Preliminary estimates of foliar absorption of $^{15}$N-labeled nitric acid vapor (HNO$_3$) by mature eastern white pine (Pinus strobus)

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We used a direct approach to quantify foliar N absorption by exposing foliage of mature eastern white pine (Pinus strobus L.) to $^{15}$N-labeled nitric acid vapor (HNO$_3$). Foliage on terminal portions of branches in a 31-year-old white pine plantation was enclosed in 9.0-L teflon film branch cuvettes and exposed to 10, 50, and 100 ppb H$_3$NO$_3$ for 12-30 h. Foliar absorption rates ranged from 0.006 $\mu$g $^{15}$N·g$^{-1}$·h$^{-1}$ at 10 ppb to 0.267 $\mu$g $^{15}$N·g$^{-1}$·h$^{-1}$ at 100 ppb. Extrapolation to the entire canopy resulted in an estimated absorption of 0.30-0.50 kg N·ha$^{-1}$·year$^{-1}$ at ambient HNO$_3$ concentrations. In contrast, canopy input-output estimates for the same forest stand indicated a depletion of 2.3 kg N·ha$^{-1}$·year$^{-1}$ by the forest canopy.


L’absorption foliaire de N a été quantifiée directement en exposant le feuillage de Pins blancs de l’est (Pinus strobus) matures aux vapeurs d’acide nitrique (HNO$_3$) marquée avec du $^{15}$N. La portion terminale du feuillage sur des branches de Pins blancs de l’est dans une plantation de 31 ans fut enfermée dans une cuvette de teflon de 9,0 L et exposée à 10, 50 et 100 ppb H$_3$NO$_3$ pendant 12 à 30 h. Les taux d’absorption foliaires allaient de 0,006 $\mu$g $^{15}$N·g$^{-1}$·h$^{-1}$ à 10 ppb jusqu’à 0,267 $\mu$g $^{15}$N·g$^{-1}$·h$^{-1}$ à 100 ppb. Une extrapolation pour l’ensemble du couvert a permis d’évaluer l’absorption à 0,30 à 0,50 kg N·ha$^{-1}$·an$^{-1}$ aux concentrations ambiantes de HNO$_3$. Par contre, des estimés «d’input-output» pour le même peuplement indiquent une perte de 2,3 kg N·ha$^{-1}$·an$^{-1}$ via le couvert.

Introduction

Increased atmospheric deposition of N to forest ecosystems in the form of gases, precipitation, and particulates has been hypothesized to alter tree physiology and nutrient cycling processes (McLaughlin 1985; Nihlgard 1985; Aber et al. 1989). An important component of the fate of these N inputs is absorption by the foliage; however, the magnitude of foliar absorption of atmospheric N inputs in mature forests is largely unknown. We used a direct approach to quantify foliar N absorption by exposing foliage of mature eastern white pine (Pinus strobus L.) to $^{15}$N-labeled HNO$_3$. Our objectives were (1) to quantify N absorption by white pine foliage across a range of H$_3$NO$_3$ concentrations and (2) to evaluate the significance of $^{15}$N absorption relative to N nutrition and cycling.

Methods

Foliation was exposed to known H$_3$NO$_3$ (99% enrichment) concentrations in FEP teflon film branch cuvettes (9.0 L volume) placed at the ends of branches in the upper canopy of a 31-year-old white pine plantation (Coweeta Hydrologic Laboratory, NC). Branches were approximately 10 m long and were sampled from three different trees. These trees were representative of dominant and codominant trees in the stand. Access to the upper canopy was facilitated by a 31-m “walk-up” tower used for atmospheric deposition monitoring. The H$_3$NO$_3$ was generated from certified, precalibrated gas permeation tubes that contained H$_3$NO$_3$ in liquid phase (KIN-TEC Laboratories, Texas City, TX). When heated to a specified calibration temperature, H$_3$NO$_3$ diffused through the teflon wall of the permeation tube at a constant rate. Permeation tubes of variable size and calibration temperature were required to generate H$_3$NO$_3$ concentrations of 10, 50, and 100 ppb when mixed with HNO$_3$ free air at a flow rate of 9.0 L·min$^{-1}$. Ambient HNO$_3$ was removed by passing air through a nylon filter (Gelman Nylasorb) prior to mixing with the permeating H$_3$NO$_3$. All tubing in the delivery system was composed of TFE teflon.

Three treatment regimes were imposed to represent a range of exposure conditions. First, foliage was subjected to 50 ppb H$_3$NO$_3$ from 09:00 to 16:00 on August 25, 1988, and from 10:00 to 15:00 on August 26, 1988 (7 and 5 h on days 1 and 2, respectively; the cuvette was removed from the branch between exposures). In the second exposure, foliage was subjected to 10 ppb H$_3$NO$_3$ from 10:00 on September 7, 1988, to 15:00 on September 8, 1988 (30 continuous hours), and in the third exposure foliage was subjected to 100 ppb H$_3$NO$_3$ from 10:00 on September 15, 1988, to 15:00 on September 16, 1988 (30 continuous hours). Exposures were conducted on rainless, sunny days. Monthly precipitation was 93 mm (34% below average) in August and 116 mm (8% below average) in September. In the 2 weeks preceding each exposure period, rainfall was 57, 63, and 70 mm for the three exposure periods, respectively. Scanning electron microscopy of needle surfaces immediately following exposures (needles were immediately fixed using procedures in Sabatini et al. 1963) showed that stomates were open at the end of all exposures (J.M. Vose and W.T. Swank, unpublished data). After exposures, foliage was (1) immediately removed and rinsed vigorously with 1000 mL deionized water spray, as previous research by Marshall and Cadle (1989) has shown that rinsing with deionized water effectively removes adsorbed N, (2) separated by age-class (i.e., foliage produced the past year and foliage produced the current year), (3) dried at 60°C for 48 h and weighed to the nearest 0.01 g, and (4) ground to 100 µm using a
Table 1. Foliar $^{15}$N absorption by age-class (current (C), past (P)) and exposure level

<table>
<thead>
<tr>
<th>Level (ppb)</th>
<th>Dosage (ppb h)</th>
<th>Age-class</th>
<th>Total $^{15}$N (%</th>
<th>Excess $^{15}$N (%</th>
<th>Total N (g)</th>
<th>Total N excess $^{15}$N (µg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>300</td>
<td>C</td>
<td>0.374 25 (0.002)</td>
<td>0.007 23</td>
<td>1.058 (0.02)</td>
<td>0.055</td>
</tr>
<tr>
<td>50</td>
<td>600</td>
<td>C</td>
<td>0.378 44 (0.003)</td>
<td>0.014 42</td>
<td>1.189 (0.001)</td>
<td>0.086</td>
</tr>
<tr>
<td>100</td>
<td>3000</td>
<td>P</td>
<td>0.378 31 (0.004)</td>
<td>0.007 79</td>
<td>1.017 (0.005)</td>
<td>0.086</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
<td>0.425 94 (0.001)</td>
<td>0.058 92</td>
<td>1.159 (0.008)</td>
<td>0.053</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P</td>
<td>0.443 34 (0.003)</td>
<td>0.076 32</td>
<td>1.043 (0.02)</td>
<td>0.044</td>
</tr>
</tbody>
</table>

Note: Total N was estimated by multiplying foliar percent total N by the dry weight of exposed foliage. Total excess $^{15}$N was estimated by multiplying percent excess $^{15}$N by total N. SE is a measure of analytical error and is given in parentheses.

Concentration in ppb x exposure duration in hours.

Results and discussion

Excess $^{15}$N was detected after all exposures. Excess at.% $^{15}$N values ranged from 0.007 23% in current foliage after the 10 ppb exposure, to 0.076 32% in past foliage after the 100 ppb exposure (Table 1). Absorption rates of $^{15}$N (µg·g$^{-1}$·h$^{-1}$) increased with concentration (Fig. 1), and this pattern was consistent across foliage age-classes. Absorption rate was linearly related to concentration in current foliage, but curvilinearly related to concentration in past foliage. Linear regression combining absorption rates for both foliage age-classes resulted in an $r^2$ of 0.96 (no-intercept model; $F = 134.51; P > F = 0.0001; \text{mean square error} = 0.0010; n = 6$), where the slope of the regression was 0.002 35. Our absorption rates are similar to simulated cloud water $^{15}$N absorption rates by red spruce foliage (Bowden et al. 1989), which ranged from 0.079 to 0.288 µg·g$^{-1}$·h$^{-1}$.

To obtain a measure of the magnitude and importance of these absorption estimates at the stand level, we extrapolated the uptake data presented in Fig. 1 to the entire forest canopy based on four assumptions: (1) canopy biomass = 9500 kg·ha$^{-1}$ from April to October and 5300 kg·ha$^{-1}$ from November to March (determined following procedures in Swank and Schreuder 1973); (2) from April to October, 50% of the canopy is current foliage and 50% is past foliage; from November to March, 100% of the canopy is past foliage (Swank and Schreuder 1974); (3) foliage is exposed to $\text{HNO}_3$ for 365 days·year$^{-1}$; and (4) uptake rates during November to March are reduced by 25% to adjust for lower stomatal conductance in winter. Extrapolated estimates of potential canopy absorption were

FIG. 1. Nitrogen-15 absorption rate by concentration and foliage age-class. Nitrogen-15 uptake rate was determined by dividing total excess $^{15}$N (µg) by the dry weight (g) of exposed foliage and by the duration of exposure (h).

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3.0, 5.3, and 15.9 kg N·ha$^{-1}$·year$^{-1}$ for the 10, 50, and 100 ppb exposures, respectively. However, ambient HNO$_3$ concentrations at our study site are typically 1-3 ppb. To obtain a first approximation of canopy absorption under ambient HNO$_3$ concentrations, we used the regression between foliar absorption rate and concentration (i.e., $15^N$N absorption rate = 0.00235 $\times$ HNO$_3$ concentration), combined with the assumptions 1, 3, and 4, and estimated N absorption at ambient levels to be approximately 0.2-0.5 kg N·ha$^{-1}$·year$^{-1}$. In contrast, we calculated a deposition (2-year average) of 2.7 kg·ha$^{-1}$·year$^{-1}$ NO$_3^-$N (from HNO$_3$) to the forest canopy (Table 2). Thus, our absorption estimates indicate that approximately 10-20% of the NO$_3^-$N deposited from HNO$_3$ is absorbed by the foliage. We recognize that the results obtained by these extrapolations are dependent on the validity of the experimental technique and assumptions used to scale-up to the stand. However, we feel that these extrapolations must be made in order to evaluate the stand-level significance of the foliar absorption data.

Our quantitative extrapolations are much lower than indicated by studies of mass NO$_3$-N balances (input-output) for the same forest stand (Table 2). For example, total NO$_3$-N input (wet and dry) to the canopy was 5.0 kg·ha$^{-1}$·year$^{-1}$ (54% of which was contributed by HNO$_3$), whereas throughfall and stem flow outputs were 2.7 kg·ha$^{-1}$·year$^{-1}$. These figures indicate a net canopy retention of 2.3 kg·ha$^{-1}$·year$^{-1}$. However, included in this net canopy retention amount are foliar absorption of both wet and dry NO$_3$-N; adsorption (i.e., not rinsed off by rainfall) of NO$_3$-N by foliage, branches, and stems; and utilization and transformation of NO$_3$-N by microflora and microfauna in the canopy. Hence, canopy retention of NO$_3$-N derived from mass balance studies (Lovett and Lindberg 1984; Lindberg et al. 1986) represents the integrated effect of canopy exchange processes and may not be appropriate for quantifying the specific fate (e.g., foliar absorption) of various forms of N within the canopy.

Assuming our approach to quantifying canopy absorption provides a reasonable estimate of absorption, N absorbed through the foliage from HNO$_3$ appears to be a minor component relative to total annual N uptake by our white pine forest. Annual N uptake is approximately 80 kg N·ha$^{-1}$ (W.T. Swank, unpublished data), of which less than 1% (i.e., 0.2-0.5 kg N·ha$^{-1}$) is contributed by foliar absorption of N from HNO$_3$. However, N may also be absorbed from NO$_2$ (Norby et al. 1989) or NH$_4$ and NO$_3$ in cloud water and rainwater (Bowden et al. 1989). Thus, the cumulative effects of foliar N absorption from a variety of N sources may be more significant nutritionally and physiologically.

Constraints imposed by working in mature forests prevented us from replicating treatments in these initial experiments. Hence, results reported in this paper should be considered as preliminary estimates. We have since devised an exposure system that treats two separate branches simultaneously. Thus, to expand on these preliminary findings, we have conducted short-term, replicated field exposures on red spruce (Picea rubens Sarg.) (tissue currently being analyzed for $15^N$). In addition, we will conduct long-term, replicated field exposures at near ambient HNO$_3$ concentrations (i.e., 5 ppb) on white pine in summer 1990.

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