# N STORAGE AND CYCLING IN VEGETATION OF A FORESTED WETLAND: IMPLICATIONS FOR WATERSHED N PROCESSING

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**Abstract.** Pools and fluxes of N in wetland vegetation and soils were compared with an adjacent upland site to assess the relative importance of wetland versus upland landscapes in watershed N-retention in the Adirondack Mountains of New York (U.S.A.). The majority of N storage occurred in forest soils and wetland peat deposits (96 and 99% of total N in upland forests and wetlands, respectively). Annual N-uptake (49 kg N ha$^{-1}$ yr$^{-1}$) was greater for wetland vegetation than that of upland vegetation (30 kg N ha$^{-1}$ yr$^{-1}$). In the wetland the supply of N from mineralization (36 kg N ha$^{-1}$ yr$^{-1}$) was less than N-uptake; in contrast, upland N mineralization (76 kg N ha$^{-1}$ yr$^{-1}$) exceeded N vegetation uptake. Annual N-storage in peat was small due to low peat accretion rates. Wetlands acted as a sink for N and stored a disproportionally high fraction (15%) of catchment N in relation to their relatively small surface area ($\sim$4%) within the catchment.

**Keywords:** nitrogen, watershed, wetlands

## 1. Introduction

Landscapes are complex systems differing in floristic composition and processes that regulate the availability and loss of N (Vitousek *et al.*, 1982). Recent studies have quantified N-cycling and drainage water NO$_3^-$ losses in northern temperate watersheds (Mitchell *et al.*, 1992a, b, 1996a, b; Friedland *et al.*, 1991), but the role of wetlands within these watersheds has received less attention. Wetlands may play an important role in N retention or less by (1) being focal points for denitrification; (2) affecting the transformation of N solutes between inorganic and organic fractions (NO$_3^-$, NH$_4^+$, and dissolved organic nitrogen (DON)) and (3) being a net sink or source of N due to vegetation uptake and organic matter accumulation or loss. Moreover, riparian wetlands, due to their high plant production and saturated organic soils, may have a greater impact on concentrations and species of N in surface waters compared to drier, upland areas (Cirmo and McDonnell, 1997).

Riparian wetlands that border agricultural lands have been shown to retain 90 to 100% of NO$_3^-$ inputs (Cooper, 1990; Lowrance *et al.*, 1983, 1984), while Precambrian shield wetlands in Canada that occupied bedrock depressions retained <50%

of $NO_3^-$ inputs (Devito *et al*., 1989). For example, a headwater riparian wetland in Ontario, Canada dominated by groundwater input retained only 26% of $NO_3^-$ (Hill, 1991, 1996). For a forested bog in Minnesota, U.S.A., Urban and Eisenreich (1988) reported 65% retention of atmospheric N but this estimate decreased to 46% with the inclusion of hillslope-derived N.

The Adirondack mountain region in upstate New York includes the headwaters for several major river basins such as the Mohawk-Hudson and St. Lawrence. This region is characterized by glacially-influenced topography resulting in blocked drainages due to the deposition of till and glacial outwash material. These geo-morphologic conditions results in numerous wetlands throughout the Adirondack region. The Adirondack Ecological Zone contains approximately 40 000 iden-tified wetlands of $\geq 0.24$ ha in size and nearly 15% of the Adirondack Park is comprised of wetlands of $\geq 0.24$ ha in size (Curran *et al*., 1989). Many of these wetlands are located along stream edges or littoral zones of lakes and likely im-pact the hydrology and water quality of surface waters (Creed *et al*., 1996) of the Adirondacks.

The objectives of this study were: (1) to quantify the pools and fluxes of N in wetland vegetation and soil, (2) to compare N-cycling in wetland vegetation to upland vegetation in the Archer Creek subcatchment and (3) to assess the relative roles of wetland and upland vegetation in watershed level N-retention. To quantify N cycling and storage, we measured wetland plant production and plant tissue N concentrations; part deposits and peat N content; and litterfall and litter N content. This information was combined with concurrents studies on N mineralization and nitrification (Ohrui *et al*., 1999) and solute mass balances (McHale *et al*., 2000) at the same study site and results compared to previous studies (e.g., Johnson and Lindberg, 1992; Mitchell *et al*., 1992a) of an adjacent upland forest.

## 2. Methods

### 2.1. SITE DESCRIPTION

Studies were conducted in the Arbutus Lake Watershed at the Huntington Forest (HF) of the State University of New York, College of Environmental Science and Forestry (SUNY-ESF) in the central region of the Adirondack Mountains of New York (43°59′N, 73°15′W) and located within the Mohawk-Hudson River drainage basin. The HF has a 50-year history of ecological research which has included intensive studies of the biogeochemistry of its upland and aquatic systems (Driscoll and van Dreason, 1993; Mitchell *et al*., 1992a, b). An upland northern hardwood site adjacent to the Arbutus Watershed was one of the sites used for the Integrated Forest Study (IFS; Johnson and Lindberg, 1992; Mitchell *et al*., 1992a, b) and the Adirondack manipulation and Modeling Project (AMMP; Mitchell *et al*., 1994, 1998). Results from these previous studies of upland forest were utilized in our

study for comparing N storage and cycling in adjacent wetland and upland zones in the Arbutus watershed.

Mean annual temperature from 1951 to 1990 was 4.4 °C, with a dormant season mean of –2.8 °C and a growing season mean of 14.3 °C. Mean annual precipitation was 101 cm (Shepard *et al.*, 1989). Within the Huntington Forest are mixed northern hardwood forests dominated by American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.), and coniferous components of eastern hemlock (*Tsuga canadensis* (L.) Carr.), red spruce (*Picea rubens* Sarg.), and balsam fir (*Abies balsamea* (L.) Miller). Upland watershed soils are dominated by Beckett-Mundal series sandy loams which are <1 m in depth and contain primarily quartz, plagioclase, and K-Feldspar while wetlands are composed of Greenwood Mucky peats (Ohrui *et al.*, 1999). Surficial geology consists of glacial till less than 3 m in depth and is sandy and non-calcareous. Bedrock outcrops are common at the higher elevations with thin till and wet soils located around the lake fringe and in wetlands.

The Archer Creek catchment of the Arbutus Watershed has an area of 135 ha and is gauged for stream discharge near the lake inlet by an H-flume (McHale *et al.*, 2000). This catchment represents the major inflow of water (∼40%) to Arbutus Lake.

The wetland in our study is a palustrine peatland dissected by a stream and rivulet that runs from a hillslope (Figure 1). Site instrumentation for vegetation sampling consisted of 37 litter traps and eight vegetation plots. In 1996, only 33 litter traps were sampled due to loss of litter traps. A tree survey was completed for the entire wetland. Speckled Alder (*Alnus incana* ssp. *rugosa*) (Furlow, 1979) is often present in wetlands of the Adirondack region (Roy *et al.*, 1996; Karlin, 1975), and occurs in this wetland. Wetland soils consist of a mostly sapric peat with several coarse sand layers.

## 2.2. SAMPLING DESIGN

### 2.2.1. *Trees*
Tree species and DBH (diameter at breast height) were ascertained for each stem within the wetland. Biomass for the upland species was from a previously published study in the same watershed (Johnson and Lindberg, 1992). Above ground tree biomass (bole, branch, and foliar mass) was determined using allometric equations derived specifically for the site (alder, equations reported below) or using published equations for conifers and hardwoods of the northeast (American beech, red maple, Briggs *et al.*, 1989; sugarmaple, Briggs, 1985; Cunia and Briggs, 1985; yellow birch and red sprice, Young *et al.*, 1980). Woody tissue of each tree was sampled using a standard tree borer, air dried and stored for chemical analyses.
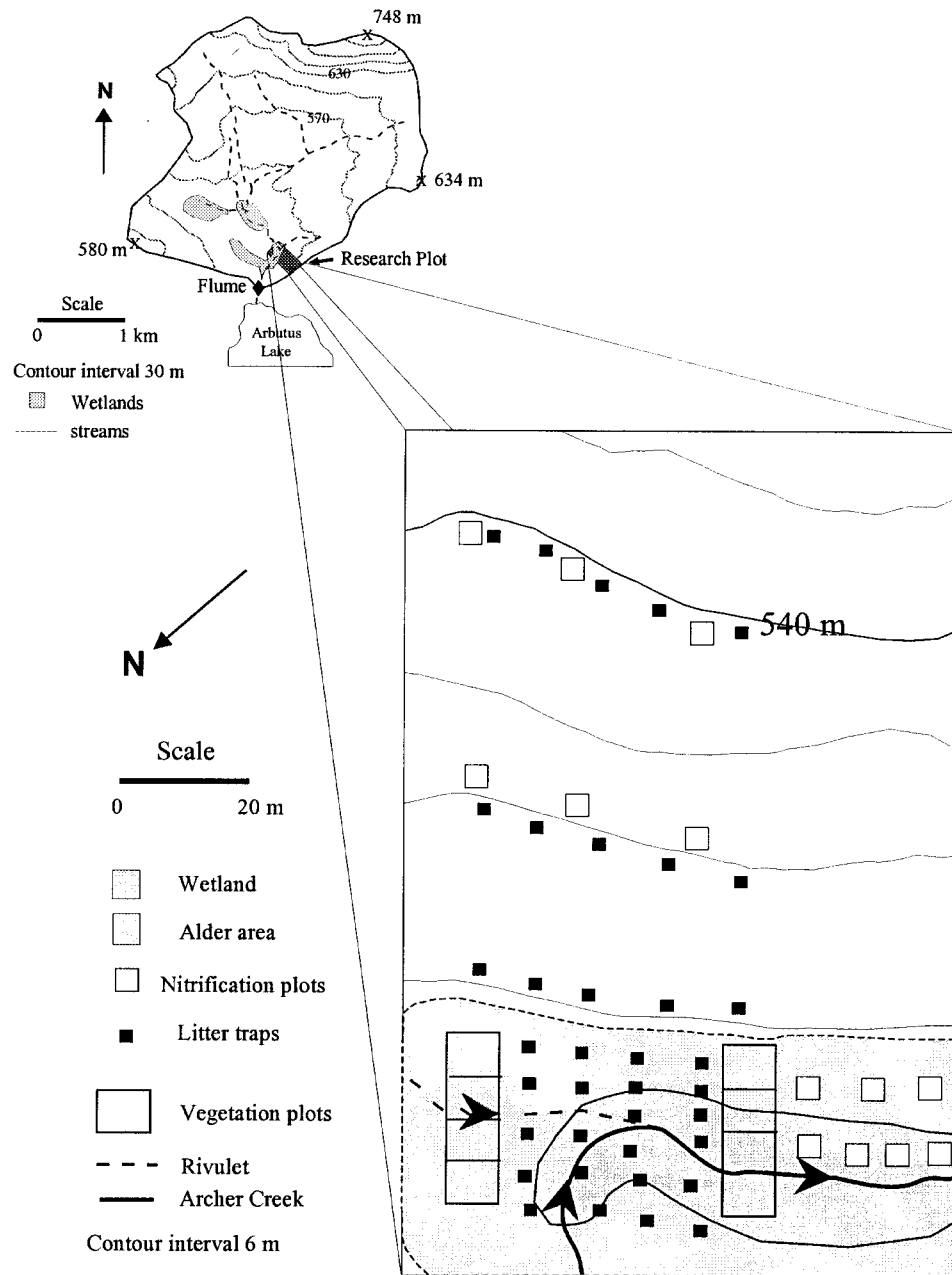
*Figure 1.* Map of sampling locations showing litter traps and plant collection plots at the intensive hillslope study site in the Archer Creek catchment at the Huntington Forest in the Adirondack Mountains of New York.

### 2.2.2. *Alder*

Alder (*Alnus incana*) biomass (bole and foliar mass) was determined using allometric equations derived from an alder stand in close proximity to the Arbutus watershed. To derive the equations, individual stems were measured for diameter (0.25 m from the base) and then cut down and foliage removed. The wood and foliage were dried at 65 °C for 48 hr and weighed. There was a strong relationship between diameter measurements (cm) at 0.25 m from the base of the alder and both foliar ($r^2 = 0.95$) and woody biomass ($r^2 = 0.98$). The biomass equations used for estimating alder biomass were:

$$\text{Foliar biomass (kg)} = e^{2.26452 \cdot (\ln(\text{diameter})) + 1.897697}$$

$$\text{Woody biomass (kg)} = e^{2.630247 \cdot (\ln(\text{diameter})) + 3.526704}$$

Biomass for the alder in the study wetland was determined from 19, 4-m$^2$ plots randomly placed throughout the alder stand. Diameter measurements at 0.25 m from the base of the stem were collected and biomass was determined from the allometric equations. Foliage was clipped from the branches and bole cores were collected in August of 1996 from five randomly selected plants in each of the 19, 4-m$^2$ plots and air fried.

### 2.2.3. *Herbaceous Vegetation*

Wetland herbaceous vegetation samples were collected in June, July, and August of 1995 and August of 1996. Aboveground herbaceous (non-woody) vegetation was clipped in eight plots (1-m$^2$) along two transects described as vegetation plots (Figure 1). A stratified random sample design was used in which the two vegetation transects were separated into four 36 m$^2$ plots from which one plot (1-m$^2$) was randomly selected in each year for sampling. The plots were stratified to account for vegetation gradients from the hillslope to the stream edge. Plants were separated by species, weighed, and air-dried. Taxonomy follows Gleason and Cronquist (1991) for all vegetation but *Alnus* which follows Furlow (1979).

### 2.2.4. *Litter*

Litter was collected using 0.25 m$^2$ litter traps with a screen bottom for both upland (N = 15) and wetland (N = 22 in 1995 and N = 18 in 1996) litter respectively. Litter was collected along thre transects of differing elevations on the hillslope plot (Figure 1). The transects represented three stand types: upland hardwood, upland conifer, and moist conifer (Ohrui *et al.*, 1999). Additional wetland litter was collected along four transects parallel to the hillslope moving from the base of the hillsplope to the stream. Litter was collected starting in September (1995 and 1996) through November after which all foliage had fallen from the deciduous trees. Litter samples were air-dried and separated into deciduous and coniferous components.

### 2.2.5.  *Peat Cores*

Six peat cores were collected along two transects using a Russian peat borer (Urso *et al.*, 1989). Peat cores were sectioned in the field, wrapped in cellophane and aluminum foil, and kept at 4 °C until processing. Peat cores were sectioned into 2 cm sections and processed as per plant samples. Carbon and N analysis was performed on a subsample of peat sections (N = 180; as described below).

### 2.2.6.  *Carbon and Nitrogen Determinations of Vegetation, Litter and Peat*

Prior to chemical analyses vegetation and peat samples were dried for 3–5 days at 55 °C, weighed, and ground (homogenized) in a Wiley mill. Carbon and nitrogen concentrations were determined from subsamples of the ground and homogenized vegetation, litter and peat samples using a Perkin-Elmer CHN®. Percentages of C and N were then multiplied by the dry mass of each respective plant species or peat core mass to obtain C and N contents per unit area.

### 2.2.7.  *N-Mineralization Rates*

N-mineralization rates were obtained from Ohrui *et al.* (1990). N-mineralization was estimated during the period of July 1995 to July 1996 and all mineralization plots were in the intensive hillslope and wetland areas. More detailed information of N-mineralization methods can be found in Ohrui *et al.* (1999).

### 2.2.8.  *Peat Accretion Rates*

Core samples were analyzed for $^{137}$Cs activity to estimate peat accretion rates. The depth of the maximum $^{137}$Cs corresponds with the period of maximum deposition of $^{137}$Cs from thermonuclear testing in 1964. Activity of $^{137}$Cs was measured for 8–24 hr using a high purity germanium gamma detector with a counting efficiency of 2%. Peat accretion rates were calculated using the depth of the $^{137}$Cs maximum as the marker for 1964 (i.e. a period of 24 yr). This technique has been successfully used to estimate peat accretion rates in the everglades (Craft and Richardson, 1993) and in estuarine marshes (Craft *et al.*, 1993). The top of the core was defined as the border between living and dead sphagnum. Living and dead sphagnum were differentiated by the color of the plant where green was considered living and white was considered dead.

### 2.2.9.  *Below Ground N-Pools*

Total peat volume was determined by a survey in which a metal rod was inserted at five meter intervals until it was stopped by till along transects located every 10 m within the wetland. The rod was inserted into the peat until reaching the peat-till interface which was identified when the rod met with substantial resistance and by the presence of sandy clay on the rod tip. Estimates of peat depth was also confirmed using ground penetrating radar (GPR). Estimates of peat volume were determined using the trapezoidal rule method where the volume was multiplied by the bulk density of the peat to obtain total peat mass. Regression analysis was

performed on each of the six peat cores to determine differences in N-storage with depth and there was a significant linear relationship found for most cores ($p < 0.05$; $r^2 = 0.18$ to $0.57$). The wetland was divided into three sections that represented the most marked differences in N content with depth. The mass of peat in each of the three sections was multiplied by its average N concentration to determine the total N mass.

### 2.2.10. *Above Ground Production*

Above ground production was estimated for each layer in the wetland (herbaceous, overstory). In the herbaceous layer, above ground production was the total biomass of the herbaceous plants assuming that all of the biomass sampled in that year was new production. In the overstory, woody production (bole increment) was not quantified since it has been shown to be only a small proportion of overall N demand on an annual basis in the upland sites of the HF ($<6\%$; Mitchell *et al.*, 1992a). Annual foliar production was assumed to equal litterfall flux and thus any loss from herbivory was not included.

Sphagnum biomass determinations present present unique difficulties since it is rather difficult to define the actively growing segment of the sphagnum plant and even more difficult to determine biomass added during any given growing season. Sphagnum plants were clipped at the base of the plant where there was separation from the green and white parts of the plant. The biomass sampled for any given year was the estimated new growth for the year, however, this is most likely an overestimate of sphagnum production.

### 2.2.11. *Nitrogen Uptake*

Nitrogen uptake is defined as the amount of N that has been assimilated into plant tissues. Nitrogen uptake in the wetland was estimated by summing N in understory vegetation at peak biomass and N in foliage litterfall (Grigal and Homan, 1994). This is the amount of annual N that is returned to the soil from the vegetation. This assumes that all of the N used in herbaceous production is new N and not from previously stored N as a result of translocation and root storage in previous years.

### 2.2.12. *Statistical Analyses*

Comparisons of biomass and nutrient concentrations among plant species were done using paired *t*-tests to detect differences in annual production and between sites. Litter data were analyzed using a two-way ANOVA with site (wetland vs. upland) and year as the factors.

TABLE I

Herbaceous vegetation composition, biomass, C:N ratios and total organic nitrogen (TON) in the Arbutus intensive wetland

| Taxon | Dry weight (kg ha$^{-1}$) | % of total biomass | C:N ratio 1995 | C:N ratio 1996 | TON (kg N) | % TON |
|---|---|---|---|---|---|---|
| *Sphagnum* spp. | 948 | 65 | 35 | 29 | 14.87 | 58.0 |
| *Osmunda cinnamomea* | 94 | 6.5 | 32 | 23 | 1.90 | 7.5 |
| *Poaceae* | 78 | 5.4 | 25 | 20 | 1.67 | 6.5 |
| *Rubus hispidus* | 74 | 5.1 | 28 | 27 | 1.42 | 5.6 |
| *Dennstaedtia punctilobula* | 70 | 4.8 | 34 | 26 | 1.35 | 5.2 |
| *Clematis virginiana* | 36 | 2.5 | 23 | 15 | 1.12 | 4.4 |
| *Onoclea sensibilis* | 33 | 2.3 | 29 | 23 | 0.66 | 2.2 |
| *Phegopteris connectilis* | 31 | 2.1 | 29 | 28 | 0.56 | 2.2 |
| *Tiarella cordifolia* | 22 | 1.5 | 26 | 23 | 0.47 | 1.8 |
| Other | 58 | <5 | | | 1.48 | 5.8 |
| Total | 1446 | 100 | | | 25.5 | 100 |

## 3. Results and Discussion

### 3.1. COMPOSITION AND BIOMASS IN THE WETLAND

Herbaceous biomass in the wetland was dominated by *Sphagnum* spp. (65% of herbaceous production), followed by *Osmunda cinnamomea* (6.5%), a variety of grasses (5.4%), *Rubus hispidus* (5.1%), *Dennstaedtia punctilobula* (4.8%), *Clematis virginiana* (2.5%), *Onoclea sensibilis* (2.3%), *Phegopteris connectilis* (2.1%), and 18 other species which collectively represented 6.3% of the total herbaceous production (Table I). No significant differences in total biomass (paired $t$-test; $p \geq 0.25$) or total N content (paired $t$-test; $p \geq 0.86$) of the herbaceous layer were observed between the two years. *Spagnum* spp. represented the largest amount of N storage in the herbaceous layer (14.87 kg N ha$^{-1}$). Overstory vegetation was dominated by *Picea* spp. (36% of overstory biomass) follow by *B. alleghaniensis* (35%), *Alnus incana* (19%) *A. rubrum* (9%), and 5 other species comprising <1% of overstory biomass (Table II). Despite accounting for only 19% of the overstory biomass, *Alnus incana* dominated the N-storage of the wetland overstory (41% of N in woody tissues and 23% of N in foliage).

TABLE II

Wetland overstory composition and biomass, C:N ratios, and total organic nitrogen (TON) in the Archer Creek hillslope-wetland study site

| Taxon | % of overstory production | Woody | | | Foliage | | |
|---|---|---|---|---|---|---|---|
| | | Dry weight (kg ha$^{-1}$) | C:N ratio | TON (kg N ha$^{-1}$) | Dry weight (kg N ha$^{-1}$ | C:N ratio | TON[a] (kg N ha$^{-1}$) |
| *Picea* spp. | 36 | 10068 | 624 | 15 | 1560 | – | 34 |
| *Betula alleghaniensis* | 35 | 9961 | 308 | 15 | 422 | – | 18 |
| *Alnus incana* | 19 | 5336 | 180 | 23 | 596 | 21 | 16 |
| *Acer rubrum* | 9 | 2642 | 557 | 2.6 | 41 | – | 0.88 |
| 4 other species | <1 | 274 | | 0.28 | 49 | – | 1.14 |

[a] Johnson and Lindberg, 1992.

TABLE III

Litterfall mass, carbon and nitrogen contents, and C:N ratios for the Archer Creek wetland and upland hillslope. Value are $\pm$ 1SE with replicates in parentheses

| | | Coniferous | | | | Deciduous | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Dry weight (kg ha$^{-1}$) | C (kg C ha$^{-1}$) | N (kg N ha$^{-1}$) | C:N Ratio | Dry weight (kg ha$^{-1}$) | C (kg C ha$^{-1}$) | N (kg N ha$^{-1}$) | C:N Ratio |
| Wetland totals | 1995 | 384±78 (22) | 207±42 (22) | 2.54±0.63 (22) | 102±11 (6) | 1245±143 (22) | 633±73 (22) | 16±2 (22) | 49±5 (6) |
| | 1996 | 409±71 (18) | 216±38 (18) | 3.70±0.63 (18) | 65±4 (6) | 1359±222 (18) | 688±112 (18) | 23±4 (18) | 37±2 (6) |
| Annual mean | | 397 | 212 | 3.12 | 84 | 1302 | 661 | 20 | 43 |
| Upland totals | 1995 | 520±95 (15) | 272±49 (15) | 5.09±0.96 (15) | 67±7 (3) | 1630±274 (15) | 820±137 (15) | 14±2 (15) | 71±9 (3) |
| | 1996 | 308±68 (15) | 160±35 (15) | 3.09±0.69 (15) | 61±1 (3) | 1521±198 (15) | 745±96 (15) | 19±3 (15) | 47±4 (3) |
| Annual mean | | 414 | 216 | 4.09 | 64 | 1576 | 783 | 17 | 59 |

## 3.2. LITTER

Nitrogen inputs from litterfall were not significantly different among sites (wetland vs. upland forest) or between years (ANOVA; $p \geq 0.13$) (Table III). Mean annual N inputs from deciduous litter were 17 kg N ha$^{-1}$ for upland litter and 20 kg N ha$^{-1}$ for wetland litter (Table III). Coniferous litter represented less than 20% of total litter N inputs for both the upland and wetland vegetation. C:N ratios for deciduous litter decreased from 1995 to 1996; 71 to 47 for upland litter and 49 to 37 for wetland litter. This decrease in C:N ratios was also seen in herbaceous vegetation (Table I). The reason for this decrease in C:N ratios is not known. C:N ratios were higher for deciduous litter in the upland zones than in the wetland, which is probably due to the influence of alder in the wetland. The C:N ratio of alder litter was 21 which is lower than either the upland or wetland means. Fresh alder foliage and foliar litter had the same C:N ratio of 21 demonstrating that there is no translocation of N in alder, a pattern consistent with other species of *Alnus* (Dawson, 1990). Coniferous litter C:N ratios decreased from 67 to 61 for upland litter and 102 to 65 for wetland litter between 1995 and 1996.

## 3.3. NITROGEN CONCENTRATIONS IN WETLAND AND UPLAND VEGETATION AND SOILS

Differences were found in N-distribution among biomass components comprising the wetland and upland ecosystems (Table IV). The greatest contrast in N-storage was between the soil component of wetlands and upland systems (42 and 9 Mg N ha$^{-1}$, respectively). Wetland soil (peat) consisted of poorly degraded plant material with a high organic content and a large pool of organically-bound N. Adirondack upland soils are often thin with a relatively shallow organic layer (0–5 cm) and a deeper mineral soil component (5–66 cm). However, the mineral soil has large organic C and N pools (Carlyle 1986) resulting in large stores of organically bound-N. The differences in N-storage of wetland and upland soils soils can also be attributed to deeper deposits of peat than mineral soils (180 and 66 cm, respectively).

Secondly, upland systems contained greater amounts of woody biomass than peatlands (193 and 26 Mg ha$^{-1}$, respectively) resulting in higher amounts of N in upland woody tissues (480 kg N ha$^-$ for upland vegetation and 130 kg N ha$^{-1}$ for wetland vegetation). Foliar production was lower in the wetland; however, wetland foliage stored approximately the same amount of N (70 kg N ha$^{-1}$ for wetlands and 80 kg N ha$^{-1}$ for upland; Table IV). This can be attributed to the presence of alder in the wetland. Alder foliage stores larger amounts of N per gram of dry weight than other species in the study (0.04 g N g$^{-1}$ dry weight for alder and 0.03 g N g$^{-1}$ dry weight for yellow birch which represents the maximum for other other species).

Lastly, there was a threefold difference in the amount of N in the herbaceous layer of the wetland and upland systems. The wetland had 30 kg N ha$^{-1}$ in the

TABLE IV

Vegetation composition for the Archer Creek wetland and upland zones

| Stratum | Dry weight biomass | Nutrient content C | N |
|---|---|---|---|
| | | (kg ha$^{-1}$) | |
| **Wetland** | | | |
| Foliage | 2000 | 980 | 70 |
| Bole + branch wood | 24000 | 10900 | 60 |
| Total | 26000 | 11880 | 130 |
| Herbaceous | 1400 | 630 | 30 |
| Peat[a] | 4000000 | 1000000 | 42000 |
| (Mineral soil) | – | – | – |
| **Upland[b]** | | | |
| Foliage | 3500 | 1700 | 80 |
| Bole + branch wood | 190000 | 87300 | 400 |
| Total | 193500 | 89000 | 480 |
| Herbaceous | 850 | 470 | 10 |
| Organic layer | 45000 | 20000 | 1100 |
| (Mineral soil)[c] | 3700000 | 300000 | 7900 |

[a] Mean peat depth was 1.9 m.
[b] Data on uplands in this table from Mitchell *et al.* (1991) and Johnson and Linberg (1992).
[c] Approximate mineral soils depth was 50 cm.

herbaceous layer whereas the upland vegetation stored only 10 kg N ha$^{-1}$ in the herbaceous layer.

N storage in wetland and upland vegetation was grouped into three classes; short term storage in foliage and herbaceous vegetation, medium term storage in woody tissues, and long term storage in peat, organic soil, and mineral soil. Wetlands stored most of their N (99%) in long-term storage with less than 1% in short and medium term storage (Table V). Upland storage of N is similar, with 96% of the N in soils (mineral + organic) and the remaining 4% in short and medium term storage.

TABLE V

Total organic nitrogen (TON) storage in the different vegetational compartments in the Archer Creek catchment

| | Compartment | Wetland storage | | Upland storage | |
|---|---|---|---|---|---|
| | | TON (kg N ha$^{-1}$) | (%) | TON (kg N ha$^{-1}$) | (%) |
| Short term | Foliage | 70 | | 77 | |
| | Herbaceous | 26 | 0.20 | 9 | 1 |
| Medium term | Woody tissues | 56 | 0.10 | 307 | 3 |
| Long term | Peat or soil | | | | |
| | organic | 42000 | 99 | 1100 | 12 |
| | mineral soil | – | – | 8000 | 84 |

TABLE VI

Vegetation fluxes for the hillslope in the Archer Creek catchment

| Flux | N (kg ha$^{-1}$ yr$^{-1}$) | |
|---|---|---|
| | Wetland | Upland |
| Understory vegetation | 26 | 9[a] |
| Foliage litterfall | 23 | 21 |
| Uptake[b] | 49 | 30 |
| Net mineralization[c] | 36 | 76 |
| Uptake-mineralization | 13 | –46 |

[a] Data from Johnson and Linberg, 1992.
[b] Equals understory vegetation + foliage litterfall (Grigal and Homan, 1994).
[c] Data from Ohrui et al., 1999.

## 3.4. ECOSYSTEM FLUXES AND DYNAMICS OF N IN WETLAND AND UPLAND VEGETATION

Wetland vegetation and soil showed an annual net gain of N (uptake was greater than N-mineralization; Ohrui et al., 1999) while upland vegetation and soil acted as a net source of N (Table VI). Bole increment and throughfall uptake were not measured; however, they typically represent less than 6% of net N-demand (Mitchell et al., 1992a). Annual uptake or N-demand was greater for wetland vegetation due to

higher production in the herbaceous layer. However, mineralization in the rooting zone of the wetland vegetation did not produce enough N to support this level of production suggesting that another source of N was being utilized (Ohrui *et al.*, 1999). It has been demonstrated that plants uptake organic forms of nitrogen, bypassing N-mineralization (Nasholm *et al.*, 1998). This may explain why wetland plants took up more nitrogen than was produced by mineralization. Upland vegetation showed a net loss of N with mineralization (76 kg N ha$^{-1}$ yr$^{-1}$; from Ohrui *et al.*, 1999) exceeding uptake (30 kg N ha$^{-1}$ yr$^{-1}$).

Another possible source of this outside N input into wetlands could be N fixation. Nitrogen accretion in speckled alder stands has been estimated to be 85 to 167 kg N ha$^{-1}$ yr$^{-1}$ (Daly, 1966). However, fixation rates of only 1 to 5 kg N ha$^{-1}$ yr$^{-1}$ were measured in pure or mixed stands of speckled alder and *Populus tremuloides* in forests of northern Wisconsin (Younger and Kapustka, 1983). The wetland in our study site has an area of approximately 0.5 ha. Given the above estimates, alder could potentially fix 43 to 84 kg N in this wetland, which could easily account for the difference of 16 kg ha yr difference in the wetland production. However, the rates of N-fixation in forested wetlands of the Adirondacks may be less due to shading, or possible negative feedback from N derived from atmospheric deposition.

## 3.5. WATERSHED N-STORAGE

Although wetlands represent only 4% of this subcatchment of the Archer Creek catchment, they stored a disproportionately high amount of N. Wetland vegetation and soil stored more N per unit area than upland vegetation and soil (42 and 10 Mg N ha$^{-1}$, respectively). Total estimated N in the Archer Creek catchment vegetation and soil was approximately 1500 Mg N with 85% stored in upland vegetation and mineral soil and 15% in wetland vegetation and soil. Inclusion of the mineral soil component is important because of the large organic C and N pools in mineral soil (Carlyle, 1986; Cole and Rapp, 1981). The relatively higher storage of N in wetlands is due to peat accretion and large pools of organic N in the peat deposits compared to that found in upland organic and mineral soils. There were well-defined $^{137}$Cs maxima in two cores taken from the intensive wetland. Peak $^{137}$Cs deposition (1964) occurred in the upper 2 cm of the cores suggesting peat accretion has occurred very slowly in the last 33 yr ($\sim$0.06 cm yr$^{-1}$). The $^{137}$Cs method for determining peat accretion rates has been successfully used in the everglades and other estuarine marshes (Craft and Richardson, 1993; Craft *et al.*, 1993).

## 3.6. IMPORTANCE OF THE WETLAND TO N CYCLING IN THE ARCHER CREEK CATCHMENT

We would expect the dominant species in N-limited systems to have higher C:N ratios since these species will add more carbon per unit of N available resulting in greater biomass. C:N ratios for *Sphagnum* have been reported in the range of 45–50

(Schindler and Bayley, 1993; Urban and Eisenreich, 1988) and have been shown to decrease (~28) when fertilized with N (Schindler and Bayley, 1993). *Sphagnum* C:N ratios in the Archer Creek wetland were lower (32) than most reported values for *Sphagnum* but higher than other plants in the herbaceous layer. Nitrogen may be in excess of demand causing the C:N ratio of *Sphagnum* to be lower than typical reported values and closer to those found in N-fertilization experiments. Atmospheric deposition of N in the Adirondacks or inputs as a result of N-fixation may have a fertilizing effect on the peatland communities causing the lower *Sphagnum* C:N ratios in this wetland.

The Archer Creek wetland stored the largest amount of N in the soil (99% of wetland N) which is typical for wetland peat and sediments (Bowden, 1984). The accretion of wetland sediments or peat is a sink for N reflects the balance between plant uptake and subsequent return as litter and N-mineralization rates. Although peat accretion in the Archer Creek wetland was low, plant uptake exceeded mineralization (Ohrui *et al.*, 1999) demonstrating that peat accretion was a sink for N while the uplands acted as a net source of N. Wetlands in the Adirondack region typically represent a relatively small proportion (4–32%) of the total watershed area. In a concurrent study on the Archer Creek subcatchment, N retention was estimated by calculating the balance of N inputs (precipitation) and outputs (streamflow) for the entire subwatershed (McHale *et al.*, 1999). The Archer Creek subcatchment showed a net retention of N with the greatest retention of n occurring during the growing season (McHale *et al.*, 1999). Net retention of N in the subcatchment was 14 Mg N representing 46% of the total atmospheric inputs. Wetland vegetation could account for up to 20% of the retained N while upland vegetation acts as a net source of N due to higher mineralization potentials in upland soils (Ohrui *et al.*, 1999). The remaining N not accounted for by vegetation may be retained through microbial immobilization or lost as $N_2$ gas a result of denitrification.

Nitrogen saturation is defined as a level of N-input that no longer increases primary production (Nilsson, 1986) or where the N input exceeds the uptake ability of the biota (Aber *et al.*, 1989). Nitrogen saturation may be detected by increased $NO_3^-$ concentrations in drainage waters (Gunderson, 1991; Aber *et al.*, 1989) as has been shown for some surface waters in the Adirondacks (Driscoll *et al.*, 1989). Using input/output budgets, wetland nitrogen retention (retention is defined as the amount of nitrogen input to the system through precipitation or in streamflow but is not lost to outflow) has been estimated in several studies. In a study by Hill (1991), a riparian wetland similar in vegetation to that of the current study retained only 26% of total N inputs although this retention was not much greater than the estimated error in the budget. This is in contrast to studies on riparian wetlands bordering agricultural lands where retention was 90–100% of $NO_3^-$-N input into the wetland through runoff (Cooper, 1990; Lowrance *et al.*, 1984; Lowrance *et al.*, 1983). In some Precambrian shield wetlands, $NO_3^-$ retention is relatively low (<50% of total N inputs) (Devito *et al.*, 1989) compared to other wetlands. Nitrogen

retention of the Arbutus watershed was 75% of atmospheric N-inputs (35% with DON export included) and Arbutus lake itself was a large sink for atmospherically deposited N (McHale *et al*., 2000).

Hence, wetlands may act as a transformer of dissolved N from inorganic forms ($NO_3^-$, $NH_4^+$) to macro-organic forms through vegetative uptake, ultimately releasing N in the form of DON. Wetlands exhibit higher amounts of transitory vegetative uptake (higher production in the herbaceous layer and foliage) which would provide an easily mineralizable source of carbon. The Archer Creek sub-catchment acted as a sink for DON in the uplands and a source of DON in the lowlands where the wetlands are located (McHale *et al*., 2000).

Wetlands may also act as a sink for N as a result of microbial immobilization and loss through denitrification. As a result of anaerobic conditions, denitrification rates in wetlands can be high resulting in loss of N in the form of $N_2$ gas. Microbial uptake can also fix nitrogen into macro-organic forms, thereby acting as a sink for N. However, neither of these two mechanisms were quantified in this study and consequently their role is unknown.

Grigal and Homann (1994) found rates of *in situ* N mineralization in upland systems of east-central Minnesota to be related to aboveground N-uptake as measured by N in annual litterfall and understory foliage. This relationship was not evident in their wetland systems. The absence of this relationship may have been due to low mineralization rates of the large organic N-pool. Moreover, the buried bag N-mineralization technique used in their study may not have provided reliable estimates of N mineralization in wetland soils. Wetlands may also rely on an outside source of N such as hillslope water that is transported into the wetland or N inputs as a result of N-fixation. Upland portions of watersheds that may be reaching N-saturation and contribute to N that may be intercepted by wetland systems (Gunderson, 1991; Aber *et al*., 1989), resulting in N-fertilization of the wetlands. Nitrogen produced by mineralization in the Archer Creek catchment exceeded uptake by upland vegetation and consequently N mineralization was a net source of N (Table VI). In a concurrent study by HcHale (1999) evaluating solute fluxes, $NO_3^-$ in wetland groundwater decreases significantly during the growing season (from 1.5 to 0.1 $\mu$mol L$^{-1}$) but it remains unclear as to whether this may be due to denitrification as a result of anoxic conditions in the wetland or due to plant uptake. The upland zone nitrate concentrations in the soil water remained constant through both the growing and dormant seasons (3.5 and 3.7 $\mu$mol L$^{-1}$, respectively) supporting the conclusion that upland soil mineralization exceeded uptake. Many Adirondack wetlands receive substantial amounts of drainage inputs from upland areas and thus may be impacted by N generated within hillslopes. Additionally, wetland N peat accretion and vegetation uptake rates suggest N contribution from either uplands or N-fixation supplement the relatively small amount of N generated by mineralization within the wetland in the Archer Creek catchment. However, the relative percentage of inputs for both fixation and hillslope derived N is unknown.

## 4. Conclusions

Overall vegetation demands for N played a small role in watershed-level retention of atmospherically-derived N since they were easily supported by internal production of N through soil mineralization. However, wetlands were a net sink for N due to vegetational uptake of N exceeding production of N through peat mineralization. Peat accretion, even though rates were low, can account for the disproportionate amount of storage of N by wetlands in the Archer Creek subcatchment while wetlands may be acting as a transformer of N from an inorganic form to organic forms with vegetative uptake acting as the mechanism. Other watershed factors that may be more important as an N sink are storage in deep groundwater (till water), loss as denitrification in wetland soils, sorption in the mineral soil, or in-lake processes (Mitchell *et al.*, 1996a, b; Rudd *et al.*, 1986).

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