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Potential canopy interception of nitrogen in the Pacific Northwest, USA

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Abstract

Nitrogen deposition is increasing worldwide from anthropogenic sources and encroaching upon previously N limited ecosystems. Recent literature reports increases in inorganic N deposition in Pacific Northwest forests of the United States due to expanding urbanization. We examined the contributions of atmospheric deposition of inorganic N to old-growth and second-growth Douglas-fir (*Pseudotsuga menziesii*) forests in the Cascade Mountains of southern Washington State. We used ion exchange resin lysimeters (IERs) to measure throughfall and compared it to data from a nearby atmospheric deposition recording station. Observed differences led us to install IERs above and throughout the canopy of an old- and second-growth forest stand at the Wind River Canopy Crane Research Facility. Total NH_4-N and NO_3-N deposition was 4.06 and 2.06 kg/ha, respectively, with NH_4-N inputs varying seasonally. Canopy interception in the first 5 m of canopy was >80% of NO_3-N deposition during the winter months, with negative net canopy exchange (NCE) accounting for nearly 90% of NO_3-N input (uptake). NCE for NH_4-N during the winter months was negligible. During the summer months, both NH_4-N and NO_3-N were taken up within the canopy. Contrary to the winter period, nearly all NH_4-N entering the canopy was retained. Although the pattern of canopy interception varied according to canopy architecture and age of stand, all species were extremely efficient in reducing the input of inorganic N to the forest floor. Greater deposition in these stands as compared to the nearby NADP site was attributed to higher precipitation. Needle concentrations of N and δ^{15}N showed no differences throughout the canopy profile, in contrast to both C and δ^{13}C that exhibited significant increases from top to the lower levels. Differences in concentrations of C, δ^{13}C, N and δ^{15}N were noted among the old-growth species.

Keywords: *Pseudotsuga menziesii*; *Tsuga heterophylla*; *Thuja plicata*; Nitrogen deposition; Pacific Northwest forests; NH_4; NO_3

1. Introduction

There has been widespread concern about the increasing effects of anthropogenic nitrogen (N) on the world's ecosystems (Vitousek, 1994; Asner et al., 1997; Holland et al., 1999; Sala et al., 2000; Matson et al., 2002; Galloway et al., 2003). Particular alarm for terrestrial systems has been raised concerning effects of N deposition on forest ecosystems, especially in heavily urbanized and industrialized regions (Rennenberg and Gessler, 1999; Driscoll et al., 2003; Holland et al., 2005). Nitrogen deposition may lead to both terrestrial and aquatic ecosystem disruption, including species changes, loss of species diversity, soil acidification, eutrophication and toxic blooms, as well as an increase in greenhouse gas emissions (Vitousek et al., 1997). However, N deposition has the potential of increasing productivity and C storage in N limited terrestrial ecosystems. Recent research has reported that N deposition is increasing around urban areas in the western US (Holland et al., 1999; Fenn et al., 2003b; Burns, 2003) with levels approaching those of the northeastern US (Aber et al., 1998; Driscoll et al., 2003). The Pacific Northwest forests of the United States have the greatest C densities of any vegetation type in the world (Smithwick et al., 2002) and have the potential of storing 671 Mg C ha^{-1} in above-ground biomass; estimates of actual storage are less than half that amount (Turner et al., 1995), primarily as a result of N limitations (Johnson, 1992; Oren et al., 2001). Nadelhoffer et al. (1999), Ollinger et al. (2002), and Aber et al. (2003) have stated that N deposition will not lead to an increase in forest C sequestration because most of the deposited N is immobilized within the organic forest floor. Both Jenkinson et al. (1999) and Sievering (1999) have debated this based on the fact that trees are capable of intercepting and utilizing much of the deposited N before it even reaches the ground. Reich et al. (2006) state that N variability, whether it is available in the soil or through atmospheric deposition,

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constrains ecosystem productivity despite increasing levels of CO_2.

Tree canopies are complex biogeochemical components of the ecosystem supporting different organisms and being sites for accumulation and processing of nutrients and other chemical elements (Hanson and Garten, 1992; Boyce et al., 1996; Knopps et al., 1996; Moffett, 2000; Heitz et al., 2002). Canopy interception studies have demonstrated that evergreen conifers intercept and retain species of inorganic N (Eilers et al., 1992; Thomas and Miller, 1992; Boyce et al., 1996) but there is discrepancy over what N species are retained and what are released (e.g., Hanson and Garten, 1992; Wilson, 1992; Lovett, 1992; Rennenberg and Gessler, 1999). Högberg (1997) notes that the fractional contribution of canopy N uptake is highly variable and difficult to measure in the field. Previous Integrated Forest Study (IFS) synthesis research (Johnson and Lindberg, 1992) has reported that an average of 40% of the incoming inorganic N is retained or transformed in the passage through the canopy. In absolute terms, the net canopy effect is greatest at those sites receiving the highest atmospheric N inputs (Lovett, 1992), but there exists a limit of N utilization and retention by forest ecosystems (Aber et al., 2003).

Deposition studies have used the stable isotope ^{15}N as an indicator of deposition pathways, although its high temporal and spatial variability, complications of separating contributions from the soil, and the difference seen within the diversity of plant parts, make that problematical (Högberg, 1997). However, ^{15}N may be used to evaluate the N status of forest ecosystems (Emmett et al., 1998; Martenelli et al., 1999) and to detect patterns of pollutant derived N (Emmett et al., 1998; Köchy and Wilson, 2001; Stewart et al., 2002).

We have been examining controls on C storage in Douglas-fir forests at and surrounding the Wind River Canopy Crane Research Facility (WRCCRF) in the southern Cascade Mountains of Washington State (Klopatek, 2002; Harmon et al., 2004). Nitrogen is considered limiting ecosystem productivity in this region (Binkley et al., 1992; Binkley, 2003) and as reported by Vanderbilt et al. (2003) many areas in the Cascades receive low precipitation N inputs. Because of this N fertilization is a common practice to increase yields in forests of the Pacific Northwest (Canary et al., 2000). However, Fenn et al. (2003b) reported significant regional increases in wet N deposition, using data from a National Atmospheric Deposition Program (NADP) recording station less than 15 km from the WRCCRF. Using lichens as indicators, Geiser and Bachman (2001) and Geiser and Neitlich (2003) correlated concentrations of inorganic N air pollutants with the loss of some lichen species in the area encompassing the above NADP site. They found that concentrations were significantly higher than on other national forests and were comparable to urban sites. As levels of N deposition are predicted to increase due to expanding urbanization and transport from Asian countries (Wilkening et al., 2000), we wanted to assess the amount of N deposited within these forests as it may generate significant ecological change (Nordin et al., 2002; Fenn et al., 2003a). We hypothesized that (i) N deposition would be greater at the WRCCRF than at the nearby NADP because of greater annual precipitation, (ii) that throughfall amounts of NH_4-N and NO_3-N would be significantly reduced by the forest canopies, and (iii) that concentrations of ^{15}N would differ according to height in the canopy, reflecting anthropogenic source of N. Here we report on inorganic N deposition in forest stands of the Pacific Northwest and the pattern of throughfall as it passes through the canopies of an old-growth and a young forest stand, as well as pattern of tree canopy N and ^{15}N concentrations.

2. Site descriptions

The research was carried out in the Wind River Experimental Forest in the Gifford Pinchot National Forest in south central Washington. We report throughfall data for three ~25-year old and three old-growth (>500 years) Douglas-fir (*Pseudotsuga menziesii var menziesii* Franco) ecosystems, referred to as crane, spur and trout. Both the young and old-growth stands were similar in vegetation composition. The canopy level research was conducted at one old-growth and one young stand (the crane sites) whose canopies were accessible through towers. That old-growth stand, located at the WRCCRF, is an Ameriflux site which is instrumented for quantifying carbon fluxes and storage. It is dominated by large Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Other species include western red-cedar (*Thuja plicata* Donn.), western white pine (*Pinus monticola* Dougl.), Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), and grand fir (*Abies grandis* (Dougl.) Forbes). The young stand is dominated by Douglas-fir with western hemlock. Stand leaf area index (LAI) for the old-growth stand is estimated to be between 8.2 and 9.3, and for the young stand between 6.1 and 7.2 (Table 1). The LAI supports a very high biomass at the Wind River stand, but it is in the low to middle portions of the range for old-growth forests in this region (Smithwick et al., 2002; Parker et al., 2004). Forest stands in this area are noted as being N limited (Binkley et al., 1992). Understory vegetation [e.g., Oregon grape (*Berberis nervosa* Pursh), salal (*Gaultheria shalon* Pursh), vine maple (*Acer circinatum* Pursh) of both the young and old-growth stands are typical of the Washington southern Cascades on

Table 1
Stand characteristics of the young Douglas-fir and the old-growth Douglas-fir sites where canopy effects were measured

Stand	Age (years)	Density (trees ha^{-1})	Aboveground biomass (Mg C ha^{-1})	LAI ($m^2\ m^{-2}$)	Height (m)
Young	25	1529	46.5	6.1–7.2[a]	17
Old-growth	~550	437	206.1[b]	8.2–9.1[c]	60

[a] Thomas and Winner (2000).

[b] Harmon et al. (2004).

[c] N. McDowell and B. Bond, Oregon State University, Corvallis (unpublished data).

well-drained soils. A complete description of the WRCCRF can be found in Shaw et al. (2004) with biomass and carbon pools of the old-growth stand in Harmon et al. (2004).

The climate is temperate winter wet, summer dry with over 2500 mm of annual precipitation, of which less than 10% falls between June and September. Mean annual temperature is 8.7 °C. The old-growth stand at the WRCCRF is situated at an elevation of 370 m, while that of the young stand is 560 m. Other stands for the initial throughfall studies were located at 500–600 m. While all stands were on similar aspects with minimal slope, the complex topography surrounding the sites undoubtably influenced their precipitation patterns that were not measured individually. All the young stands were previously old-growth before they were cut and all exhibited gaps and without canopy closure.

3. Materials and methods

We set up a series of ion exchange resin lysimeters (IERs) to evaluate patterns of inorganic N throughfall in the second- and old-growth forest stands. We constructed the IERs similar to those described by Susfalk and Johnson (2002). The lysimeters were constructed of ABS (rigid, black plastic) pipe couplers, 6 cm deep with an inner diameter of ca. 5.25 cm. Two sections of ABS pipe [4 cm deep (top) and 1 cm deep (bottom) with an i.d. of 5 cm] were cut and used to sandwich in two layers of nylon fine-mesh netting that held 20 g of mixed-bed ion-exchange resin (Rexin^{TM}, Fisher Scientific Co., Fair Lawn, NJ). We set out the lysimeters in Spring 2001 and collected them the following Spring, 2002. Twelve IERs were placed in each of three young and three old-growth stands in a stratified-random framework. All IERs were positioned using a stratified, random design. We also installed lysimeters beneath the forest floor and 20 cm below the soil surface; the belowground data from that experiment will be reported in a future publication. Preliminary results from the lysimeters on the forest floor initiated our examination of the effects of the tree canopy.

In the following autumn, to examine the N interaction within the tree canopy, we constructed a series of gimbals attached to 15 cm long ABS pipe so that the IERs could be fitted to the top of the pipe. The gimbals were made to ensure that the surface of the lysimeter remained parallel to the ground surface and could be attached to the branches with plastic zip ties. We installed the series of lERs above and down through the canopy to the forest floor at the WRCCRF old-growth and a nearby second-growth stand where access to the canopy was possible. The old-growth stand, with numerous trees >65 m tall, was instrumented from the WRCCRF canopy tower, a model Liebherr 550 HC (Morrow Crane Inc., Salem, OR) with a jib height of 74.5 m and a range of 87 m to position the lysimeters. Lysimeters were placed on the jib of the crane 20 m above the canopy and on meteorological towers in a nearby meadow away from the influence of the forest. IERs were placed in four replicate trees of three species, Douglas-fir, western hemlock and western red cedar in the old-growth stand, while only Douglas-fir was available in the second growth stand. Individual trees were fitted with IERs at the mid-point of the branch 5 m below the top in a selected tree with subsequent instruments placed below at 10 m intervals until the last of that tree's branches above the forest floor. Throughfall was measured with IERs (without gimbals) placed on the forest floor below the selected tree canopies distance 0.5 m from the bole. Trees in the second-growth stand were ~17 m tall, and were instrumented from a temporary tower constructed within the stand. All three species differ in their canopy architecture (Van Pelt, 2002; Parker et al., 2004). Douglas-fir concentrates its leaf area in the mid to upper canopy. Western hemlock stratifies its leaf area throughout the entire canopy. Western red cedar, being somewhat shorter than the other two species, has a conical distribution of leaf area.

The canopy IERS were initially installed in September 2002 and replaced in mid-April 2003 (the winter sampling period) when the lysimeters were taken from the gimbals and replaced with lysimeters with fresh resin. The second set of IERs were collected in the following September and represented the summer sampling period. The timing of the sampling periods corresponds to the water year for the region. The collected lysimeters were taken back to the laboratory and air dried. The resin was extracted, shaken in 100 ml of 2 M KCl for 1 h, filtered, and the elutrant analyzed for NO_3-N and NH_4-N on a Bran-Luebbe TrAAcs 800 Autoanalyzer.

Our adsorption and recovery of dissolved N with the ion-exchange resins was determined by dripping various standard solutions of NO_3-N and NH_4-N through IERs in the laboratory. It was found to be similar to that of Langlois et al. (2003) with an efficiency of >90% for NO_3-N and approximately 80% for NH_4-N. For calculation of the total levels of adsorbed N we corrected our data for the adsorption efficiency to reflect total for NO_3-N and NH_4-N. (The concentrations obtained were divided by the absorption efficiencies to obtain the corrected values of NO_3-N and NH_4-N.) Snowfall, especially heavy accumulations, presents a problem as the catchment area of the lysimeters was only 4 cm deep. Fortunately, during the collection period only two or three periods occurred where snowfall exceeded this depth for a brief period in December.

3.1. NADP data

Atmospheric N deposition data were available from the NADP monitoring location OR98 located at Bull Run, Oregon that closed operation in October 2003. This site was located along the Columbia River at an elevation of 267 m, approximately 20 km from the WRCCRF (Fig. 1). A new site, WA98 Columbia River Gorge, has been established on the Washington State side of the river, but comprehensive data were not available for the study period. The deposition data were obtained from the NADP web site (http://nadp.sws.uiuc.edu). Urbanization has been substantially increasing in upwind areas from the NADP station and this has been reported to be increasing N deposition. Total wet deposited inorganic N at the NADP station is shown in Fig. 2. High interannual variability is present and although an increasing trend is apparent, it is non-significant ($r^2 = 0.156$, $Pr > F = 0.069$). Similar results were obtained for both NH_4-N and NO_3-N deposition.

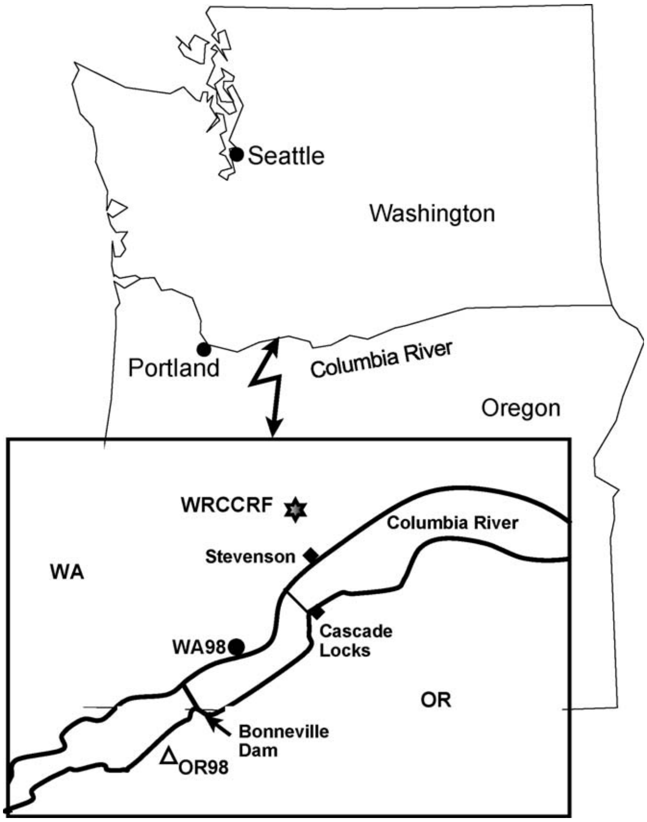

Fig. 1. Location of Wind River Canopy Crane Research Facility (WRCCRF) in the southern Cascade Mountains of Washington State. OR98-location of NADP station that ended monitoring in October 2003; WA98-NADP station that began recording data in summer 2003.

3.2. Plant sampling and analysis

In September 2003, at the time of the final lysimeter collection, plant needles from branches adjacent to each of the IERs were collected. We selected the most recent needles (second year) that were present during the entire collection period. The age of the needles and the time of sampling were chosen to examine stable isotopic N (Chang and Handley, 2000; Chambers et al., 2004) to highlight any pattern from atmospheric deposition (Stewart et al., 2002). Needles were dried at 65 °C and ground with a Wiley mill to pass an 80 mesh sieve. The samples were analyzed for concentrations and natural abundances of total C and N. Isotope ratios and concentrations of C and N were measured with a PDZ-Europa IRMS consisting of an elemental analyzer and a gas purification module interfaced to a mass spectrometer. All N isotope ratios are expressed relative to the international standard (N_2 in air) while C isotopes use the Pee Dee Belemite. All ratios are expressed in delta notation (δ) calculated according to the following equation:

$$\delta x = \left(\frac{R_{\text{sample}}}{R_{\text{standard}} - 1} \right) \times 1000\,(‰)$$

δx is the isotope ratio of C and N in δ units, relative to the standards and R_{sample} and R_{standard} are the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios of the samples and standards respectively.

3.3. Statistical analyses

Statistical analyses were performed on a personal computer using SAS (SAS, 1995). For the IER data, a one-way analysis of variance was performed using Tukey's test. For evaluating differences in the elemental concentrations and isotope ratios of the needles by height and species, the ANOVA routine of the PROC GLM was used. For this study, effects with probabilities of $p < 0.05$ were assumed to be significant.

4. Results

4.1. Throughfall

Precipitation from 2001 to 2003 showed the typical wet-winter dry summer pattern, but also showed interannual variability (Fig. 3). Annual precipitation varied from just over 1900 mm in 2001 to 2230 mm in 2003. No distinct pattern was

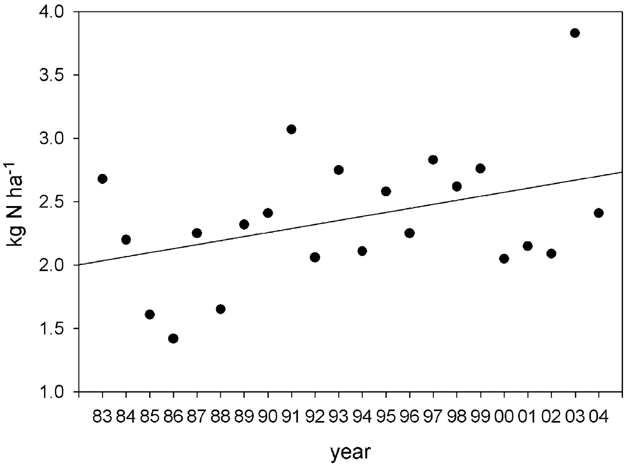

Fig. 2. Annual inorganic N deposition at the NADP station located 15 km from the WRCCRF.

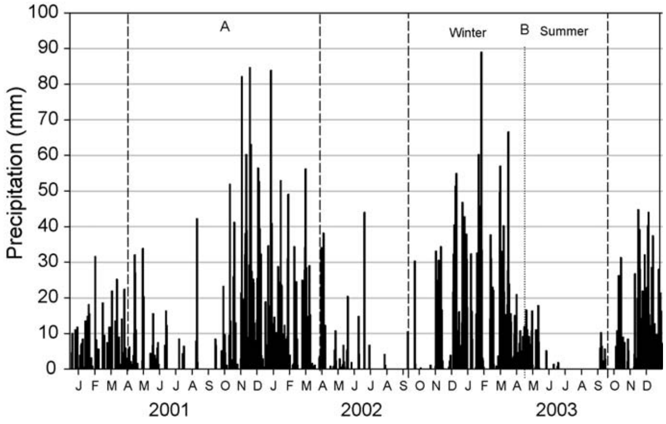

Fig. 3. Daily precipitation amounts recorded at the Carson Fish Hatchery near the study sites. (A) The period during which the three second- and three old-growth stands were sampled for throughfall. (B) When the intensive canopy interception studies were performed.

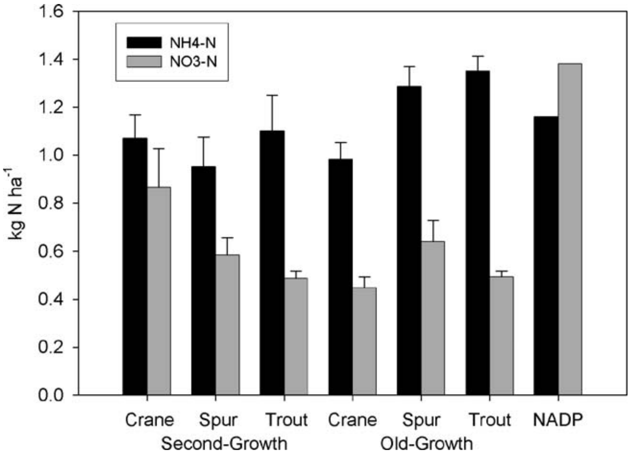

Fig. 4. Amount of NH_4-N and NO_3-N collected in throughfall IERs in three second- and old-growth stands in the Wind River Experimental Forest. Error bars are standard error of the mean. Names underneath the stands correspond to their location. The crane stands were the primary stands for the canopy research in this study.

observed across the stands during the sampling period from 2001 to 2002, although between stand differences were observed (Fig. 4). The N deposited at the NADP station was 1.16 and 1.38 kg ha^{-1} of NH_4-N and NO_3-N, respectively. Greater NO_3-N was observed at the NADP station than in the forest stands, despite the NADP station receiving nearly 300 mm less precipitation. The throughfall amount measured by the IER's averaged 1.07 NH_4-N and 0.86 NO_3-N at the young and 0.98 NH_4-N and 0.45 NO_3-N at the old growth stands, respectively.

4.2. Canopy interception

Canopy data reflect the 2002 to 2003 precipitation period (Fig. 3). During the winter period in the old-growth stand the total measured amount of NH_4-N and NO_3-N entering the canopy was 1.17 and 1.11 kg ha^{-1}, respectively (Fig. 5). No trend was observable for NH_4-N as it fell through the canopy; the total amount reaching the forest floor was approximately equal to that entering the canopy. However, in the old-growth stand all three tree species displayed significant interception of NO_3-N with the pattern differing by height between species

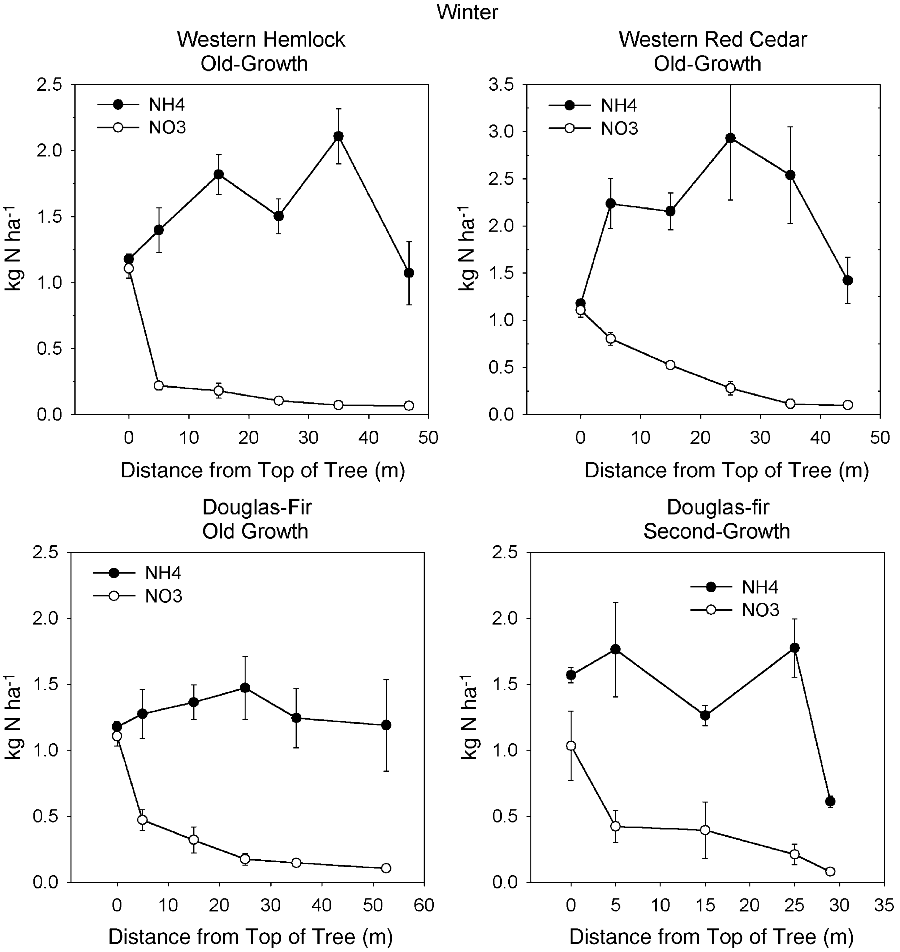

Fig. 5. Change in amounts of the NH_4-N and NO_3-N deposition as collected through the canopy in an old-growth and young Douglas-fir stand in the Cascade Mountains of South Central Washington. The left-most point of each graph represents the concentration before entering the canopy. The right-most point indicates the amount captured at the forest floor. The winter sampling period was from mid-September 2002 to mid-April 2003. Error bars are standard error of the mean.

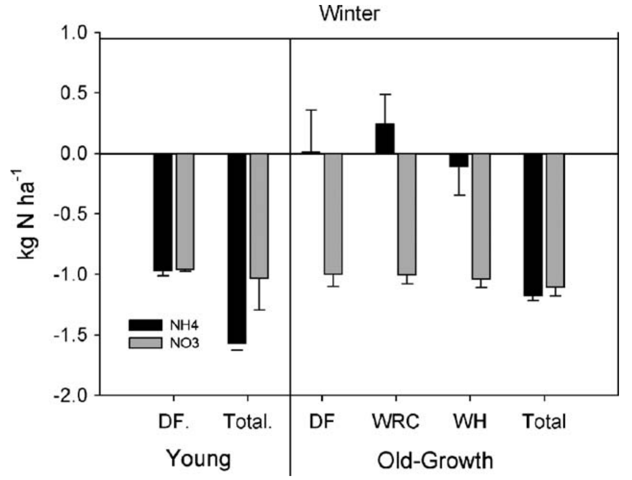

Fig. 6. Winter differences in net canopy exchange (NCE) of NH_4-N and NO_3-N in the old-growth and young Douglas-fir stand at the WRCCRF. NCE was determined as the difference between bulk deposition (total), measured above the canopy, and throughfall, measured at the forest floor. DF: Douglas-fir; WH: western hemlock; WRC: western red cedar. Error bars are standard error of the mean.

(Fig. 5). There was a significant decline of the NO_3-N in the first 5 m of canopy with both Douglas-fir and western hemlock reducing input levels by nearly 80%. The young Douglas-fir also exhibited a significant reduction in NO_3-N although deposition levels were lower. Stemflow in these species is minimal (Kimmins, 1997) and thus we can attribute the difference between bulk deposition and throughfall as the net canopy exchange (NCE). Simply stated NCE is the amount of element entering the forest from the atmosphere that never reaches the ground. Our use of NCE (a negative value indicates a reduction in throughfall) refers to the particular species not the ecosystem as throughfall was only measured underneath the selected trees. NCE of NO_3-N was more than 90% in all trees sampled in the old-growth stand (Fig. 6). In the young Douglas-fir stand there was positive NCE for both NH_4-N and NO_3-N. No differences among species nor between stands were detected in the amount of NO_3-N retained by the canopy.

For the summer period the total amount of NH_4-N and NO_3-N entering the canopy was 2.82 and 0.95 kg ha^{-1}, respectively. Similar to the winter period, a decline in NO_3-N was also significant, but not as precipitous (Fig. 7). During the summer, in contrast to the winter period, NH_4-N exhibited a significant

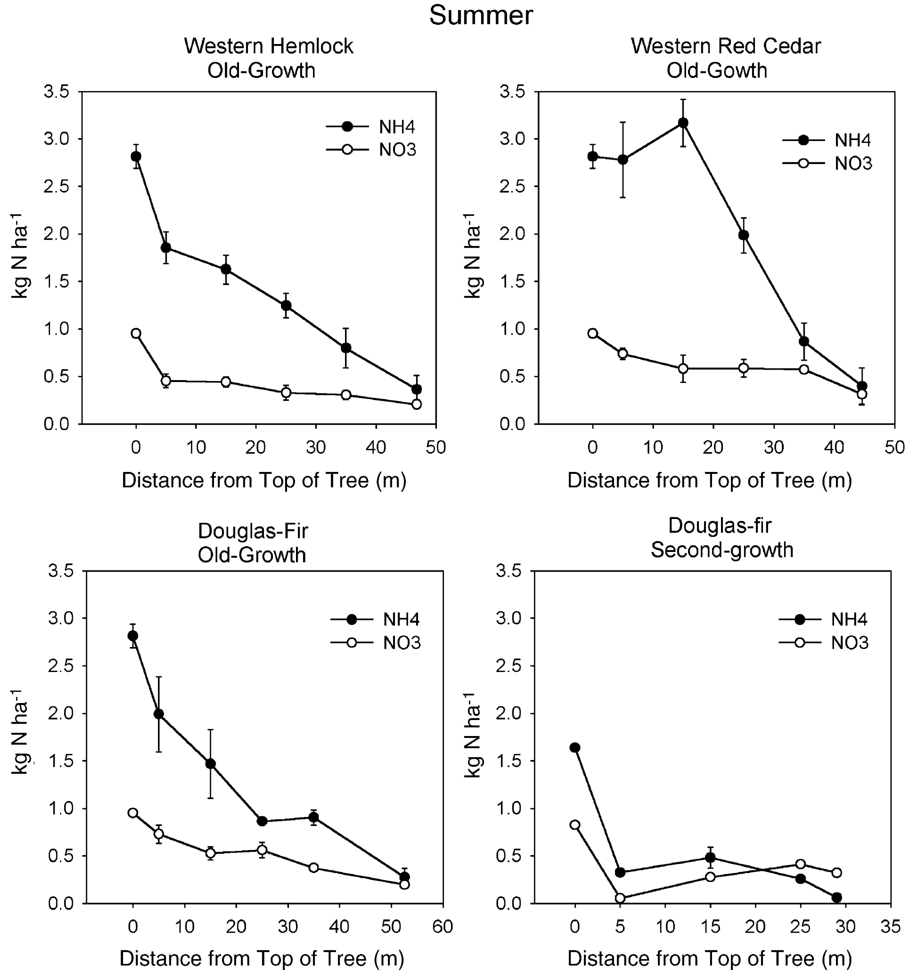

Fig. 7. Change in amounts of the NH_4-N and NO_3-N deposition as collected through the canopy in an old-growth and young Douglas-fir stand in the Cascade Mountains of South Central Washington. The left-most point of each graph represents the concentration before entering the canopy. The right-most point indicates the amount captured at the forest floor. The summer sampling period was from mid-April to mid-September 2003. Error bars are standard error of the mean.

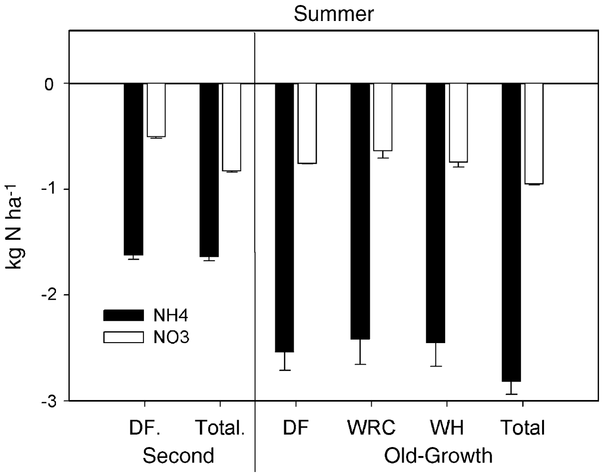

Fig. 8. Summer differences in net canopy exchange (NCE) of NH_4-N and NO_3-N in the old-growth and young Douglas-fir stand at the WRCCRF. NCE was determined as the difference between bulk deposition (total), measured above the canopy, and throughfall, measured at the forest floor. DF: Douglas-fir; WH: western hemlock; WRC: western red cedar. Error bars are standard error of the mean.

decline with canopy height, with a NCE ranging from 86–90% of NH_4-N and 67–79% of NO_3-N in the old-growth stand (Fig. 8). In contrast to the winter period, the NH_4-N levels collected on the forest floor were lower than those of NO_3-N. Samples taken in the young stand showed a different pattern for both NH_4-N and NO_3-N where both elements declined substantially in the first 5 m of the canopy, with NH_4-N leveling off and NO_3-N actually increasing. The young Douglas-fir stand again showed the greatest retention of NH_4-N of approximately 95%. Inputs (1.65 kg ha^{-1} NH_4-N and 0.83 kg ha^{-1} NO_3-N) into the young stand were significantly lower than in the old-growth stand (Fig. 8). There were no differences in amount of inorganic N retained among tree species, nor between elements in the old growth stand (Fig. 8).

4.3. Needles

There was no significant pattern for either N or $\delta^{15}N$ with canopy position (Table 2), although there were significant differences between tree species that corresponded to patterns found with the stable carbon isotope (Table 3). A distinct pattern for $\delta^{13}C$ existed for all three species with the discrimination being less in the upper as compared to the lower canopy and the pattern differed among the three species due to stomatal limitations of carbon use (Winner et al., 2004). Western hemlock exhibited also showed more C per needle weight in the upper canopy (Table 2).

5. Discussion

Inorganic N deposition has been increasing with expansion of urban areas in the Pacific Northwest, although we did not find the trend statistically significant in wet deposition N at NADP stations downwind from Portland, Oregon (Fig. 2). Our initial throughfall data surprised us in that they showed no significant difference between the second- and old-growth stands, although the stands differed in species composition and biomass. Unfortunately, we cannot compare that data with precipitation values as only the data from the NADP site were available for comparison, and that site received at least 300 mm less precipitation than the forest stands. However, the individual stand NO_3-N throughfall values reflect the relative LAI of each stand and that of the NH_4-N the overall N status of each stand (Klopatek, unpublished data).

For the 1-year period from mid-September, bulk deposition inputs of NH_4-N and NO_3-N at the old-growth stand were 3.99 and 2.06 kg ha^{-1}, respectively. These values were somewhat greater than that experienced for the same time period at the Bull Run NADP station (3.84 NH_4-N and 1.76 NO_3-N kg ha^{-1}) and supported our initial hypothesis that increased precipitation results in increased deposition. Precipitation at the NADP site for the period was 1664 mm, whereas the recorded precipitation at the Carson Fish Hatchery near the WRCCRF, was 2748 mm of which 85% fell during the winter period of this study. By using the volume-weighted mean concentration (load/concentration) of the NADP, the greater precipitation at the WRCCRF easily accounts for the increased N loading. The annual wet deposition values of NH_4-N and NO_3-N are similar to those reported earlier for the IFS sites located in Washington (Lovett, 1992) where they reported wet fall or bulk deposition accounting for approximately 60% of the deposited inorganic N. The IERs are similar to the bulk deposition collectors used by Lovett and Lindberg (1993) in that they are constantly open and do not discriminate between wet and dry deposition. Their capacity for measuring dry and fog deposition is unknown and there is a considerable amount of cloud and fog activity at the old-growth stand during the fall and winter months, which may

Table 2
Mean ($n = 4$) concentrations of C and N and isotopic signatures, $\delta^{13}C$ and $\delta^{15}N$, of second year needles descending from the top of the canopy (0 m) down through the canopy of three tree species in an old-growth forest stand at the Wind River Canopy Crane Research Facility, Washington State

Height (m)	Douglas-fir				Western red cedar				Western hemlock			
	%C	$\delta^{13}C$	%N	$\delta^{15}N$	%C	$\delta^{13}C$	%N	$\delta^{15}N$	%C	$\delta^{13}C$	%N	$\delta^{15}N$
−5	50.3	**−26.7**	1.21	−3.47	51.5	**−25.5**	1.17	−3.31	**51.6**	**−26.9**	0.97	−5.28
−15	49.7	−26.9	1.10	−3.92	51.7	−26.4	1.03	−3.35	50.8	−27.9	0.95	−5.60
−25	49.2	−27.9	1.35	−3.72	50.9	**−27.0**	1.17	−3.12	50.6	−28.5	1.02	−5.69
−35	50.0	**−28.2**	1.21	−3.75	50.7	**−27.6**	1.15	−3.44	**49.9**	**−29.4**	1.03	−5.80

Values in bold within a column, comparing upper canopy to lower canopy, are significantly different ($p < 0.01$).

Table 3
Mean concentrations of C and N and isotopic signatures, $\delta^{13}C$ and $\delta^{15}N$, of second year needles from three old-growth and one second-growth tree species at the Wind River Canopy Crane Research Facility

Stand species element	Old-growth			Second-growth
	Douglas-fir	Western red cedar	Western hemlock	Douglas-fir
%C	49.5 a	51.2 c	50.7 b	49.7 a
$\delta^{13}C$	−27.4 b	−26.5 a	−28.3 c	−29.9 d
%N	1.22 c	1.13 bc	1.00 a	1.07 ab
$\delta^{15}N$	−3.71 ab	−3.30 a	−5.58 c	−4.18 b

Means are derived from samples taken throughout the canopy of four trees per species (old-growth, $n = 16$; second-growth, $n = 11$). Different letters following values in each row indicate significant differences ($\alpha = 0.05$).

account for its higher depositional rates than the second-growth stand. If we use the 60% ratio (bulk or wet/total) found by Lovett and Lindberg (1993), we estimate that approximately 10 kg ha^{-1} of inorganic N was deposited in the old-growth stand. The source of much of the N is probably attributable to the encroaching urbanization up wind from the WRCCRF (Lovett et al., 2000; Fenn et al., 2003b). Trans-Pacific air pollution has also added to increases in regional N deposition (Wilkening et al., 2000).

Our use of the IER on the forest floor 0.5 m from the bole may have biased the NCE estimations. Both Bouten et al. (1992) and Keim et al. (2005) have shown that Douglas-fir tends to channel intercepted precipitation to the outer edges of the branches producing a drip line. However, our data show that over 90% of the NO_3-N was reduced before it reached the lower level. Only the data for summer NH_4-N, which often was erratic, was affected by this bias. Lovett and Lindberg (1993) reported net canopy uptake of NH_4-N in most forest stands, including a Douglas-fir forest on the western slopes of the Cascade Mountains in Washington State. Our data showed no measurable NH_4-N canopy uptake during the winter months but did show uptake during the summer collection period. Our findings were consistent with Lovett and Lindberg (1993) wet deposition results for the other Washington site showing a negative net-throughfall of NO_3-N as it passed through the canopy. Higher fluxes in precipitation than throughfall of NO_3^- were apparent in both collection periods. Canopy interception loss of rainfall was similar for both young and old-growth stands, ranging from 20 to 25% (Pypker et al., 2005)

Our values of NCE are considerably greater than those reported in IFS synthesis research (Johnson and Lindberg, 1992). Our study showed that there were seasonal differences in NCE for NH_4-N with no measurable canopy effect during the winter months. This may be a function of the physiological state of the trees and epiphytes during these months—low photosynthesis, reduced growth, and limited seasonal demand for N (Paw et al., 2004). As indicated by Lovett and Lindberg (1993) and shown by Rennenberg and Gessler (1999) the NCE of inorganic N is greatest in stands with epiphytes. Epiphytic lichens and mosses are a major component within the old-growth canopy (Harmon et al., 2004). The biomass of the lichens in the WRCCRF old-growth stand has been reported to be nearly 200 g m^{-2} as compared to over 1800 g m^{-2} for tree foliage (Harmon et al., 2004). Lichens in this area have shown effects of an increase in N deposition as some sensitive species have declined (Geiser and Neitlich, 2003). Lichens and bryophytes definitely affect the flux of nutrients in the throughfall (Knopps et al., 1996), yet they are virtually absent from the upper 5 m of the canopy in the old-growth stand and from nearly the entire canopy of the young stand where interception was significant (Figs. 5 and 7).

Based on 3 years data, annual litterfall in the old-growth stand is 255 kg ha^{-1} and 2200 kg ha^{-1} for epiphtyes and conifer foliage, respectively accounting for 0.23 kg N ha^{-1} and 9.5 kg N ha^{-1} (Klopatek, unpublished data). If we can assume that the old-growth stand is in quasi-steady state (Field and Jörg, 2004), then lichens and bryophytes can only be potentially responsible for only a fraction of the N taken up within the canopy. Most of the reduction in inorganic N, as it descends through the forest canopy, is probably taken up by the trees themselves supporting our second hypothesis (Lovett and Lindberg, 1993; Eilers et al., 1992; Gebauer et al., 1994; Boyce et al., 1996; Tietema et al., 1998). Furthermore, the amount of N measured as NCE represents a substantial portion of the N lost in litterfall emphasizing the N limitations in this ecosystem.

Our selection of second-year needles should have highlighted any differences in $\delta^{15}N$ (Chang and Handley, 2000; Chambers et al., 2004). Yet, similar to Gebauer and Schulze (1991) who examined other conifers, no pattern was observed in either $\delta^{15}N$ or N concentration through the canopy. There was no corresponding trend relative to the observed interception patterns (Figs. 5 and 7), and thus our third hypothesis was not proven. Western hemlock foliage had the most depleted ^{15}N values and western red cedar the least. Western red cedar is a facultative arbuscular mycorrhizal species and dependent on mineralized N (Chang and Handley, 2000), thus its $\delta^{15}N$ should be more positive than the other two species that are ectomycorrhizal. Ectomycorrhizal species are thought to discriminate against ^{15}N, yielding more negative values in the foliage (Högberg, 1997). In addition, western red cedar occurs in areas of the WRCCRF with wetter soils and higher N concentrations. Both these factors may contribute to its foliage being less isotopically N depleted. However, there was no correlation between leaf C isotope discrimination and foliar N contents for any of the species as suggested by Sparks and Ehleringer (1997). The pattern of $\delta^{13}C$ was consistent with earlier findings of Fessenden and Ehleringer (2003) and Winner et al. (2004) who reported greater discrimination with increased moisture stress moving higher in the canopy. The second-growth Douglas-fir had lower tissue concentrations of N than the old-growth, as well as more depleted ^{15}N indicating a greater N limitation. This was supported by N use efficiency being greater in the second-growth stand (Klopatek, unpublished data). The $\delta^{13}C$ were also more depleted at the second-growth stand indicating less moisture stress.

N emissions are predicted to increase in this region with increasing urbanization (Geiser and Bachman, 2001; Fenn et al., 2003b) and trans-Pacific origins (Wilkening et al., 2000; Richter et al., 2005). It is assumed that added N will increase ecosystem productivity and C sequestration within many of these N limited forests (Fenn et al., 1998; Reich et al., 2006). However, structural changes may occur and not only within the forest canopy (Geiser and Neitlich, 2003). For example, western red cedar with greater ^{15}N depletion and less foliar N as compared to the other two species may be construed as experiencing a greater N deficiency and a tighter N cycle (e.g., Martenelli et al., 1999). Catovsky and Bazazz (2002) have shown that hemlock seedlings were the only species showing positive survival responses to added inorganic N in eastern temperate forests. The addition of added N to these forests may promote changes in species composition as well as biomass (Nordin et al., 2002). Nordin et al. (2002) showed that changes in key ecosystem components can occur at low rates of additional N input. They found that a critical load of 6 kg ha^{-1} $year^{-1}$ was enough to cause vegetation change in the boreal forest. While the resulting effects of increased N deposition may be debated (e.g., Nadelhoffer et al., 1999; Fenn et al., 2003a), it is assumed that added inorganic N will increase productivity and C sequestration of most second-growth forests in the region (Reich et al., 2006). However, the ecosystem consequences of added N to the old-growth stands remains a question.

The two forest stands in this study showed a marked reduction of inorganic N as it passed through the canopy. However, many of the second-growth forest stands in the region have a considerable amount of red alder (*Alnus rubra* L.), known for its contribution of N through fixation. As discussed by van Miegroet et al. (1992) and Compton et al. (2003), even small additions of N to these systems can lead to an increased leaching of NO_3-N from the ecosystem. In one of our highly fertile Douglas-fir study plots with red alder (not reported on in this article), leaching of NO_3-N down the soil profile was readily apparent. This emphasizes the need for careful monitoring of N deposition and ecosystem processes in this region with long term studies.

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