Canopy uptake of atmospheric nitrogen and new growth nitrogen requirement at a Colorado subalpine forest

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Abstract: A field study at a Rocky Mountain spruce–fir–pine forest was undertaken to obtain canopy N uptake (CNU), N reallocation, and foliar N requirement. Wet deposition, dry deposition, and throughfall fluxes of ammonium and nitrate were measured during the 2000 and 2001 growing seasons. Estimation of CNU, for both ammonium and nitrate, was obtained by subtracting throughfall (TF) flux from the sum of wet deposition (WD) and dry deposition (DD): CNU = WD + DD – TF. CNU efficiency (CNU/(WD + DD)) for ammonium (0.9) was consistent across 2000 and 2001. For nitrate, this efficiency was 0.8 and 0.7 for 2000 and 2001, respectively. Foliar N requirement for growth in 2000 and 2001 was about 19 and 22 kg N·ha^{-1}·year^{-1}, respectively. Growing season estimates of CNU for 2000 and 2001 were approximately 2 and 3 kg N·ha^{-1}, respectively. Thus, CNU may contribute 10%–15% of the foliar N requirement for canopy growth. Mountain upslope winds bring substantial amounts of anthropogenic N to this forest during the growing season, thereby contributing to CNU. Given that a sizable fraction of CNU is anthropogenic in origin, the forest's N cycle has likely undergone substantial changes on a decadal time scale.

Résumé : Une étude au champ a été réalisée dans une forêt d'épinette et de sapin des Montagnes Rocheuses afin de quantifier le prélèvement de N par la canopée, la réallocation de N et le besoin en N foliaire. Les dépôts humides, les dépôts secs et les flux d'ammonium et de nitrate du pluviolessivage ont été mesurés durant les saisons de croissance 2000 et 2001. L'estimation du prélèvement de N, tant pour l'ammonium que pour le nitrate, a été obtenue en soustrayant le flux du pluviolessivage de la somme des dépôts humides et des dépôts secs. L'efficience du prélèvement de N par la canopée pour l'ammonium (0,9) était uniforme pour 2000 et 2001. Pour le nitrate, l'efficience était de 0,8 en 2000 et de 0,7 en 2001. Le besoin en N foliaire pour la croissance a été de 19 kg N·ha^{-1} en 2000 et de 22 kg N·ha^{-1} en 2001. Les estimations du prélèvement de N par la canopée ont été de 2 kg N·ha^{-1} en 2000 et de 3 kg N·ha^{-1} en 2001. En conséquence, le prélèvement de N par la canopée peut contribuer pour 10 à 15 % du besoin foliaire en N pour la croissance de la canopée. Les vents ascendants sur la montagne apportent des quantités substantielles de N anthropique sur cette forêt durant la saison de croissance, contribuant ainsi au prélèvement de N par la canopée. Étant donné qu'une fraction significative du prélèvement de N par la canopée est d'origine anthropique, le cycle de N dans cette forêt a vraisemblablement subi des changements substantiels sur un horizon de 10 ans.

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Introduction

Nitrogen is typically a limiting nutrient at forest ecosystems (Cole and Rapp 1981), with forest ecosystem processes generally adapting to conditions of N limitation. Thus, atmospheric deposition of anthropogenic N may significantly perturb forest processes (Rennenberg et al. 1998). A review of atmospheric N deposition impacts in the Rocky Mountains of Colorado and southern Wyoming (Burns 2002) notes that up to 7 kg N·ha^{-1}·year^{-1} is deposited to the east slope portion of this region, which lies nearer to agricultural and urban sources of N. In contrast, west slope areas of this region receive about 2 kg N·ha^{-1}·year^{-1} (Baron et al. 2000). European studies at spruce forests indicate that atmospheric N deposition >20 kg N·ha^{-1}·year^{-1} has contributed to spruce decline at sites in the Netherlands (Boxman et al. 1995) and in Germany (Harrison et al. 2000). However, atmospheric N deposition <5–10 kg N·ha^{-1}·year^{-1} at N-limited conifer for-

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est sites may stimulate growth (Schindler and Bayley 1993). Given that anthropogenic N deposition can yield both forest growth and forest decline, there is concern regarding the response of forests to increased N deposition.

Our study site is a subalpine forest (Niwot Forest) east of Niwot Ridge and the Continental Divide in Colorado. During the growing season, this site is exposed to episodic mountain upslope flow conditions that transport N-laden air to the site. This site receives 4–8 kg N·ha^{-1}·year^{-1} (Sievering 2001), which is at least twice the deposition rate to forests on the western slope of the divide. Although many subalpine forests in Colorado receive a significant amount of anthropogenic N deposition, they are generally considered to be N limited with minimal export of N across their forested landscapes (Campbell et al. 2000). One indication that the Niwot Forest is N limited comes from a study of stream chemistry (Hood et al. 2003). High inorganic N concentrations were found in tundra stream water as it entered the subalpine forest (Niwot Forest) area, but these concentrations dropped to zero quite rapidly within the subalpine forest. This forest's N limitation and magnitude of anthropogenic N deposition make it ideal for studying N cycle perturbations.

At coniferous forests, where stemflow is insignificant (Lovett 1992), canopy N uptake (CNU) may be estimated by CNU = wet deposition + dry deposition – throughfall (Sievering et al. 2000). We determined CNU of inorganic (NH_4^+, NO_3^-) and organic (total dissolved N minus inorganic N) N species by measuring the N flux in throughfall, wet deposition, and dry deposition. Uptake and emission of ammonia were found to very nearly cancel each other out (Torizzo et al. In press.)[2]; therefore, ammonia flux was not included in the determination of CNU.

The uptake of N by the canopy is primarily the result of ion uptake by foliar and branch tissues and uptake by canopy lichens and microorganisms (Lovett et al. 1989). These uptake mechanisms lack adequate characterization; thus, one may speculate that canopy microbes and lichens are as important for canopy retention of N as are foliar, twig, and branch retention. However, we measured canopy lichen biomass at the Niwot Forest using methods adapted from Lang et al. (1980) and determined that lichen biomass was <50 kg dry matter·ha^{-1}. Considerably larger lichen biomass densities, at subalpine forests in New Hampshire (120–1630 kg dry matter·ha^{-1}), were found to have inconsequential influence on the productivity and flux of elements within the forested ecosystem (Lang et al. 1980). In addition, canopy microorganisms presumably reach small and steady population sizes (Lovett 1992) as a result of competition for space and frequent drying of leaf surfaces. Therefore, lichens and canopy microorganisms at this site are not a significant sink of N.

CNU has been defined to quantify the uptake by canopy elements of atmospherically deposited N (Sievering et al. 2000). As such, it is determined per unit area of the canopy. At forest sites with a closed canopy, per unit canopy area and per unit ground area are identical. However, at forest sites with significant canopy gaps, CNU magnitudes will differ from a corresponding per unit ground area estimation of N uptake by the forest as a whole. Since N uptake by canopy elements is desired (and not the forest as a whole), CNU is determined on a per unit canopy area basis.

Coniferous forests often display significant CNU efficiencies (Sievering et al. 2000; Ignatova and Dambrine 2000; Arthur and Fahey 1993; Friedland et al. 1991), indicating that the canopy may represent a large sink for atmospherically deposited N. Therefore, the N deposition growth response may be closely tied to CNU at coniferous forests displaying significant CNU. Since the mechanism and fate of CNU are not fully known, it is unclear how CNU contributes to forest growth. However, studies utilizing ^{15}N-labeling methods indicate that wet and dry deposited N is taken up and assimilated by foliage with a portion of the ^{15}N going into the foliar amino acid pool (Vose and Swank 1990; Nussbaum et al. 1993; Boyce et al. 1996; Garten et al. 1998). Photosynthesis is known to increase with the increasing N concentration of foliage (Field and Mooney 1986); therefore, foliar uptake of atmospheric N deposition may increase photosynthesis and C sequestration at forests having N-limited growth.

High elevation spruce–fir forests may derive a substantial fraction, or even a majority, of their annual N requirement for growth from reallocation (Friedland et al. 1991). CNU has been noted to account for 8%–40% of the annual N requirement for growth (Boyce et al. 1996; Harrison et al. 2000). Although CNU measures are useful in their own regard, they are more meaningful when compared with a measure of total new growth N requirement (Lovett 1992). While the annual growth of foliage, fruiting bodies, roots, branches, and boles requires N, the new growth foliage and roots demand the largest fraction (Schlesinger 1997). Therefore, the magnitude of CNU, at forests receiving significant anthropogenic N deposition compared with the magnitude of annual foliar N requirement, may be a useful method for assessing the potential perturbation of a forest's N cycle. The objectives of this study were to (*i*) estimate N fluxes to the canopy (unit area of canopy basis) at the Niwot Forest due to reallocation, root uptake, and CNU, (*ii*) characterize CNU with respect to NH_4^+, NO_3^-, and organic N, and (*iii*) evaluate the contribution that CNU makes to the annual N requirement for foliar growth at this subalpine forest site.

Materials and methods

Study site

The research area is located at the University of Colorado's Mountain Research Station (40°01′58″N, 105°32′47″W) approximately 6 km east of the Continental Divide and approximately 60 km west of greater Denver's urban, agricultural, and industrial areas. In summer, episodic upslope winds bring polluted air from these urban, agricultural, and industrial areas. Consequently, this easterly air is often significantly laden with N compounds.

The study site, known as Climate Station 1 and referred to in this paper as the Niwot Forest, was formerly deforested by logging but is now a 90-year-old slowly aggrading forest at an approximate elevation of 3000 m. Composition of the

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[2] J. Torizzo, C. Seibold, T. Tomaszewski, A. Turnipseed, and H. Sievering. Atmospheric deposition of nitrogen species to a coniferous, subalpine forest at Niwot Ridge, Colorado. Environ. Pollution. In press.

previous forest is not known; however, spruce and fir are the dominant species for this ecotone. Soils are classified as well-drained sandy loams (0–6 cm) and sandy clay loams (6–12 cm) at this site (Marr 1961). The forest consists of, nearly entirely, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud.). Tree density is 16, 10, and 9 per 100 m^2 for spruce, fir, and pine, respectively (Monson et al. 2002). The canopy height is approximately 11 m and the canopy gap fraction is 17%. The Niwot Forest averages about 80 cm of precipitation a year, and about 35 cm falls during the months of May–October. The period of May–October has been identified as the seasonal interval when net ecosystem CO_2 exchange favors CO_2 uptake (Monson et al. 2002). Thus, May–October is viewed as the growing season.

Wet deposition and throughfall flux

Event precipitation was collected in a clearing with two Aerochem precipitation collectors (26 cm in diameter). For throughfall collection, 22 troughs of various dimensions, for a total sampling area of 1.55 m^2, were distributed beneath spruce, fir, and pine. The allocation of troughs beneath these species approximated the relative cover of each species. The 22 throughfall collection troughs were partitioned into five collection sites with collection areas of 0.28, 0.31, 0.29, 0.31, and 0.36 m^2.

Care was taken to ensure that troughs were completely beneath the crown. The throughfall collection troughs slope slightly downhill so that throughfall will drain into subterranean Nalgene bottles. An aluminum screen at the bottom of the trough prevents litter from entering into the Nalgene collection bottle. A segment of vinyl tubing connected the throughfall troughs to their collection bottles. Throughfall troughs were typically oriented such that one end was against the bole, while the other end approached the edge of the crown. The bottles were placed in holes measuring 20 cm deep to ensure cooler temperatures and downward flow and their tops were covered with opaque plastic wrap. The cooler underground environment, coupled with the lack of light, constituted an effort to prevent microbial and photolytic degradation of the sample.

During sample collection, throughfall volumes were bulked for each of the five sites and volumes were recorded. A 60- to 125-mL aliquot from each of the five bulk samples was taken for analysis of total dissolved N and inorganic N ($NH_4^+ + NO_3^-$). Wet deposition collectors were taken to the laboratory for weighing (to determine volume) prior to taking a 60- to 125-mL aliquot for analysis. During transport, throughfall samples were kept cool with ice packs. Event wet deposition and throughfall collection troughs were rinsed with deionized water every 1–2 days. Rinsing cleaned the collection troughs of debris and accumulated dry fall. Wet deposition and throughfall samples were collected within 2–4 h of each precipitation event's endpoint.

Throughfall and wet deposition collectors become contaminated with small amounts of dry fall, pollen, insects, and litter, which may contain N compounds. Determination of the appropriate blank subtraction for wet deposition and throughfall inorganic and total dissolved N was measured by pouring known amounts of deionized water into throughfall and wet deposition collectors. Subsequently, this water was analyzed for total dissolved N and inorganic NH_4^+ and NO_3^-. This rinsing procedure was performed after collectors had ample time to become contaminated. The greatest length of time that a collector went without an event or a rinse was 3 days. Therefore, in an effort to be conservative, blanks were measured only after 3 days of going without a rinse. The blank mean and standard deviation, calculated with several blanks, were added together in the determination of the blank subtraction.

Growing season uncertainty estimates for wet deposition and throughfall are the products of their blank subtractions and seasonal precipitation events (Table 1). The uncertainty for the sum of the 25 total dissolved N events was determined similarly (Table 2). Moreover, the uncertainty associated with the growing season CNU and sum of the 25 organic N events is the added uncertainties of their component fluxes (Tables 1 and 2).

Dry deposition

Dry deposition of N is in the form of several nitrate species (total is designated as NO_y), NH_4^+, and ammonia. Ammonia deposition and emission have been shown to very nearly cancel each other at this site (Torizzo et al. In press.)[2]; thus, it is not considered further. HNO_3 has been shown to contribute about 80% of NO_y dry deposition (Torizzo et al. In press)[2]. The HNO_3 dry deposition contribution was determined by flux-gradient measurement (Sievering et al. 2001). Nitric oxides (NO_x) and NO_3^- deposition contribute essentially all of the remainder (~20%) to the dry deposition of NO_y; their contributions were estimated using combined site-specific concentration and deposition velocity data (Fahey et al. 1986; Parrish et al. 1986; Torizzo et al. In press.[2]).

New growth foliar N requirement

Branches were harvested periodically, throughout the growing season of 2001, for new growth foliar dry mass and mass %N measures. Branches were cut at the bole–branch interface. A single branch was taken from the bottom, middle, and top of the crown for each tree sampled. Harvested branches were removed from spruce, fir, and pine trees across five size classes. The size classes were defined by diameter at breast height (0–5, 5–10, 10–15, 15–20, and >20 cm). The branch length, determined by the longest axes, was measured. New growth foliage was removed and dried. New growth foliage dry mass per centimetre of branch was determined. The mass %N of foliage was determined on a LECO-CHN (St. Joseph, Mich.) element analyzer. Scaling from a grams of N per centimetre of branch basis to a kilograms of N per hectare basis was made possible through the use of allometric formulations developed by Sparks et al. (2001).

Sparks et al. (2001) developed these allometric formulations by synthesizing information obtained from tree harvests and forest surveys at the Niwot Forest. Harvesting whole trees of various size classes and species led to the parameterization of total branch length (sum of the longest axes per branch) per upper, middle, and lower portions of the crown. Forest surveys provide the frequency of each tree species size class per hectare of forest.

Table 1. Growing season (May–October) flux estimates and uptake efficiencies for NH_4^+ and nitrate (DD is $NO_y = HNO_3 + NO_x$ + PAN + particulate N) at the Niwot Ridge subalpine forest canopy.

Growing season	Ammonium					Nitrate					Inorganic CNU
	WD	DD	TF	CNU	Uptake efficiency	WD	DD (NO_y)	TF	CNU	Uptake efficiency	
2000	0.78 (0.05)	0.06 (0.03)	0.07 (0.01)	0.77 (0.09)	0.92 (0.12)	0.78 (0.05)	0.81 (0.29)	0.29 (0.02)	1.30 (0.35)	0.82 (0.27)	2.07 (0.45)
2001	1.66 (0.12)	0.05 (0.03)	0.17 (0.02)	1.54 (0.17)	0.90 (0.11)	1.51 (0.11)	0.31 (0.12)	0.54 (0.03)	1.28 (0.26)	0.70 (0.20)	2.82 (0.43)

Note: Numbers in parentheses are ± uncertainty estimates. Units are in kilograms N per hectare per growing season. WD, wet deposition; DD, dry deposition; TF, throughfall; CNU, canopy N uptake.

Table 2. Total dissolved nitrogen (TDN), inorganic N, and organic N flux estimates (kilograms N per hectare) in wet deposition (WD) and in throughfall (TF).

	TDN	Inorganic N	Organic N
WD	2.92 (0.20)	1.99 (0.28)	0.93 (0.48)
TF	1.57 (0.11)	0.59 (0.08)	0.99 (0.19)
Net exchange	1.35 (0.31)	1.40 (0.36)	−0.07 (0.67)

Note: Numbers in parentheses are ± uncertainty estimates. Flux estimates, the sum of 25 precipitation events sampled during the 2001 growing season, are based on 60 days of essentially contiguous sampling taken within the 180-day growing season of Table 1.

In the calculation of new growth foliar N (kilograms of N per hectare), branch dry mass is divided by branch length to yield grams dry mass per centimetre of branch. This value is then multiplied by the corresponding mass %N value to produce units of grams of N per centimetre of branch. The total branch length of the appropriate crown section multiplied by grams of N per centimetre of branch yields the total grams of N for the crown section. The total grams of N of each crown section is appropriately combined to yield total grams of N for a species size class. The known number of trees per hectare of forest for each species size class is then multiplied by the corresponding grams of N of each species size class. The total grams of N per hectare of each of the three species' five size classes may then be combined to yield total foliar new growth grams of N per hectare. This value is converted to units of kilograms of N per hectare and divided by 0.83 to adjust for canopy gap fraction (17%). Consequently, the new growth foliar values are presented on a canopy area basis, since 1.0 ha of forest floor would correspond to 0.83 ha of canopy cover. This correction was needed to perform the by-difference calculations of N reallocation and the portion of root uptake contributing to foliar growth. A propagation of error produced estimated uncertainties (–, +) for the 2000 (19 kg $N \cdot ha^{-1}$) and 2001 (22 kg $N \cdot ha^{-1}$) new growth foliar N requirements of (5, 25) and (6, 29), respectively.

Laboratory analysis

Wet deposition and throughfall samples were filtered with a hand pump using Whatman 0.45-µm filter paper. A 10- to 60-mL sample for inorganic analysis of NH_4^+ and NO_3^- was refrigerated at 4 °C for later analysis. Volume permitting, an additional aliquot of 10–60 mL was frozen for analysis of total dissolved N using an Antek 9000 N analyzer. Samples were stored in Nalgene bottles. Inorganic N from wet deposition and throughfall was measured on a Lachat Quick Chem 8000 spectrophotometric flow injection analyzer (detection: NH_4^+, 0.36 $\mu equiv. \cdot L^{-1}$, relative standard deviation 1.00%; $NO_3^- + NO_2^-$, 0.05 $\mu equiv. \cdot L^{-1}$, relative standard deviation 0.39%).

Results and discussion

Wet deposition

During the growing season of 2000, the wet deposition of both NO_3^- and NH_4^+ was 0.78 kg $N \cdot ha^{-1}$. This is half as much inorganic N in wet deposition as occurred during the growing season of 2001 (Table 1). The mean inorganic N concentration of wet deposition events was 1.41 $mg \cdot L^{-1}$ (SD = 1.26) and 1.30 $mg \cdot L^{-1}$ (SD = 0.71) for the 2000 and 2001 growing seasons, respectively. The 50-year mean for May–October precipitation flux to the forest is 35 cm (SD = 7.3 cm) (T. Ackerman, personal communication); however, in 2000, it was only 20 cm whereas in 2001, it was 30 cm. Since wet deposition N concentrations did not differ significantly from 2000 to 2001, the increase of inorganic N deposition during the 2001 growing season is largely due to increased precipitation. Precipitation during both growing seasons was below the 50-year mean so that recorded wet deposition inorganic N fluxes may be less than long-term mean values.

Dry deposition

The dry deposition of NO_y in 2000 was greater than nitrate wet deposition; yet, in 2001, nitrate wet deposition was nearly five times greater than the dry deposition of NO_y. This is partly due to the 50% greater precipitation during the growing season of 2001 but is primarily due to the much lower 2001 HNO_3 air concentrations. Ammonium dry deposition was about the same in 2000 and 2001, reflecting the fact that its concentration did not vary significantly in these two years. Overall, despite 2001 N dry deposition being only 40% of that in 2000, the total inorganic atmospheric N deposition was 45% greater for 2001 (Table 1).

Canopy N uptake

The majority of CNU during 2000 was as nitrate-N (Table 1), while CNU in 2001 was distributed almost evenly between nitrate and NH_4^+. A substantial decrease in nitrate dry deposition was responsible for the smaller contribution of nitrate (relative to 2000) towards total inorganic CNU in 2001. Just as the inorganic N flux in wet deposition increased proportionally with greater precipitation, so did the magnitude of CNU. Therefore, the long-term trend for growing season N deposition and CNU is likely greater than the rates measured during 2000 and 2001, since both years exhibited below-average precipitation.

Nitrogen uptake efficiencies

The NH_4^+ uptake efficiency [CNU/(wet deposition + dry deposition)] of 0.9 (Table 1) was consistent across both the 2000 and 2001 growing seasons. Uptake efficiencies for NO_3^- were found to be 0.8 and 0.7 during the 2000 and 2001 growing seasons, respectively. Comparison of N uptake efficiencies on an event basis, across our 2001 growing season, yielded some interesting results. For example, uptake efficiencies for NO_3^- were highly variable across precipitation events (SD = 0.36), whereas event variability of NH_4^+ uptake efficiency was relatively small (SD = 0.07). High canopy NH_4^+ uptake is often reported for coniferous forests, while uptake of NO_3^- is less common (Parker 1983). Measurements at a northeastern U.S. forest have indicated NO_3^- uptake efficiencies as high as 0.9 (Sievering et al. 2000).

A study at a Rocky Mountain subalpine forest (Loch Vale), similar to the Niwot Forest, found an NH_4^+ uptake efficiency of approximately 0.7 with no significant uptake of nitrate (Arthur and Fahey 1993). However, the Loch Vale forest canopy may exhibit a positive uptake efficiency for nitrate and a larger than approximately 0.7 uptake efficiency for NH_4^+. Throughfall collectors were scattered randomly about the forest floor during the Loch Vale study (Arthur and Fahey 1993). Therefore, incident precipitation may have entered throughfall collectors through gaps in the forest canopy, thereby masking N uptake by the canopy. The Niwot Forest and Loch Vale subalpine forest may be more similar than they appear. For example, our NH_4^+ uptake efficiency on a unit area of canopy basis (0.9) is actually approximately 0.7 on the unit area of ground basis used by Loch Vale researchers.

The greater N loading to the forest in 2001 did not elicit any substantial changes in the NH_4^+ uptake efficiencies. Therefore, there is no evidence to suggest that we are approaching a maximum level of NH_4^+ uptake by the forest canopy. Although nitrate uptake efficiency dropped from 0.8 in 2000 to 0.7 in 2001, the nitrate uptake flux (1.3 $kg\ N \cdot ha^{-1}$ per growing season) was unchanged across the two growing seasons (Table 1). Thus, there does not appear to be any substantial resistance of nitrate or NH_4^+ uptake despite the increases in atmospheric N deposition. However, the decreased nitrate uptake efficiency in 2001 may be in some way related to the increased NH_4^+ loading that season.

Organic N deposition: canopy neutrality

Total dissolved N was determined for 2001 wet deposition and throughfall samples (Table 2). Organic N in wet deposition and throughfall was then determined by difference: total dissolved N – (NH_4^+ + NO_3^-). Net canopy exchange of organic N was estimated by subtracting organic N in throughfall from that in wet deposition. There was no statistically significant net canopy exchange of organic N, although the trend does suggest a slight leaching of organic N. Interestingly, for 18 of the 25 precipitation events, canopy retention of organic N was recorded. Net canopy organic N losses for seven other events, which also exhibited relatively larger precipitation volumes, were relatively large and more than compensated for the accumulation during the remaining 18 events. Accumulating organic N may not be flushed out of the canopy until large-volume precipitation events occur. However, this remains speculative until data regarding organic N speciation in wet deposition and throughfall are available.

A substantial portion of the total N in wet deposition is organic, about one-third; in throughfall, it is two-thirds. The majority of precipitation events exhibited an increase in the organic N concentration of throughfall versus that in wet deposition. Typically, this increase was not sufficient to make the throughfall organic N flux exceed the wet deposition organic N flux, since throughfall water flux was only 25%–30% of the wet deposition water flux at this site. Despite the large inorganic N uptake, the canopy appears to be neutral with respect to net organic N uptake.

Canopy new growth N: CNU contribution

To determine foliar new growth N requirement, foliage is typically sampled at the time of maximum tissue N content. For conifer first-year foliage, this condition is often the case at the end of the growing season (Fahey and Birk 1991). We observed this pattern to be true across our periodic sampling throughout the growing season of 2001. In 2000, the foliar N requirement had been estimated to be 19 $kg\ N \cdot ha^{-1}$ (Sparks

Table 3. Foliar N requirement, root N uptake into foliage, canopy N uptake (CNU), and reallocation (by difference) in kilograms N per hectare per growing season during the 2000 and 2001 growing seasons.

Source	Foliar N requirement	Root N uptake	CNU	Reallocation
2000				
N contributed	19	5–6	2	11–12
% of N required		~30	~10	~60
2001				
N contributed	22	4–5	3	14–15
% of N required		~20	~15	~65

Note: Best estimate values are shown (see text).

2001). Therefore, the 2000 growing season CNU of 2.1 kg N·ha^{-1} contributed about 10% of the foliar N requirement. In 2001, the foliar N requirement was about 22 kg N·ha^{-1} (Table 3). Therefore, CNU of 2.8 kg N·ha^{-1} during the growing season of 2001 contributed about 15% of the foliar N requirement.

Canopy N budget: reallocation and root uptake

Changes in N concentration over the life of needles roughly reflect reallocation rates. Nambiar and Fife (1991) pointed out that it is more quantitatively accurate to measure changes in needle mass in addition to changes in N concentration. However, to assess the approximate magnitude of foliar reallocation, we examined new growth and litterfall foliar N concentrations. The C to N ratios of foliar new growth (at the end of 2001) and of litterfall needles were about 50 and 110, respectively. Therefore, reallocation of N within the forest canopy over the life of the needles is on the order of 50%–60% of the foliar N requirement, assuming that additional C gain over the life of the needle is minimal. New growth N provided by reallocation varies greatly across species and study sites; mature conifer forests range from 30% to 80% (Cole and Rapp 1981; Friedland et al. 1991; Helmisaari 1992; Birk and Vitousek 1986).

A more accurate approximation of the magnitude of N supplied to foliage by reallocation was obtained using the following formula: Reallocation = N_{required} − litterfall N (Fahey and Birk1991). Three years (1999–2001) of litterfall data (L. Scott-Denton, personal communication) were used to estimate that litterfall foliar N loss was 7–8 kg N·ha^{-1}·year^{-1} as needle litter. Considering that the canopy is nearly in steady state (Sparks 2001), root N uptake into foliage and CNU must replenish this lost N in needle litter. Given that the foliar new growth N requirement for 2000 and 2001 was found to be 19 and 22 kg N·ha^{-1}, respectively, reallocation was approximately 11–12 and 14–15 kg N·ha^{-1}, respectively, more than half of the N required for foliar new growth (Table 3). Reallocation, as a percentage of foliar N requirement, appears to corroborate the observations of foliar and litterfall N concentrations. Given that CNU contributed 2–3 kg N·ha^{-1} per growing season, the portion of root N uptake partitioned to the canopy should be in the range of 4–6 kg N·ha^{-1}·year^{-1} (Table 3).

Canopy N uptake: perturbation of the natural N cycle

Forests on the eastern slope of the Continental Divide (where N deposition is enhanced) are known to have lower organic horizon and foliar C to N ratios (Baron et al. 2000; Rueth and Baron 2002). This is strong evidence that anthropogenic N deposition has been altering the N cycle at these east slope forests. Nitrogen wet deposition at the Niwot Saddle, which is in near proximity to the Niwot Forest, is nearly the highest in Colorado (Rueth and Baron 2002). The Niwot Forest's canopy takes up approximately 85% of the growing season wet plus dry inorganic N deposition, making the canopy the largest forest sink for N deposition. If the N concentration of foliage increases with CNU, then photosynthesis and current-year growth (bole, branch, root, foliage) may be enhanced. Furthermore, given that CNU may represent 10%–15% of the new growth foliar N requirement, it is likely that changes are occurring on a shorter time scale than chronic N loading might otherwise suggest. The high N uptake efficiencies at the Niwot Forest, together with the high NH_4^+ uptake efficiency of 0.7 observed at the Loch Vale forest (Arthur and Fahey 1993), indicate that the canopy may be a large sink for N deposition across a broad region of Colorado.

Conclusions

Organic N contributed about one-third of N in wet deposition during the 2001 growing season. However, the magnitude of organic N flux in throughfall was essentially the same as the organic N flux in wet deposition; thus, the canopy was neutral with respect to net organic N exchange. The canopy retained inorganic NH_4^+ and nitrate with relatively high efficiency, 90% and approximately 75%, respectively. CNU of atmospherically deposited N contributed 10%–15% of the total N requirement for new growth foliage. Reallocation supplied more than half of the foliar N requirement. Disruption of the background natural N cycle at this forest is likely, given that a majority of the atmospherically deposited N is anthropogenic. Since the canopy is the largest sink for N deposition, understanding the fate of CNU and its potential role in C sequestration is paramount to understanding the impacts of N deposition at this and possibly other Colorado subalpine forests.

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References

Arthur, M.A., and Fahey, T.J. 1993. Throughfall chemistry in an Engelmann spruce – subalpine fir forest in north central Colorado. Can. J. For. Res. **23**: 738–742.

Baron, J.S., Rueth, H.M., Wolfe, A.M., Nydick, K.R., Allstott, E.J., Mincar, J.T., and Moraska, B. 2000. Ecosystem responses to nitrogen deposition in the Colorado Front Range. Ecosystems, **3**: 352–368.

Birk, E.M., and Vitousek, P.M. 1986. Nitrogen availability and nitrogen use efficiency in loblolly pine stands. Ecology, **67**: 69–79.

Boxman, A.W., Van Dam, D., Van Dijk, H.F.G., Hogervorst, R.F., and Koopmans, C.J. 1995. Ecosystem responses to reduced nitrogen and sulphur inputs into two coniferous forest stands in the Netherlands. For. Ecol. Manage. **71**: 7–29.

Boyce, R.L., Friedland, A.J., Chamberlain, C.P., and Poulson, S.R. 1996. Direct canopy nitrogen uptake from ^{15}N-labeled wet deposition by mature red spruce. Can. J. For. Res. **26**: 1539–1547.

Burns, D.A. 2002. The effects of atmospheric nitrogen deposition in the Rocky Mountains of Colorado and southern Wyoming — a synthesis and critical assessment of published results. U.S. Geol. Surv. Water Resour. Invest. Rep. 02-4066.

Campbell, D.H., Baron, J.S., Tonnessen, K.A., Brooks, P.D., and Schuster, P.F. 2000. Controls on nitrogen flux in alpine/subalpine watersheds of Colorado. Water Resour. Res. **36**: 37–47.

Cole, D.W., and Rapp, M. 1981. Elemental cycling in forest ecosystems. *In* Dynamic properties of forest ecosystems. *Edited by* D.E. Riechle. Cambridge University Press, New York. pp. 341–409.

Fahey, T.J., and Birk, E.M. 1991. Internal redistribution and resorption. *In* Techniques and approaches in forest tree ecophysiology. *Edited by* J.P. Lassoie and T.M. Hinckley. CRC Press, Inc., Boca Raton, Fla. pp. 225–245.

Fahey, D., Hubler, G., Parrish, D., Williams, E., Norton, R., Singh, H., and Fehsenfeld, F. 1986. Reactive nitrogen species in the troposphere: measurements of NO, NO_2, HNO_3, PAN, and total reactive odd nitrogen (NO_y) at Niwot Ridge, CO. J. Geophys. Res. **91**: 9781–9793.

Field, C., and Mooney, H.A. 1986. The photosynthesis–nitrogen relationship in wild plants. *In* On the economy of plant form and function. *Edited by* T.J. Givnish. Cambridge University Press, Cambridge, U.K. pp. 25–55.

Friedland, A.J., Miller, E.K., Battles, J.J., and Thorne, J.F. 1991. Nitrogen deposition, distribution and cycling in a subalpine spruce–fir forest in the Adirondacks, New York, USA. Biogeochemistry, **14**: 31–55.

Garten, C.T., Schwab, A.B., and Shirshac, T.L. 1998. Foliar retention of ^{15}N tracers: implications for net canopy exchange in low- and high-elevation forest ecosystems. For. Ecol. Manage. **103**: 211–216.

Harrison, A.F., Schulze, E.-D., Gebauer, G., and Bruckner, G. 2000. Canopy uptake and utilization of atmospheric pollutant nitrogen. *In* Carbon and nitrogen cycling in European forest ecosystems. Ecological studies. Vol. 142. *Edited by* E.-D. Schulze. Springer-Verlag, Berlin and Heidelberg. pp. 171–187.

Helmisaari, H.S. 1992. Nutrient retranslocation in three *Pinus sylvestris* stands. For. Ecol. Manage. **51**: 347–367.

Hood, E.W., Williams, M.W., and Caine, N. 2003. Landscape controls on organic and inorganic nitrogen leaching across an alpine–subalpine ecotone. Ecosystems, **6**: 31–45.

Ignatova, N., and Dambrine, E. 2000. Canopy uptake of N deposition in spruce (*Picea abies* L. Karst.) stands. Ann. For. Sci. **57**: 113–120.

Lang, G.E., Reiners, W.A., and Pike, L.H. 1980. Structure and biomass dynamics of epiphytic lichen communities of balsam fir forests in New Hampshire. Ecology, **6**: 541–550.

Lovett, G.M. 1992. Atmospheric deposition and canopy interactions of nitrogen. *In* Atmospheric deposition and forest nutrient cycling: a synthesis of the Integrated Forest Study. Ecol. Stud. 91. *Edited by* D.W. Johnson and S.E. Lindberg. Springer-Verlag, New York. pp. 152–166.

Lovett, G.M., Reiners, W.A., and Olson, R.K. 1989. Factors controlling throughfall chemistry in a balsam fir canopy: a modeling approach. Biogeochemistry, **8**: 239–264.

Marr, J.W. 1961. Ecosystems of the east slope of the Front Range in Colorado. Univ. Colo. Stud. Ser. Biol. 8.

Monson, R.K., Turnipseed, A.A., Sparks, J.P., Harley, P.C., Scott-Denton, L.E., Sparks, K., and Huxman, T.E. 2002. Carbon sequestration in a high-elevation, subalpine forest. Global Change Biol. **8**: 459–478.

Nambiar, E.K.S., and Fife, D.N. 1991. Nutrient retranslocation in temperate conifers. Tree Physiol. **9**: 185–207.

Nussbaum, S., Ballmoos, P.V., Gfeller, H., Schlunegger, U.P., Fuhrer, J., Rhodes, D., and Brunold, C. 1993. Incorporation of atmospheric $^{15}NO_2$-nitrogen into free amino acids by Norway spruce *Picia abies* (L.) Karst. Oecologia, **94**: 408–414.

Parrish, D., Norton, R., Bollinger, M., Albritton, D., and Fehsenfeld, F. 1986. Measurements of HNO_3 and NO_3^- particulates at a rural site in the Colorado mountains. J. Geophys. Res. **91**: 5379–5393.

Rennenberg, H., Kreutzer, K., Papen, H., and Weber, P. 1998. Consequences of high loads of nitrogen for spruce (*Picea abies*) and beech (*Fagus sylvatica*) forests. New Phytol. **139**: 71–86.

Rueth, H.M., and Baron, J.S. 2002. Differences in Englemann spruce forest biogeochemistry east and west of the Continental Divide in Colorado, USA. Ecosystems, **5**: 45–57.

Schindler, D., and Bayley, S. 1993. The biosphere as an increasing sink for atmospheric carbon: estimates from increased nitrogen deposition. Global Biogeochem. Cycles, **7**: 717–733.

Schlesinger, W. 1997. Biogeochemistry: an analysis of global change. Academic Press, San Diego, Calif. pp. 166–223.

Sievering, H. 2001. Atmospheric chemistry and deposition. *In* Structure and function of an alpine ecosystem Niwot Ridge, Colorado. *Edited by* W.D. Bowman and T.R. Seastedt. Oxford University Press, New York. pp. 32–44.

Sievering, H., Fernandez, I., Lee, J., Hom, J., and Rustad, L. 2000. Forest canopy uptake of atmospheric nitrogen deposition at eastern US conifer sites: carbon storage implications? Global Biogeochem. Cycles, **14**: 1153–1160.

Sievering, H., Kelly, T., McConville, G., Seibold, C., and Turnipseed, A. 2001. Nitric acid dry deposition to conifer forests: Niwot Ridge spruce–fir–pine study. Atmos. Environ. **35**: 3851–3859.

Sparks, K.L., Sparks, J.P., Scott-Denton, L.E., Harley, P.C., Turnipseed, A.A., Huxman, T.E., and Monson, R.K. 2001. Carbon balance in a high elevation subalpine forest. Poster Abstract, 2001 Ecological Society of America Conference, Madison, Wis. Allen Press, Inc., Kansas.

Vose, J.M., and Swank, W.T. 1990. Preliminary estimates of foliar absorption of ^{15}N-labeled nitric acid vapor (HNO_3) by eastern white pine (*Pinus strobus*). Can. J. For. Res. **20**: 857–860.