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Nitrogen mineralization in high-elevation forests of the Appalachians. II. Patterns with stand development in fir waves

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Abstract. Wave-like patterns of mortality and regeneration of balsam fir (*Abies balsamea* {L.} Mill.) and Fraser fir (*A. fraseri* {Pursh.} Poir.) forests at high elevations in the Appalachian Mountains offer a unique opportunity to study the effects of stand development on nitrogen cycling. We sampled two fir waves, one with Fraser fir on Mt. LeConte in the Great Smoky Mountains National Park, and one with balsam fir on Whiteface Mountain in New York. Net nitrogen mineralization for 3 summer months at Mt. LeConte was high in the dead fir zone (47 kg-N/ha), lower in the regeneration and juvenile zones (24 and 21 kg-N/ha), and highest in the mature zone (61 kg-N/ha). This sampling period probably accounted for about 60% of the annual total. The pattern was similar in the balsam fir wave on Whiteface Mountain, with N mineralization rates of 39 and 33 kg-N/ha over 2 months for the regenerating and juvenile zones, and 43 and 54 kg-N/ha for the mature and dead zones. Throughfall nitrogen followed a fairly similar pattern, with rates ranging from 4.5 to 10 kg-N/ha for 2 or 3 months across all zones at both sites. Tension-free lysimeters indicated very little leaching of nitrogen below 30 cm depth (the maximum was 2.6 kg-N/ha), but these estimates may be low. We conclude that nitrogen mineralization is high at all stages of stand development, perhaps exceeding the uptake capacity of the trees. Rates of nitrogen leaching may be high in these ecosystems and should receive further attention.

R.H. Whittaker (1956) eloquently described the high-elevation Fraser fir (*Abies fraseri* (Pursh.) Poir.) forest on Mt. LeConte in the Great Smoky Mountains:

> ...the forest appears appropriate to the subalpine extremity in the Appalachians, a dwarf conifer forest which on a fair day has a charm of its own but at other times, with the summits involved in cloud and a raw wind whipping fog through the firs, assumes the bleakness of the climate in which it lives.

Partly as a result of the influence of cloud cover and high winds, these forests are subject to much higher deposition of inorganic nitrogen and other substances from the atmosphere than are lower elevation forests (Lovett et al. 1982; Lovett 1984). The fertilization effect of high deposition rates may result in greater nitrogen availability, production of litter with lower C:N ratios, and a greater amount of nitrogen cycling through litterfall (Vitousek et al. 1982). Some fir and spruce (*Picea rubens* Sarg.) forests in the Appalachians show symptoms of decline (Johnson & McLaughlin 1986; Woodman 1987), and high nitrogen availability has been speculated to be a possible cause or contributing agent (c.f. Friedland et al. 1984).

Very little information is available on changes in nutrient cycling through stand development following gap-phase turnover of forests (Vitousek 1985). The presence of wave-regeneration patterns in high-elevation Fraser fir (> 1800 m) and balsam fir (*A. balsamea* (L.) Mill.) (>1200 m) forests, as elucidated by Sprugel (1976, 1984), provides a unique opportunity to study changes in nitrogen dynamics across a gap-phase/stand development sequence. White et al. (1985) concluded the "patch-wise blowdown" pattern in Fraser fir stands was similar to balsam fir waves, but without the regularity and directionality observed by Sprugel (1976). In both types of forests, these mortality and regeneration patterns provide a gradient of stand development over short (< 100 m) distances.

In this study, we examined nitrogen dynamics in relation to stand development across a Fraser fir wave on Mt. LeConte in the Great Smoky Mountains National Park in Tennessee, and a balsam fir wave on Whiteface Mountain in New York. We expected that the zones of dead trees would show relatively low N deposition (as indexed by throughfall), high mineralization rates (after Vitousek 1985) due to greater insolation and lower evapotranspiration, and high leaching losses due to low plant uptake. We expected that the developing canopy in the regenerating and juvenile zones would be moderately efficient at trapping fog and nitrogen compounds from the atmosphere, but that mineralization rates and leaching rates would be low due to shading of the forest floor and rapid uptake. We expected the mature stands would show greatest deposition due to greatest canopy surface area, low mineralization rates due to shading of the forest floor, and moderate leaching losses due to low acumulation in biomass. To test these hypothesized patterns, we used ion exchange resin bags to estimate the N content of throughfall at the surface of the forest floor as a surrogate for N deposition. Incubations of open soil cores with resin bags on bottom gave an index of nitrogen mineralization, and tension-free lysimeters coupled with ion exchange resins provided an estimate of N leaching.

Methods

The fir wave on Mt. LeConte is to the northwest of the peak on a northeast-facing slope at an elevation of 1900 m. Precipitation exceeds 2000 mm/yr, and the mean monthly temperature is 8 C. The bedrock of the area is metamorphosed sedimentary sandstones and shales of Precambrian age, and the soils in the Fraser fir wave belong to the Craggey series (loamy, mixed, frigid Lithic Haplumbrept). The soils are thin (< 0.5 m), high in organic matter and very acidic (Springer 1984). Balsam woolly adelgid (*Adelges piceae* Ratz.) damage has been reported on Mt. LeConte, but the wave we examined was not related to adelgid activity (P. White, National Park Service, pers. comm.).

The fir wave near Whiteface Mountain is to the northeast of the main peak, at about 1200 m on a south-facing slope on the trail to Mount Lookout from the Whiteface Memorial Toll Road. We located a wave in the vicinity of Sprugel's (1976) study sites; this wave resembled the fir patches described by Reiners & Lang (1979). Whiteface Mountain receives less precipitation (about 1200 mm/yr) than Mt. LeConte, and is considerably cooler (monthly mean temperature 2 C). Bedrock is Whiteface anorthosite, composed mainly of plagioclase feldspars. The soils in the fir wave were not classified to series, but are thin (15 to 50 cm deep), high in organic matter, and very acidic (Sprugel 1976). Adelgid damage is minimal (Sprugel 1976).

In both fir waves, four 50-m transects were laid out parallel with the stages of stand development. The dead zones were characterized by standing and fallen dead trees, with little understory growth (the disturbance stage of Oliver 1981). The regenerating zones had dense stands of firs less than 2 m in height (Oliver's stand initiation stage). The juvenile zones had closed canopies and average tree height of 2 to 4 m (Oliver's stem exclusion stage). The mature zones also had closed canopies, with average tree heights greater than 4 m (Oliver's old growth stage).

Ten sampling points were spaced at 5 m intervals along each transect. Sharpened PVC tubes (3.8 cm diameter, 15 cm length) were hammered into the soil and the top 12 cm of forest floor + mineral soil were removed (Strader et al. in review). The bottom 2 cm of soil were replaced by an ion exchange resin bag (after DiStefano & Gholz 1986) constructed of nylon stockings containing 14 mL of anion resin (J.T. Baker strongly basic resin, OH-saturated) and 14 mL of cation resin (Dowex 50W-X8 strongly acidic resin, H^+ saturated). The bags were pretreated with 100 mL of 2 *M* NaCl each to minimize later interference with nitrogen analyses. A second bag was placed on top of the tubes to catch throughfall. Additional soil cores were removed for determination of initial soil concentrations of ammonium and nitrate.

Tension-free lysimeters were constructed of 6-cm diameter plastic funnels covered with nylon stockings, with a 30-cm tube of ion exchange resins (about 6 mL of anion + cation resin) attached. The funnels were installed in the sides of soil pits at depths ranging from 20 cm (in shallow bedrock sites) to 30 cm.

At Mt. LeConte, the incubation tubes and funnels were installed on May 5 and 6, 1986, and removed on July 28 and 29, 1986. Tubes and funnels were installed at Whiteface Mountain on June 4 and 5, 1986, and removed August 14, 1986. After removal, soil samples were stored cool (at about 4 C) for 2 to 4 days until 4 g subsamples were extracted with 40 mL of 2 *M* KCl. Resin bags were air-dried and extracted with 100 mL of 2 *M* KCl. This extraction procedure does not remove all adsorbed N from the resins; recovery of known amounts of N from resins averaged 70%, so resin values reported here have been increased proportionally. Resins from the lysimeters were extracted with 30 mL of 2 *M* KCl. Ammonium and nitrate in the extracts were determined colorimetrically (Scientific a and b).

Throughfall nitrogen was extrapolated to a hectare basis by multiplying the ammonium and nitrate content of the top resin bag by the area of the tube. Net nitrogen mineralization was calculated as the increase in ammonium and nitrate in the soil core relative to initial values, plus the ammonium and nitrate accumulated on the bottom resin bags. Mineralization values were extrapolated to a hectare level based on the area of the soil cores, reduced by the proportion of unsamplable points along each transect. The incubation cores needed to be shifted up to 1 m away from the designated sample points due to soil rocks; the proportion of unsamplable points was determined by inserting a metal rod to a depth of 15 cm at 100 points along each transect. The proportion of soil rocks was similar among transects within each mountain, so a composited value was used for all zones. Leaching losses (past the 20–30 cm depth) were extrapolated to a hectare level based on the area of the funnels.

Statistical analyses were performed with SAS on a mainframe computer (SAS 1985), or by hand calculation. Log transformation of throughfall and mineralization data improved the normality of the distributions and equalized variances (Martin & Games 1977). Means were compared with Tukey's HSD test at alpha = 0.10 (Sokal & Rohlf 1981).

Results and discussion

Contrary to our expectations, throughfall nitrogen showed no significant differences among transects within either mountain (Fig. 1). In fact,

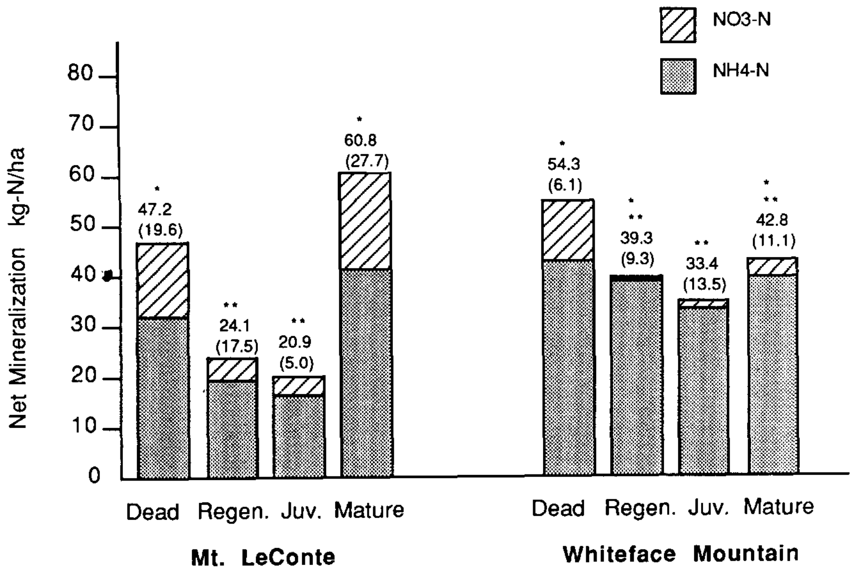

Fig. 1. Mean (standard deviation) of net nitrogen mineralization by stage of stand development at Mt. LeConte (3 months) and Whiteface Mountain (2 months). Bars with same number of asterisks do not differ at $p = 0.10$.

throughfall appeared highest in the dead zones where we predicted the lowest capture of fog and nitrogen would occur. The overall average for Mt. LeConte was 6.5 kg-N/ha, and 7.9 kg-N/ha for Whiteface mountain. Based on the annual pattern determined by Strader et al. (1988) for nearby Clingman's Dome, the annual throughfall at Mt. LeConte may be about 15 to 35 kg-N/ha. The variability among samples was very large, so the area represented by the resin bags on top of the incubation tubes may have been too small to provide a good estimate of throughfall nitrogen. Interestingly, about 75% of the throughfall N was ammonium. Cronan & Reiners (1983) estimated that throughfall nitrogen in fir forests in the White Mountains in New Hampshire was comprised of 75% nitrate, whereas Olson et al. (1981) estimated equal amounts of ammonium and nitrate. Strader et al. (1988) found higher proportions of ammonium than nitrate in throughfall in 19 spruce-fir stands in the southern Appalachians during the growing season, but equal amounts on an annual basis.

Net nitrogen mineralization rates generally followed our hypothesized pattern. On Mt. LeConte, the dead and mature zones showed about twice the rates ($p < 0.0001$) of the regenerating and juvenile zones (Fig. 2). The high rate in the mature zone was unexpected, indicating that either the dense canopy does not impair the microenvironment for mineralization, or the

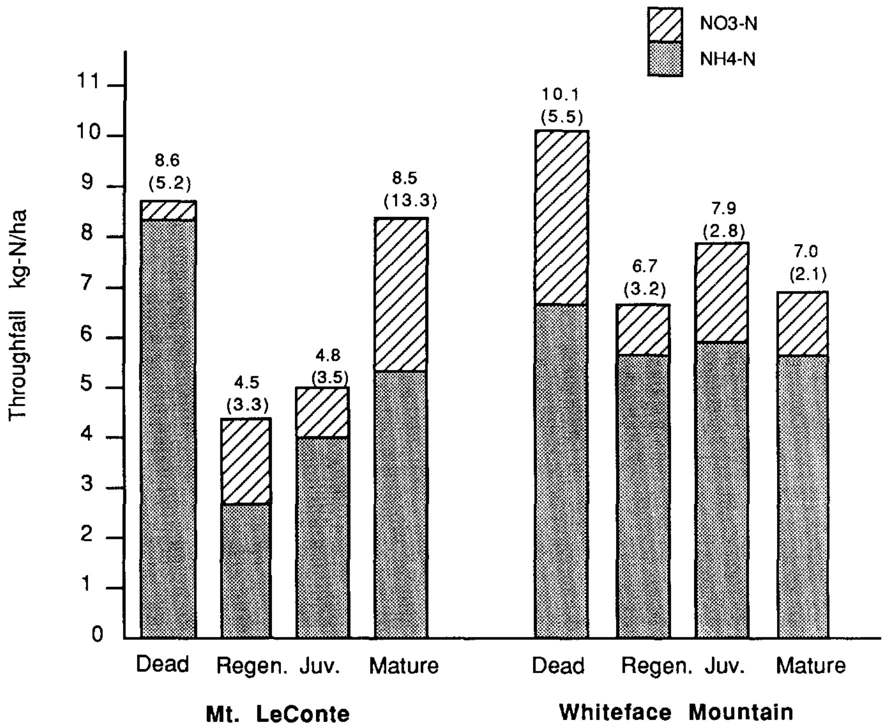

Fig. 2. Mean (standard deviation) of throughfall nitrogen at Mt. LeConte (3 months) and Whiteface Mountain (2 months). Means of log-transformed values did not differ ($p > 0.10$) did not differ among stages of stand development within each mountain.

substrate quality is better in the mature stage of stand development. The pattern was similar at Whiteface Mountain, except that the only significant differences were between the dead zone and the juvenile zone. Ammonium was the dominant form in all transects, comprising about 75% of mineralized N at Mt. LeConte, and 92% at Whiteface Mountain. In contrast, Bloss & Binkley (1988) found that mineralized nitrogen in nearby beech stands was about 80% nitrified during the same period. Most of the mineralized nitrogen accumulated on the resin bags in both studies; about 60 to 75% of mineralized N was found in the bottom resin bags.

The rates of mineralization were very high, especially considering the short (2 to 3 month) incubation periods. Based on the annual pattern determined by Strader et al. (1988) for stands on Clingman's Dome, our 20 to 60 kg-N/ha mineralization rates for Mt. LeConte extrapolate to annual rates of about 35 to 100 kg-N/ha. If a similar pattern holds for Whiteface Mountain, the extrapolated annual mineralization rate may be from about 80 to over 100 kg-N/ha.

Table 1. Means (and ranges) of nitrogen captured in tension-free funnel lysimeters during 3 months at Mt. LeConte, and 2 months at Whiteface Mountain

Mountain	Zone	Ammonium kg/ha	Nitrate kg/ha
LeConte	Dead	0.0 (0.0–0.0)	2.6 (0.1–12.6)
	Regenerating	0.0 (0.0–0.0)	0.2 (0.0–0.8)
	Juvenile	0.0 (0.0–0.0)	0.2 (0.0–1.5)
	Mature	0.1 (0.0–0.8)	1.3 (0.0–4.3)
Whiteface	Dead	0.1 (0.0–0.8)	0.2 (0.0–0.9)
	Regenerating	0.1 (0.0–0.6)	0.0 (0.0–0.1)
	Juvenile	0.3 (0.0–2.5)	0.3 (0.0–1.1)
	Mature	0.1 (0.0–0.8)	0.8 (0.0–2.9)

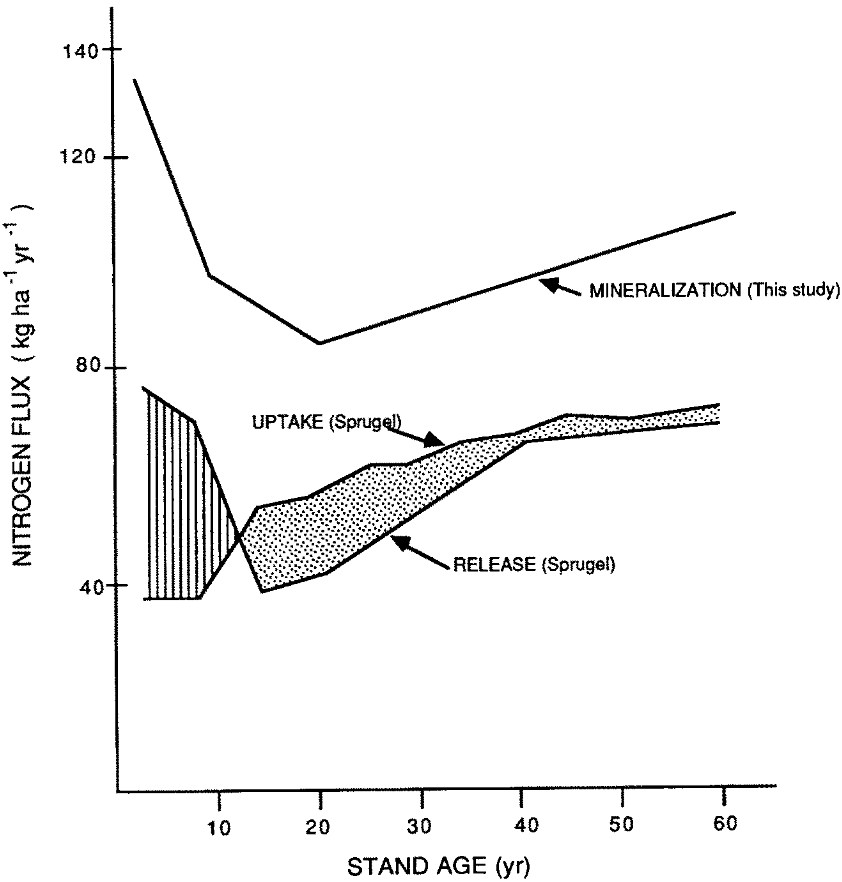

Fig. 3. Nitrogen uptake (sum of N accumulation in biomass plus return in litterfall) by trees and release by decomposition in fir waves as modelled by Sprugel (1984), and net nitrogen mineralization estimates for Whiteface Mountain from this study.

The nitrogen contained in the resin tubes of the tension-free funnel lysimeters was small relative to the mineralization rates; the maximum rate was about 2.6 kg-N/ha (Table 1). Either the lysimeters failed to sample soil leachate adequately, or uptake by the vegetation was sufficient during the growing season to minimize leaching.

Sprugel (1984) estimated the rate of uptake of N into aboveground biomass across a fir wave on Whiteface Mountain, and compared that to a calculated release of nitrogen from decomposition of the forest floor. Our pattern of mineralization at Whiteface Mountain is strikingly similar to Sprugel's (Fig. 3), but our rates are about twice as high. Sprugel's estimate of release included only the decomposition of aboveground litter; ours included the top 10 cm of litter plus mineral soil. Our mineralization estimate exceeds Sprugel's rate of N uptake in aboveground tissues at all stages, but inclusion of the N uptake for belowground tissues might reduce the difference. No information is available on the rate of N uptake for belowground portions of fir forests in the eastern US; Vogt et al. (1986) found that belowground N turnover rates for cool, temperate coniferous forests averaged about 60 kg-N/ha annually. If the rate of N uptake for belowground production across the fir waves matched this average, then our estimated rate of mineralization would almost precisely match the estimated uptake rate at all stages after about 10 years of age. Based on this rough N budget, N leaching might be important in the dead and early-regeneration stages of the fir waves. However, it is possible that roots from adjacent mature and regenerating stages could occupy the dead zone, and reduce any leaching of N that would otherwise occur. Improved sampling of the soil solution is needed to test these patterns.

We conclude that nitrogen availability is fairly high in all stages of the fir waves, perhaps exceeding uptake by the vegetation in the early stages. These high mineralization rates provide evidence that "excess nitrogen" speculations about causes of decline in spruce and fir forests would be tenable for mature stands only if the rate of N uptake for belowground production is considerably less than the average rate for cool, temperate, coniferous forests.

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