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High Nitrate Retention during Winter in Soils of the Hubbard Brook Experimental Forest

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Abstract

Stream export of nitrogen (N) as nitrate (NO_3^-; the most mobile form of N) from forest ecosystems is thought to be controlled largely by plant uptake of inorganic N, such that reduced demand for plant N during the non-growing season and following disturbances results in increased stream NO_3^- export. The roles of microbes and soils in ecosystem N retention are less clear, but are the dominant controls on N export when plant uptake is low. We used a mass balance approach to investigate soil N retention during winter (December through March) at the Hubbard Brook Experimental Forest by comparing NO_3^- inputs (atmospheric deposition), internal production (soil microbial nitrification), and stream output. We focused on months when plant N uptake is nearly zero and the potential for N export is high. Although winter months accounted for only 10–15% of annual net nitrification, soil NO_3^- production (0.8–1.0 g N m^{-2} $winter^{-1}$) was much greater than stream export (0.03–0.19 N m^{-2} $winter^{-1}$). Soil NO_3^- retention in two consecutive winters was high (96% of combined NO_3^- deposition and soil production; year 1) even following severe plant disturbance caused by an ice-storm (84%; year 2) We show that soil NO_3^- retention is surprisingly high even when N demand by plants is low. Our study highlights the need to better understand mechanisms of N retention during the non-growing season to predict how ecosystems will respond to high inputs of atmospheric N, disturbance, and climate change.

Key words: forest ecosystem; land-water interactions; mass balance; nitrification; nitrogen cycle; stream export.

Introduction

Nitrogen (N) is often a limiting nutrient to plant growth, but in excess it is exported from terrestrial ecosystems mainly as the mobile anion, nitrate (NO_3^-), where it is a concern as a drinking water pollutant and a cause of eutrophication (for example, Galloway and others 2003). The roles of forest succession, disturbance, and N deposition in regulating the export of NO_3^- from forest catchments have been investigated for many years (for example, Odum 1969; Likens and others 1970; Vitousek and Reiners 1975; Bormann and Likens 1979; Aber and others 1998). These investigations have shown that plants play a major role in forest N retention, such that reductions in plant uptake are directly linked to increased NO_3^- export in streams. There can be considerable interannual variation in stream NO_3^- export, and models indicate that disturbances and climatic factors control this variation (Aber and others 1992; Hong and others 2005), although there is disagreement as to the relative importance of each factor. Few studies, however, have approached the question from the other direction and asked: what controls forest N retention when plant uptake is low?

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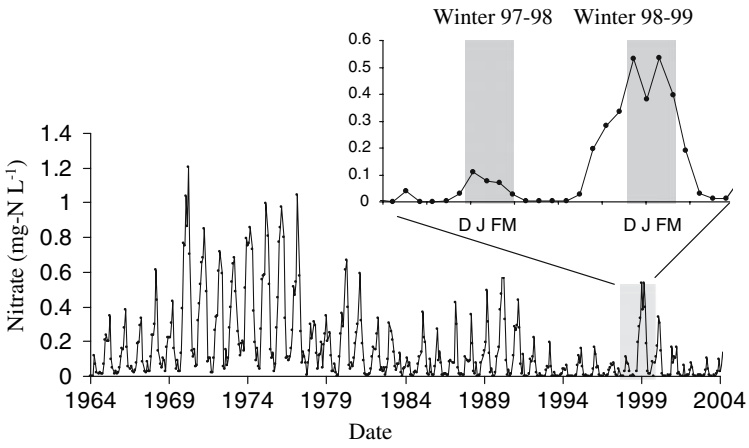

Figure 1. Monthly, volume weighted concentrations of NO_3^- (as mg N L^{-1}) in stream water for Watershed 6 of the HBEF (updated from Likens 2004). Severe insect defoliations (1969–1971) and the January 1998 ice storm are indicated with *. The *inset* depicts NO_3^- concentrations (mg N L^{-1}) during the study period (winters 1997–1998 and 1998–1999).

Forest ecosystems have great potential for N retention, as demonstrated by the build up of N in soils and biomass that occurs over long time periods (for example, thousands of years), especially in soils with little or no N release from bedrock weathering, such as those of the Hubbard Brook Experimental Forest (HBEF; Likens and Bormann 1995). These ecosystems are thought to be highly retentive of N during early stages of development and become ''leakier'' with maturation (Vitousek and Reiners 1975). Elevated levels of atmospheric N deposition are predicted to accelerate this transition (Aber and others 1998), and N saturation and increased NO_3^- export has been observed in some North American and European forests (for example, Peterjohn and others 1996; Kortelainen 1997; Aber and others 2003). However, NO_3^- concentrations in headwater streams in the region around the HBEF have unexpectedly declined (Goodale and others 2003), highlighting the gaps in our knowledge of NO_3^- retention and export in aggrading forested ecosystems receiving elevated N deposition.

Long-term records from the HBEF (Figure 1) and other temperate, boreal, and alpine ecosystems (for example, Sickman and Melack 1998; Williams and others 2001; Worrall and others 2003; Langan and Hirst 2004) show a consistent pattern of elevated stream NO_3^- concentrations during the nongrowing season when plant activity is minimal. By and large, undisturbed forest ecosystems are very retentive of N, resulting in low stream NO_3^- export, even though there are larger internal fluxes between soil, plant, and microbial pools. Nitrate is made available for export from soils through microbial nitrification of remineralized ammonium (NH_4^+), a process thought to be enhanced by high availability of NH_4^+ in excess of plant uptake, and through atmospheric deposition. However, there have been few analyses of production, consumption, and retention of NO_3^- during the dormant season (Campbell and others 2005).

Recent evidence from stable isotope studies indicates that NO_3^- in streams originates primarily from microbial nitrification and not directly from atmospheric inputs. Microbially produced NO_3^- appears to dominate stream NO_3^-, even during the spring snowmelt, when water is flushing quickly through soils (Burns and Kendall 2002; Pardo and others 2004; Piatek and others 2005). Winter microbial activity in soils can be important to annual carbon and N cycling activity in many alpine and boreal ecosystems (for example, Clein and Schimel 1995; Hobbie and Chapin 1996; Williams and others 1996; Brooks and others 1996). Because a disproportionate amount of the annual NO_3^- export occurs during winter and spring, the build up of NO_3^- in soils over the winter months may be an important source of exported NO_3^-. To better understand the controls on N cycling and NO_3^- export during periods of minimal plant uptake of inorganic N, we investigated the relationship between soil microbial NO_3^- production and stream NO_3^- export during the winter at the HBEF. We used a mass balance approach, synthesizing previously published data on winter microbial NO_3^- production in soils (Groffman and others 2001), long-term stream chemistry (Likens 2004), and atmospheric deposition (Likens and Bormann 1995; Likens 2001) to address the following questions: (1) Is winter microbial NO_3^- production in soils sufficient to account for stream NO_3^- export? And, if so, (2) how much of the NO_3^- produced during winter months is retained in soils in the absence of high plant demand for inorganic N?

Methods

Study Site

The HBEF is located in the White Mountains of New Hampshire, USA (43°56′N, 71°45′W). Vegetation is characteristic of a mature, northern hardwood forest ecosystem and is dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghenienssis*). Soils are acidic (pH 3.9), well-drained spodosols (Haplorthods) of sandy loam texture with a thick (3–15 cm) surface organic layer (Likens and Bormann 1995). Annual precipitation averages about 1,400 mm and is evenly distributed throughout the year. About one third to one quarter of annual precipitation is snow, and snowpack generally persists from mid-December until mid-April, with a peak depth in March. However, occasional midwinter thaws result in elevated streamflow. The snowpack normally melts during March–May. Some 68% of the annual streamflow occurs during this period (Likens and Bormann 1995). Snow-covered soils typically do not freeze, but in the absence of snowpack, soil frost can occur (Likens and Bormann 1995). Average soil temperatures in the plots for the two study years were above freezing at 10 (1.4°C), 20 (3.4°C), and 30 (3.8°C) cm (for daily soil temperatures see Hardy and others 2001). For climate data throughout the HBEF see http://www.hubbardbrook.org.

We used a mass balance approach to calculate winter N fluxes using data from a previously published study of winter soil microbial N production (Groffman and others 2001) and long-term data from the Hubbard Brook Experimental Forest. Our study focused on 1997–1998 and 1998–1999, the two years of the winter soil microbial-N production study. We designated winter as the period from 1 December through 31 March to coincide with months of minimal plant activity (that is, low inorganic N uptake). A large ice-storm occurred in January of 1998, which resulted in elevated NO_3^- export the following winter (Houlton and others 2003). The two years of our study thus include ''typical'' and ''post-disturbance'' winters.

Winter Soil Incubations

Overwinter soil inorganic N production was measured using an in situ, intact core method (Robertson and others 1999; Stottlemyer and Toczydlowski 1996). Four plots were used, two each were dominated (>80%) by sugar maple and yellow birch (see Groffman and others 2001 for details). These species were chosen because sugar maple and yellow birch are two key species in the northern hardwood forest, and they are expected to vary in cold-hardiness (that is, the elevation range of birch exceeds that of maple). In the winter of 1997–1998, 25 intact cores (25 cm × 2 cm) were collected from each plot in late November and then harvested in groups of 5 at approximately four-week intervals (after 40, 60, 105 and 147 days of incubation). Harvested cores were separated into forest floor (depth ranged from 5–10 cm) and mineral soil and inorganic N (NH_4^+ and NO_3^-) were extracted with 2 N KCl. Quantifying accumulation of inorganic N over time in the incubated cores provides estimates of in situ net N mineralization and nitrification rates. Inorganic N was quantified colorometrically using a Perstorp™ 3000 flow-injection analyzer. The late November samples served as the ''initial'' extractions for all overwinter months (December through March) due to the difficulty of sampling frozen soil (Stottlemyer and Toczydlowski 1996). Values were converted to an areal basis (g N m^{-2}) using forest floor-depth and bulk-density values and mineral-soil (to 10 cm) density values from Bohlen and others (2001). Seasonal data on net nitrification and mineralization appear in Groffman and others (2001).

Stream N Export

Streamwater samples have been collected and analyzed weekly for NO_3^- and NH_4^+ concentrations at the HBEF since 1964 (Likens and Bormann 1995; Buso and others 2000), and long-term patterns for stream NO_3^- concentrations were most recently published in Likens and others (2004). In this study (as in Likens 2004), we report values from the biogeochemical reference watershed (W6). Methods followed standard protocols developed for the HBES over the last 43 years (Likens and Bormann 1995; Buso and others 2000). In summary, streamwater samples were collected above gauging weirs weekly in clean, polyethylene bottles and shipped to the Rachel Carson Analytical Facility at the Institute for Ecosystem Studies for chemical analysis. Export is calculated by multiplying streamflow (mm ha^{-1} d^{-1}) by the concentration (mg L^{-1}) on that day. For dates between samples, the average of the beginning and ending concentration values for the weekly period is applied to the daily flow. Intermediate samples are taken frequently during episodes of high flow (see Buso and others 2000 for details). All values are reported as NO_3^-–N or NH_4^+–N in g N m^{-2}.

Table 1. Environmental and N Cycling Data during the Winter Period (December through March) from the HBEF during 1997–1998 and 1998–1999

Variable	1997–1998	1998–1999
Precipitation (mm)	461	463
Stream flow (mm)	411	460
Average air temperature (°C)	−4.47	−4.80
NO_3^- deposition (g N m^{-2})	0.13	0.17
NH_4^+ deposition (g N m^{-2})	0.03	0.05
Net NO_3^- production[1] (g N m^{-2})	0.8	1.0
Net NH_4^+ production[1] (g N m^{-2})	1.4	1.9
Peak [NO_3^-] (mg N l^{-1}) (month)	0.19 (Jan)	0.75 (Jan)
Average [NO_3^-] (mg N l^{-1})	0.06	0.43
N–NO_3^- export (g m^{-2})	0.03	0.19
Production:export (NO_3^-)	26.7	5.3
Production:export (NH_4^+)	350	950
Percentage of NO_3^--N retention	96.6	84.1
Percentage of NH_4^+–N retention	99.7	99.9

[1]*Data from Groffman and others 2001*

Mass Balance Calculations

Soil retention of NO_3^- was calculated as the difference between sources of NO_3^- to the soil pool (N-deposition and nitrification) and losses of NO_3^- through stream export for W6. Because rates of N fixation (Roskoski 1980) and denitrification (Groffman and others 2001) are very low during winter months and do not contribute significantly to overall NO_3^- budgets, these fluxes were not included in our calculations. We did not include estimates of stream N retention because stream NO_3^- processing is small relative to soil pools (Bernhardt and others 2002; Mulholland and others 2004), particularly in winter.

Results

The long-term record at the HBEF characterizes a remarkably consistent pattern of alternating low and high stream NO_3^- concentrations during the growing (May through September) and non-growing (December through March) seasons, respectively, with a rapid shift between the two patterns (Likens and Bormann 1995, Figure 1). Average winter NO_3^- concentrations were higher in 1998–1998 than 1997–1998 (Table 1) due to lagged effects of an ice storm in January 1998.

Total winter precipitation was virtually identical in the two study years, but its timing and distribution differed. In 1997–1998, average winter air temperature was 0.72°C warmer and December was colder and wetter (http://www.hubbardbrook.org), resulting in earlier and greater snow accumulation. The two years had similar patterns in snow melt, but in 1997–1998 snow melt occurred slightly earlier (~1 week) and was larger because of greater snow accumulation throughout the winter and more precipitation in March (Table 1).

Production of inorganic N in soils occurred over the winter (Figure 2), and there was no difference between stand types (data not shown). Soil NO_3^- production during winter months was similar in the two study years (average of 0.9 g NO_3^-–N for the two study years), an amount exceeding the long-term average annual stream NO_3^- export (0.24 g NO_3^-–N m^{-2} y^{-1}). Although winter soil NO_3^- production was only 8–12% of annual soil NO_3^- production during the 2 study years (Groffman and others 2001), it was 27 and 5 times greater than stream NO_3^- export in winters 1997–1998 and 1998–1999 respectively, and even exceeded annual export (11.4 and 3.6 times respectively; Table 2). Ratios of soil NO_3^- production to stream export were lower in the second year, because stream NO_3^- export was over six times greater than in the previous year (Table 1). Compared to atmospheric inputs of NO_3^- (0.15 g NO_3^-–N m^{-2} during winter), winter soil production of NO_3^- was greater.

Soil NO_3^- retention was high in both years, but slightly lower in the second year because of greater NO_3^- export (97 and 84% respectively; Figure 3). Ammonium retention was very high in both years (>99%). In the second winter of the study (1998–1999) peak NO_3^- concentration and export were higher (~5 times) than in year 1 (1997–1998), but

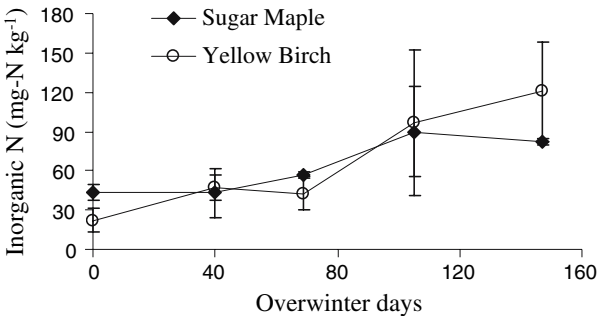

Figure 2. Inorganic N accumulation in soil core incubations. Combined average NO_3^- and NH_4^+ accumulation summed for forest floor and mineral soils in sugar maple and yellow birch plots (Note that NO_3^- production levels off in experimental cores, likely due to immobilization or denitrification. In the field, NO_3^- produced during winter months is likely to leach before these processes can occur). *Bars* indicate standard error ($N = 4$).

NH_4^+ export was (~3 times) lower (Figure 4, Table 1).

Discussion

We focused our attention on the months of minimal plant activity because NO_3^- retention is expected to be lowest during this period. In contrast to summer, which is characterized by large and highly variable internal fluxes among pools and consistently low streamwater export (in the absence of disturbance), winter months are characterized by much smaller internal fluxes but greater export. Thus winter may be a critical period for annual ecosystem N export in these forested ecosystems because NO_3^- export is high relative to internal fluxes at this time and, therefore, may be more sensitive to factors regulating export. The two main findings of our study are, (1) that NO_3^- production in soils during winter months is more than sufficient to account for winter and spring stream NO_3^- export, and (2) that NO_3^- retention by soils is high during the non-growing season, even following major disturbances.

Stream NO_3^- concentrations typically increase in the fall, are sustained throughout the winter, peak during spring run-off, then decline to nearly undetectable levels during the summer growing season. Consequently, the non-growing season dominates annual NO_3^- export. In fact, about 90% of annual export occurs between November and June, and the primary months during which snowmelt occurs (March and April at the HBEF) account for 68% of annual NO_3^- export (Likens and Bormann 1995). At least part of the high export during the spring melt may be due to NO_3^- accumulated in soils over the winter (NO_3^- in snow pack (Brooks and others 1999) and increased decomposition following soil thawing (Peterson and Rolfe 1985) may also contribute to the spring NO_3^- pulse). Because soils rarely freeze and because atmospheric NO_3^- deposition (and therefore snowpack accumulation) is low, soil NO_3^- production is the main source of NO_3^- exported by streams at the HBEF.

One limitation of a mass balance approach is the errors associated with scaling up from point measurements to a catchment. For example, we used measurements of net nitrification from sugar maple and yellow birch stands to estimate average watershed values of NO_3^- release from soils, but ''hot-spots'' of NO_3^- immobilization or denitrification would reduce the magnitude of our soil NO_3^- sink. Denitrification in the plots averaged close to zero (Groffman and others 2001), but showed considerable variation, and denitrification is likely to be higher in hyporheic or lowland areas where organic carbon sources are high. ''Hot moments'' (McClain and others 2003) of denitrification may also account for reduced NO_3^- export. High rates of denitrification have been observed during the snowmelt period (Nyborg and others 1997), and could also account for reduced NO_3^- export when plant N uptake is low. The accuracy of our mass balance is also influenced by the degree to which in situ incubations accurately measure inorganic N production in soils. Nonetheless, our results are consistent with one or more of the following findings found in other systems: (1) winter microbial activity can be important to annual N budgets (Brooks and others 1999), (2) abiotic retention of nitrate may be quite high (Davidson and others 2003) during winter months (Campbell and others, unpublished data), and (3) NO_3^- in streams is largely of microbial origin (Burns and Kendall 2002; Pardo and others 1994).

Microbial activity can be significant under snow cover (for example, Brooks and others 1996; Schadt and others 2003; Schmidt and Lipson 2004), and models indicate that microbial processes in soils can be at least as important as plant uptake in controlling terrestrial N losses (Hong and others 2005). A number of recent studies have shown that atmospheric inputs of inorganic N cycle through microbial pools prior to stream export. For example, stable isotope studies at the HBEF (Pardo and others 2004) and elsewhere (Burns and Kendall 2002; Paitek and others 2005) indicate that stream NO_3^- originates from microbial nitrification, however, the timing of the soil processes that contribute

Table 2. Ecosystem Annual N Fluxes and Pools Measured at the HBEF

Fluxes	g-N m^{-2} y^{-1}	Reference
Plant uptake	9.32	Hong and others (2005)[1]
NO_3^-	0.6	
NH_4^+	8.7	
Nitrification	7–12	Groffman and others (2001)
Mineralization	12–22	Groffman and others (2001)
Denitrification	0–0.65	Groffman and others (2001)
Stream export	0.24	(1964–2002) this study
Stream processing	(±~30%)	Bernhardt and others (2002)
Atmospheric deposition (inorganic)	0.74	This study
Net N cycling	2–14	Aber (1991)
		Likens and Bormann (1995)
		Reich and others (1997)
NO_3^- retention	6–12	(Calculated, this study)
Pools (N)	g-N m^{-2}	
Soil N	130–590	Huntington and others (1998), Bohlen and others (2001)
Above ground biomass	35	Likens and Bormann (1995)
Below ground biomass	18	Likens and Bormann (1995)

[1]*Based on data from Tierney and others (2001), Whittaker and others (1979), Fahey and others (1998), Tierney and Fahey (2001).*

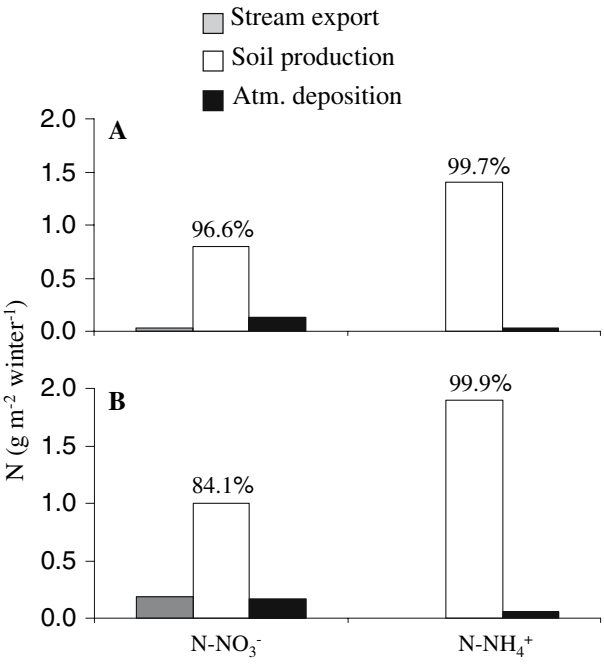

Figure 3. Comparison of NO_3^- inputs, release, and output during the winter season (December–March) for **A** 1997–1998 and **B** 1998–1999. The percent of NO_3^- supplied by inputs and retained in soils is indicated above the *bars*.

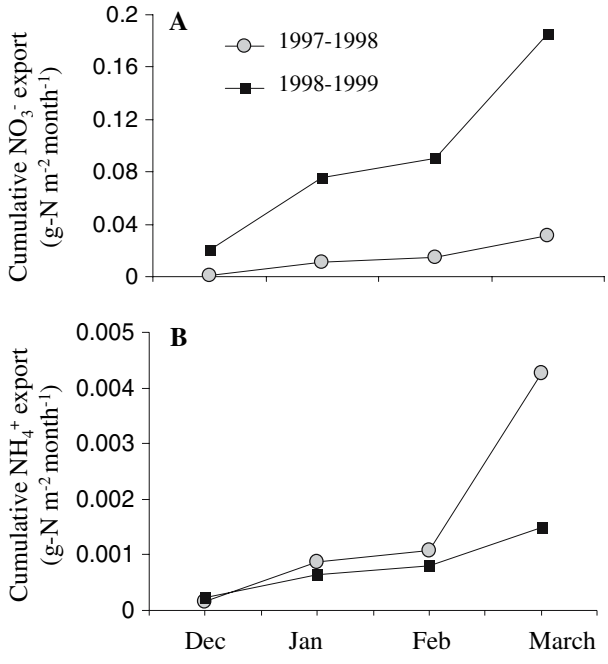

Figure 4. Cumulative stream export of NO_3^- (**a**) and NH_4^+ (**b**) (g N m^2 mo^{-1}) over the course of the winter in (**A**) 1997–1998 and (**B**) 1998–1999.

to stream NO_3^- has not yet been determined. Our study suggests that over-winter soil NO_3^- production is more than sufficient to account for annual stream NO_3^- export. Because plant demand is low during winter, this finding suggests that winter nitrification controls annual catchment NO_3^- export.

Mechanisms of N retention over long time periods (thousands of years) are critical for forest growth and development, particularly in areas with low or negligible amounts of N in geologic substrates. Preferential retention and biological assimilation of NH_4^+ over NO_3^- is thought to be common in forest ecosystems, but biological (for example, Nadelhoffer and others 1984; Stark and Hart 1997) and abiotic (Davidson and others 2003) mechanisms of NO_3^- immobilization may also contribute to the retention of N in forest soils. Microbial immobilization of NO_3^- has been observed in other alpine and boreal ecosystems during snow melt (Brooks and others 1996; Sickman and others 2003). A tracer study at the HBEF, in which $^{15}NO_3^-$ was applied to the snow pack, found that NO_3^-retention in soils during winter and spring was high, but abiotic rather than biological mechanisms dominated (Campbell and others unpublished data). These results are consistent with recent evidence that abiotic immobilization could be an important soil sink for NO_3^- (Berntson and Aber 2000; Dail and others 2001; Perakis and Hedin 2001). Although little is known about the mechanisms of abiotic NO_3^- retention, NO_3^- appears to be rapidly converted to soluble organic N (Dail and others 2001), perhaps through reduction by iron (II) in organic soils and subsequent reactions of nitrite with dissolved organic matter to produce dissolved organic N (Davidson and others 2003).

The two study years included a year of very low export (typical of recent years), and a year of higher export (Figure 1), due to forest disturbance by a severe ice storm (~30% canopy damage in W6; Rhoads and others 2002). Comparing the two years shows that soil NO_3^- retention at HBEF is high even during years of high export. In fact, in the year of the highest NO_3^- export on record (1974, 0.37 g NO_3^-–N m^{-2} $winter^{-1}$), 59% of NO_3^- that was produced in soils over the winter was retained (calculated using winter nitrification rates from Groffman and others 2001). Thus, strong mechanisms of NO_3^- retention operate even during natural disturbances.

Changes in winter climatic conditions have the potential to impact N export through both physical and biological mechanisms, although we lack a clear understanding of the extent and direction of these effects. Current evidence suggests that physical effects may be stronger than biological effects. For example, increased NO_3^- leaching occurs at the HBEF with reduced snow cover (and increased soil freezing) due to root mortality and altered root-soil-microbe interactions (Mitchell and others 1992; Fitzhugh and others 2003), whereas reductions in snow pack had only weak effects on microbial immobilization and production (Groffman and others 2001). Effects of climate change on an abiotic retention mechanism are not known. Thus our current understanding points to increased NO_3^- losses with reduced winter snow-pack.

This study shows that a mass balance of NO_3^- in the HBEF reveals high soil NO_3^- retention during the winter months, despite low plant N uptake and high stream NO_3^- export at this time. These unexpected results are consistent with a strong abiotic retention mechanism and point to the need for studies aimed at elucidating this mechanism. Because the magnitude of soil NO_3^- retention is great, small changes in retention could have a dramatic effect on watershed NO_3^- export. Therefore, understanding the controls on soil NO_3^- retention is critical if we are to predict how changing winter climate regimes will impact overall N budgets in forest ecosystems.

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