

# Abundance of *Alnus incana* ssp. *rugosa* in Adirondack Mountain shrub wetlands and its influence on inorganic nitrogen

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Received 25 September 2001; accepted 26 July 2002

**“Capsule”:** *The presence of the nitrogen-fixing shrub, Alnus incana ssp. rugosa, influences the concentration of inorganic nitrogen in surface waters in the Adirondack Mountain region of northern New York.*

## Abstract

The purpose of this research was to determine the abundance of the nitrogen-fixing shrub, *Alnus incana* ssp. *rugosa* (speckled alder), in shrub wetlands of the Adirondack Mountain region of New York State and to determine whether its abundance affects the concentration or accumulation of inorganic nitrogen in wetland substrates. Alder/willow wetlands are the second most common wetland type in the Adirondack region. The Adirondack Park Agency’s digital GIS database of wetland types was used to determine the areal extent of alder/willow wetlands in the Adirondacks. Randomly selected wetlands were sampled to determine the size and abundance of alder. Alder densities averaged  $\sim 7000$  stems  $\text{ha}^{-1}$  and alder was present in 75% of the wetlands. As an indication of short-term accumulation of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  in wetland substrates, ion exchange resins were used to sample ground water in high and low alder density wetlands as well as from wetlands lacking alder and dominated by conifers. Additionally,  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations in ground water samples were measured.  $\text{NH}_4^+$  accumulation levels from exchange resins were low for all wetland types while groundwater  $\text{NH}_4^+$  concentration was highest in the low-density alder sites. Wetlands with high alder density had approximately six times higher  $\text{NO}_3^-$  accumulation than other wetlands. Substrate groundwater  $\text{NO}_3^-$  concentrations in wetlands of high-density alder exceeded by three times levels in low or no alder wetlands, showing the importance of alder to local N budgets. To assess the recovery of shrub wetlands from acidification, future studies should determine the fate of fixed N in wetland systems. © 2003 Elsevier Science Ltd. All rights reserved.

**Keywords:** *Alnus incana*; Soil nitrogen; Nitrogen fixation; Shrub wetlands; Adirondack Mountains

## 1. Introduction

While the concentrations of sulfate and hydrogen ions in precipitation in the eastern United States have been reduced since implementation of the Clean Air Act Amendments of 1990, nitrate concentrations have not generally declined (Lynch et al., 2000a, b). Atmospheric deposition of nitrate may contribute to nitrogen saturation and chronic acidification of surface waters (Galloway, 1995) delaying anticipated ecosystem recovery from anthropogenic acidification (Driscoll et al., 2001).

Palustrine wetlands may commonly serve as net sinks for nitrogen (Driscoll et al., 1998; Howarth et al., 1995; Richardson, 1990) because of their substantial capacity

to store nitrogen in both living biomass and necromass, including peat. Further, return of gaseous nitrogen to the atmosphere through denitrification processes that occur under anaerobic substrate conditions found in wetlands may decrease  $\text{NO}_3^-$  export to surface waters. The recovery of surface waters from acidification in response to changes in atmospheric deposition remains a topic of intensive interest and investigation (Driscoll et al., 1998, 2001) and the role of wetlands, particularly those with nitrogen-fixing shrubs, in the anticipated recovery is poorly understood.

Wetlands are abundant in the Adirondack Mountains of New York State, a region subjected to high amounts of atmospheric deposition relative to other regions of the United States (Ito et al., 2002). For example, within the Oswegatchie-Black watershed, a major Adirondack drainage system, 60,766 ha of the total 398,783 ha or 15% of the area is classified as “wetland”. Of these,

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spruce-fir forests constitute 47% of the wetlands and shrub-dominated wetlands comprise about 28% of the wetland complex (Roy et al., 1996).

Shrub-dominated wetlands of the Adirondacks typically support vigorous populations of the nitrogen-fixing species speckled alder [*Alnus incana* (L.) Moench ssp. *rugosa* (DuRoi) Clausen (Mitchell and Tucker, 1997)]. In symbiotic association with an actinomycete of the genus *Frankia*, this colonial shrub fixes 37–43 kg N ha<sup>-1</sup> year<sup>-1</sup> in Adirondack wetlands (Hurd et al., 2001) and rates of N accretion as high as 87–167 kg ha<sup>-1</sup> year<sup>-1</sup> have been reported elsewhere (Daly, 1966; Voigt and Steucek, 1969). Alder leaf litter contributes about 90% of its N content to the labile soil fraction (Swanston and Myrold, 1997) and N content does not change at senescence (Bischoff et al., 2001). Nitrogen mineralization rates in stands of *Alnus* spp. range from 43 to 100 kg ha<sup>-1</sup> year<sup>-1</sup> (Danieri et al., 1986; Stottlemeyer et al., 1995). In an Adirondack forested watershed, the presence of speckled alder increased NO<sub>3</sub><sup>-</sup> content and net nitrification rates of wetland soil (Ohrui et al., 1999).

This study was undertaken to quantify the abundance, size and biomass of alder shrubs in wetlands typed as “Scrub-shrub 1” (SS1) in the National Wetlands Inventory (Cowardin et al., 1979). SS1 wetlands, supposedly typified by the abundance of alder and willow, are the second most abundant wetland type in the Adirondack region (Roy et al., 1996). A second objective was to determine whether there are indications that the presence of alder affects N concentration in wetland substrates, thereby warranting a more intensive study of alder–surface water chemistry relationships. Nitrogen inputs from alder foliage were used to project foliar N inputs by alder at the regional watershed scale.

## 2. Methods

### 2.1. Site selection

Because of the availability of remotely sensed data labeling wetland type, the Oswegatchie-Black (OB) and Upper Hudson (UH) watersheds of the Adirondack Park were selected for study. Together, these watersheds include more than 800,000 ha of land surface. To determine the abundance of alder in “alder/willow” wetlands, 10 wetlands in each watershed were randomly selected using the Adirondack Park Agency’s electronic geographic information system (GIS) database. Wetlands designated as “SS1” (scrub–shrub vegetation) and “SS1/EM1” (scrub–shrub with emergent herbaceous vegetation) were included in the sample (Table 1). In the area considered in this study, there were 7827 wetlands greater than 0.33 ha (the resolution level of the database) with SS1 and SS1/EM1 designations. Of the 4563 such wetlands in the OB, 33% were SS1 wetlands and

67% were SS1/EM1 wetlands. There were 3265 considered wetlands in the portion of the UH included in this study, 36% SS1 and 64% SS1/EM1.

### 2.2. Vegetation sampling

Three belt transects, each 2 m wide, were established at random distances perpendicular to the long axis of each wetland (Stehman and Salzer, 2000). Within these transects, alder stems >0.7 m in height were counted and diameter measured with calipers at 25 cm above the substrate. The following equations from Bischoff et al. (2001) were used to estimate alder stem and foliar mass:

$$\ln(\text{stem mass, g}) = 2.6253\ln(\text{diameter, cm}) + 3.5231$$

$$R^2 = 0.98$$

$$\ln(\text{foliar mass, g}) = 2.2655\ln(\text{diameter, cm}) + 1.8978$$

$$R^2 = 0.95$$

Mean alder density was calculated. The total number of alder stems and total biomass were determined using procedures for two-stage cluster sampling (Cochran, 1977). Foliar N content was calculated using N concentrations from Hurd (1999). Non-parametric analysis of variance (ANOVA) tests were used to evaluate differences among wetlands and between watersheds.

### 2.3. Nitrogen accumulation and concentration

Six wetlands in the UH varying in alder abundance were chosen to determine whether alder density might affect N accumulation in the substrate. Four of the six were selected from sites where alder abundance and biomass were estimated, two with dense (~14,500 stems ha<sup>-1</sup>) alder populations (Deer Pond and Rock Lake) and two with lower (~1650 stems ha<sup>-1</sup>) alder density (Cheney and Gull Ponds). Alder density is significantly correlated to basal area ( $\rho=0.81$ ; Kiernan, 2000). Two sites with no alder present (Wolf Lake and Arbutus Pond) were randomly selected from spruce-fir forested wetlands (FO4), the most common wetland type in the Adirondack Park (Roy et al., 1996). While many factors determine wetland type and cover species, FO4 wetlands were chosen due to their extensive area in the region. This study was not designed to determine what specific factors influence the type of wetland found in any given area. Wetland microtopography was characterized as hummock and hollow and all sub-sampling sites were located in hollows.

The loci of N accumulation sampling at each site were chosen using the sub-sampling procedure of Keuhle (1994). Three sub-samples were randomly located in each wetland. Ion exchange resin (IER) bags, approxi-

Table 1  
Site descriptions of wetlands included in this study (alder density is stems ha<sup>-1</sup>; percent alder is out of total number of shrub stems)

Watershed <sup>a</sup>	Site	Label <sup>b</sup>	Lat	Long	Elev (m)	Alder density	Percent alder
OB	Mitchell Pond 1	SS1	43 40 15 N	74 44 50 W	625	0	0
OB	Big Moose Lake	SS1	43 48 56 N	74 53 03 W	578	6207	26
OB	Nick's Lake	SS1	43 40 33 N	74 59 26 W	527	11,504	99
OB	Red River	SS1	43 40 47 N	74 46 15 W	577	9396	45
UH	Cedar River Flow	SS1	43 41 18 N	74 29 45 W	645	25,620	38
UH	Deer Pond 2	SS1	44 02 50 N	74 14 21 W	544	4125	49
UH	Gull Pond Outlet	SS1	43 50 00 N	73 42 32 W	358	0	0
UH	Rock Lake 1	SS1	43 49 38 N	74 19 28 W	541	14,172	38
OB	Bisby Road	SS1/EM1	43 41 09 N	74 58 06 W	601	0	0
OB	Cascade Lake	SS1/EM1	43 47 36 N	74 47 28 W	602	1985	60
OB	Brandy Brook	SS1/EM1	44 12 22 N	74 46 28 W	457	6897	98
OB	Limekiln Lake	SS1/EM1	43 4 214 N	74 47 00 W	642	0	0
OB	Mitchell Pond 2	SS1/EM1	43 40 14 N	74 45 11 W	621	0	0
OB	Moss Lake	SS1/EM1	43 46 58 N	74 50 37 W	548	18,524	60
UH	Cheney Pond	SS1/EM1	43 56 15 N	73 58 59 W	527	1757	6 <sup>c</sup>
UH	Deer Pond 1	SS1/EM1	44 02 21 N	74 15 46 W	509	14,895	58 <sup>c</sup>
UH	Gull Pond	SS1/EM1	43 49 57 N	73 42 35 W	359	1479	6 <sup>c</sup>
UH	Mineville Road	SS1/EM1	44 04 25 N	73 38 22 W	328	7484	60
UH	Northwoods Road	SS1/EM1	43 48 39 N	74 00 28 W	547	6802	63
UH	Rock Lake 2	SS1/EM1	43 49 24 N	74 19 41 W	532	2398	11 <sup>c</sup>
UH	Arbutus Pond	FO4	43 59 06 N	74 14 39 W	518	0	0 <sup>c</sup>
UH	Wolf Lake	FO4	44 00 48 N	74 13 07 W	561	0	0 <sup>c</sup>

<sup>a</sup> UH, upper Hudson watershed; OB, Oswegatchie/Black River watershed.

<sup>b</sup> SS1, scrub shrub 1 wetland; SS1/EM1, scrub shrub 1/emergent 1 wetland.

<sup>c</sup> Included in the IER study.

mately 4 cm<sup>2</sup>, were constructed from nylon hosiery and filled with 7 g each of IONAC A-554 anion exchange resin and DOWEX HCR-W2 cation exchange resin. The material was loosely mixed and enclosed within the bags (Binkley, 1984). Bags were then twice rinsed in 1 N HCl and triple rinsed with doubly-deionized water. A bag was placed 10 cm deep at each sub-sampling location in mid-September, 1998. After 2 weeks, the bags were collected and new ones installed. This process was repeated until mid-November, 1998, when the wetland icing began. Collected samples were frozen until extraction as suggested by Giblin et al. (1994). Nitrate concentrations of samples in cold storage remain stable for weeks; NH<sub>4</sub><sup>+</sup> may be less stable (Yorks and McHale, 2000).

Prior to analysis, IER bags were thawed and air-dried. Then 5.0 g of mixed resins from each bag were extracted individually in 100 ml 2M KCl for 24 h (Wyland and Jackson, 1993; Binkley, 1984). The extract was analyzed for NH<sub>4</sub><sup>+</sup> using the Wescan Ammonia Analyzer (Alltech Assoc., Deerfield, IL), and for NO<sub>3</sub><sup>-</sup> using the Technicon AutoAnalyzer II (Technicon Instrument Corp., 1973, Tarrytown, NY) (Ohrui et al., 1999). Results were analyzed under the one-way ANOVA with sub-sampling protocol (Keuhle, 1994), using SAS 6.12 (SAS Institute, 1996).

Groundwater wells were constructed from 5.7 cm inner diameter PVC pipe, 30 cm long. In each wetland, one well was installed to a depth of 10 cm at each of the three sub-sampling stations, using another PVC pipe as

a corer. Water was collected using a hand pump, and samples were stored in 100 ml plastic bottles. The samples were kept refrigerated until analysis (~4 weeks). Samples were collected at the time of IER bag replacement. Groundwater samples were analyzed for NO<sub>3</sub><sup>-</sup> using Dionex DX-120 ion chromatograph (Dionex Corporation, Sunnyvale, CA), and for NH<sub>4</sub><sup>+</sup> using the Wescan Ammonia Analyzer. Results were analyzed using the same statistical procedure as for the IER results.

### 3. Results

#### 3.1. Wetland size and area

Across the study area, wetlands considered in this study were larger in the OB (3.4 ha) than in the UH (2.0 ha). SS1/EM1 wetlands were larger (3.8 ha) than SS1 wetlands (1.0 ha). Within each watershed, the mean size of SS1/EM1 wetlands in the OB was 4.6 ha, significantly larger than the UH average of 2.6 ha. Wetlands with only the SS1 label averaged approximately one ha in both watersheds.

In the OB, SS1/EM1 wetland area is 14,220 ha, while SS1 wetlands cover 1545 ha. The wetlands included in this study represent 19% of total wetland area in the OB, although 27% of all wetlands in the watershed had an SS1 designation in the label. Of the UH wetlands, 22% had an SS1 designation in the label, but the wet-

land types included in this study represent 16% of total wetland area. SS1/EM1 wetlands covered 5487 ha in the UH, and SS1 wetlands covered 1101 ha.

### 3.2. Distribution, density, and biomass of alder

In the OB watershed, *Alnus incana* averaged 30% of total shrub density in SS1 wetlands and 36% in SS1/EM1 wetlands. Alder accounted for 49% of all stems in UH SS1 wetlands, 28% in the SS1/EM1 wetlands and in total accounted for 35% of all stems in this study. Where it occurred, alder density ranged from 1985 stems  $\text{ha}^{-1}$  at Cascade Lake Inlet to 25,620 stems  $\text{ha}^{-1}$  at Cedar River Flow, averaging 8883 stems  $\text{ha}^{-1}$ .

In the OB watershed, four wetlands studied had no alder in them, three classified as SS1/EM1, and one in the SS1 category. The UH survey had only one wetland lacking alder (an SS1). However, total alder density did not significantly vary between type ( $P=0.37$ ). SS1 averaged 8878 stems  $\text{ha}^{-1}$ , while SS1/EM1 averaged 5185 stems  $\text{ha}^{-1}$ . Alder density did not vary significantly between the OB and UH watersheds ( $P=0.42$ ); density in the OB averaged 5451 stems  $\text{ha}^{-1}$  and averaged 7873 stems  $\text{ha}^{-1}$  in the UH. In the OB SS1/EM1 wetlands averaged 4568 stems  $\text{ha}^{-1}$ , and SS1 wetlands averaged 6777 stems  $\text{ha}^{-1}$ . SS1/EM1 wetlands in the UH averaged 5803 stems  $\text{ha}^{-1}$  and SS1 wetlands averaged 10,979 stems  $\text{ha}^{-1}$  (Table 2).

Since alder biomass is logarithmically related to stem diameter (Bischoff et al., 2001; Beuch and Rugg, 1995), differences in diameter distribution strongly influence biomass. In the OB SS1 wetlands, 23.7% of the total stems were over 3.0 cm compared to 7.0% in the UH. Diameters in UH SS1/EM1 wetlands had 16.3% of alder stems over 3.0 cm, compared to 12.1% in the OB. In the OB, foliar biomass in SS1/EM1 wetlands averaged 206  $\text{kg ha}^{-1}$  (Table 3) and stem biomass averaged 1626  $\text{kg ha}^{-1}$ . SS1 wetlands averaged 502  $\text{kg ha}^{-1}$  foliar and 4264  $\text{kg ha}^{-1}$  stem biomass. The UH SS1/EM1 wetlands averaged 391  $\text{kg ha}^{-1}$  foliar biomass and 3457  $\text{kg}$

$\text{ha}^{-1}$  stem biomass. SS1 wetlands in the UH averaged 407  $\text{kg ha}^{-1}$  foliar biomass and 3046  $\text{kg ha}^{-1}$  stem biomass.

### 3.3. Comparison of inorganic N accumulation and groundwater concentration among sites

Nitrate in IER extracts was significantly higher in high-density alder wetlands ( $P=0.04$ ) though there was no significant difference in ammonium among treatments ( $P=0.46$ ; Fig. 1). High-density alder wetlands (DP and RL) averaged 1.19  $\text{mg g}^{-1}$  and low-density alder (CP and GP) and non-alder (AR and WL) wetlands averaged 0.15  $\text{mg g}^{-1}$ . The maximum value at DP (8.01  $\text{mg g}^{-1}$ ) was considered aberrant at  $>2.5$  standard deviations above the mean for that site, and was excluded from further analysis. High-density alder sites averaged 0.07  $\text{mg g}^{-1}$ ; low-density alder and no alder sites averaged 0.02 and 0.04  $\text{mg g}^{-1}$ , respectively.

Groundwater  $\text{NO}_3^-$  levels were significantly higher in the high-density alder wetlands than in either low-density or non-alder wetlands ( $P=0.05$ ), while groundwater  $\text{NH}_4^+$  was significantly higher in low-density alder wetlands than in either high density or non-alder wetlands ( $P=0.03$ ; Fig. 2). High-density alder wetlands averaged 13.05  $\mu\text{eq NO}_3^- \text{ l}^{-1}$  of compared to 3.75  $\mu\text{eq NO}_3^- \text{ l}^{-1}$  in low-density alder and 1.17  $\mu\text{eq NO}_3^- \text{ l}^{-1}$  in non-alder wetlands. Low-density alder wetlands had an average of 225.3  $\mu\text{eq NH}_4^+ \text{ l}^{-1}$  of  $\text{NH}_4^+$ , compared to 117.3  $\mu\text{eq NH}_4^+ \text{ l}^{-1}$  in high-density alder wetlands. The non-alder wetlands averaged 52.0  $\mu\text{eq NH}_4^+ \text{ l}^{-1}$ .

## 4. Discussion

### 4.1. Alder abundance

Speckled alder was widespread in both the OB and UH watersheds, although three SS1/EM1 wetlands in the OB were devoid of alder. Alder was generally abundant, averaging 35% of the total stems and 6662 stems  $\text{ha}^{-1}$  in the wetlands in this study. The average density of alder in Adirondack wetlands was similar to the 7850 stems  $\text{ha}^{-1}$  found in a central New York wetland (Tilton and Bernard, 1975). In Adirondack wetlands that contained alder, alder averaged 50% of the stems. In 10% of the wetlands sampled, alder accounted for at least 98% of the total stems. Alder density did not significantly vary between watersheds or between wetland types, although SS1/EM1 wetlands were larger in the OB, and both types were more abundant in the OB. The total number of alder stems did not significantly vary between watersheds.

Estimates of foliar N in dense alder stands in Adirondack wetlands ranged from 55 to 70  $\text{kg N ha}^{-1}$  (Bischoff et al., 2001; Hurd et al., 2001). Alder foliar N is derived primarily from fixation (85–100%, Hurd et al., 2001). Alders therefore assimilate little of the inorganic

Table 2  
Mean total shrub layer density (stems  $\text{ha}^{-1}$ ), mean alder density, and percent alder in studied wetlands

		Total	Alder	%
OB	SS1/EM1	12,880	4568	35
	SS1	22,620	6777	30
	Total	16,776	5451	32
UH	SS1/EM1	20,597	5802	28
	SS1	22,373	10,979	49
	Total	21,307	7873	37
Overall		19,041	6662	35 <sup>a</sup>

<sup>a</sup> Range from 0 to 99%.

Table 3  
Estimated foliar biomass and foliar N contribution to studied wetlands

OB	Foliar biomass	Foliar N (kg ha <sup>-1</sup> )	UH	Foliar biomass	Foliar N (kg ha <sup>-1</sup> )
<i>SSI/EMI</i>					
Bisby Rd.	0	0	Cheney Pond	75	2
Cascade Lk	57	1	Deer Pond 1	339	8
Brandy Brook	577	13	Gull Pond	35	1
Limekiln Lk	0	0	Mineville Rd	996	23
Mitchell Pnd 2	0	0	Northwoods Rd	640	15
Moss Lake	601	14	Rock Lake 2	263	6
Means	206	5	Means	391	9
<i>SSI</i>					
Mitchell Pnd 1	0	0	Cedar River Fl	342	8
Big Moose Lk	139	3	Deer Pond 2	319	7
Nick's Lake	1261	30	Gull Outlet	0	0
Red River	608	14	Rock Lake 1	968	23
Means	502	12	Means	407	10

N entering the wetland from external or internal sources yet they contribute large quantities of fixed N to wetland soils when its litter is mineralized. It has been shown that both alder foliage and fresh foliar litter have the same N content (2.7%) and C:N ratios of 21, indi-

cating minimal translocation of N from alder foliage prior to senescence (Bischoff et al., 2001). Those findings agree with those of Dawson (1990).

Foliar biomass of alder ranged from 0 to 1261 kg ha<sup>-1</sup> in individual wetlands, but averaged 377 kg ha<sup>-1</sup> over all

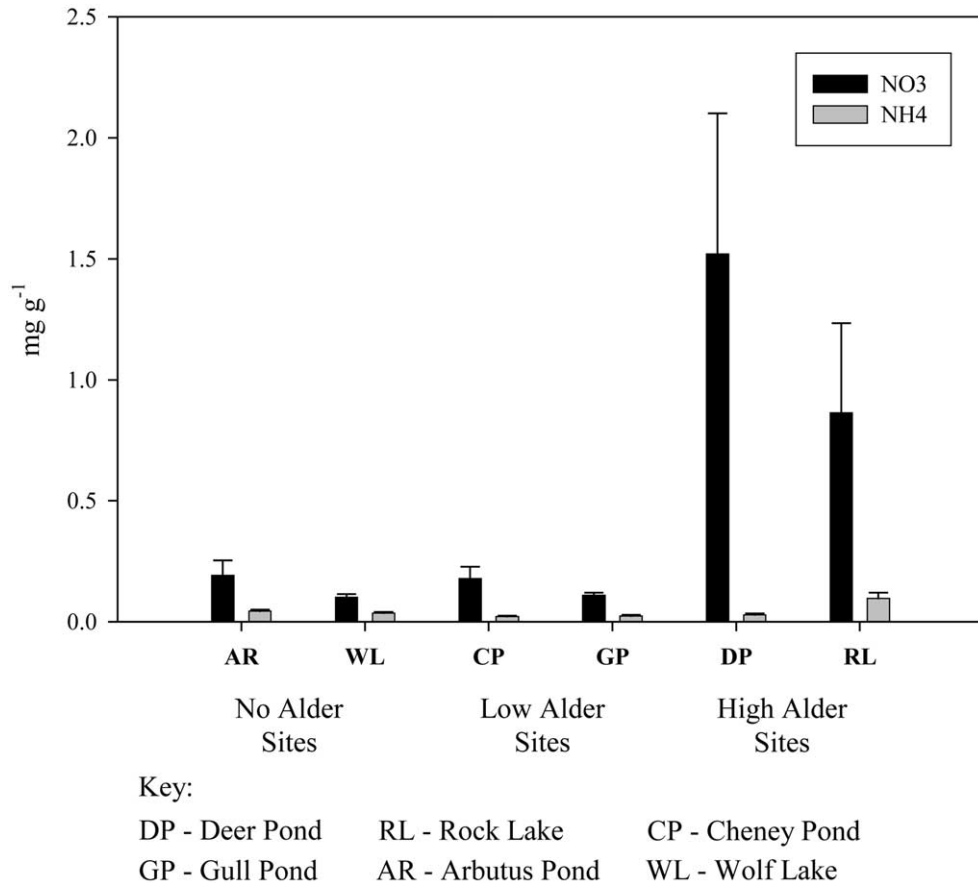


Fig. 1. Mean (±standard error) nitrate and ammonium concentrations in IER extracts over the four collection periods.

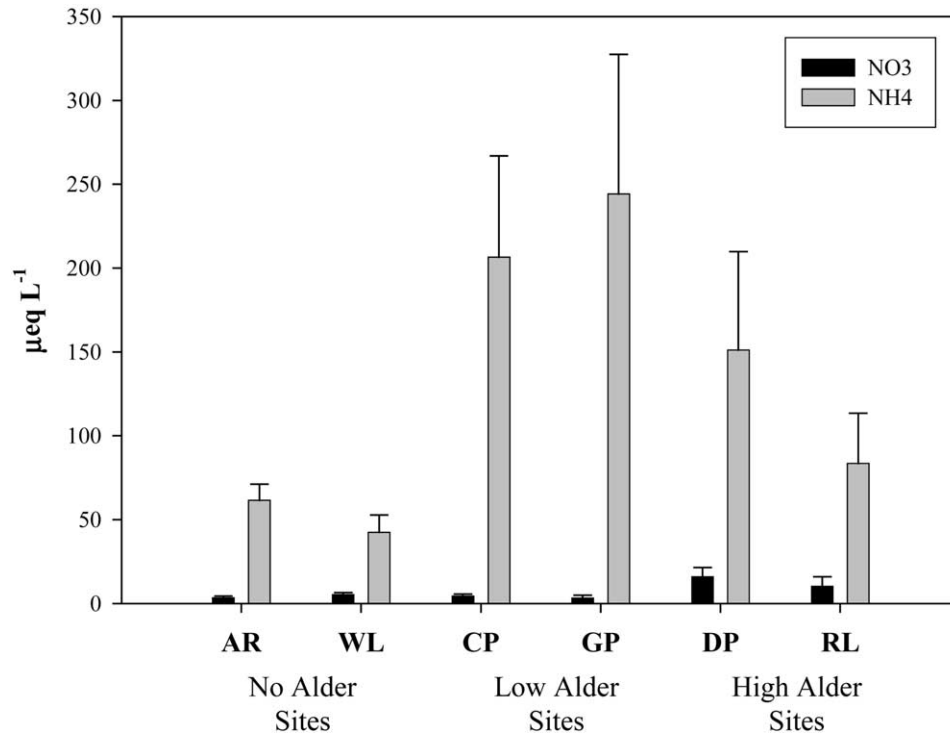


Fig. 2. Mean ( $\pm$ standard error) nitrate and ammonium concentrations in groundwater samples of the four collection periods.

wetlands. This is considerably lower than the 3070 kg ha<sup>-1</sup> found in a central New York wetland (Tilton and Bernard, 1975), a study that included both leaves and twigs. The diameter distribution in the Tilton and Bernard study had a high number of large stems; stems larger than 5.0 cm diameter accounted for 41% of the total stems. Hurd et al. (2001) measured 2060 kg foliage ha<sup>-1</sup> in an UH SS1/EM1 wetland. The difference between the findings of this study and those of Hurd et al. (2001) can be explained by the greater frequency of large diameter stems within that wetland than was found in this study. Further, most wetlands in this study included large areas dominated by other shrubs, herbs, or open water. These were areas not considered by Hurd et al. (2001).

The SS1 and SS1/EM1 wetlands included in this study accounted for only 70% of the wetlands with "SS1" in the identification label. Alder abundance in wetlands with other label types should be determined to obtain a more complete estimate of alder abundance. Additionally, alder appears common in smaller riparian zones, not accounted for in the Adirondack Park Agency database. The importance of alder in these wetland areas was not considered in this study.

#### 4.2. Comparison of N accumulation and concentration among sites

Binkley (1984) concluded that use of IER is well suited to comparisons of ionic concentration of soil between sites or across treatments. However, the lack of

specific information of hydrologic flow paths restricts use of IER results as more than a short-term index of accumulation. We found that NO<sub>3</sub><sup>-</sup> accumulation in IER bags was greater in high-density alder wetlands than in wetlands of low alder abundance or devoid of alder, regardless of Cowardin et al. (1979) wetland type labeling. The IER NO<sub>3</sub><sup>-</sup> levels were six times greater in high-density alder wetlands and low or non-alder wetlands.

Groundwater NO<sub>3</sub><sup>-</sup> concentrations were three to four times greater in high-density alder wetlands than in other sites. Nitrification, and consequent production of nitric acid, has been shown to increase acidification in forest soils beneath red alder (van Miegroet et al., 1989; van Miegroet and Cole, 1984). Nitrate levels in stream and groundwater in an UH alder wetland during the dormant season was found to be up to six times higher than in a reference wetland devoid of alder (Hurd and Raynal, in press). Alder accounted for 59% of the stems in that wetland.

Because speckled alder density in these wetlands was strongly correlated with basal area, density (a more ready measurement) was chosen for comparison. Groundwater NH<sub>4</sub><sup>+</sup> concentrations were highest in low-density alder wetlands. Accumulation of NH<sub>4</sub><sup>+</sup> in the IER bags was uniformly low across all sites and thus it appears likely that the higher groundwater NH<sub>4</sub><sup>+</sup> concentration in low-density alder wetlands was not directly linked to alder. Because depth to water strongly influences redox potential (Mitsch and Gosselink, 1993),

it uncertain whether  $\text{NH}_4^+$  emanated from internal flushing or from other sources. It is possible that the low-density alder wetlands are less aerated in the upper peat than wetlands of abundant alder and most inorganic N is in the form of  $\text{NH}_4^+$ . High-density alder systems generally have a greater number of larger roots and hummocks around stem clumps, and the sprawling growth habit of alder results in variable microtopography. Some alder species have also been shown to increase aeration in the substrate (Schröder, 1989). Analyses of both accumulation and concentration indicate greater  $\text{NO}_3^-$  levels in wetlands of high alder density. However,  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations were greatest in low-density alder and higher in alder wetlands than non-alder wetlands.

A density of 14,000 alder stems  $\text{ha}^{-1}$  was associated with six times more  $\text{NO}_3^-$  than a density of 1500 stems  $\text{ha}^{-1}$ . Since there were no differences in  $\text{NO}_3^-$  accumulation between 1500 alder stems  $\text{ha}^{-1}$  and no alder, there may be a threshold density at which alder effects on wetland N cycles are detectable. While further study is needed to accurately define that threshold, it is useful to consider the variation in density found in this study. Eight of the 20 wetlands were estimated to have less than 3000 alder stems  $\text{ha}^{-1}$ , and five were estimated to have greater than 10,000 stems  $\text{ha}^{-1}$ . The other seven wetlands averaged 6000 stems  $\text{ha}^{-1}$ . About 50% of the SS1/EM1 wetlands and at least 75% of the SS1 wetlands in these watersheds are characterized by elevated  $\text{NO}_3^-$  levels. On a watershed scale, alder dominated wetlands may encompass 5–10% of total wetland area. However, the capacity of wetlands to function as N sinks may be diminished beyond that figure, as 20% of the wetlands in this study exceeded 14,000 alder stems  $\text{ha}^{-1}$ , and therefore may not function as a N sink, but serve as a source of N to downstream systems. Future studies determining the fate of fixed N should address root turnover and exudation.

Based on the reported C:N ratio of 21 in both foliage and fresh leaf litter, and assuming that there is negligible translocation of N from alder foliage (Bischoff et al., 2001; Dawson, 1990), we estimated total foliar N contribution from fixation in alder dominated wetlands using the biomass estimates from this study and data from Hurd (1999). We assumed that the foliar N concentration was 2.6%, with 90% N derivation from fixation (Hurd et al., 2001). Alder foliage contribution ranged from 0–30  $\text{kg ha}^{-1} \text{ year}^{-1}$  (Table 3). At nine sites, fixed foliar N addition equaled or exceeded estimated total atmospheric deposition ( $\sim 10 \text{ kg ha}^{-1} \text{ year}^{-1}$ ), and deposition was exceeded by more than 150% in 20% of the wetlands studied. To assess the recovery of shrub wetlands from acidification and their response to changing N deposition, storage or export of fixed N in wetlands should be determined.

## Acknowledgements

We gratefully acknowledge the contributions of Drs. Donald Leopold, Russell Briggs of SUNY-ESF and Charles Driscoll of Syracuse University toward the design and implementation of this study and for comments on the manuscript. We thank three anonymous reviewers who suggested clarifications and improvements in the presentation. Mark Watson, Guest Editor, facilitated publication. This study was funded by contracts from the Niagara Mohawk Power Corporation and New York State Energy Research and Development Authority (NYSERDA) as well as by the McIntire–Stennis program. We thank Mr. Dan Spada and Dr. Avram Primack of the Adirondack Park Agency and Dr. Don Bogucki and Ms. Eileen Allen of SUNY-Plattsburgh who provided access to GIS data and support crucial to the success of this study.

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