Variation in overstory nitrogen uptake in a small, high-elevation southern Appalachian spruce–fir watershed¹

M. Barker, H. Van Miegroet, N.S. Nicholas, and I.F. Creed

Abstract: High-elevation red spruce (*Picea rubens* Sarg.) – Fraser fir (*Abies fraseri* (Pursh) Poir.) forests of the southern Appalachians exhibit considerable spatial heterogeneity in structure, and possibly in N uptake, because of a combination of natural disturbances and heavy fir mortality caused by infestations of the exotic balsam woolly adelgid (*Adelges piceae* Ratz.). The objectives of this study are to determine spatial variability in tree N uptake in a small high-elevation catchment in the Great Smoky Mountains National Park, compare outcomes among calculation methods, and assess the influence of stand and landscape properties on N uptake. Tree N uptake is estimated for fifty 20 × 20 m plots in the Noland Divide Watershed (NDW). Components considered in the calculations are stem growth, foliage increment, and mortality of spruce, fir, and yellow birch (*Betula alleghaniensis* Britt.) from 1993 and 1998 stand inventories; throughfall N flux measured in summers 1998 and 1999; litterfall N return for 1 year in a subset of 12 plots; tissue N analyses; and atmospheric N deposition and root turnover estimates from the literature. Overstory N uptake varies spatially within NDW, with a CV of 9–41% depending on the calculation method. Variability among methods is even higher, with an almost 15-fold difference between the smallest and largest average overstory uptake estimate (5 vs. 74 kg·ha⁻¹·year⁻¹). Only 5 and 3 kg·ha⁻¹·year⁻¹ of N is sequestered in wood and foliar increment, respectively, while 36 kg·ha⁻¹ of N returns annually as aboveground litterfall. Uptake and its components are correlated with measures of stand structure but not with elevation or aspect.

Résumé : Des forêts de haute altitude d'épinette rouge (*Picea rubens* Sarg.) et de sapin Fraser (*Abies fraseri* (Pursh) Poir.) du Sud des Appalaches montrent une hétérogénéité spatiale considérable dans leur structure et probablement dans leur prélèvement en azote du fait d'une combinaison de perturbations naturelles et d'une mortalité importante du sapin causée par des infestations du puceron lanigère du sapin (*Adelges piceae* Ratz.). Les objectifs de cette étude consistaient à déterminer la variabilité spatiale du prélèvement en azote des arbres dans un petit bassin de haute altitude localisé dans le parc national des Great Smoky Mountains, comparer les résultats entre les méthodes d'estimation et évaluer l'influence des propriétés du peuplement et du paysage sur le prélèvement en azote. Le prélèvement en azote des arbres a été estimé pour 50 placettes de 20 × 20 m dans le bassin du Noland Divide (BND). Les éléments considérés dans les calculs sont : la croissance de la tige, la croissance foliaire et la mortalité de l'épinette, du sapin et du bouleau jaune (*Betula alleghaniensis* Britt.) à partir des inventaires de peuplement de 1993 et 1998; le flux d'azote dans le pluviollessivage mesuré pendant les étés 1998 et 1999; le retour en azote par la litière pour une année dans un sous-ensemble de 12 placettes; les analyses d'azote dans les tissus; les dépôts atmosphériques d'azote et le taux de renouvellement des racines estimés à partir de la littérature. Le prélèvement d'azote du couvert varie spatialement dans le BND, avec un CV de 9 à 41 % en fonction de la méthode de calcul. La variabilité parmi les méthodes est même plus forte, avec une différence de près de 15 fois entre la valeur estimée de prélèvement moyen du couvert la plus élevée et la plus faible (5 vs 74 kg·ha⁻¹·an⁻¹). Seuls 5 et 3 kg·ha⁻¹·an⁻¹ d'azote sont respectivement séquestrés dans l'accroissement du bois et du feuillage alors que 36 kg·ha⁻¹·an⁻¹ d'azote retourne annuellement comme litière aérienne. Le prélèvement et ses composantes sont corrélés avec des mesures de structure du peuplement mais pas avec l'altitude ou l'exposition.

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Introduction

Nitrogen (N) has long been considered a limiting nutrient in forests. However, increases in atmospheric N deposition

from fossil fuel combustion has greatly increased N availability in some locations often to the point where it now exceeds biological N demands (Skeffington and Wilson 1988; Aber et al. 1989). There are concerns that this excess N may

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reduce forest productivity because of frost damage or other physiological impairments (Friedland et al. 1984; Aber et al. 1998), that accelerated nitrate (NO_3) mediated leaching may cause nutrient imbalances in the soil through cation depletion and (or) Al mobilization, and that these exports may in turn adversely impact stream water quality (Stoddard 1994; Fenn et al. 1998). Disturbance and land-use history influence the rate at which ecosystems approach N saturation; in the long-term by repeated reductions in soil N capital associated with prior extractive land-use practices (Aber et al. 1998) and, in the short term, through changes in N fluxes such as plant uptake or N mineralization following disturbance (Vitousek and Melillo 1979; Perry 1994).

Stand vigor is an important predisposing factor in the degree of N saturation (Fenn et al. 1998), and vegetation N increment accounts for a large portion of forest N retention capacity (Johnson 1992; Perry 1994). Overstory N uptake changes with time, with the greatest N increment into biomass in the aggrading phase of forest development (Cole and Rapp 1981), while the lowest N retention capacity is typically observed in older forests (Emmett et al. 1993; Olsson et al. 1997). Species composition may also affect N uptake, as annual N requirements have been reported to be higher in deciduous than coniferous species (Cole and Rapp 1981). Nadelhoffer et al. (1995) observed that deciduous species were more effective at taking up NO_3 than red spruce, suggesting that in ecosystems with a high NO_3 abundance, species composition could also influence N retention capacity.

The high-elevation southern Appalachian (SA) red spruce (*Picea rubens* Sarg.) – Fraser fir (*Abies fraseri* (Pursh) Poir.) forests receive among the highest atmospheric N inputs in North America, estimated at $28 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ (Johnson et al. 1991; Lovett and Lindberg 1993). They are characterized by high soil NO_3 leaching rates ($10\text{--}20 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$; Johnson et al. 1991; Joslin and Wolfe 1992) and considerable stream water exports ($15 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$; Nodvin et al. 1995). Historically, these high-elevation spruce–fir forests have largely escaped logging and associated burning because of inaccessibility (Pyle 1988), and fires are rare as a disturbance agent (Harmon et al. 1983); the result is large soil N pools with high N mineralization potential (Van Miegroet et al. 1992; Garten 2000). More recently, the spruce–fir forest has been impacted by an exotic insect infestation, the balsam woolly adelgid (*Adelges picea* Ratz.), causing dieback of mature Fraser fir and creating a heterogeneous forest structure with numerous gaps and a large variation in stand age, number of live and dead standing trees, and amount of coarse woody debris on the forest floor (Nicholas et al. 1992; Pauley et al. 1996; Rose 2000). It is expected that such structural heterogeneity would be reflected in significant spatial variation in N uptake by the overstory trees.

Assessing the role of overstory N uptake in ecosystem N retention is further complicated by the fact that several uptake calculation methods are currently in use that differ in complexity and terms included (Cole and Rapp 1981; Bockheim and Leide 1990). Many uptake calculations are based on aboveground processes only (increments, litterfall), because belowground measurements are destructive and often difficult to obtain. The only published overstory N up-

take estimates for SA spruce–fir forests are in the order of $7 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ and were derived from a total of four plots at only two sites in the Great Smoky Mountains National Park (GSMNP) during the Integrated Forest Study (IFS) (Johnson et al. 1991; Johnson and Lindberg 1992). While this earlier study alludes to the limited N sink capacity of overstory trees, the question remains if these N uptake estimates can be used for the spruce–fir system at large, especially in light of the ecosystem's recent disturbance history and the ensuing heterogeneity in forest structure (Nicholas et al. 1992; Pauley et al. 1996). Indeed, little is known about the variation in overstory N uptake on a small spatial scale, the factors controlling it, and its influence on N dynamics.

The objectives of this study were to determine (i) the magnitude and spatial variation in overstory soil N uptake across a small watershed; (ii) the variation in N uptake estimates among different calculation methods; and (iii) the relationship between overstory N uptake, forest growth, and stand or landscape characteristics. This study was designed to put the earlier overstory N uptake estimates in context by providing a range of minimum to maximum values that could be used in future modeling and assessment efforts. Quantifying relationships between overstory N uptake and stand or landscape characteristics further allows for N uptake predictions outside the study area without the need for time- and resource-intensive measurements.

The Noland Divide Watershed (NDW), a small, high-elevation headwater catchment in GSMNP is well suited to investigate variation in overstory N uptake because of the considerable heterogeneity in stand structure throughout the watershed (Nicholas et al. 1992), a strong elevational gradient that affects overstory species composition and deposition regime (Lindberg and Owens 1993; Shubzda et al. 1995; Pauley et al. 1996), and the pre-existing plot infrastructure and available data sets. Furthermore, the watershed is small enough that parent material is not a significant source of variation in the uptake estimates. While uptake of understory vegetation is undoubtedly important to N dynamics, this study focuses only on the N uptake of the three dominant overstory species: Fraser fir, red spruce, and yellow birch (*Betula alleghaniensis* Britt.).

Materials and methods

Study site

The NDW ($35^{\circ}34'N$, $83^{\circ}29'W$) is a small (17.4 ha), high-elevation (1700–1910 m) first-order drainage in the red spruce – Fraser fir ecosystem located near Clingman's Dome in the GSMNP on the North Carolina and Tennessee border. It is in close proximity to the IFS Tower site described in Johnson et al. (1991). The watershed is dissected at 1800 m by the Clingman's Dome road built in 1938. The NDW has not been impacted by logging or fire (Pyle 1988). At the onset of the study, live basal area (LBA) of overstory trees ranged from 14.9 to $67.5 \text{ m}^2 \cdot \text{ha}^{-1}$. Red spruce accounts for 77% of the LBA of the watershed, while yellow birch and Fraser fir account for 19 and 2.5%, respectively. The relative abundance of fir increases with elevation, while that of yellow birch declines. Fraser fir accounts for 56% of the standing dead basal area, indicating the large impact of the

adelgid infestation (Pauley et al. 1996). Pauley et al. (1996) estimated total biomass of live overstory trees at $220 \text{ Mg}\cdot\text{ha}^{-1}$ and aboveground N content in live overstory trees at $375 \text{ kg}\cdot\text{ha}^{-1}$, with the highest N on east-facing slopes of the lower watershed.

The soils in the NDW are Inceptisols with spodic characteristics classified as Dystrochrepts or Haplumbrepts (McCracken et al. 1962; Van Miegroet et al. 1993), underlain by Thunderhead Sandstone (King et al. 1968). They have a silt loam to sandy loam texture and are generally shallow throughout the catchment (<50 cm depth to bedrock; J. Branson, unpublished data). Mean annual precipitation in NDW varies from 200 to 300 cm and is fairly evenly distributed throughout the year (Johnson et al. 1991; Johnson and Lindberg 1992; Shubzda et al. 1995). Snow accounts for about 10% of the mean annual precipitation and typically covers the ground for 50 days a year (Johnson et al. 1991). The cloud base typically occurs at 1800 m (Johnson and Lindberg 1992), roughly matching the elevation of Clingman's Dome Road. Mean air temperatures at the base of the watershed range from about -2°C in February to 17°C in August, with a frost-free period from May through September (Johnson et al. 1991; Shanks 1954).

Uptake calculations

Overstory N uptake is estimated from retention, the amount of N incorporated in above- and below-ground biomass increment, and restitution, the amount of N returned to the soil via above- and below-ground litterfall and canopy leaching, using different calculation methods found in the literature (after Bockheim and Leide 1990). Net woody biomass increment represents the simplest form of N uptake. Foliage increment is generally excluded from uptake calculations for forests under steady-state conditions (Cole and Rapp 1981; Bockheim and Leide 1990). Vitousek and Reiners (1975) suggested that if a disturbance patch size was small relative to the size of watershed, the watershed as a whole could incorporate disturbance into a watershed-level, steady-state condition. However, if the disturbance patch size was relatively large, then steady-state conditions could not be measured at the scale of the watershed. Because of significant changes in forest composition and structure following the extensive balsam woolly adelgid infestation, SA spruce-fir forests cannot be considered at steady state (Nicholas et al. 1999). Hence, potential net increment in foliar biomass is explicitly considered in our uptake calculations. As per Bockheim and Leide (1990), restitution via aboveground litterfall includes all fine components (foliage, twigs, bark, and reproductive components), except in one equation, modeled after the IFS uptake calculation (Johnson and Lindberg 1992), which contains only foliage litterfall. Net canopy exchange (NCE) is calculated as atmospheric N deposition minus throughfall N flux. A positive NCE value represents N taken up from the soil and subsequently leached from the canopy and must be added to the other fluxes to obtain total (= soil) N uptake. A negative NCE value indicates foliar uptake, and this flux is subtracted from biomass N increment and litterfall N return to obtain soil N uptake (Johnson et al. 1991). Total N uptake is then simply the sum of foliar and soil uptake. The most complete uptake

Fig. 1. Location map of the Noland Divide Watershed, near Clingman's Dome, North Carolina, in the Great Smoky Mountains National Park (prepared by the Cartographic Section of the Geography Department, University of Western Ontario, London, Ont. Map No. 2001/95-00).

calculation considers N sequestered in belowground root turnover, which in this study, is based on values from the literature. For clarity, the formulas of the seven calculation methods used in this study are included with the actual calculation results later in this paper.

Field measurements

Fifty 20×20 m plots were established systematically along nine elevation bands in the NDW (Pauley et al. 1996) (Fig. 1). Woody and foliar biomass increments were determined using allometric equations developed by Nicholas (1992) and diameter at breast height (DBH) measurements in 1993 and 1998 for all overstory (>5 cm DBH) trees within the 50 plots. In ecosystems with significant tree mortality, the calculation of overstory N uptake must also consider the amount of nutrients sequestered in the trees that died within the measurement period. Thus, in this study, gross rather than net growth was used to calculate aboveground N sequestration, using the following equation:

$$(\text{live biomass } 1998 - \text{live biomass } 1993 + \text{ingrowth biomass} + \text{biomass of trees that died between } 1993 \text{ and } 1998) / 5$$

Ingrowth refers to those trees in the 1998 survey with a DBH of ≥ 5 cm that were too small for inclusion in the 1993 survey. The 1993 biomass for these trees was set at zero. Net forest growth was calculated as the difference in biomass between two inventory periods, minus mortality plus ingrowth (after Shiver and Borders 1996). The allometric equations used in this study were developed by Nicholas (1992) based on mostly second-growth trees from the Black Mountains in North Carolina and Mount Rogers National

Recreation Area (MRNRA) in Virginia. Since the DBH–height relationships were likely different in the old-growth Great Smoky Mountains, tree heights were also measured for a subsample of spruce, fir, and birch overstory trees in the NDW with a clinometer, using methods for sloped terrain (Long and Mohai 1986).

Live tissue sampling and litterfall collection occurred near 12 plots selected in a stratified random design. All 50 plots were categorized into four leaf area index (LAI) classes ($\text{m}^2\cdot\text{m}^{-2}$) (class 1, 3.44–6.57; class 2, 6.58–9.71; class 3, 9.72–12.85; class 4, 12.86–16.00) and three elevation bands (low, 1705–1768 m; medium, 1798–1828 m; and high, 1859–1920 m). The LAI (projected area) was determined from LBA using allometric equations (Nicholas 1992). One plot was randomly selected from each of the resulting 12 categories, and a total of 24 dominant and codominant trees were identified within 10 m from the four plot corners, striving for two candidates per species and plot corner. Trees with dead tops or inaccessible branches were not considered. From this pool of potential sampling trees ($n \cong 288$), five trees per species were randomly selected for sampling in each of the three elevation bands, for a total of 45 trees. From each tree, bolewood, dead branches, live branches, bark, and foliage samples were collected. Needles were divided into two age-classes: old and current year. After collection, samples were dried for 24 h at 65°C and ground in a Wiley Mill (0.85 mesh). Tissues from two or three sample trees per elevation were composited by species, tissue type, and elevation then analyzed for N by combustion using a LECO CN analyzer (CHN 1000, Leco Corp., St. Joseph, Mich.).

Litterfall was collected over a 1-year period (September 1998–1999) at a total of 12 plots using four 0.07- m^2 traps per plot placed outside the plot about 3 m from each corner stake. Collection occurred on or around the first day of October, November, and December 1998 and March, April, May, July, and September 1999. Litter was dried at 65°C, weighed within 48 h of collection, and then separated into four tissue types (needles, foliage, bark and twig, other). The biomass and N concentrations of litterfall components collected in the fall (October–December) were determined separately from those collected the remainder of the year. A linear relationship between LAI and fall litterfall biomass ($Y = 91.2 + 8.6X$, $r^2 = 0.42$, $p = 0.02$) was used to estimate fall litterfall biomass for the remaining plots. Since the relationship between LAI and litterfall biomass was very weak ($r^2 < 0.05$) for the nonfall period, plots were uniformly assigned the average litterfall biomass value obtained from the 12 sampling plots. Needle N concentration was analyzed by individual plot for the two periods ($n = 24$). Because of funding limitations, twig plus bark, foliage, and other components were composited by elevation and collection period ($n = 6$ per litter type) prior to N analysis by a LECO CN analyzer.

To date, no direct information pertaining to the SA spruce–fir is available for belowground N litterfall via fine-root turnover. To approximate belowground N return in this study, we applied the belowground N return of 29 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ from a Norway spruce (*Picea abies* (L.) Karst.) site in Belgium (Duvigneaud and Kestemont 1977, as cited in Vogt et al. 1986), which climatically most closely resembles NDW con-

ditions. Other studies involving spruce have found above- and below-ground N litterfall fluxes to be similar (e.g., 22 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ for fine root N turnover vs. 28 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ for foliar litterfall in Wisconsin (Nadelhoffer et al. 1995)). Thus, the Duvigneaud and Kestemont (1977) estimate used did not seem unreasonable given the aboveground litterfall N estimate for SA spruce–fir (22 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) determined earlier (Johnson et al. 1991).

Throughfall N flux was estimated from eight mixed anion–cation exchange resin bags placed on the soil surface along the perimeter of the 50 plots during the growing season (mid-June – September 1998; May–August 1999). At the end of the growing season (approximately 10 weeks), resins bags were retrieved, extracted with a 1-M KCl solution, and the extract frozen until analysis for inorganic N on a Lachat autoanalyzer (Quick CHEM, Zellweger Analytics, Milwaukee, Wis.). Seasonal throughfall patterns determined earlier by Strader et al. (1989) using similar field techniques, and a mean adsorption–recovery efficiency of 49% for $\text{NH}_4\text{-N}$ and 35% for $\text{NO}_3\text{-N}$ determined for this exchange resin type (H. Van Miegroet, unpublished data) were applied to estimate the annual throughfall N flux for each plot. Throughfall N fluxes used in the calculation for each plot were based on 1998–1999 means. Atmospheric N deposition estimates for a high- (35 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) and low-elevation site (27 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) in the NDW (Shubzda et al. 1995) along with these throughfall N flux estimates were used to estimate net canopy exchange (NCE) in each plot (Table 1).

Data analysis

Statistical analyses of the data were performed with SAS software, version 7 (SAS Institute Inc. 1998) and SURFER software, version 7 (Golden Software 1999). The CORR procedure was used to determine general associations between uptake or its components with landscape and stand characteristics using an alpha level of 0.05. Landscape characteristics included elevation and aspect. Aspect was transformed using a sine function after Beers et al. (1966) to increase the weight of those slopes that have a lower numerical azimuth but typically have higher productivity in the northern hemisphere, namely northern and eastern slopes. Stand characteristics included the proportion of LBA to total standing basal area (BA) (dead and live), as well as the respective proportions of the BA of live or dead spruce, fir, or birch to total standing BA. Correlations with the stand density index (SDI) of all live trees, as well as the SDI of fir, birch, and spruce, were also examined. Stand density index is a relative density measurement based on tree diameter and stand density (Reineke 1933) that differs from BA in that each DBH measurement is raised to 1.6 prior to summation rather than squared as for BA (Shaw 2000). Studies have indicated that SDI may be a better predictor of relative density, the amount of crowding in a stand, than BA (Jack and Long 1996).

Trends between uptake and its components with elevation or aspect were examined using general linear models (GLM), using three elevation classes (low, 1705–1768 m; medium, 1798–1828 m; high, 1859–1920 m) and four aspects (NE, E, SE, S). To determine if a relationship existed between N uptake and net or gross forest growth, a simple REG procedure was performed. To determine if soil N up-

Table 1. Live aboveground overstory N content (kg·ha⁻¹) in southern Appalachian spruce–fir forests.

Species	Foliage	Live branch	Dead branch	Bark	Bole	Total
Fir						
1993, live ^a	2.4	3.4	0.2	1.4	0.4	7.8
1998, live ^a	4.7	6.5	0.37	2.8	0.86	15.2
1998, dead ^{a,b}	0.2	0.3	0.03	0.1	0.04	0.7
1998, total ^a	4.9	6.8	0.4	2.9	0.9	15.9
Pauley et al. 1996 ^c	3.5	1.7	—	—	1.3	6.5
IFS Becking ^d	—	—	—	—	—	2.2
Spruce						
1993, live ^a	167.5	65.5	11.1	43.7	31.4	319.2
1998, live ^a	156.5	61.7	10.4	40.7	29.4	299.0
1998, dead ^{a,b}	22.5	8.3	1.5	6.1	4.3	42.4
1998, total ^a	179.0	70.0	11.9	46.8	33.7	341.4
Pauley et al. 1996 ^c	140.1	37.5	—	—	89.4	266.9
IFS Tower ^d	75	38	—	—	115	229
IFS Becking ^d	80	32	—	—	125	237
Birch						
1993, live ^a	12.4	21.9	0.6	61.7	14.0	110.6
1998, live ^a	13.0	22.9	0.6	65.5	14.8	117.0
1998, dead ^{a,b}	0.4	0.7	0.1	1	0.3	2.4
1998, total ^a	13.4	23.6	0.7	66.5	15.1	119.4
Pauley et al. 1996 ^c	15.1	14.4	—	—	72.3	101.8
IFS Tower ^d	44	17	—	—	39	100
IFS Becking ^d	—	—	—	—	—	<2

^aThis study.^bRefers to N sequestered in trees that died since 1993 survey.^cPauley et al. (1996) used N tissue concentrations from IFS.^dJohnson et al. (1991).

take could be predicted by stand or landscape characteristics, multiple regression analysis was used. First, the RSQUARE multiple regression procedure, looking at all possible regressions, was performed. After ranking every combination of variables, from one to m for m number of independent variables; the best model was determined by the highest adjusted and Mallows's $C(p)$ value that most closely approximated p , i.e., the number of variables in the model plus 1 (Hamilton 1992). After the best number and combination of variables was selected, the REG procedure was used to create a regression model and determine coefficients for the model variables (SAS Institute Inc. 1998).

Kriged surfaces of overstory N uptake, based on selected calculation methods, were generated using SURFER version 7.0 (Golden Software 1999). Nondirectionally biased exponential variogram models that incorporated a nugget effect, which includes the spatial variability that occurs at a distance closer than the 50 permanent sample plots, provided the interpolation weights that were applied in the calculation of the kriged surfaces.

Results and discussion

Aboveground biomass and N increment

Live aboveground overstory N content for NDW was 438 kg·ha⁻¹ in 1993 and declined to 431 kg·ha⁻¹ in 1998 (Table 1). While this would suggest little or no N sequestration, it should be noted that the forest experienced severe mortality during that period. More than 10% of the 1993 live overstory N pool (46 kg·ha⁻¹) was contained in trees that subsequently died (Table 1) and, therefore, were not counted

in the 1998 live tree inventory. Including this overstory N pool, the total amount of N sequestered in aboveground overstory biomass increased to 477 kg·ha⁻¹ in 1998, corresponding to a mean annual N increment in aboveground woody and foliar tissues of 7.8 kg·ha⁻¹·year⁻¹ in that 5-year period. On average, spruce accounted for 60% of the total N increment, while fir and birch each accounted for about 20% of the increment. Increase in foliage accounted for 40% of the total aboveground biomass N increment, with spruce accounting for the majority (77%) of the foliar N increment. The mean woody N increment value from this study, 4.8 kg·ha⁻¹·year⁻¹ (Table 2), was considerably larger than that reported for the IFS Tower site, 0.5 kg·ha⁻¹·year⁻¹, based solely on red spruce (Johnson et al. 1991).

There may be some inaccuracies in our estimation of biomass and, therefore, of N increment. A comparison of DBH–height relations in the Black Mountains and MRNRA (Nicholas 1992) versus the GSMNP indicated that for a given diameter, trees at NDW were shorter than those in other SA spruce–fir forests (Fig. 2). Thus, tree biomass, based on available allometric equations (Nicholas 1992), may have been somewhat overestimated. However, discrepancies in DBH–height relationships between the two areas were least pronounced for spruce, the greatest component in our biomass estimates. Since the actual 1993 DBH of ingrowth trees (trees with DBH < 5 cm in 1993) was not known, but set at zero, biomass increment associated with ingrowth was likely overestimated. Conversely, many trees that died between 1993 and 1998 may have accrued some biomass during that period, but since no growth was assigned, N sequestration in those trees may have been under-

Table 2. Annual N increment in aboveground biomass (including dead stems) between 1993 and 1998 ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$).

Species	Foliage	Branch	Bark	Bole	Total woody	Total
Fir	0.5 (0.8)	0.7 (1.1)	0.3 (0.4)	0.1 (0.2)	1.1 (1.6)	1.6 (2.5)
Spruce	2.3 (1.1)	1.1 (0.6)	0.6 (0.3)	0.5 (0.3)	2.2 (0.3)	4.5 (2.2)
Birch	0.2 (0.2)	0.3 (0.3)	1.0 (1.4)	0.2 (0.3)	1.5 (2.0)	1.7 (2.1)
Total	3.0 (1.2)	2.1 (1.0)	1.9 (1.3)	0.8 (0.3)	4.8 (2.0)	7.8 (2.8)

Note: Values are means with SDs given in parentheses.

Fig. 2. Height–DBH relationship for the NDW overstory trees: (a) Fraser fir; (b) yellow birch; (c) red spruce. The triangles are the actual tree measurements, the broken line is the DBH–height regression for NDW, and the solid line is the DBH–height regression developed by Nicholas (1992) for the Black Mountains, North Carolina, and Mount Rogers National Recreation Area, Virginia.

estimated. Although several factors could have influenced the accuracy of our biomass estimates, the calculated aboveground N content was close to the worldwide mean for temperate coniferous forests ($479 \pm 221 \text{ kg}\cdot\text{ha}^{-1}$ (mean $\pm$ SD); Cole and Rapp 1981) and was in line with the range of values ($361\text{--}518 \text{ kg}\cdot\text{ha}^{-1}$) reported in Johnson et al. (1991), using allometric equations from North Carolina spruce–fir forests.

Nitrogen return fluxes

Total litterfall mass averaged $3471 \pm 280 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ and consisted, on average, of 40% needles, 20% deciduous foliage, and the remaining 40% of a combination of twigs, bark, and reproductive tissues. Mean annual litterfall N flux for the entire watershed was $36 \pm 3 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ but showed considerable spatial variation among plots and among elevations. The mean total litterfall biomass fell within the range of values reported by Weaver (1972) for the Balsam Mountains, North Carolina ($3400 \pm 800 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$). Mean needle biomass and N return, 1322 and $10 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, respectively, closely matched those reported by Johnson et al. (1991), $1200 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ for needle biomass and $7 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ for N return. Deciduous foliage accounted for a disproportionately higher N flux (20% of biomass vs. 30% of N flux).

The calculated throughfall N return averaged across all plots was $32 \pm 9 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, with a minimum of $17 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ and a maximum of $63 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ (Table 3). It did not follow a distinct nor consistent pattern with elevation, contrary to earlier observations by Shubzda et al. (1995) and Lindberg and Owens (1993) who measured higher throughfall N fluxes at 1720 m compared with 1940 m at NDW. There was also considerable temporal variation; individual plot-level throughfall estimates for 1999 were not correlated with the 1998 estimates, even though the mean, standard deviation, and range of throughfall N values for the entire NDW were almost identical among measurement years. Our throughfall N flux was on the high end of values reported earlier for the region: between 15 and $35 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ using the same methodology (Sasser and Binkley 1989; Strader et al. 1989) or $24 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ from actual throughfall collections over a 3-year period (Johnson et al. 1991). There is some uncertainty associated with our throughfall N flux estimates in that they were derived from $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ adsorbed to exchange resins over a 10-week period in 1998 and in 1999 and were then extrapolated to a mean annual N flux using reported relationships between summer and yearly throughfall N (Strader et al. 1989).

The mean NCE for NDW was positive but low ($2 \pm 10 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) (Table 3), which was not that dissimilar from the IFS results, where N deposition and N throughfall fluxes were also quite close, resulting in an estimated mean foliar N uptake of $3 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ (Johnson et al. 1991). We found an almost even distribution among plots with net foliar N leaching ($n = 27$) ranging from 1 to $36 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, mainly in the lower part of the catchments; and plots exhibiting foliar N uptake ($n = 23$) in the order of $1\text{--}18 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, mostly at the higher elevations. Shubzda et al. (1995) also reported higher foliar N uptake with in-

Table 3. Nitrogen flux components ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) used in soil uptake equations.

Component	Mean (SD)	Minimum	Maximum
Woody N increment	5 (2)	2	10
Foliar N increment	3 (1)	1	6
Total aboveground litterfall N return	36 (3)	30	40
Leaf litterfall N return	20 (2)	15	25
Belowground litterfall N return	29 ^a		
N throughfall	32 (9)	17	63
N deposition ^b		27	35
Net canopy exchange ^c	2 (10)	-18	36

^aDuvigneaud and Kestemont (1977, as cited in Vogt et al. 1986).^bShubzda et al. (1995).^cNet canopy exchange (NCE) < 0, foliar uptake; NCE > 0, foliar leaching.

creasing elevation. Foliar N uptake, however, is strongly driven by N deposition estimates (Johnson and Lindberg 1992; Lovett and Lindberg 1993). Thus, the distinction in NCE pattern between the upper and lower catchment may simply reflect our deposition assumptions, since throughfall N fluxes followed no apparent trend with elevation, and only two discrete N deposition values were used ($27 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ <1800 m and $35 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ >1800 m), derived from Shubzda et al. (1995). While they represent the best available data for NDW, there is some uncertainty associated with this approach, as other studies have shown that N deposition can vary with elevation, stand structure, and especially with the presence of forest edges (Lovett and Kinsman 1990; Emmett et al. 1993; Lindberg and Owens 1993). Also, annual N deposition estimates were obtained in different years (1986–1989 and 1993–1994; Shubzda et al. 1995) from the throughfall estimates (1998 and 1999).

The mean value and range of all N fluxes used in the various soil uptake equations is given in Table 3. None of the fluxes was strongly correlated with elevation, and they each exhibited different spatial patterns in the watershed. The kriged surface of annual N sequestration in wood and foliage increment (U_2), for example, had peaks distributed throughout the watershed (Fig. 3), while litterfall N fluxes were lowest in the high-elevation plots (data not shown). Belowground litterfall N flux was not measured directly in this study nor were any data available for the SA spruce–fir in general. The literature value of $29 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ for Norway spruce (Duvigneaud and Kestemont 1977; as cited in Vogt et al. 1986) was only slightly below the measured aboveground litterfall N flux ($36 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$). This consistency with the 1:1 relationship between fine root turnover and leaf litterfall noted by Nadelhoffer et al. (1995), and the lack of a clear spatial trend in litterfall N return would suggest that this was not an unreasonable estimate to apply to the entire catchment.

While N sequestration in wood was by far the smallest among the fluxes, the amount of N returned annually to the forest floor via litterfall was, on average, four times the N incorporated in new tissue growth and represented the continuously cycling part of overstory N uptake. The restitution

Fig. 3. Kriged surface showing spatial pattern of N increment ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) in woody and foliar biomass increment (U_2) across the NDW.

flux increased even more when belowground dynamics were also considered. Consequently, the way overstory N uptake for a given ecosystem is calculated and interpreted may vary significantly and may be dictated by specific ecological questions (e.g., N biogeochemistry, N availability, retention of anthropogenic N addition).

Comparison of calculation methods

The amount of N taken up from the soil varied throughout the watershed, and calculation method influenced the magnitude of that variability (Table 4). There was a two- to five-fold difference between minimum and maximum values in NDW within a given method, with coefficients of variation (CV) ranging from <10 to 45% (Table 4). The largest difference between minimum and maximum and the greatest CV were observed for equation U_5 . Soil N uptake estimates including belowground N return (eqs. U_6 and U_7) generally had a smaller range and lower CV, because of the inclusion of a large uniform flux ($29 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) in all plots. Differences between calculation methods, however, were considerably larger than the variation within each calculation method.

The most basic uptake equation, U_1 , considering only N sequestered in woody biomass increment, yielded the lowest soil N uptake estimate, $5 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, ranging from 2 to $10 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$. Our estimates were within the range of values reported in Johnson and Lindberg (1992) ($1\text{--}7 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) but below the $11 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ calculated for a spruce–fir site on Whiteface Mountain in the northern Appalachians (Friedland et al. 1991). Comparison with worldwide means for temperate coniferous forests, $12\text{--}15 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ (Cole and Rapp 1981), further substantiated that the forest at NDW was slow growing. Spruce contributed approximately 50% to woody N increment, while fir and birch contributed 20 and 30%, respectively. Branch and bark increment both contributed about 40% each to the total; birch accounted for the greatest bark N increment. Ascribing aboveground N increment solely to N sequestered in wood is appropriate for forests that have reached a steady state in canopy biomass. However, in forests like the SA spruce–fir, which are undergoing a new disturbance regime, the amount

Table 4. Soil N uptake estimates ($\text{kg N}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) derived from various equations for Noland Divide Watershed.

	U_1^a	U_2^b	U_3^c	U_4^d	U_5^e	U_6^f	U_7^g
Mean (SD) uptake	5 (2)	8 (3)	44 (4)	45 (11)	26 (12)	73 (4)	74 (11)
Coefficient of variation (%)	41	35	9	25	45	6	15
Maximum	10	13	50	85	66	79	114
Minimum	2	3	34	20	3	63	49

^a U_1 = woody increment_(aboveground).^b U_2 = woody increment_(aboveground) + foliage increment.^c U_3 = woody increment_(aboveground) + foliage increment + total litterfall_(aboveground).^d U_4 = woody increment_(aboveground) + foliage increment + total litterfall_(aboveground) + NCE.^e U_5 = woody increment_(aboveground) + leaf litterfall + NCE (this is similar to the equation used at the IFS Tower site, although Johnson and Lindberg (1992) included stemflow in net throughfall and used only needle litterfall).^f U_6 = woody increment_(aboveground) + foliage increment + total litterfall_(aboveground) + belowground litterfall.^g U_7 = woody increment_(aboveground) + foliage increment + total litterfall_(aboveground) + belowground litterfall + NCE.

of N allocated towards the expansion of foliage must also be considered in addition to woody increment (Table 4, eq. U_2). Adding net annual foliage increment increased mean soil N uptake for NDW by 60% ($8 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$), while variability remained similar (CV 35%), with a fourfold difference between the low ($3 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) and high estimates ($13 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$).

Including aboveground litterfall (U_3) increased mean N uptake more than fivefold ($44 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) compared with N uptake based on biomass increment only (U_2) but considerably reduced spatial variability across the watershed (CV 9%). Traditionally, only N return with foliage litterfall (leaves and needles) is included in uptake calculations (Bockheim and Leide 1990). In our study, needle and leaf litterfall accounted for a little over half of the mean total litterfall N return, at $10 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ each. Thus, limiting N return to foliage litter would have reduced the mean N uptake estimate from 44 to $27 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$. Since most nonfoliage constituents (i.e., reproductive tissues, twigs, etc.) were not included in our biomass increments, the N demands associated with this biomass production needed to be included somewhere in our calculations. Therefore, all litterfall components were included in U_3 , U_4 , U_6 , and U_7 . In U_5 , which was fashioned after Johnson et al. (1991) and derived for comparative purposes, only foliar litterfall was included.

While the mean soil N uptake for NDW was not greatly altered by the inclusion of NCE in this study ($45 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ for U_4 vs. $44 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ for U_3), within-catchment variability increased significantly (from CV 9 to 25%, Table 4), reflecting the occurrence of either foliar N leaching or foliar N uptake in NDW (Table 3). Based on our best estimates of N deposition and N throughfall in NDW, foliar uptake occurred in about 45% of the plots, accounting for 2–44% of N needed for tissue increment and litterfall N return. Earlier soil uptake calculations (e.g., Cole and Rapp 1981) recognized only the need to account for nutrient return via canopy leaching as an additive factor in the uptake calculations. However, recent improvements in atmospheric input assessments have suggested considerable canopy N uptake in many forests (Johnson and Lindberg 1992; Lovett and Lindberg 1993), reducing the ecosystem's reliance on N derived from the mineral soil. Johnson et al. (1991) further demonstrated that the type of deposition estimate (bulk vs. wet + dry) could cause a two- to four-fold difference in calculated total and soil N uptake, respectively. The mean total

Fig. 4. Kriged surface showing spatial pattern of calculated total N uptake ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) based on soil uptake using U_4 and foliar uptake in the NDW.

N uptake (soil uptake U_4 + foliar N uptake) for NDW was $49 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, ranging from 34 to $85 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$. This was in line with a mean N uptake of $48 \pm 17 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ in temperate coniferous forests reported by Cole and Rapp (1981) and $40 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ for cold temperate coniferous forests reported by Aber and Melillo (1991). Total N uptake was highest in the lower catchment and appeared to decline with elevation, although the elevational pattern was not very strong ($r^2 = 0.14$) (Fig. 4).

A more conservative variant of the above calculation, eq. U_5 , considered only woody N increment and only foliage litterfall N return, while still considering the impact of NCE. The catchment mean, $26 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, was about 60% of the mean for equation U_4 , and ranged from 3 to $66 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$. Our estimate was considerably larger than the values obtained at nearby spruce–fir sites in the GSMNP using the same calculation method. Johnson et al. (1991) calculated a mean soil N uptake of $4 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$; while a later paper reported values between -9 and $9 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ at the two nearby IFS Tower plots and around $3.5 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ at the Becking site, a more distant location from the NDW (Johnson and Lindberg 1992). These differences possibly reflect forest structure and growth differences with location and elevation. Total N uptake based on U_5 plus foliar uptake, averaged $29 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ and ranged from 17 to $66 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$.

Equations U_6 and U_7 (mean 73 and 74 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, respectively) illustrated how the inclusion of belowground litterfall N return further increased uptake estimates by 65% relative to the corresponding eqs. U_3 and U_4 . As indicated earlier, there is some uncertainty associated with applying belowground litterfall values from another related species. While this estimate may be reasonable, the true importance of roots in N cycling and retention in this ecosystem remains largely unknown.

Relationship between N uptake and stand and landscape characteristics

The complexity of the equations used to calculate soil uptake increases from U_1 to U_7 , as does the potential error, resulting from uncertainty in the estimation of the contributing factors. Because belowground litterfall N flux estimates used in eqs. U_6 and U_7 were derived from outside the NDW, eqs. U_1 , U_2 , and U_5 did not incorporate all components considered important in estimating uptake; eqs. U_4 and U_5 included the NCE, which had the greatest uncertainty; soil N uptake based on eq. U_3 (Fig. 5) was considered most reliable and robust. Therefore, U_3 was used to examine the relationship between soil N uptake and growth, stand characteristics, and landscape features in the NDW. The results from individual correlations and multiple regression analysis consistently pointed at stand-related parameters rather than landscape features as significant drivers of N uptake.

Soil N uptake was most strongly correlated with total SDI ($r = 0.54$, $p < 0.0001$). It also showed significant correlations with the proportion of live to total BA ($r = 0.53$, $p < 0.0001$), SDI of birch ($r = 0.41$, $p = 0.0032$), and the proportion of live spruce BA to total BA ($r = 0.36$, $p = 0.0093$). Uptake was negatively correlated with the proportion of total BA as standing dead fir ($r = -0.52$, $p < 0.0001$). The observation that N uptake was positively correlated with measures of live overstory biomass was logical as that is typically the location for growth and associated N sequestration. Also, N sequestration in biomass increment, a small subcomponent of N uptake ($<20\%$ of U_3), and BA and SDI were ultimately derived from the same DBH measurements. The strong correlation with relative BA of spruce likely reflected the dominance of this species in the live overstory. The correlation with birch SDI was interesting in that birch accounted for only a relatively small proportion of total overstory biomass. This may be due to the deciduous nature and high N content of birch foliage (two times greater than fir or spruce needles) and their influence on N uptake flux. The negative correlation with dead fir was consistent with stand dynamics, as lower overstory N demands would be expected in areas with high fir mortality. There were no correlations between uptake and either aspect or elevation. Although the relative abundance of the three overstory species varied with elevation in NDW (Pauley et al. 1996), this was insufficient to cause a strong elevational trend in N uptake. Regression analysis further indicated the lack of a significant relationship between N uptake and net growth ($r^2 = 0.06$, $p = 0.09$). However, N uptake was significantly correlated with gross growth ($r^2 = 0.67$, $p < 0.0001$), which accounted for increases in total standing (dead + live) overstory biomass, and was more appropriate for ecosystems undergoing significant forest structure changes due to mortality.

Fig. 5. Kriged surface showing spatial variation in overstory N uptake ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) across the NDW using U_3 .

We also examined the influence of landscape and stand characteristics on the individual components of equation U_3 . Total N sequestration in wood and foliage biomass increment were significantly correlated with SDI of fir ($r = 0.38$, $p = 0.007$), the proportion of live fir BA ($r = 0.33$, $p = 0.02$), and total SDI ($r = 0.31$, $p = 0.04$). While the positive correlation with total SDI was logical, the correlation with measures of live fir abundance was unexpected, given the generally small contribution of fir to total live standing biomass. It may reflect accelerated growth and N uptake in the remaining live fir trees following canopy opening. Net N increment did not show any strong elevational pattern and did not differ significantly with aspect. Litterfall N flux was most strongly and positively correlated with total SDI ($r = 0.86$, $p < 0.0001$), was positively correlated with SDI of spruce ($r = 0.69$, $p < 0.0001$), and was negatively correlated with relative BA of dead fir ($r = -0.63$, $p < 0.0001$). Weaker correlations existed with the proportion of live to total BA ($r = 0.54$, $p < 0.0001$), the relative proportion of live spruce BA ($r = 0.51$, $p = 0.0001$), and the relative proportion of live fir BA ($r = -0.32$, $p = 0.02$). Again, the positive correlations with measures of live overstory biomass and the negative correlation with dead fir were reasonable, given that live overstory trees were the source of litterfall input, and LAI was directly correlated with LBA. Aspect did not influence litterfall N. The latter was negatively correlated with elevation, although only weakly and not significantly at an $\alpha = 0.05$ level ($r = -0.27$, $p = 0.054$). Results from the GLM analysis indicated significantly lower litterfall N return at the higher elevations compared with low and medium elevations, consistent with the lower abundance of live biomass in the upper catchment (Pauley et al. 1996). A negative correlation between litterfall N and live fir may be spurious, simply reflecting the co-occurrence of an increase in live fire abundance with an overall decline in total live biomass at higher elevation.

To assess which combination of stand and landscape descriptors best predicted soil N uptake, two separate multiple regression analyses were performed, each using the RSQUARE and REG procedure (SAS Institute Inc. 1998). In the first analysis, which simultaneously considered seven

Table 5. Regression equations using (A) basal area proportions or (B) stand density index (SDI) to predict N uptake using equation U_3 .(A) U_3 versus basal area ($r^2 = 0.49$)

	Intercept	Proportion of basal area as					
		Live spruce	Dead spruce	Live fir	Dead fir	Live birch	Dead birch
Coefficient	236.2	-188.2	-196.2	-174.3	-207.9	-190.6	-208.9
Significance	0.0026	0.0147	0.0112	0.0274	0.0070	0.0138	0.0078

(B) U_3 versus SDI ($r^2 = 0.60$).

	Intercept	Spruce SDI	Fir SDI	Birch SDI
Coefficient	31.59	0.0177	0.0301	0.0216
Significance	<0.0001	<0.0001	0.0001	<0.0001

BA variables (proportions of live trees, and live and dead spruce, fir, and birch components) in addition to elevation and aspect, the model with the highest adjusted r^2 (0.49) included six variables: the proportion of BA as live and dead spruce, fir, and birch. The second analysis used four SDI parameters for stand structure (total SDI, spruce SDI, fir SDI, and birch SDI) in addition to elevation and aspect, and the model with the highest adjusted r^2 (0.60) included metrics for each overstory species. There was some collinearity among the variables, but both models and all the individual coefficients were statistically significant (Table 5). The models consistently showed (i) the influence of the biomass of all three overstory species on aboveground N uptake and (ii) the lack of correlation with either aspect or elevation. Thus, at NDW, parameters describing stand structure appeared better predictors of N uptake than landscape characteristics.

Conclusions

Our study clearly demonstrates that caution should be exercised when applying plot-level growth and uptake values to a forest at large, especially when that ecosystem is or has been undergoing drastic structural changes, as is the case with the SA spruce–fir forest. Even at a small scale (17 ha) we noted a 2- to 5-fold difference (in one case more than 20-fold) between the minimum and maximum overstory N uptake value within a given calculation method. Spatial variation in N uptake in this study was most strongly correlated with measures of stand structure, rather than landscape parameters such as elevation or aspect. While elevation proved a poor quantitative predictor of overstory N uptake in this catchment, overstory species composition and live biomass, important drivers of N uptake, varied with elevation in SA spruce–fir forests (Nicholas et al. 1992; Pauley et al. 1996). Also, certain N fluxes used in calculating N uptake (e.g., litterfall, NCE) appeared to be influenced by elevation, albeit not always at statistically significant levels. Hence, for high-elevation spruce–fir forests outside the NDW and the GSMNP, elevation should not be ignored in future analyses, as it may still be a reasonable driver of overstory N uptake.

It should also be noted that while BA and SDI are indicators of forest structure and canopy density, they provide limited information on developmental stage or stand vigor (and, therefore, total ecosystem N uptake potential) other than through stem size distribution. An even greater source of variability in forest N uptake potential may be associated with understory dynamics, which was not specifically ad-

dressed in this study. At NDW, natural stand dynamics, the balsam woolly adelgid infestation, and windthrows have created considerable heterogeneity in overstory canopy cover as well as in understory and regeneration density. Thus, a potentially important ecosystem N uptake mechanism and its spatial variability currently remain unaccounted for.

Finally, our study has important implications for the interpretation of the ecosystem N sink strength. There was an almost 15-fold difference in mean N uptake values from the simplest (U_1) to the most comprehensive (U_7) equation, much larger than the two- to three-fold difference among calculation methods reported by Bockheim and Leide (1990). On average, only 5 kg·ha⁻¹ of N were sequestered annually in woody biomass at NDW. Even including the additional 3 kg·ha⁻¹·year⁻¹ used towards an increase in canopy foliage, this N uptake potential remained fairly small (~25%) compared with annual N inputs from the atmosphere. The amount of N returned in aboveground litterfall, which constituted a significant portion of annual tree uptake, averaged 36 kg·ha⁻¹·year⁻¹. This N flux approximately doubled if root turnover was also considered. Only N incorporated into perennial (woody) tissue represents long-term sink of N. Foliar increment and litterfall (above- and below-ground), the dominant and biogeochemically active component of soil N uptake, does not represent long-term N storage but plays an important role in site N availability. Deciduous leaves are only retained for a single growing season, needles up to several years, after which they return to the forest floor, and N is released again during microbial decomposition. While the mean residence time of this N pool is not known, it is doubtful that it would be much longer than 10 years and certainly significantly shorter than that of dead wood. The turnover of this detrital N pool is critical to N availability, and N cycling in general.

The choice of the calculation method and the interpretation of overstory N uptake fluxes will depend on context and intended use of the information. Where site productivity and N availability is of interest, the more complete N uptake formulas may be more appropriate to evaluate annual overstory N demands and growth potential relative to the N supplying capacity soils. On the other hand, when assessing ecosystem N retention capacity relative to anthropogenic inputs, a more conservative approach may be more appropriate. Indeed, overstory N uptake in NDW using equation U_3 (34–50 kg·ha⁻¹·year⁻¹) was equal to or even greater than the atmospheric deposition N flux in the NDW (27–35 kg·ha⁻¹·year⁻¹). However, less than 10% of this N was sequestered in long-term storage (wood), while the majority

actively cycled through the system, representing at best a temporary storage of this N. Our study suggests that despite spatial differences in forest structure, the overstory component of the high-elevation spruce–fir forest in the SA plays a limited role in the retention of current atmospheric N loads.

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