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# FOLIAR ABSORPTION OF $^{15}N$-LABELED NITRIC ACID VAPOR ($HNO_3$) IN MATURE EASTERN WHITE PINE (*Pinus strobus* L.)

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**ABSTRACT** Foliage of mature white pine in cuvettes was exposure to 50 ppb N labeled nitric acid vapor ($H^{15}NO_3$) for 4 to 12 h to quantify foliar absorption. Net photosynthesis, transpiration, and leaf conductance were measured and foliage was observed with a scanning electron microscope (SEM). Physiological data were variable, but results indicated that transpiration and leaf conductance were reduced after exposure. Potential mechanisms include a humidity build-up within the cuvette (e.g., cuvette humidity was 7% to 20% higher than ambient conditions), and the direct effects of H $^{15}NO3$ exposure. SEM of young foliage after one exposure revealed substantial cuticular disruption, which may have enhanced $^{15}N$ movement across the cuticle. Nitrogen-15 was absorbed in all exposures, with rates ranging from 0.009 25 to 0.156 50 $\mu$g $^{15}N$/g foliage/exposure h. Extrapolation to the entire canopy resulted in an estimated foliar uptake of 5.5 kg N/ha/yr. This represents approximately 10% of the annual canopy N requirement.

## INTRODUCTION

Increased atmospheric deposition of nitrogen (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). Studies comparing atmospheric chemical inputs to forest canopies with the chemistry of below-canopy throughfall and stemflow solutions have documented both depletion and enrichment of a variety of ions (Parker 1983, Lovett & Lindberg 1984, Swank & Reynolds 1987). In conifers, N ions (particularly nitrate) are usually lower in throughfall and stemflow than in atmospheric deposition to the forest canopy (Parker 1983). This budgeting implies a retention of atmospheric N within the canopy through foliar uptake or microbial and lichen immobilization. Foliar absorption of nitrogeneous gases are known to occur in herbaceous plants (Rogers *et al.* 1979); but only a few studies have quantified gaseous N deposition and

uptake in tree species (e.g., Marshall & Cadle 1987, P.J. Hanson, pers. comm), and these studies have been restricted to seedlings or excised foliage in growth chambers. Growth chamber approaches limit interpretation and extrapolation of the magnitude and impacts of foliar N absorption on physiological processes and nutrient relations to the mature forest.

The majority of research on the effects of gaseous N on plants has been concerned with $NO_x$ gases and herbaceous vegetation. However, measurements of $HNO_3$ vapor concentrations above an eastern white pine ( Pinus strobus L.) forest canopy in our study show that ambient levels can exceed 8 $\mu g/m^3$ (3 ppb). Coupled with a high deposition velocity (Lindberg *et al.* 1986) and large leaf area index of pine canopies, $HNO_3$ represents a significant form of atmospheric N input to the forest canopy. Biochemical assimilation pathways of $NO_x$ and $HNO_3$ are probably similar; however, research at Oak Ridge National Laboratory (P.J. Hanson, pers. comm.) indicates that NO2 deposition is totally regulated by stomatal conductance, whereas a substantial amount of $HNO_3$ is also deposited to the leaf surface. Thus, $HNO_3$ uptake can potentially occur: (1) directly through the stomata in vapor phase, (2) indirectly across the cuticle through ectodesmata-like channels, and (3) through areas where the cuticle has been disrupted by weathering, pollution, or insect damage (Leece 1976). Fumigation studies have found both positive and negative responses following exposure to NO2. For example, Zeevart (1976) and Wellburn *et al.* (1980) reported that NO2 can act as a fertilizer and stimulate physiological activity and growth. In contrast, other researchers have reported adverse effects on photosynthesis (Hill & Bennett 1970, Capron & Mansfield 1976). The fate of $HNO_3$ deposition in forest canopies, and the subsequent impacts on physiology and nitrogen nutrition are unknown.

In this paper, we report initial results of a study which has the general objective of quantifying uptake and biochemical assimilation of $HNO_3$ in a 30-year-old white pine plantation across a range of $HNO_3$ concentrations. Here, our specific objectives were to determine the amount of $^{15}N$ (in $H^{15}NO_3$ vapor) absorbed by white pine foliage exposed for 4 h and 12 h at 50 ppb concentration, and to evaluate its significance relative to foliar nitrogen nutrition.

## SITE DESCRIPTION AND METHODS

### Site Description

The study site is at the Coweeta Hydrologic Laboratory in the Southern Appalachian Mountains of North Carolina, USA. The climate of the region is characterized by cool summers, mild winters, and abundant rainfall in all seasons. Average annual precipitation at Coweeta ranges from 1800 mm at lower elevations (700 m) to 2400 mm at the highest elevation (1600 m). The average monthly temperature ranges from 3.3 °C in January to 21.6 °C in July.

The present study was conducted in a 16.2-ha, 30-year-old white pine plantation located on Coweeta Watershed 1 (WS 1). This watershed is part of the Integrated Forest Study on the Effects of Atmospheric Deposition (IFS) established in several North American forests and one forest in Norway (Johnson and Lindberg 1986). Studies at these sites are evaluating the role of atmospheric deposition in altering forest nutrient cycles and soil chemistry with detailed research on deposition rates and transfer processes. Chemical constituents in the atmosphere, precipitation, throughfall, stemflow, and soil solution have been measured by event sampling and longer-term integrated sampling since fall 1985 (Swank and Reynolds 1987). A summary of $HNO_3$ concentrations measured since April 1986 is presented

in Table 1. These data were obtained using filter packs and nylon (nylasorb) filters from a 31 m tower extending 5 m above the white pine canopy of WS 1 as described by Swank and Reynolds (1987).

**Table 1** $HNO_3$ concentrations (ppb) above a white pine canopy

| Season: | Growing | Dormant | Growing | Dormant |
|---|---|---|---|---|
| Years: | 1986 | 1986-87 | 1987 | 1987-88 |
| Months: | [Apr-Oct] | [Nov-Mar] | [Apr-Oct] | [Nov-Mar] |
| Mean (SE) | 0.96(0.18) | 0.68(0.19) | 0.53(0.05) | 0.55(0.06) |
| Maximum | 3.01 | 1.62 | 0.78 | 0.67 |
| Minimum | 0.35 | 0.41 | 0.23 | 0.48 |

Methods

Foliage was exposed to a known $H^{15}NO_3$ vapor concentration in FEP Teflon Film branch cuvettes (9.0 1 volume) positioned on the terminal portions of branches in the upper canopy. Access to the upper canopy was facilitated by a 31 m *"walk-up"* tower used for atmospheric deposition monitoring. The $H^{15}NO_3$ was generated from a gas permeation tube which contained $H^{15}NO_3$ in liquid phase (KIN-TEC Laboratories, Texas City, TX, USA). When the tube was heated to 60 ° C, $H^{15}NO_3$ vapor permeated through its walls at a rate of 1200 ng/min. The $H^{15}NO_3$ vapor was then mixed with $HNO_3$ free air (i.e., ambient $HNO_3$ was removed with nylasorb filters) at a flow rate of 9.0 l/min to generate a $H^{15}NO_3$ concentration of 50 ppb. Air flowed through the cuvette at a rate of 9.0 1/min (i.e., one air turnover/min). All tubing was composed of TFE Teflon.

Cuvettes were tested for $HNO_3$ losses to their interior surface using an $HNO_3$ exposure system at Oak Ridge National Laboratory (Oak Ridge, TN, USA). Losses were evaluated by comparing inlet and outlet $HNO_3$ concentrations. In the first two tests, inlet $HNO_3$ concentration was maintained at 50 ppb and relative humidity was set at 35% for the first test and 70% for the second. Results showed that $HNO_3$ losses to the cuvette were negligible ($<$0.5 ppb) at both relative humidities. In the final test, the cuvette was injected with 3 ml deionized water, and water droplets soon coated the interior surface of the cuvette. $HNO_3$ losses increased to about 5 ppb, indicating that condensation absorbed $HNO_3$.

Results reported in this paper are from two experiments. In the first experiment, foliage on the terminal portions of two separate branches was exposed to 50 ppb $H^{15}NO_3$ for 4 h (1000 h to 1400 h) on consecutive days (20 & 21 July 1988). After the 20 July exposure, the exposed foliage was removed from the branch and immediately rinsed with deionized water to remove $^{15}N$ deposited to the needle surface. Foliage was then separated into current and older needles (i.e., white pine produces new foliage each year and retains foliage produced the previous year), dried for 48 h at 60 ° C, weighed to the nearest 0.01 g, and ground to 100 microns using a ball mill. After the 21 July exposure, the entire exposed portion of the branch was removed from the tree, enclosed in a plastic bag, and allowed to sit at room temperature for 72 h. Foliage was then removed from the branch, rinsed, separated by age class, dried, weighed, and ground. In the second experiment, an individual branch was exposed for a total of 12 h on two

consecutive days (25 & 26 August 1988). On 26 August, the foliage was exposed for 7 h (0900 h to 1600 h) at $H^{15}NO_3$ concentration of 50 ppb and the cuvette was then removed from the branch. On 26 August, an additional 5 h (1000 h to 1500 h) exposure was repeated on the same branch. No rainfall occurred between exposures. After the final exposure, foliage was removed from the branch and separated by age class. Foliage from each age class was rinsed with deionized water to remove $^{15}N$ deposited on the surface, dried, weighed, and ground as above.

During exposures, temperature and humidity within the cuvette were monitored at 15-min intervals in the July experiments, and at approximately hourly intervals in the August experiments. Concurrent measurements (i.e., within one min.) were taken under ambient conditions. Temperature was measured with a thermister and humidity was measured with a capacitive thin-film sensor (ADC-PLC, Hoddesdon, UK). To determine cuvette effects on photosynthetically active radiation (PAR), PAR was measured outside and within the cuvette in full sunlight using a selenium cell and filters for the 400-700 nm wavelengths (ADC-PLC).

Photosynthesis ($\mu mol/m^2/sec$), transpiration ($mmol/m^2/sec$), and leaf conductance ($mmol/m^2/sec$) were measured (ADC-LCAII Portable Photosynthesis Meter) on both unexposed branches and fumigated branches immediately following exposures. In the 25 August exposure, we placed an additional 9.0 1 cuvette on a branch proximal to the treated branch and circulated ambient air through the cuvette at 9.0 l/min. This provided an estimate of *"cuvette effects"* on photosynthesis, transpiration, and leaf conductance, as well as a control for scanning electron microscopy (SEM). Due to equipment failure, physiological measurements were not obtained following the 26 August exposure.

Following the 25 August exposure, three fascicles were immediately excised from each of the treated and control branches and prepared for SEM. Preparation procedures followed Sabatini *et al.* (1963).

Tissue samples were analyzed for N abundance using mass spectrometry (ISO-TEC Laboratories, Miamisburg, Ohio, USA). Excess atomic $^{15}N$ was determined by subtracting natural abundance levels of $^{15}N$ (i.e., 0.366 32%) from $^{15}N$ levels detected in exposed foliage. Total N was determined using micro-Kjeldahl digestion (ISO-TEC Labs.). Total $^{15}N$ deposition and uptake were expressed on a foliage weight basis.

## RESULTS AND DISCUSSION

### Environmental Conditions

Exposures were conducted on relatively clear days and no rainfall occurred during any exposure period. Solar radiation inputs during exposure periods were 405, 150, 500, and 431 langleys for the 20 July, 21 July, 25 August, and 26 August exposures, respectively. Average ambient (i.e., outside the cuvette) relative humidity ranged from 32.8% to 62.7% whereas average humidity within the cuvette ranged from 7% to 20% higher than ambient conditions (Table 2). This difference was anticipated because the cuvette restricts vapor diffusion away from the foliage. In no case, however, did water vapor condense on the cuvette surface. Air temperatures within the cuvette were comparable to ambient air temperatures (Table 2). Photosynthetically active radiation was approximately 10% lower (e.g., 839 ambient vs. 754 $\mu mol/m^2/s$ cuvette) within the cuvette.

**Table 2** Environmental conditions during $HNO_3$ exposures

| Date | Time(h) | | Relative Humidity (%) | | | Air Temperature (°C) | | |
|---|---|---|---|---|---|---|---|---|
| | | | $\bar{X}$ | max | min | $\bar{X}$ | max | min |
| 7/20 | 1000-1400 | cuvette | 69.8 | 77.4 | 64.9 | 29.2 | 33.0 | 24.9 |
| | | ambient | 52.3 | 64.9 | 41.6 | 29.2 | 32.8 | 24.9 |
| 7/21 | 1000-1400 | cuvette | 69.6 | 73.8 | 65.6 | 28.1 | 30.0 | 24.8 |
| | | ambient | 62.7 | 74.2 | 49.1 | 28.1 | | 30.9 |
| 8/25 | 0900-1600 | cuvette | 52.2 | 67.1 | 27.0 | 29.1 | 33.6 | 23.8 |
| | | ambient | 32.8 | 53.1 | 16.3 | 29.5 | 34.3 | 24.3 |
| 8/26 | 1000-1500 | cuvette | 50.3 | 80.1 | 28.6 | 29.3 | 34.1 | 18.7 |
| | | ambient | 43.0 | 76.1 | 25.3 | 29.1 | 34.0 | 18.4 |

### Photosynthesis, Transpiration, and Leaf Conductance

On each exposure date, photosynthesis, transpiration, and leaf conductance were compared by foliage age class (Table 3). Results showed that there were no significant differences in photosynthesis rates ($p < 0.10$) between treated, control, and proximal branches. In general, photosynthesis rates were higher in the current foliage than in older foliage. This is a typical pattern observed in many pine species (e.g., Higginbotham 1974). Transpiration and leaf conductance were significantly reduced in treated foliage following the 20 July exposure. Response patterns were similar for the 21 July exposure; however, the data were too variable to detect statistically significant differences. There were no statistically significant differences in transpiration or leaf conductance following the 25 August exposures, but leaf conductance and transpiration were lowest for exposed current foliage (0.70 $mmol/m^2/s$ and 29.2 $mmol/m^2/s$ for leaf conductance and transpiration, respectively).

Due to high variability and small sample size it is difficult to make definitive statements about the impacts of $HNO_3$ on physiological processes. Our primary purpose for collecting those data was to provide background information for evaluating $H^{15}NO_3$ uptake. As a result, we collected a minimum number of samples. These data do suggest, however, that transpiration and leaf conductance may be altered within the leaf cuvette. Potential mechanisms include a reduction in vapor pressure gradients between the leaf interior and the atmosphere as a result of higher cuvette humidity, and/or the direct effects of $HNO_3$ exposure. Gas exchange processes appear less impacted by cuvette/exposure effects than do water vapor exchange processes. Clearly, more refined experimentation is required to understand the extent and magnitude of these effects. In particular, we recognize the need to reduce the humidity build-up within the cuvette (e.g., by increasing air flow) and to increase sample size for physiological measurements.

### Scanning Electron Microscopy

Based on a limited sample, it appears that the 25 August $H^{15}NO_3$ exposure resulted in visible damage to the surface of current needles (Figure 1). This damage was not observed in exposed older foliage or foliage from the

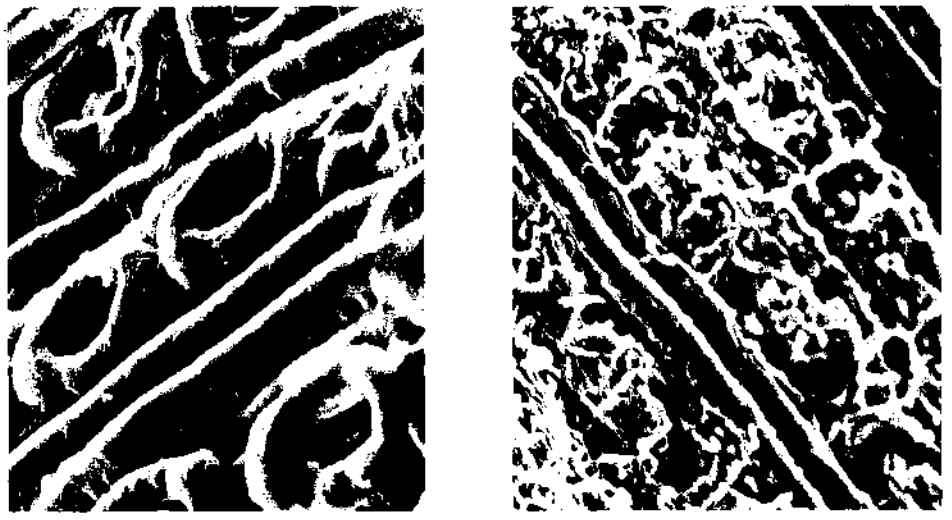
**Table 3** Photosynthesis (A in $\mu mol/m^2/s$), transpiration (E in $mmol/m^2/s$), and leaf conductance (gl in $mmol/m^2/s$) following $H^{15}NO^3$ exposure. Data are mean (n=2) and standard error. Significant differences were determined with t-tests ($p < 0.10$; denoted by *) between treated and proximal/control foliage within a date and for the same age class of foliage

| Date | Treatment | Foliage [1] Age Class | A | E | gl |
|---|---|---|---|---|---|
| 7/20 | proximal | C | 4.90(2.27) | 1.03(0.02)* | 50.8(0.6)* |
| | | O | 2.37(0.30) | 1.21(0.01)* | 63.4(1.2)* |
| | $H^{15}NO_3$ cuvette | C | 4.48(2.67) | 0.57(0.14) | 25.9(6.5) |
| | | O | 2.02(0.19) | 0.25(0.17) | 11.2(7.6) |
| 7/21 | proximal | C | 1.22(0.95) | 1.00(0.61) | 44.9(28.3) |
| | | O | 1.99(0.39) | 0.88(0.03) | 41.9(2.3) |
| | $H^{15}NO_3$ | C | 5.02(1.67) | 0.72(0.03) | 36.2(1.3) |
| | | O | 3.08(1.11) | 0.75(0.02) | 39.9(1.4) |
| 8/25 | proximal | C | 1.64(0.61) | 1.08(0.15) | 44.2(7.5) |
| | | O | 1.47(0.52) | 1.10(0.17) | 44.0(9.4) |
| | control cuvette | C | 1.93(0.12) | 1.29(0.15) | 54.9(6.4) |
| | | O | 1.79(0.23) | 0.84(0.30) | 34.8(13.2) |
| | $H^{15}NO_3$ cuvette | C | 0.97(0.50) | 0.70(0.38) | 29.2(16.7) |
| | | O | 2.05(0.04) | 1.53(0.11) | 67.9(5.5) |

[1] C=current foliage; O=older foliage.

control cuvette. We hypothesize that the damage observed in current foliage was a disruption of the cuticle caused by exposure to $H^{15}NO_3$. Interestingly, when exposures began on 25 August there was substantial condensation (i.e., dew) on the foliage. Thus, until the condensation evaporated (approximately 2 h), the foliage was probably exposed to a *"bath"* of $H^{1}NO_3$ acid which may have disrupted the cuticle. The lack of damage on older exposed foliage may have been a result of a greater protection by polymerized cuticular waxes.

It is important to note that the $HNO_3$ concentration used in these experiments was more than ten times higher than measured ambient levels at Coweeta. Thus, cuticle disruption observed in these exposures may only occur where $HNO_3$ concentrations are much higher (e.g., urban areas). Disruption of the cuticle could alter $HNO_3$ uptake pathways by enhancing movement across the cuticle (Leece & Kenworthy 1972). It also appears that the disrupted cuticle may have reduced stomatal conductance by covering many of the stomatal openings (Figure 1). However this phenomenon was only weakly supported by the physiological data because, although photosynthesis, transpiration, and leaf conductance were lowest in



A B

**Figure 1** SEM of nonfumiated (A) and fumigated (B) current white pine needles. Magnification: (A) x550; (B) x390.

the current exposed foliage (Table 3), differences were not statistically significant.

Foliar Absorption of $^{15}N$

As shown in Table 4, $^{15}N$ absorption occurred in all of the exposures. Very small levels of excess $^{15}N$ were detected in the 20 July exposure; however, $^{15}N$ absorption was at least ten times greater in the 21 July and 25 & 26 August exposures. The primary difference between the 20 July and 21 July exposures was the total time between exposure and sampling. On both dates, exposures were for 4 h, but sampling was conducted 72 h after cessation of exposure on 21 July. Results suggest that cuticular absorption is an important uptake pathway. In the 25 & 26 August exposure, exposure time was increased to 12 h and the total time between exposure and sampling was 30 h. Higher levels of excess $^{15}N$ in the August exposures were probably a result of the longer exposure period. There were also differences in $^{15}N$ absorption between foliage age classes. In the 20 July and 21 July exposures, uptake by older foliage was nearly double that of current foliage. In contrast, $^{15}N$ absorption was greater in the current foliage than in the older foliage in the 25 & 26 August exposure. This difference may be a result of increased cuticular absorption by current foliage as a result of the apparent damage observed in the SEM (Figure 1). We have no SEM data for the July exposures so we cannot evaluate the integrity of the cuticle during those exposures. Uptake rates ranged from 0.009 25 to 0.156 50 $\mu$g $^{15}N$/g foliage/exposure h (Table 4).

To evaluate the significance of foliar $H^{15}NO_3$ uptake to nitrogen nutrition, $^{15}N$ uptake rates were extrapolated to the entire forest canopy for a year. Estimates were based on the average of $^{15}N$ uptake rates for the 21 July and 25 August exposures and the following assumptions:

**Table 4** Foliar $^{15}N$ absorption following exposure to 50 ppb $H^{15}NO_3$

| Date | Foliage Age Class | Total N | Total N | Excess Atom % $^{15}N$ | Total Excess $^{15}N$ | $^{15}N$ Uptake Rate[1] |
|---|---|---|---|---|---|---|
| | | % | g | % | μg | μg/g/h |
| 7/20 | C | 1.179 | 0.072 | 0.000 32 | 0.23 | 0.009 25 |
| | O | 1.121 | 0.083 | 0.000 55 | 0.46 | 0.015 50 |
| 7/21 | C | 1.257 | 0.057 | 0.002 93 | 1.68 | 0.093 25 |
| | O | 1.132 | 0.105 | 0.005 54 | 5.81 | 0.156 50 |
| 8/25&26 | C | 1.173 | 0.085 | 0.012 14 | 10.32 | 0.118 42 |
| | O | 1.029 | 0.087 | 0.008 51 | 7.39 | 0.073 08 |

[1]Uptake rate unit is: μg $^{15}N$/g dry wt foliage/exposure h.

1. canopy biomass (kg/ha) = 9500 for Apr-Oct, and 5300 for Nov-Mar,
2. for Apr-Oct, 50% canopy — current foliage, 50% = older foliage; for Nov-Mar, 100% canopy = older foliage,
3. foliage exposed to 50 ppb $HNO_3$ for 24 h/day, 365 days,
4. nighttime (12 h/day) uptake rates one-half of measured rates (i.e., measured = cuticular (50%) + stomatal (50%); and, no stomatal uptake at night), and
5. stomatal uptake rates during Nov-Mar reduced by 50%.

Based on these assumptions, approximately 5.5 kg/ha (4.1 kg/ha in Apr-Oct and 1.4 kg/ha in Nov-Mar) could be absorbed by the foliage. Assuming that the canopy replaces approximately one-half of its foliage each year (i.e., 5000 kg/ha), and that the new foliage has an N concentration of 1.20%, 60 kg N/ha would be necessary for the development of new foliage. At a $HNO_3$ concentration of 50 ppb, approximately 10% of the N requirements of the developing canopy could be met by foliar absorption.

Initial results using 50 ppb $H^{15}NO_3$ clearly show that $^{15}N$ is absorbed by white pine foliage. However, $H^{15}NO_3$ concentrations used in these initial experiments were ten times greater than ambient. In our current experiments, we are exposing foliage to 10 ppb $H^{15}NO_3$ for longer time periods (i.e., 30 h). These chronic, low level exposures are more representative of ambient conditions. Due to high variability, the impacts of $H^{15}NO_3$ on physiological processes are difficult to discern. In addition, humidity increases within the cuvette make distinction between *"cuvette effects"* and *"treatment effects"* quite difficult. Thus, our future experiments will focus on increasing sample size for physiological measurements and minimizing cuvette effects.

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