium concentrations in water samples were higher in above-ground samples than in below-ground samples (Fig. 1). Presumably, ammonium is rapidly taken up by plants or immobilized by microorganisms in the soil. Nitrate solution concentrations were fairly similar above and below the canopy and throughout the soil profile. Organic N solution concentrations above the forest canopy were below detection limits. Organic N solution concentrations were highest in the O horizon (Fig. 1), where soil organic matter concentrations were the largest (Table 2).
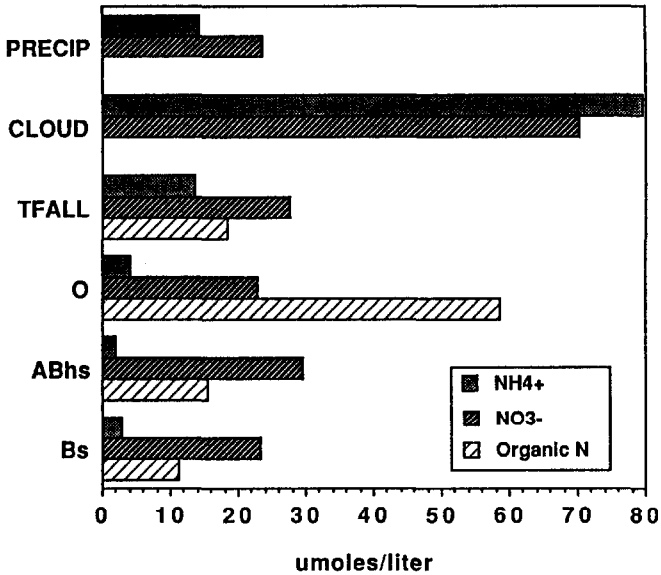
Fig. 1. Average solution concentrations from precipitation, cloudwater, throughfall, O horizon lysimeter, ABhs horizon lysimeter and Bs horizon lysimeter samples collected from Whiteface Mountain, New York between 1986 and 1990. TFALL = throughfall.

Average N concentrations in water samples from Whiteface differ by as much as a factor of two from values reported for other montane coniferous forests. Ammonium concentrations are higher and nitrate concentrations are lower than values reported for cloudwater in the White Mountains by Lovett et al. (1982) from a much smaller data set (part of one growing season only). Throughfall concentrations are almost double the values reported by Cronan (1980) in the White Mountains during two growing seasons, although Cronan did not analyze for organic N (which accounted for 32% of the N in our throughfall samples). Soil water ammonium is less and nitrate greater than values reported by Cronan (1980). These differences may reflect differences in sampling intensity and collector type as well as site variation and temporal variations in N concentrations.

Many investigators have reported a decline in solute concentrations with depth in the soil profile (e.g. Shepard et al. 1990; Foster et al. 1989). However, given the large variation inherent in soil solution chemistry (e.g. Shepard et al. 1990), it is not clear in some of those studies if the decrease would be deemed statistically significant. Nevertheless, in the present study there is no evidence of a significant decrease in either ammonium or

nitrate with depth in the soil (Fig. 1). Ammonium is consumed in the O horizon and organic N is retained in the Bhs as part of the podsolization process (illuviation of organic matter).

Nitrogen amounts in biomass, soils and litterfall

Nitrogen concentrations shown in Table 2 were combined with calculated biomass estimates (data not shown) and measured soil mass values (data not shown) to yield values presented in Fig. 2. Nitrogen amounts in vegetation and soils are within the ranges reported for New England forests. Nitrogen in vegetation (628 kg ha^{-1}) (440 kg ha^{-1} not including roots) was not greatly different from values reported for a low elevation spruce forest (540 kg ha^{-1} (including roots) in Ontario, Canada) by Gordon (1983) and was even closer to values reported for slightly higher elevations on Whiteface Mountain (494 kg ha^{-1} not including roots) by Sprugel (1984).

Nitrogen amounts in the O horizon (2640 kg ha^{-1}) are high compared to other temperate forests but are similar to amounts found in boreal red spruce forests (e.g. 2630 kg N ha^{-1} determined by Gordon 1983). Nitrogen in litterfall averaged approximately 24 kg ha^{-1} yr^{-1} (Fig. 2). Total dry weight of litterfall was 2590 kg ha^{-1} yr^{-1}. Litterfall mass is similar to a low-elevation spruce stand in Maine (2510 kg ha^{-1} yr^{-1}) (Rustad & Cronan 1989). However, N concentration and thus N content of litterfall are higher at our site (0.91% at Whiteface vs. 0.7% in Maine). The higher N concentration of litterfall at the Whiteface site is likely due to the relative abundance of balsam fir versus red spruce compared to the Maine site. Balsam fir has a higher foliar N concentration (approximately 13.9 g kg^{-1} in new foliage for balsam fir versus 10.2 g kg^{-1} for red spruce) (Table 2).

The B horizons of the mineral soil have low total N concentrations compared to the O horizon, but because of large mass they contribute substantially to the total N pool of the forest (Fig. 2). Richter et al. (1989) and Johnson et al. (1991) report similarly high values for N content in the mineral soil of southern subalpine forests. These high N amounts may be due in part to the age of the soil and the lack of disturbance in recent centuries.

Dead wood lying on the forest floor was determined to be approximately 14,700 kg ha^{-1} (J. J. Battles, unpublished data) compared to a forest floor mass of 141,000 kg ha^{-1} (Table 2). Based on live bole wood N determinations shown in Table 2 (which may underestimate N concentrations in decaying boles, Arthur & Fahey 1990), N content of dead wood lying on the forest floor is less than 15 kg ha^{-1}, which is less than
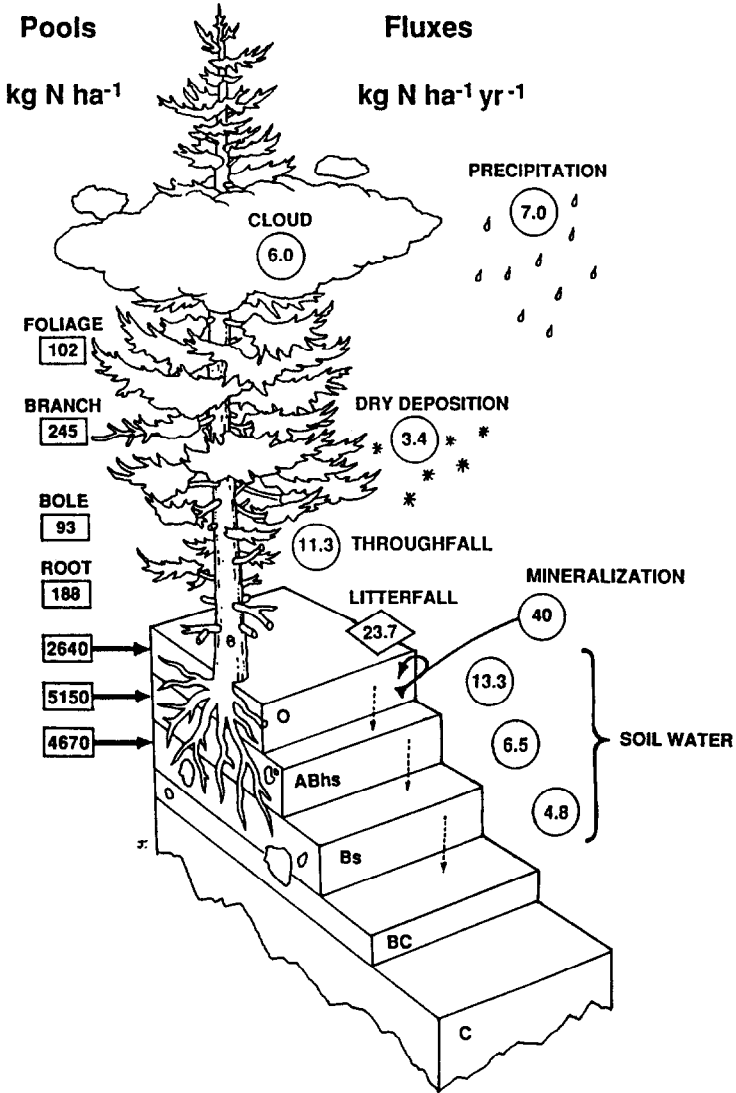
Fig. 2. Pools and fluxes of N in the spruce-fir-birch forest at 1000-m elevation on Whiteface Mountain, NY. Pools (kg N ha^{-1}) are shown in boxes while fluxes (kg N ha^{-1} yr^{-1}) are shown in circles. A diamond is used to represent litterfall, which is a flux but is not in an immediately available form. Mineralization is an internal flux that represents the rate at which organic N is converted to ammonium.

2.5% of the N pool. Other investigators have shown that decaying boles do not contribute substantially to N pools in subalphine fir forests (Arthur & Fahey 1990; Lang et al. 1981). The N in decaying boles is not included in Fig. 2.

Nitrogen mineralization

Our estimate of forest floor ammonification (conversion of organic N to ammonium) is 40 kg ha^{-1} yr^{-1} (Fig. 2) (Thorne & Miller 1991) and is similar to that of Sprugel (1984) for estimates at slightly higher elevations on Whiteface Mountain. Ammonification values from the forest floor appear to be within the range reported for other New England forests, particularly those in spruce-fir forests (e.g. Federer 1983), both in terms of activities and amounts per hectare per year. Ammonification activities vary slightly among sites (Thorne & Miller 1991) and areal rates of N mineralization in the forest floor vary with forest floor mass. Nitrification (production of nitrate from ammonium) was essentially 0 (Thorne & Miller 1991). Federer (1983) also found 0 nitrification in forest floor in northern New England during 28 day incubations. One study on White-face Mountain (McNulty et al. 1990) found that nitrification potential was 22% of N mineralization.

An early paper by us (Thorne et al. 1987) reported that N mineraliza-tion differed among stands of various ages. This assessment was based on forest floor mass determinations from 10 × 10 cm samples that varied in mass with age of the stand of trees growing in a particular part of the forest. Quantitative, larger (70.7 × 70.7 cm and 50 × 50 cm) samples collected during this and other studies on Whiteface Mountain revealed that forest floor mass is not related to a minimum measure of mean age of the live trees in the stand, as estimated by regressing mean dbh of trees in that stand with forest floor mass ($r^2 = 0.03$; $p > 0.1$; $n = 43$) (data not shown). Leak (1975) showed that age of red spruce was correlated with diameter of red spruce ($r^2 = 0.88$). Furthermore, we believe that our forest floor mass values determined from the larger, quantitative samples yielded more accurate estimates of forest floor mass (average 141,000 kg ha^{-1}) than those reported in Thorne et al. (1987). Accordingly, we do not believe there is evidence for a difference in N mineralization with differ-ences in stand age, as reported for our data by Pastor et al. (1987).

An attempt to quantify mineralization in the mineral horizon using the same buried bag technique as in the forest floor (Thorne & Miller 1991) yielded extremely high values (320 kg ha^{-1} yr^{-1}). Because we cannot account for this value or verify this number (for example, if that much N were being mineralized in the mineral soil, we should see much more N in lysimeters), we have not included it in our figures and calculations. A similar very high N mineralization value was found in the mineral soil of a southern Appalachian spruce-fir forest (Johnson et al. 1991). We recog-nize that the value for N mineralization at our site is greater than 0 and less than 320 kg ha^{-1} yr^{-1}. Federer (1983) found N mineralization rates of

4.1 kg ha^{-1} yr^{-1} in a 28-day period in Maine and northern New Hampshire. This suggests that up to 3—4 times this amount of mineralization could occur (corresponding to approximately 3—4 months when soil temperature is warm enough to mineralize N). However, we have not quantified differences in temperature and moisture between our site and those studied by Federer (1983), and thus we do not know how mineralization differs. Nitrogen mineralization in the mineral soil has not been included in Table 5 or Fig. 2 because of this uncertainty.

Canopy and ecosystem fluxes

By using water flux estimates for total input to the canopy and measured throughfall amounts, N fluxes above and below the canopy were determined (Fig. 3). Input to the canopy is approximately 16.4 kg N ha^{-1} yr^{-1} (Fig. 2), roughly 60% nitrate and 40% ammonium (Fig. 3). This value is substantially lower than a previous estimate for a sub-alpine fir stand 200-m higher in elevation in the White Mountains of New Hampshire (44.1 kg N ha^{-1} yr^{-1} Lovett et al. 1982) and at a number of elevations in the Green Mountains, Vermont (37.5 kg N ha^{-1} yr^{-1} Scherbatskoy & Bliss
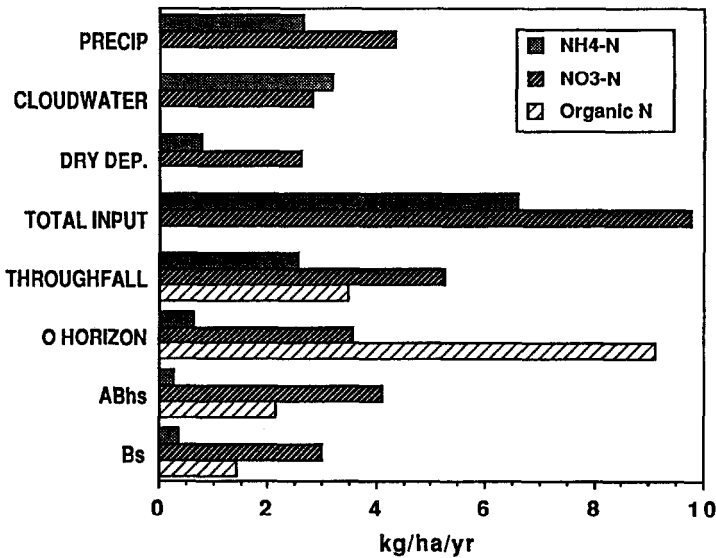

Fig. 3. Total amounts (in kg ha^{-1} yr^{-1}) of ammonium-N, nitrate-N and organic N from precipitation, cloudwater, dry deposition, throughfall, O horizon lysimeter, ABhs horizon lysimeter and Bs horizon lysimeter samples collected from Whiteface Mountain, New York, between 1986 and 1990. Total input is the sum of precipitation, cloudwater and dry deposition.

1984). Our value (which represents four continuous years of sampling) differs from previous estimates primarily because our estimates of cloud immersion time and cloudwater deposition are much lower. More recent data from montane regions of the eastern United States (summarized in Lovett & Kinsman 1990) suggest that mean cloudwater deposition for 1000—1200 m in elevation is somewhat lower than the estimate reported by Lovett et al. (1982) and Scherbatskoy & Bliss (1984) and is much closer to the values reported by us. Throughfall flux is approximately 11.3 kg N ha^{-1} yr^{-1} (Fig. 2) and is dominated by nitrate (46% of total) and organic N (31% of total) (Fig. 3). A decrease in N from above to below the canopy has been observed previously (as reviewed by Parker 1983).

There are at least two important aspects to the change in N amount (Fig. 2) and speciation (Fig. 3) above and below the forest canopy. First, it appears that total N amount has been reduced by the forest canopy. This reduction could represent an immobilization of N by the canopy surface, microbes and epiphytes living on the forest canopy (Lang et al. 1980) or it could represent uptake through foliage or bark (a suggested pathway for water, Katz et al. 1989). Bowden et al. (1989) reported that less than 1.5% of annual N requirement in red spruce seedlings was taken in through foliage, when the nitrogen was applied as an aqueous solution. Norby (1989) reported that HNO$_3$ vapor induced nitrate reductase activity and was assimilated in red spruce foliage. It is not clear how these findings relate to mature, canopy trees but it does suggest that N can enter trees through the foliage or twig bark. In view of the results of Norby (1989), we believe that the estimated 2.6 kg N ha^{-1} yr^{-1} of HNO$_3$ vapor deposition (Fig. 3) is a possible source of nitrogen to either foliage or twig bark.

Some N could be taken up by epiphytes. However, Lang et al. (1980) found that epiphytic lichens contributed little to a subalpine fir forest in terms of biomass or elemental pools or fluxes. Reiners & Olson (1984) determined ammonium and nitrate uptake by lichens in a balsam fir forest for a number of three-hour periods during cloud events. When we extrapolated these uptake rates to a year based on our observed cloud immersion times at Whiteface Mountain, we calculated less than 0.2 kg N ha^{-1} yr^{-1} of uptake by lichens. Accordingly, we do not believe that uptake or retention by lichens accounts for very much of the nitrogen that is immobilized in the canopy. Twig, branch and bole bark can immobilize or act as a temporary sink for elements (Reiners & Olson 1984; Friedland & Johnson 1985). It is possible that some N is immobilized on bark surfaces, but here again, calculations based on data from Reiners & Olson (1984) indicate that less than 0.2 kg N ha^{-1} yr^{-1} could be retained. The second aspect of N reductions through the canopy is that the decrease in ammo-

nium from above to below the canopy (4.0 kg ha^{-1} yr^{-1}) is close to the increase in organic N (3.5 kg ha^{-1} yr^{-1} Fig. 3). Above the canopy, N speciation is predominately nitrate and some ammonium; the increase in organic N below the canopy suggests that ammonium in solution has been replaced by or metabolized to organic N.

Nitrogen mass balance

Data from the current study were used to construct a mass balance for nitrogen. Atmospheric input to the forest is 16 kg N ha^{-1} yr^{-1} (Fig. 2). An estimated 40 kg N ha^{-1} yr^{-1} is generated from mineralization in the organic horizon plus an undetermined amount (see discussion in *Nitrogen mineralization* section) in the mineral horizon (Fig. 2). Thus a minimum of 56 kg N ha^{-1} yr^{-1} is available to the forest. Nitrogen uptake, requirement and translocation were calculated for our site (using the methods defined by Cole & Rapp 1981 as modified by Waring & Schlesinger 1985) and the results are shown here (Table 3). The calculated uptake for the overstory forest is 43 kg N ha^{-1} yr^{-1} (Table 3). We did not determine N pools or uptake in understory vegetation but we estimated from other coniferous sites a minimum annual uptake by understory vegetation of 0.6 kg N ha^{-1} yr^{-1} (values ranged from 0.6—4.0 kg N ha^{-1} yr^{-1}; Gordon 1983; Cole & Rapp 1981). Lower soil horizon N export is 4.8 kg N ha^{-1} yr^{-1} (Fig. 1). Thus our mass balance shows a N supply to the system of at least 56 kg N ha^{-1} yr^{-1} and we can account for at least 48 kg N ha^{-1} yr^{-1} (above- and below-ground uptake + export + minimum understory vegetation uptake of 0.6 kg N ha^{-1} yr^{-1}), or 86% of total input. If atmospheric deposition were completely utilized by forest vegetation, it could provide 38% of the annual N uptake (Table 3). However, some of the N was deposited during times of the year when canopy trees were not actively taking up N.

   Currently, forest ecosystems in the Northeast are receiving more atmospheric N deposition than earlier in this century. In the absence of any unimpacted 'control' stands, we compared N cycling in the current study site to that in a variety of other temperate forest ecosystems to see if differences exist that might be related to red spruce decline. Using the IBP data in Cole & Rapp (1981), we made a series of comparisons of N use and retention times to gain some insights into N availability at our site compared to other sites (Table 4). The values in columns 1 and 2 of Table 4 are taken directly from Cole & Rapp (1981). Column 3 contains data from the current study calculated with the amount of information and type of data available to the IBP investigators. For example, even though we had estimates of root biomass and production, these were not included in

Table 3. Annual deposition, leaching, requirement[a], uptake[a] and translocation for the subalpine spruce-fir forest at Whiteface Mountain, NY.

	Total N
	kg N ha^{-1} yr^{-1}
Total deposition[b]	16.4
Mineralization[b]	40
Requirement	
New foliage	34.5
Wood increment[b]	10.8
Root increment[b]	8.3
Canopy leaching	0
Total requirement	53.6
Uptake	
Aboveground increment	10.8
Belowground increment	8.3
Litterfall	23.7
Net canopy effect (if > 0)	0
Total uptake	42.8
Translocation = requirement − uptake =	10.8
Atmospheric deposition/uptake =	38%
Leaching loss (export)[c]	4.8

[a] As defined by Cole & Rapp (1981) and modified by Waring & Schlesinger (1985).

[b] Wood and root increment were determined from Whittaker et al. (1974) and possibly underestimate actual increment because roots < 2-mm diameter were not considered.

[c] Values from Fig. 2.

the values in column 3 of Table 4 because these data were not available to most IBP investigators (Cole & Rapp 1981). Because the IBP investigators did not measure cloudwater or dry deposition, throughfall minus precipitation was used to calculate crownwash in column 3. However, all of the information obtained in the present study was included in the estimates shown in column 4 in order to present a more complete estimate of the same parameters.

Our site contains approximately 15% white birch by basal area (Table 1) and thus might be expected to behave similar to but not exactly like the temperate coniferous sites from Cole & Rapp (1981). However, the relatively large atmospheric N deposition at our site, compared to most (but not all) of the IBP sites, might cause nutrient cycling in our forest to resemble that of deciduous forests where N is often more abundant. Foliar biomass and N residence times for our site are similar to temperate

Table 4. Comparison of N retention and use parameters from temperate coniferous and deciduous sites (from International Biological Programme (IBP) Cole & Rapp 1981) and from the current study. Current study values were calculated using parameters available to most IBP investigators and using additional parameters available today but not available to most IBP investigators.

	Deciduous	Temperate coniferous	Whiteface (IBP methods)[a]	Whiteface (contemporary)[b]
Foliar biomass Residence time[c] (yrs)	0.86	2.75	2.79	2.79
Foliar N Residence time[d] (yrs)	1.46	3.74	3.64	5.5
$\left(\dfrac{\text{N translocation}}{\text{N requirement}^e} \right)$ (%)	23	9.9	14	20
N use efficiency[f]	138	184	151	172

[a] Estimated from the current study using only the amount and quality of information available to IBP investigators.

[b] Estimated from the current study using additional information not available to IBP investigators including estimates of cloudwater and dry deposition, canopy uptake and root biomass and increment.

[c] Foliar biomass/litterfall biomass: for Whiteface, this value was determined from foliar biomass of 7250 kg ha^{-1} divided by litterfall biomass of 2590 kg ha^{-1} yr^{-1}.

[d] Foliar N mass/return N mass: for the Whiteface IBP method, we used foliar N mass (102 kg ha^{-1} from Fig. 2) and N return from litterfall (23.7) plus the amount delivered to the forest floor from leaching (which using IBP methods was throughfall minus precipitation or 11.3 kg ha^{-1} yr^{-1} minus 7.0 kg ha^{-1} yr^{-1} = 4.3 from Fig. 2). For the Whiteface contemporary method, we calculated return as litterfall (23.7 kg ha^{-1} yr^{-1}) minus canopy uptake of N (5.1 kg ha^{-1} yr^{-1} from Fig. 2).

[e] For the Whiteface IBP method, we removed belowground increment from the calculation of requirement (Table 3) yielding an IBP-compatible requirement of 45.3 kg ha^{-1} yr^{-1}. For uptake, the belowground increment was removed and canopy effect added, yielding an IBP-compatible uptake of 38.8 kg ha$^-$ yr^{-1}.

[f] Annual net primary productivity/Annual N uptake (in kg ha^{-1}): for the Whiteface IBP method, we did not include root primary productivity, so NPP was (5850 kg ha^{-1} yr^{-1}) and N uptake was 38.8 kg ha^{-1} yr^{-1} as in c. For the Whiteface modern method, we included roots in our NPP estimate (7380 kg ha^{-1} yr^{-1}) and we used the estimate of uptake from Table 3 (42.8 kg ha^{-1} yr^{-1}).

coniferous IBP sites (Table 4). Nitrogen reabsorption as a percent of N requirement for our site is greater than the temperate coniferous IBP sites but not as great as the value for the deciduous sites. Nitrogen use efficiency (net primary productivity per unit uptake of N) from our site is less than that for temperate coniferous IBP sites and is closer to the average value for the deciduous sites, which are, in general, less nutrient limited

(Table 4). These findings suggest that our site is not severely limited by N. A more definitive way to test this hypothesis would be to reevaluate the parameters reported in Table 4 in five or ten years as well as compare N cycling across an N deposition gradient (cf. McNulty et al. 1991, this issue).

The role of N in forest decline

Although previous investigators have concluded that boreal forests and montane coniferous forests are N-poor (Vitousek et al. 1982; Lea et al. 1979), our results suggest this may not be the case at Whiteface Mountain. Pastor et al. (1987) hypothesized that declining red spruce forests are experiencing a decrease in N availability as part of a periodic cycle of N availability, in part due to periodic accumulation of inhibitory compounds from litterfall which should limit N mineralization. We found rates of mineralization of 40 kg N ha^{-1} yr^{-1} (Fig. 2) which do not appear to be low when compared to the N uptake for the forest (Table 3) or when compared to other spruce-fir forests (Federer 1983). In addition, some nitrate leaves the system (Fig. 2). Nitrate concentrations in soil solution do decrease during the growing season (average nitrate concentration during the growing season is 18.6 μmoles liter^{-1}; 40.2 μmoles liter^{-1} during the remainder of the year) indicating nitrate is taken up from the soil solution by biological activity or less nitrate is produced. Nevertheless, some N leaves the system at all times of the year, indicating that this forest is probably not N limited.

Aber et al. (1989) suggested a number of 'early indicators' of the onset of nitrogen saturation in a forested ecosystem including elevated nitrate in solutions and increased nitrate losses from the system. Aluminum and hydrogen ion losses are discussed as secondary effects of N saturation. Aber et al. (1989) further state that N saturation can be determined by increased leaching of nitrate and ammonium as compared to background levels. We are unable to determine if the concentrations (Fig. 1) and net fluxes (Table 5) we have observed in the current study are higher than 'background levels' because we do not have any N values with which to compare our present values. The N values reported in the present study do not appear to be excessively high; however, Tables 3 and 5 show that some leaching is taking place.

Schulze (1989) constructed a decline scenario for Norway spruce (*Picea abies* L. Karst)-dominated forests in Europe that included foliar uptake of ammonium and nitrate which led to modification of tree nutrition. Schulze stated that additional N may stimulate growth which is ultimately impaired by the induced deficiency of other elements such as Ca or Mg. In this paper, we noted the probable foliar uptake of N

Table 5. Net canopy and net ecosystem fluxes from Whiteface Mountain, NY determined from June 1986 through May 1990.

	NH$_4^+$-N	NO$_3^-$-N	Organic N	Total N
		kg ha^{-1} yr^{-1}		
Total deposition	6.6	9.8	0.0	16.4
Total export	0.4	3.0	1.4	4.8
Net canopy	4.0	4.5	−3.5[a]	5.0
Net ecosystem	6.2	6.8	−1.4[a]	11.6

[a] The negative sign designates a net loss from that component of the system.

(previous section on Canopy Fluxes and Fig. 3). We have noted relative deficiencies of Mg in red spruce foliage in Vermont and New York (Friedland et al. 1988) and at the study site (Friedland & Miller, unpublished data). We have also observed elevated N to Mg ratios in red spruce foliage at high elevations throughout Vermont (Friedland et al. 1988) and at our study site (Friedland & Miller, unpublished data).

The results presented in this paper lack a quantitative assessment of variability (as briefly discussed in the section *Solution nitrogen concentrations*) and it is therefore difficult to test particular hypotheses regarding N abundance or deficiency and its impact on red spruce decline. Furthermore, since we do not have data from previous decades, it is difficult to compare our results to what might be the case if our study area had been impacted by less substantial N deposition from air pollution. Finally, we recognize that the recent death of large numbers of red spruce trees (Johnson & Siccama 1983; Scott et al. 1984; Craig & Friedland 1991; Battles et al. 1991) is in itself a disturbance agent. Again, we lack baseline data with which to compare our present results. Since our data are observational in nature, we can only state that some aspects of our data are consistent with some of the hypothesized 'symptoms' of excess N while other aspects are not.

Conclusions

During four years of continuous monitoring in the subalpine spruce-fir forest at approximately 1000-m elevation in the Adirondacks of New York, an average of 16 kg N ha^{-1} yr^{-1} was delivered to the forest canopy as precipitation, cloudwater and dry deposition from the atmosphere. This value is somewhat lower than previous reports of cloudwater deposition to

high-elevation forests in the northeastern United States. Approximately 30% of the input was retained by the canopy. Canopy retention is probably the result of immobilization by bark and foliar uptake with minor immobilization by microorganisms. Approximately 40 kg N ha^{-1} yr^{-1} is generated within the forest floor by mineralization of organic matter. Virtually all ammonium is consumed in the forest floor. The most abundant N components of soil water solutions are organic N in the organic soil horizon and nitrate in the mineral soil horizons. Most organic N is retained in the Bhs soil horizon, which is consistent with processes of podsolization. The net canopy and ecosystem fluxes for ammonium and nitrate indicate accumulation of both compounds in the ecosystem. Atmospheric deposition could fulfill up to 30% of the calculated annual overstory forest requirement for N. Mineralization of forest floor material and calculated translocation from older foliage easily fulfilled the remainder of the above- and below-ground annual N requirement. Comparisons with other sites suggest that N use efficiency may not be as great as in some other temperate coniferous systems. This could in part be a result of the deciduous component of the current study site or the increased availability of N from atmospheric deposition.

Acknowledgments

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