

The Long-term Effects of Disturbance on Organic and Inorganic Nitrogen Export in the White Mountains, New Hampshire

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ABSTRACT

Traditional biogeochemical theories suggest that ecosystem nitrogen retention is controlled by biotic N limitation, that stream N losses should increase with successional age, and that increasing N deposition will accelerate this process. These theories ignore the role of dissolved organic nitrogen (DON) as a mechanism of N loss. We examined patterns of organic and inorganic N export from sets of old-growth and historically (80–110 years ago) logged and burned watersheds in the northeastern US, a region of moderate, elevated N deposition. Stream nitrate concentrations were strongly seasonal, and mean (\pm SD) nitrate export from old-growth watersheds (1.4 ± 0.6 kg N ha⁻¹ y⁻¹) was four times greater than from disturbed watersheds (0.3 ± 0.3 kg N ha⁻¹ y⁻¹), suggesting that biotic control over nitrate loss can persist for a century. DON loss averaged $0.7 (\pm 0.2)$ kg N ha⁻¹ y⁻¹ and accounted for 28–87% of total dissolved N (TDN) export. DON concentrations did not vary seasonally or with suc-

cessional status, but correlated with dissolved organic carbon (DOC), which varied inversely with hardwood forest cover. The patterns of DON loss did not follow expected differences in biotic N demand but instead were consistent with expected differences in DOC production and sorption. Despite decades of moderate N deposition, TDN export was low, and even old-growth forests retained at least 65% of N inputs. The reasons for this high N retention are unclear: if due to a large capacity for N storage or biological removal, N saturation may require several decades to occur; if due to interannual climate variability, large losses of nitrate may occur much sooner.

Key words: disturbance; dissolved organic carbon; dissolved organic nitrogen; fire; logging; nitrate leaching; nitrogen saturation; nitrogen retention; old growth; succession.

INTRODUCTION

Human activities have vastly changed the global nitrogen (N) cycle (Galloway and others 1995; Vitousek and others 1997). Nitrogen deposition to the eastern United States has increased at least five- to

10-fold since preindustrial times, and even higher N deposition rates occur in western Europe (Galloway and others 1995; Holland and others 1999). In order to anticipate the downstream consequences of this large change in N inputs, it is important to understand the mechanisms that control ecosystem N retention. Traditional biogeochemical theories suggest that ecosystem N losses are controlled by varying degrees of biotic N limitation, with N losses increasing as N availability exceeds plant and microbial demand. Essentially:

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$$\text{N losses} = \text{N availability} - \text{biotic N demand}, \quad (1)$$

with N availability affected by N mineralization and N inputs from deposition and fixation, and biotic N demand controlled by plant uptake and microbial immobilization. More than two decades ago, Vitousek and Reiners (1975) proposed that changes in the rate of plant and soil accumulation over the course of ecosystem succession should affect the loss of limiting nutrients, from tight cycling and few losses in rapidly growing early- and mid-successional systems, to elevated losses and essentially no net retention in steady-state old-growth systems (see also Bormann and Likens 1979; Gorham and others 1979; Reiners 1981). Increasing N supplies from atmospheric deposition should also affect biotic N retention, as elevated N inputs gradually satisfy biotic N demands and lead to increased nitrification and N losses through a series of stages of N saturation (Aber and others 1989). Together these theories suggest that elevated N deposition should accelerate the succession-related decline in N retention and that old-growth forests should be closer to N saturation than aggrading forests (for example, van Miegroet and others 1992; Stoddard 1994; Aber and Driscoll 1997).

This conceptual model largely focuses on processes affecting dissolved inorganic N (DIN) pools, even though dissolved organic N (DON) makes up the majority of hydrologic N loss from many systems (Sollins and others 1980; Hedin and others 1995; Lajtha and others 1995; Lewis and others 1999; Campbell and others 2000). Are DON losses also controlled by biotic N demand? Hedin and others (1995) speculate that DON export from unpolluted temperate old-growth forests represents a chronic loss that is free from direct biotic control but subject to indirect biotic control via the production, transport, and leaching of dissolved organic matter. Neff and others (2000) and suggest that stream export of DON is controlled both by biotic factors affecting dissolved organic carbon (DOC) production in the forest floor (for example, McDowell and Likens 1988; Qualls and others 1991; Currie and others 1996) and by abiotic factors such as soil texture and mineralogy, which affect DOC sorption to mineral soil (for example, McDowell and Wood 1984; Moore and others 1992). DON production has been shown to increase with N inputs (Currie and others 1996; McDowell and others 1998), a response consistent with partial biotic regulation of N loss as DON. However, Neff and others (2000) demonstrate that increases in DON production are slow and small relative to increases in N input; they

occur only at the most N-limited sites; and they are largely due to declining soil C:N ratios rather than to decreasing microbial N demand. Losses of DON despite strong N limitation suggest a largely abiotic control over this form of N loss, which in turn may act to maintain chronic N limitation (Hedin and others 1995; Vitousek and others 1998; Neff and others 2000).

Vitousek and others (1998) recognized the oversights of the traditional conceptual model of wholly biotic control over N losses, and they used a simple, quantitative model of N cycling to predict the long-term impacts of chronic losses of DON and N gases, with DON losses assumed to be essentially independent of plant and microbial demand for N. Under natural conditions of low N deposition, they predicted that DON loss could induce long-term ecosystem N limitation, with total dissolved N (TDN) loss dominated by DON and with trivial increases in TDN loss over 5000 years of succession. When they modeled N deposition at elevated rates similar to those in the eastern US, Vitousek and others (1998) predicted that TDN loss increased greatly over time due to a large increase in DIN loss and a small increase in DON loss.

We tested whether stream N export from forests in the White Mountain National Forest (WMNF), New Hampshire, followed predictions from this revised conceptual model of biotic and abiotic controls over the amount and form (DIN or DON) of ecosystem N loss. This region has received moderately elevated N deposition for at least three decades (Likens and Bormann 1995). We hypothesized that variation in biotic demand would affect the pattern and magnitude of DIN loss, whereas DON loss would follow patterns of DOC loss. We expected that biotic control over N loss would be reflected in seasonal and successional differences in plant and microbial uptake, with elevated DIN losses during the dormant season relative to the growing season and in old-growth stands relative to successional stands. The WMNF has a relatively well-defined disturbance history, largely consisting of extensive logging and slash fires 80–110 years ago. Remnant old-growth stands exist, and limited forest harvests have continued through the present. Additional modeling studies suggested that watersheds that had experienced severe losses of N in slash fires would presently have lower losses of DIN than forests that had experienced less severe N losses through biomass harvest only (Aber and Driscoll 1997). We tested this hypothesis by comparing N export from logged and burned watersheds.

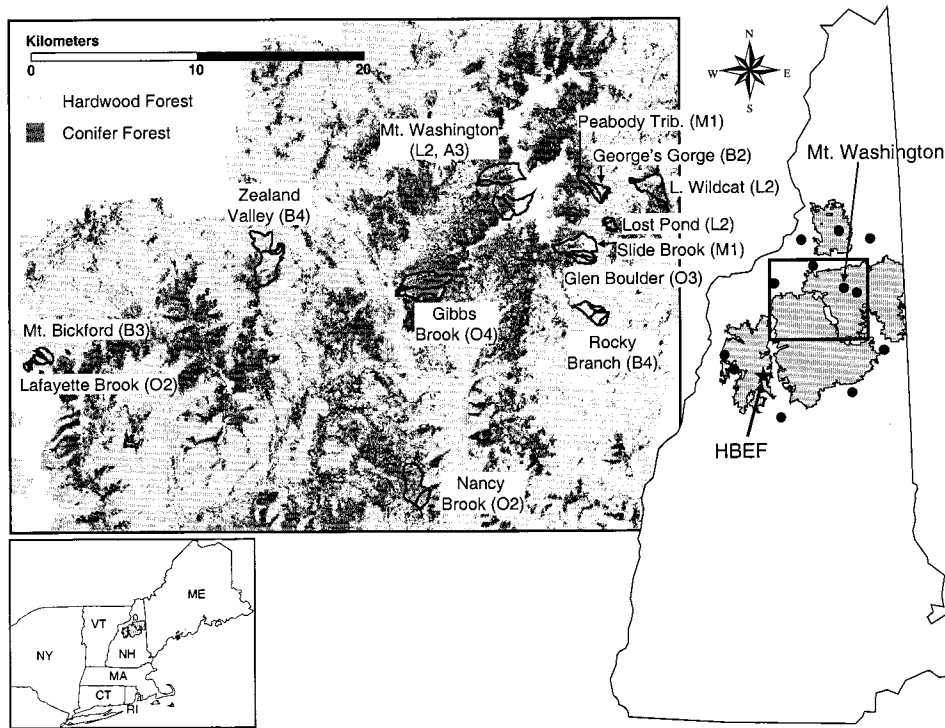


Figure 1. Location of precipitation gauging stations within New Hampshire (●) and watershed boundaries in the White Mountain National Forest. Site names are followed by letters and numbers indicating disturbance type (B, burned; L, logged; O, old-growth; A, alpine; M, mixed) and the number of watersheds at each site.

METHODS

Site Description

The WMNF contains 3000 km² of forest in north-central New Hampshire (Figure 1). Northern hardwoods cover the lower slopes and largely consist of yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), red spruce (*Picea rubens*), and eastern hemlock (*Tsuga canadensis*). Paper birch (*B. papyrifera*), red maple (*A. rubrum*), poplar (*Populus spp.*), and white pine (*Pinus strobus*) are common in early- and mid-successional forests (Leak 1991). Subalpine spruce and fir (*Abies balsamea*) dominate above 750 m, until the treeline gives way to alpine tundra around 1400 m (Leak and Graber 1974; Reiners and Lang 1979).

Over 40 peaks exceed 1200 m, but nearly 90% of the land area falls below 750 m. Bedrock geology consists primarily of highly metamorphosed Devonian aluminum schists and Mesozoic granites (Hatch and Moench 1984). Soils are generally Spodosols: Haplorthods occur at low elevations and grade to Cryorthods, Cryohumods, and Cryofolists at high elevations (Huntington and others 1988, 1990). Precipitation is distributed evenly throughout the year (Federer and others 1990) and increases with elevation (Dingman 1981) from a long-term average of 100 cm y⁻¹ at 300 m elevation

to 230 cm y⁻¹ at the summit of Mount Washington (1917 m). Snowpacks accumulate in winter, and stream flow usually peaks with April snowmelt (Federer and others 1990). The Hubbard Brook Experimental Forest (HBEF) in the southwestern WMNF (Figure 1) has maintained long-term measurements of watershed hydrology and chemistry (Likens and Bormann 1995). During the early 1990s, bulk deposition of inorganic N (NH₄⁺ - N + NO₃⁻ - N) was 6.2–9.1 kg ha⁻¹ y⁻¹ at the HBEF and nearby Cone Pond, with DON contributing an additional 1.4–2.4 kg ha⁻¹ y⁻¹ (Hornbeck and others 1997, Campbell and others 2000). Nitrogen deposition generally increases with elevation, due to increased precipitation, wind-driven dry deposition, and cloud cover (Lovett and Kinsman 1990).

Forest History

Widespread clear-cutting and slash fires in the late 1800s and early 1900s arguably represent the most extensive disturbances to White Mountain forests during the last several millennia. The northern hardwood community was established in its current form at least 7000 years ago, although red spruce did not join the present spruce-fir zone until 2000 years ago (Spear and others 1994). Fires occurred rarely (Spear and others 1994), with return intervals estimated at 1500 to 2500 years (Lorimer 1977; Fahey and Reiners 1981). Wind is generally consid-

ered to be the primary mechanism of natural disturbance in northern New England. Large (more than 25 ha), infrequent blowdowns recur approximately every 1150 years (Lorimer 1977), although small windthrow gaps are much more common (Bormann and Likens 1979).

Starting in 1867, the state of New Hampshire sold large tracts of White Mountain forest to timber and paper companies. Intense clear-cutting and slash fires followed over the next several decades, peaking around 1907. Public criticism of these forest practices led to passage of the Weeks Act in 1911, which funded the federal purchase of forest land. Prior to government purchase (generally 1911–39), foresters surveyed and mapped each forest tract. Most of these historical surveys still exist (USDA Forest Service, Laconia, New Hampshire), and they provide a relatively complete record of the spatial extent of logged, burned, second-growth, and old-growth forest in the early 1900s.

The historical survey maps were used to locate 11 sites with relatively homogeneous land-use histories. Each site contained two to four small watersheds (Figure 1). Four sites (13 watersheds) burned between 1886 and 1914; three sites (six watersheds) were heavily logged between 1885 and 1910; and four sites (11 watersheds) have no record of human disturbance (Table 1). We sampled two additional watersheds with mixed land-use histories and three watersheds draining alpine tundra, for a total of 35 streams. Only 11 streams were named; the rest were referred to by letter and site name (Table 1). Soil charcoal fragments were found at the sites mapped as having been burned, but not at the logged or old-growth sites. Disturbance dates were estimated from tree increment cores, from the historical surveys, or from other historical records (Chittenden 1904; Belcher 1980). Three of the four old-growth sites have been documented previously: the Gibbs Brook Scenic Area (Foster and Reiners 1983), the Nancy Brook Research Natural Area (Oosting and Billings 1951; Leak 1975), and the Lafayette Brook Scenic Area (Sperduto and Engstrom 1993). (These sites contain several small streams in addition to their namesake brooks.) The fourth old-growth site, Glen Boulder, was identified from historical survey maps and stand compartment records (USDA Forest Service, Conway, New Hampshire).

Sample Collection and Analysis

Stream-water samples were collected monthly from October 1996 to September 1997, except at the Nancy Brook, Mount Washington, and Mount Bickford sites, which were sampled from May to September 1997. Nancy Brook and Mount Wash-

ington are difficult to access in winter, and Mount Bickford was added late in the study. These three sites were included in comparisons of growing season stream chemistry, but were not included in estimates of annual N flux. Two streams were added to the Gibbs Brook site in January and February (streams A and D, respectively); missing chemistry was approximated from values from the two other streams at this site. Stream samples were collected over 2–3 days in the middle of each month, but could not be collected in December 1996. For annual flux calculations, December concentrations were estimated as the mean of November 1996 and January 1997 values, as indicated by the long-term (1965–92) mean pattern of monthly stream chemistry at HBEF Watershed 6 (data online at: <http://www.hbrook.sr.unh.edu/>).

After prerinsing with stream water, samples were collected in 250-mL acid-washed (10% HCl), well-rinsed, high-density polyethylene (HDPE) bottles. Samples were refrigerated after collection until processing the following day. An Orion combination electrode was used to measure the pH of subsamples allowed to warm to room temperature. The remaining sample was vacuum-filtered through ashed (1 h at 425°C), rinsed, Whatman GF/F glass fiber filters (nominal pore size 0.7 μm), and subsamples were frozen in 30-mL polyethylene (NO_3^- and NH_4^+) or HDPE (DOC and TDN) vials. After thawing, NO_3^- samples were refiltered through 0.2 μm nominal pore-size Acrodisks (Gelman Sciences) to conform with protocol for analysis on a Waters ion chromatograph and a Dionex AS4A column with micromembrane chemical suppression. Ammonium was measured with flow injection analysis using the automated phenate method on a Lachat QuikChem AE. DOC and TDN were measured in separate analyses of thawed samples using high-temperature (680°C) catalytic (Pt) oxidation with a Shimadzu TOC 5000. DOC samples were acidified and sparged prior to analysis. TDN was determined by reaction with ozone and chemiluminescent detection with an Antek 720C N detector (Merriam and others 1996). DON was calculated by difference: $\text{DON} = \text{TDN} - \text{DIN}$.

Forest Cover Determination

Satellite-derived land cover information was obtained from the New Hampshire Geographically Referenced Analysis and Information Transfer System (NH GRANIT, Durham, New Hampshire). NH GRANIT classified Landsat TM images (spatial resolution of 30 m) from 1986 to 1990 into the following 10 types of land cover: agriculture, developed land, open/disturbed land, rock, tundra,

Table 1. Site, Disturbance Type and Date, and Watershed Characteristics

Site (Disturbance date)	Stream (name)	Area (ha)	Elev (m)		Vegetation (%)			
			Min.	Mean	Hard.	Mix.	Con.	Non.
Burned								
Rocky Branch (1912–14)	A	16	509	637	100			
	B	44	519	694	100			
	C	65	533	878	99	1	<1	
	D	17	540	708	100			
George's Gorge (c. 1903)	A (Peabody Brook)	37	637	797	75	9	15	1
	B	7	644	746	73	7	20	
Zealand Valley (1886)	A	114	511	654	87	4	9	1
	B	4	522	574	76	17	7	
	C	17	526	631	99	1		<1
	D (Hale Brook)	225	531	878	54	15	30	1
Mount Bickford ^a (1903)	B	9	572	576	70	13	17	
	C	27	570	618	72	13	15	
	D	8	576	595	100			
Logged								
Little Wildcat (c. 1895)	A (L. Wildcat Brook)	175	533	872	38	14	47	<1
	B	6	533	580	97	1	2	
Lost Pond (c. 1895)	A	12	615	659	63	15	22	1
	B	26	614	715	17	21	62	1
Mount Washington ^a (c. 1910)	B	22	888	949	13	10	68	9
	C	4	873	890	5	6	89	
Old growth								
Glen Boulder	B	36	543	905	75	6	13	6
	C	14	540	767	93	2	1	6
	D	42	534	929	61	6	31	2
Gibbs Brook	A (Gibbs Brook)	218	640	966	7	11	80	2
	B	10	670	678	34	14	52	
	C (Elephant Head)	123	583	930	9	10	73	7
	D	4	586	598	88	10	2	
Lafayette Brook	A	9	587	604	n/a			
	B	7	588	611	n/a			
Nancy Brook ^a	A (Nancy Brook)	215	733	995	9	23	62	6
	B	58	724	856	6	43	45	5
Alpine or mixed land uses								
Subalpine/landslide	Slide Brook	186	558	1005	58	7	26	9
Subalpine/logged	Peabody Tributary	68	632	963	32	9	56	2
Mount Washington ^a	A (Clay Brook)	232	876	1212	12	15	44	30
	D (Monroe Brook)	105	983	1316	3	7	63	28
	E (Ammonoosuc)	108	1049	1499	1	<1	25	74

Hard., hardwood; Con., conifer; Mix., mixed hardwood/conifer; Non., nonforest (rock, tundra, or wetland).

Most streams were unnamed and are indicated by letter.

^aStreams sampled May–September 1997; all others sampled October 1996–September 1997.

Table 2. Predicted (PnET-II) and Observed Stream Flow for the October 1996–September 1997 Water Year for Five White Mountain Watersheds

	Size (ha)	Mean Elev. (m)	Stream flow (cm)	
			Observed	Predicted
Hubbard Brook Watershed 6 ^a	13	670	105	100
Hubbard Brook Watershed 7 ^a	76	760	105	112
Ammonoosuc River at Bethlehem ^b	22757	740	94	103
Ellis River above Jackson ^b	2832	958	129	134
East Branch Pemigewasset River ^b	29875	803	112	118

^aStream flow for the Hubbard Brook watersheds was obtained from <http://www.hbrook.sr.unh.edu/>.

^bUSGS stream flow was obtained from <http://bowdnhbow.er.usgs.gov/annual.html>.

wetlands, water, and hardwood, conifer, and mixed hardwood/conifer forest. Accuracy assessments indicated a statewide accuracy of 70% across all cover types (Rubin and others 1993).

Exact stream sampling locations were identified with a Trimble Pro XR Global Positioning System (Sunnyvale, California). Automated methods of watershed definition were not used because several watersheds were too small to delineate with the available digital elevation models (DEM). Watersheds were delineated by hand on 1:24,000 USGS topographic maps and digitized with Arc/Info 7.1.1 (ESRI, Redlands, California). Watershed boundaries (Figure 1), land cover, and DEM data were overlaid with ERDAS Imagine 8.3 (Atlanta, Georgia).

Streamflow and Nitrogen Export

None of the sampled streams was gaged. Stream flow was estimated for all of the sampled watersheds by using available climate data and a model of carbon and water balance, PnET-II (Aber and others 1995). The model uses inputs of precipitation, temperature, and solar radiation to calculate monthly evapotranspiration, snowpack development, and stream flow. The model has captured temporal patterns of monthly stream flow at Hubbard Brook (Aber and others 1995) and spatial patterns of mean annual flow across New England (Ollinger and others 1998). PnET-II was run for each 30-m pixel in each sampled watershed, for a total of over 30,000 pixels.

Monthly precipitation data were obtained for the following 12 US cooperative or National Weather Service stations in the White Mountain region: Benton, Berlin, Bethlehem, Glenduff, Jefferson, Lancaster, Mount Washington, North Conway, Pinkham Notch, Plymouth, Tamworth, and York Pond (Figure 1) (NOAA data online at: <http://www.ncdc.noaa.gov/pub/data/coop-precip/>). During

the 1996–97 water year, precipitation exceeded long-term (1971–90) averages by 6%–20%. Monthly averaged maximum and minimum daily temperature data were obtained for the Bethlehem and Mount Washington weather stations and for four stations at the HBEF (Federer and others 1990; and online at: <http://www.hbrook.sr.unh.edu/>). Precipitation and temperature were estimated at each 30-m pixel using its elevation and linear orographic factors developed from the available climate data. Elevation-based regressions explained 67% of the spatial variability in monthly precipitation measurements and predicted annual precipitation within 2 and 21 mm of measured values at HBEF Watersheds 6 (W6) and 7 (W7), respectively.

Monthly stream N export (kg ha^{-1}) was estimated by multiplying measured N concentration by modeled monthly stream flow, with monthly fluxes totaled for the water year. The reliability of this approach depended on (a) the accuracy of modeled stream flow, and (b) the ability of stream chemistry from a single day to represent mean monthly values. To verify PnET-II estimates of stream flow during 1996–97, the model was tested at the following five gaged watersheds in the WMNF: the Ellis, Ammonoosuc, and East Branch of the Pemigewasset Rivers, all gaged by the USGS, and W6 and W7 of the HBEF (Table 2). W6 and W7 are similar in size to the watersheds we sampled; the USGS watersheds are much larger but are in closer proximity to the sampled watersheds. During 1996–97, gaged stream flows exceeded long-term averages by 10%–20%.

PnET-II predicted annual flow within 4%–10% of measured values at all five watersheds (Table 2) and largely reproduced monthly stream flow patterns (Figure 2). The model slightly overestimated flow in October and late summer, and it underestimated flow in December. PnET-II predicted a later

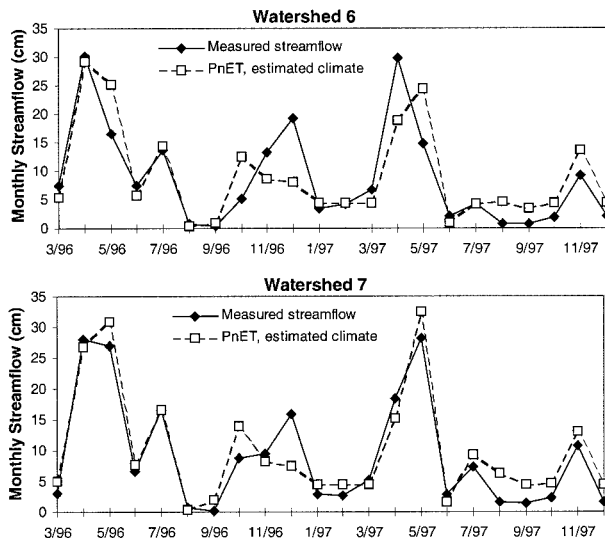


Figure 2. Predicted and observed monthly stream flow for Watersheds 6 and 7, Hubbard Brook Experimental Forest.

snowmelt than observed at the south-facing W6, but it accurately predicted peak snowmelt flows in May at the north-facing W7 (Figure 2) and at the three USGS watersheds (not shown). These errors in predicting W6 stream flow led to an underestimate of W6 NO_3^- -N flux by approximately $0.1 \text{ kg ha}^{-1} \text{ y}^{-1}$ for June 1996–May 1997 (chemistry from Campbell and others 2000). If similar errors occurred at the streams sampled in this study, then NO_3^- -N flux may have been underestimated by an average of $0.1 \text{ kg ha}^{-1} \text{ y}^{-1}$, or 18% (range, less than 0.01 to $0.46 \text{ kg ha}^{-1} \text{ y}^{-1}$), with the largest errors occurring in streams with the highest NO_3^- concentrations. Stream-flow errors similar to those at W7 would lead to mean underestimates of NO_3^- -N flux by only $0.05 \text{ kg ha}^{-1} \text{ y}^{-1}$, or 7% (range, $+0.05$ to $-0.22 \text{ kg ha}^{-1} \text{ y}^{-1}$).

The use of a single sample to represent monthly mean stream chemistry can also lead to errors in estimates of annual element flux. Concentrations of NO_3^- (Murdoch and Stoddard 1992; Creed and Band 1998), DOC (McDowell and Likens 1988; Hornberger and others 1994), and DON (McHale and others 2000) often increase at the start of high-flow events due to changes in hydrologic flowpaths and flushing of upper soil horizons; failure to sample high-flow periods may cause underestimates of annual flux. Most sampling dates in this study occurred during base flow conditions, although April and May sampling coincided with high snowmelt flows. During the growing season, both event (June and July) and base flow (August and September)

conditions were sampled by chance without discernible effects on NO_3^- concentrations, although DOC and DON concentrations in some streams responded to the summer events. McHale and others (2000) indicate that inclusion of storm-flow sampling affected estimates of annual NO_3^- -N and DON flux by 0.14 and $0.25 \text{ kg ha}^{-1} \text{ y}^{-1}$, respectively, compared to biweekly sampling alone. Swistock and others (1997) and Eshleman and others (1998) report that monthly sampling of stream chemistry coupled with continuous stream-flow measurements usually yielded estimates of annual NO_3^- flux within 10% (range, -25% to $+41\%$) of estimates based on near-continuous chemical sampling. Hence, we expect that our estimates of stream N flux could have been biased by several tenths of a $\text{kg ha}^{-1} \text{ y}^{-1}$, but that these errors were likely small relative to the large uncertainties regarding N inputs.

Nitrogen Retention

Net N retention was assessed across watersheds by comparing annual stream N export (TDN_{out}) with simple estimates of N inputs (TDN_{in}): N Retention (%) = $(\text{TDN}_{\text{in}} - \text{TDN}_{\text{out}}) / \text{TDN}_{\text{in}} \times 100$. Nitrogen inputs were estimated roughly as N deposition of varying precipitation amount and constant N concentration, similar to Ollinger and others (1993) and Miller and others (1993), and supported by a review by Lovett and Kinsman (1990). Precipitation amount was estimated from the elevation-based regressions, and N concentration was set at 0.60 mg/L . This value is the mean TDN concentration of bulk deposition collected at HBEF and Cone Pond during 1995–97, consisting of 54% NO_3^- -N, 28% NH_4^+ -N, and 18% DON (Campbell and others 2000). Bulk deposition includes both wet and some dry deposition, but it generally underestimates total (wet + dry) deposition (Lovett 1994; Lovett and others 1997). Mount Washington and other eastern US mountain peaks receive substantial N inputs through cloud deposition (Lovett and others 1982; Weathers and others 1988; Lovett and Kinsman 1990; Miller and others 1993), but we did not include this mechanism of deposition because of the lack of data quantifying local cloud chemistry or cloud exposure. Because we did not include cloud deposition and probably underestimated dry deposition, we expect that our estimates of N deposition substantially underestimated true values but provide a minimal index of N inputs.

Statistical Analyses

Differences in stream N concentration due to land-use history (burned, logged, or old-growth) (Table

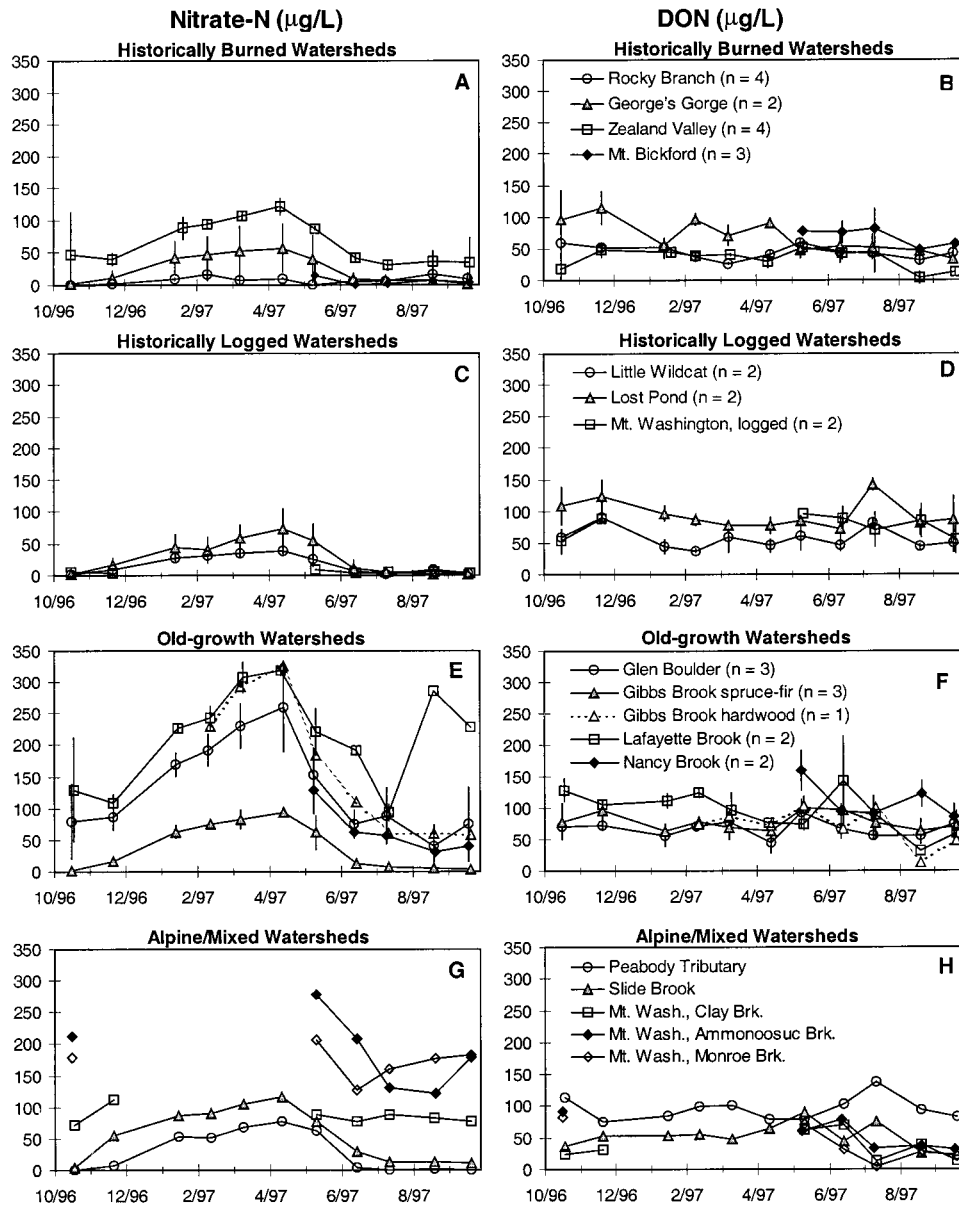


Figure 3. Monthly NO_3^- -N and DON concentrations of burned (A, B), logged (C, D), old-growth (E, F), and alpine or mixed-history (G, H) sites. Plotted concentrations are the mean (± 1 SD) of two to four streams at each site (n in parentheses).

1) were determined by repeated measures analysis of variance. A nested design was used to evaluate the effects of land-use history during each measurement period after considering the variability of neighboring streams within the same site and among sites with the same land-use history. Land-use history effects on N flux were assessed with similarly nested ANOVAs. Scheffe's tests were used for all post hoc pairwise comparisons. Sites with only growing-season collections (Nancy Brook, Mount Washington, and Mount Bickford) were excluded from the ANOVAs, so that statistical analyses of the effects of land-use history included three burned sites (10 streams), two logged sites (four streams), and three old-growth sites (nine streams),

for a total of 23 streams. All streams ($n = 35$) were included in analyses of mean growing-season chemistry, although the three watersheds containing large areas of tundra and two watersheds with missing land cover data were not included in analyses of forest cover ($n = 30$).

RESULTS

Watershed Characteristics

The GIS analyses provided estimates of watershed area, mean elevation, and forest cover (Table 1). Watersheds ranged in size from 4 to 232 ha, with a median size of 27 ha. Mean watershed elevation

ranged from 574 to 1499 m, with a median of 746 m. Northern hardwoods dominated most watersheds, although spruce-fir forests were common on the higher watersheds, and three watersheds on Mount Washington had at least 28% alpine tundra cover. On average, the historically burned watersheds had less spruce-fir cover (9%) than the logged (27%) or old-growth (33%) watersheds. These differences in forest cover could be attributed to the differences in land-use history or to differences in mean elevation: the burned watersheds were slightly lower (696 m) than the logged (778 m) or old-growth watersheds (804 m).

Stream Chemistry

Nitrate concentrations were strongly seasonal in all streams, with relatively high concentrations during the dormant season and low concentrations during the growing season (Figure 3). Old-growth watersheds had significantly higher NO_3^- -N concentrations than historically disturbed watersheds, particularly during the dormant season (Figure 4). Nitrate concentrations did not differ significantly between historically logged and burned sites in any month. Three of the four streams sampled at the old-growth Gibbs Brook Scenic Area had low NO_3^- -N concentrations relative to the other old-growth watersheds, whereas the fourth stream had some of the highest NO_3^- -N concentrations in the study (Figure 3E). Growing-season NO_3^- -N concentrations were constantly elevated at two watersheds draining alpine tundra and unlogged subalpine forest on Mount Washington (Monroe and Ammonoosuc brooks) (Figure 3G). Forests on the lower part of the third alpine watershed (Clay Brook) were logged around 1910, and its NO_3^- concentrations (Figure 3G) were intermediate to the unlogged alpine/subalpine watersheds and the near-zero values of adjacent logged watersheds (Figure 3C).

The seasonal and successional patterns in NO_3^- -N concentrations drove seasonal and successional differences in TDN concentrations, because NH_4^+ -N concentrations were low (6–16 $\mu\text{g/L}$, not shown) and DON concentrations did not vary seasonally or by land-use history (Figure 4). DON concentrations varied moderately from stream to stream, and some streams responded to high-flow events in June and July, but otherwise DON varied little (Figure 3). DON accounted for over half of unweighted mean annual TDN concentrations in the burned (57%) and logged (69%) watersheds, and slightly less than half (42%) in the old-growth watersheds. These differences were due not to vary-

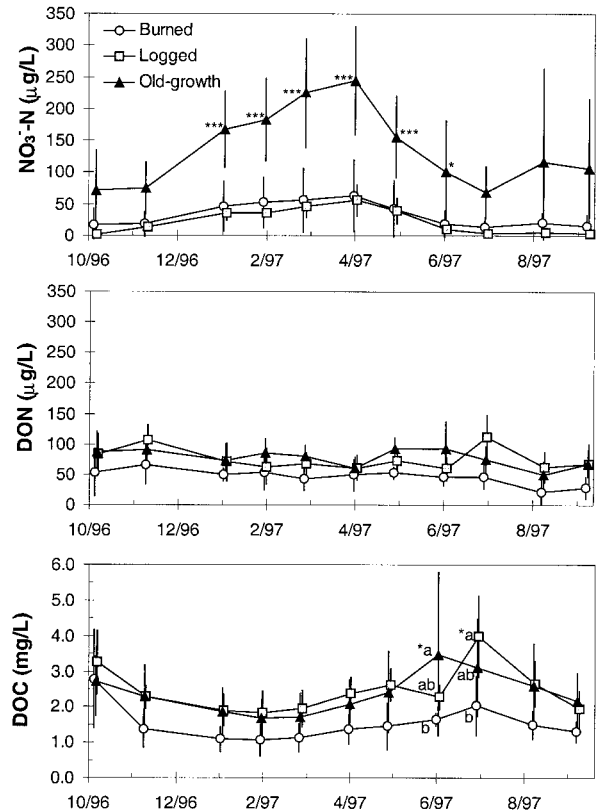


Figure 4. Stream concentrations by land-use history. Error bars are the standard deviation of concentrations among different sites. * $P < 0.05$, *** $P < 0.0001$ for significantly different concentrations within a month.

ing DON concentration but to increased NO_3^- -N concentration in the old-growth streams.

Patterns of stream DOC concentration were generally similar to patterns of DON concentration. DOC concentrations appeared to be slightly lower in burned watersheds than in old-growth or logged watersheds, but this difference was statistically significant only in June and July, respectively, following precipitation events (Figure 4). DOC concentrations were usually between 1.0 and 2.5 mg/L, although concentrations reached 5.0–8.0 mg/L in several streams after summer rainstorms. While DON concentration varied little throughout the year, DOC concentrations were slightly higher during the growing season (base flow mean = 2.1 mg/L) than during the winter (mean = 1.5 mg/L). These small differences in DOC concentration led to higher mean DOC:DON ratios during the growing season (37) than during the winter (24). DOC:DON ratios did not differ significantly by land-use history in any month.

Compared across all streams during the growing season, DON concentrations generally correlated

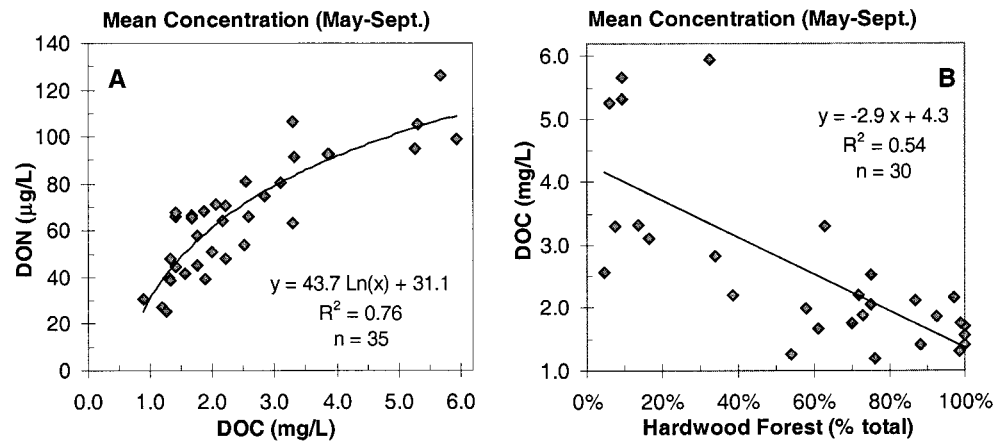


Figure 5. Relationships between mean growing season (May–September) DON and DOC concentrations (A), and DOC concentration and forest type (B).

with DOC concentrations (Figure 5A). However, the best fit to this relationship suggested that DOC:DON ratios increased at high DOC concentrations, from a DOC:DON ratio of about 35 for DOC concentrations less than 3.0 mg/L to ratios of more than 50 for DOC concentrations greater than 5.0 mg/L. DOC concentrations correlated with vegetation type, decreasing as the fraction of hardwood forest cover increased (Figure 5B).

Fluxes of Water and Nitrogen

Elevation-based regressions were used to predict monthly precipitation values, which in turn were used to estimate annual N deposition. Estimated precipitation ranged from 144 cm y^{-1} at the lowest watersheds to 237 cm y^{-1} at the alpine watersheds (not shown), with an overall median of 161 cm y^{-1} (Table 3). Corresponding estimates of bulk N deposition ranged from at least 8.7 to 14.2 kg $ha^{-1} y^{-1}$ (median, 9.6 kg $ha^{-1} y^{-1}$), although actual N deposition was likely higher due to additional dry and cloud deposition. Stream flow was predicted to increase with watershed mean elevation from 87 to 201 cm y^{-1} , due primarily to the predicted increase in precipitation, but also to a modeled decrease in evapotranspiration from 57 to 35 cm y^{-1} . PnET-II predicted substantial differences among watersheds in the timing and magnitude of snowmelt at different elevations (for example, Figure 2), with snowmelt peaks predicted in April for the lowest watersheds and in June for the high alpine streams on Mount Washington.

Differences among streams in predicted N export resembled differences in mean N concentration. The median NO_3^- -N loss was 0.6 kg $ha^{-1} y^{-1}$, with a range from 0.05 kg $ha^{-1} y^{-1}$ in the burned Rocky Branch watersheds to approximately 2.0 kg $ha^{-1} y^{-1}$ in the Glen Boulder and Lafayette Brook old-

growth sites (Table 3). We estimate that Ammonoosuc Brook, an alpine stream, exported nearly 3.0 kg NO_3^- -N ha^{-1} during May–September alone. If this stream had maintained its peak May N concentrations all winter, annual NO_3^- -N export hypothetically could have reached 4.0 kg $ha^{-1} y^{-1}$ and TDN export, 5.3 kg $ha^{-1} y^{-1}$. Across all streams, NH_4^+ -N export averaged 0.1 kg $ha^{-1} y^{-1}$ and varied little. The median DON loss was 0.7 kg $ha^{-1} y^{-1}$, with a range from 0.4 kg $ha^{-1} y^{-1}$ in the Zealand Valley to 1.4 kg $ha^{-1} y^{-1}$ in one of the Gibbs Brook streams (C-Elephant Head Brook) (Table 3). On average, DON made up 54% of total N export and ranged from 35% in the Zealand Valley to over 80% in Rocky Branch streams. Patterns of DOC loss were similar to patterns of DON loss, with lowest export in the Zealand Valley (11 kg $ha^{-1} y^{-1}$) and highest export in Elephant Head Brook (62 kg $ha^{-1} y^{-1}$) and a tributary to Peabody Brook (67 kg $ha^{-1} y^{-1}$). The median DOC loss was 20 kg $ha^{-1} y^{-1}$.

TDN export from the old-growth watersheds was double that from the logged or burned watersheds ($F_{2,5} = 6.46$, $P = 0.04$), due to three- to fourfold differences in NO_3^- -N loss (Figure 6). TDN export differed significantly among sites with the same land use ($F_{5,15} = 7.4$, $P = 0.001$), largely because the Gibbs Brook site had lower NO_3^- -N losses than the other two old-growth sites with annual flux estimates (Table 3). Although it may appear that DON loss at burned sites was lower than that from logged or old-growth sites (Figure 6), this difference was small (approximately 0.2 kg $ha^{-1} y^{-1}$), not statistically significant ($F_{2,5} = 1.0$, $P = 0.43$), and covaried with differences in forest composition. DON loss did not vary by land-use history, but instead followed patterns of DOC loss (Table 4, and Figure 5A). Both DON and DOC flux increased with

Table 3. Estimated Annual Water, N, and DOC Flux by Watershed

Site	Stream	Precip.	Flow	N Dep.	DON	NO ₃ ⁻	NH ₄ ⁺	Reten.	DON	DOC	DOC:DON
		cm y ⁻¹	kg N ha ⁻¹ y ⁻¹								
Burned watersheds											
Rocky Branch											
	A	151	95	9.0	0.5	<0.1	<0.1	8.5	87	11	24
	B	156	103	9.4	0.5	<0.1	0.1	8.8	78	16	34
	C	175	128	10.5	0.6	0.1	0.1	9.7	80	25	39
	D	158	105	9.5	0.6	0.1	0.1	8.8	79	18	31
George's Gorge											
	A	167	117	10.0	0.8	0.5	0.1	8.6	58	30	36
	B	162	110	9.7	0.7	0.2	0.1	8.7	73	19	26
Zealand Valley											
	A	152	98	9.1	0.6	0.8	<0.1	7.7	42	14	24
	B	144	88	8.7	0.3	0.6	0.1	7.7	30	9	31
	C	150	95	9.0	0.4	0.7	0.1	7.8	36	10	24
	D	176	127	10.5	0.4	1.0	<0.1	9.0	29	14	32
Logged watersheds											
Little Wildcat											
	A	174	125	10.4	0.7	0.2	0.1	9.4	65	30	46
	B	145	88	8.7	0.5	0.2	0.1	7.9	68	17	31
Lost Pond											
	A	153	99	9.2	1.0	0.5	0.1	7.6	61	29	30
	B	158	107	9.5	1.0	0.2	0.1	8.2	74	31	31
Old-growth watersheds											
Glen Boulder											
	B	177	132	10.6	1.1	2.1	0.1	7.3	33	23	22
	C	164	115	9.8	0.8	1.8	0.1	7.1	28	18	24
	D	180	133	10.8	0.8	1.2	0.1	8.7	39	20	24
Gibbs Brook											
	A	183	135	11.0	0.9	0.6	0.1	9.4	57	40	45
	B	155	102	9.3	0.8	0.5	0.1	7.9	59	27	33
	C	180	132	10.8	1.4	0.4	0.1	8.9	73	62	45
	D	147	90	8.8	0.7	1.3	0.1	6.7	33	12	17
Lafayette Brook											
	A	147	92	8.8	0.9	2.0	0.1	5.8	29	27	31
	B	148	93	8.9	0.8	1.8	0.1	6.2	30	17	22
Mixed land-use watersheds											
Slide Brook											
		187	142	11.2	0.8	0.7	0.1	9.6	51	28	34
Peabody Tributary											
		183	135	11.0	1.3	0.4	0.2	9.2	70	68	53

N Dep., N deposition; *DON*, NO₃⁻-N, NH₄⁺-N, and DOC; *stream fluxes*; *Reten.*, watershed N retention; *Reten.*, watershed N retention; *DON %*, DON flux as a percentage of TDN export. *PNET-II* was used to estimate stream water fluxes, which in turn were used to estimate stream N and DOC export fluxes.

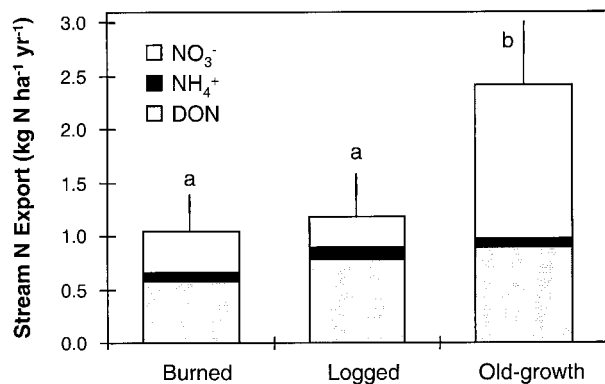


Figure 6. Mean stream NO_3^- -N, NH_4^+ -N, and DON export ($\text{kg ha}^{-1} \text{y}^{-1}$) by land-use history. Error bars indicate the standard deviations among sites. Different letters indicate significantly different TDN fluxes.

mean watershed elevation (and hence with calculated precipitation and stream flow) and varied inversely with fractional cover by northern hardwoods (Table 4). Forest type covaried with elevation, so it is unclear whether forest composition, elevation, or some other correlated property (for example, temperature or soil type) best explains the observed differences in DOC and DON export. DOC:DON ratio was the only watershed property correlated with annual NO_3^- -N flux (Table 4), a relationship that was particularly strong among old-growth and mixed-history watersheds (Figure 7). Several logged or burned watersheds followed this relationship (for example, Zealand Valley streams), but others had much lower NO_3^- losses than expected based on DOC:DON ratio alone (for example, Rocky Branch streams).

Net N retention appeared to decrease with increasing time since disturbance, due largely to increasing NO_3^- loss rather than to changes in DON loss (Figure 8). However, N retention exceeded 65% in all watersheds. On average, the historically disturbed sites retained 88% of N inputs, while the old-growth sites retained 75%.

DISCUSSION

The traditional conceptual model of biotic control over ecosystem N retention has received renewed attention with recognition of the importance of DON as a mechanism of N loss and recent concern over the fate of elevated N deposition. Although the traditional theory suggests that biotic demand for limiting nutrients prevents their loss (for example, Vitousek and Reiners 1975), recent observations (Hedin and others 1995; Neff and others 2000)

suggest that significant losses of N can occur as DON during the production and loss of dissolved organic matter, despite strong biotic demand for N. Under pristine conditions with low N inputs from the atmosphere, hydrologic losses of DON may contribute to the chronic N limitation pervasive in most unpolluted temperate forests (Hedin and others 1995; Vitousek and others 1998; Neff and others 2000). In regions where anthropogenically enhanced N inputs more than compensate for DON losses, N availability should gradually satisfy biotic N demands, particularly when biotic demands for N decline in late succession. This revised conceptual model predicts that in regions of elevated N deposition, DIN loss should increase in late succession, whereas losses of DON should correlate with losses of DOC rather than with patterns of biotic N demand. Our results conformed to expectations of this revised model, in that NO_3^- -N loss increased with successional status while DON did not, instead correlating with patterns of DOC loss.

Stream N Export in the Northeastern US

Although there were uncertainties in our estimates of stream N export, these values (Table 3) were similar to others in the northeastern US during the mid-1990s. Loss of NO_3^- -N from nine northern New England watersheds ranged from less than 0.1 to 2.1 $\text{kg ha}^{-1} \text{y}^{-1}$, while DON loss ranged from 0.5 to 2.4 $\text{kg ha}^{-1} \text{y}^{-1}$ (Campbell and others 2000). Both N deposition (Ollinger and others 1993) and stream NO_3^- -N export were slightly higher in New York than in New England, while DON losses were generally similar. In the Adirondack Mountains, New York, McHale and others (2000) report stream export of 3.0 $\text{kg ha}^{-1} \text{y}^{-1}$ as NO_3^- -N and 1.8 $\text{kg ha}^{-1} \text{y}^{-1}$ as DON. Streams in the Catskill Mountains, New York, had variable losses of NO_3^- -N that averaged about 3.5 $\text{kg ha}^{-1} \text{y}^{-1}$, with relatively constant losses of DON at rates similar to those in this study (Lovett and others 2000).

Seasonal and Successional Patterns of Nitrate Loss

Patterns of NO_3^- -N loss conformed to expected patterns of greater biotic uptake during the growing season relative to the dormant season and in successional stands compared to old-growth stands. The strong seasonality of NO_3^- -N concentrations in all of the forested watersheds (Figure 3) suggests biotic control over NO_3^- -N loss during the growing season. Confirming predictions of decreased demand for N in the old-growth stands, NO_3^- -N concentrations in old-growth watersheds greatly ex-

Table 4. Linear Correlations (R) among Annual NO_3^- -N, DON, and DOC Fluxes ($\text{kg ha}^{-1} \text{y}^{-1}$) and Other Watershed Properties

	<i>n</i>	NO_3^- -N	DON	DOC	DOC:DON	pH	Elev. (m)	Area (m)
DON ($\text{kg ha}^{-1} \text{y}^{-1}$)	25	0.19						
DOC ($\text{kg ha}^{-1} \text{y}^{-1}$)	25	-0.16	0.85 ^c					
DOC:DON ratio	25	-0.48 ^a	0.43 ^a	0.77 ^c				
Mean annual pH	25	0.03	-0.66 ^c	-0.65 ^c	-0.34			
Mean elevation (m)	25	-0.04	0.52 ^b	0.61 ^c	0.56 ^b	-0.03		
Area (ha)	25	-0.11	0.10	0.32	0.46 ^a	0.03	0.69 ^c	
Hardwood cover (%)	23	0.05	-0.67 ^c	-0.73 ^c	-0.54 ^b	0.67 ^c	-0.54 ^c	-0.51 ^a

Significant correlations (uncorrected for multiple comparisons) are indicated by ^a $P < 0.05$, ^b $P < 0.01$, and ^c $P < 0.001$.

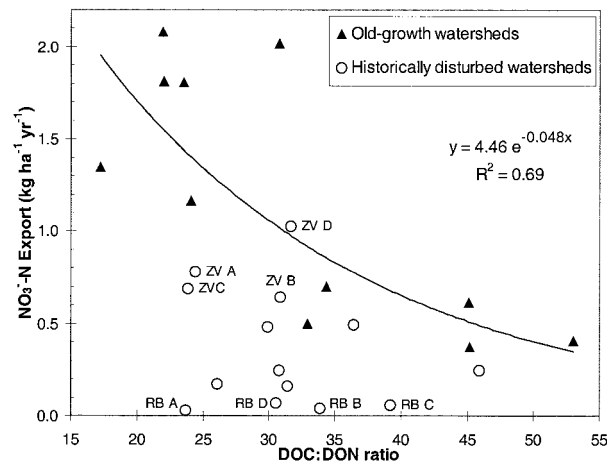


Figure 7. Scatterplot of annual NO_3^- -N loss and DOC:DON ratio for old-growth and historically disturbed watersheds. Curve and equation pertain to old-growth streams only. ZV = Zealand Valley and RB = Rocky Branch streams (A–D).

ceeded those of successional watersheds (Figure 4). This pattern of elevated NO_3^- -N loss from old-growth forests relative to successional forests has been demonstrated elsewhere in the eastern US (Leak and Martin 1975; Vitousek and Reiners 1975; Silsbee and Larson 1982; Flum and Nodvin 1995), a region that receives N deposition at rates five to 10 times higher than during preindustrial times (Galloway and others 1995; Holland and others 1999). In contrast, temperate old-growth forests in regions receiving little N deposition generally lose very little NO_3^- -N (Sollins and others 1980; Hedin and others 1995). Chronic losses of N as DON may slow or prevent N from accumulating to levels sufficient to induce net nitrification and nitrate loss from unpolluted stands. This regional contrast is consistent with the revised conceptual model that DIN loss should be minimal in regions with little N deposition, but that late-successional systems should have

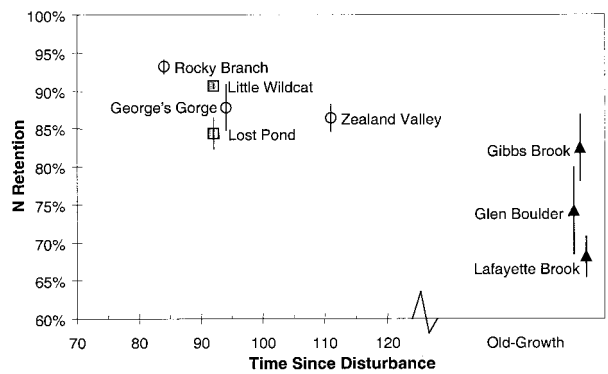


Figure 8. Net N retention and time since disturbance (○ = burned, □ = logged, ▲ = old-growth). Error bars are the standard deviations among streams within sites.

reduced biotic control over the loss of DIN in regions of elevated N deposition. Our results indicate that despite chronic N deposition, this control can persist for 80–110 years.

One site departed from the general trend of elevated NO_3^- -N losses in old-growth watersheds, suggesting that additional controls may be needed to explain variability of DIN loss among watersheds. At the Gibbs Brook Scenic Area, three old-growth, conifer-dominated watersheds had very low losses of NO_3^- -N, whereas a fourth stream, draining a small northern hardwood cove, had relatively high NO_3^- -N loss (Figure 3E). Vegetation type alone does not necessarily explain the low NO_3^- -N losses, however, in that NO_3^- -N concentrations at another old-growth red spruce site (Nancy Brook) were relatively high (Figure 3E). Recent internal disturbance and its effects on woody debris, growth rates, and species composition may be affecting current N losses from the three Gibbs Brook watersheds. Foster and Reiners (1983) and Lawrence and others (1997) noted extensive mortality of red spruce at Gibbs Brook in recent decades. Spruce mortality likely added large quantities of woody debris to the

forest floor and placed much of the watersheds' living vegetation in an earlier successional state than presumed. In a similar stand in the Adirondack Mountains, New York, Friedland and Miller (1999) noted that declining NO_3^- -N loss coincided with spruce mortality and replacement by N-demanding balsam fir.

The two forms of disturbance—logging and fire—were expected to have had different effects on current NO_3^- -N loss, due to presumed differences in past N removal (Aber and Driscoll 1997). Historical records were not sufficient to determine the relative intensity of logging or fire across sites. We presumed that logged sites had incurred N losses through bole removal and disturbance-induced NO_3^- -N leaching (for example, Hornbeck and Kropelin 1982) and that burned sites had incurred these losses, as well as losses by volatilization of slash and soil organic N (for example, Raison 1979; Little and Ohmann 1988; Johnson and others 1998). However, present-day NO_3^- -N loss did not differ significantly between logged and burned sites (Figures 4 and 6). A related study of soil and vegetation in several of these and similar watersheds detected no significant differences between logged and burned sites in aboveground biomass, forest floor C and N pools, or net mineralization and nitrification rates (Goodale and Aber forthcoming). The historical fires may have been less severe than presumed, such that small differences in past N removal mattered less in controlling current DIN losses than differences in forest age and N demand (Figure 8). In contrast, NO_3^- -N export from Cone Pond watershed in the southwestern WMNF remains extremely low (under $0.1 \text{ kg ha}^{-1} \text{ y}^{-1}$), despite 175 years of recovery from a severe fire around 1820 (Hornbeck and others 1997; Campbell and others 2000). This fire may have been more severe than the ones we studied, and the red spruce that dominate Cone Pond watershed may prolong microbial N limitation at the site by producing poor quality litter. Soil C:N ratios at Cone Pond are quite high (Campbell and others 2000), suggesting continued microbial demand for N and little net production of nitrate.

C:N Ratio Effects on Nitrification and Nitrate Loss

In order for NO_3^- -N to be leached from a forested system, it must first be produced through nitrification, and both net nitrification and NO_3^- -N export generally increase as forest floor C:N ratios decrease (van Miegroet and others 1992; Dise and others 1998; Gundersen and others 1998). Leachate DOC: DON ratios often correlate with soil C:N ratios

(Campbell and others 2000; Neff and others 2000), and reported correlations between stream NO_3^- -N export and DOC: DON ratio (Kortelainen and others 1997; Campbell and others 2000) probably reflect patterns of soil C:N ratio and nitrification. In this study, NO_3^- -N export correlated with DOC: DON ratio in streams draining the old-growth and mixed-history stands, yet several streams draining historically disturbed stands had much lower NO_3^- -N export than predicted based on DOC: DON ratio alone (Figure 7). DOC: DON ratios are often higher than bulk soil C:N ratios, reflecting a source of dissolved organic matter other than simple solubilization of the bulk humus (Qualls and Haines 1991; Currie and others 1996). Dissolved organic matter and nitrification/ NO_3^- -N loss may derive from related but slightly different sources in soil organic matter.

Patterns of DON Loss

In the forest floor at the Harvard Forest, Massachusetts, DOC and DON production peak in late summer and early fall (Currie and others 1996; McDowell and others 1998). However, stream DON concentrations in this study showed little seasonal variation (Figure 3), similar to observations in similar watersheds (Creed and Band 1998; Lovett and others 2000; Campbell and others 2000). Retention of dissolved organic matter in the mineral soil (McDowell and Wood 1984; Qualls and Haines 1991) likely damped any seasonal signal of DON production in the forest floor. Although the increased DOC: DON ratio during the growing season could have reflected microbial N limitation on DON production, the overall lack of seasonality in DON loss suggests that DON export is regulated not by biotic N demand, but by abiotic factors such as sorption to mineral soil.

DON loss did not vary with successional status (Figure 6), but instead correlated with DOC loss (Figure 5A, Table 4) and variables associated with DOC production and retention such as vegetation or soil type. At Harvard Forest, forest floors in hardwood stands produce less DOC and DON, often with lower DOC: DON ratios, than do forest floors in adjacent conifer stands (Currie and others 1996). Similarly, DOC concentrations in mid- and low-elevation northern hardwood watersheds are lower than those in high-elevation spruce-fir watersheds (Lawrence and others 1986). We observed a similar decrease in DOC concentration with increasing percent cover by hardwood forest (Figure 5B). However, it is unclear whether differences in DOC and DON loss were due to species-level differences in DOC production or to covarying differences in ele-

vation, climate, or soil type and texture effects on DOC sorption.

The patterns of DON loss corresponded little with expected seasonal and successional differences in biotic N demand, suggesting that DON losses occur despite conditions of N limitation. To what extent could chronic loss of DON offset N input in deposition? Under unpolluted or preindustrial conditions with N deposition rates generally less than $1 \text{ kg N ha}^{-1} \text{ y}^{-1}$ (Holland and others 1999), DON loss may balance a large fraction of N input (Sollins and others 1980; Hedin and others 1995). Anthropogenic N deposition may increase DON loss (Currie and others 1996; McDowell and others 1998), but the increase in DON production is likely to be small relative to increases in N input (Currie and others 1996; Neff and others 2000). In regions of moderate to high N deposition, DON loss offsets little of the N received in deposition, except perhaps in coarse-textured soils that have little capacity to sorb dissolved organic matter (Lajtha and others 1995; Seely and others 1998). In the present study, even though DON was a large fraction of total N export, loss of DON accounted for only 3%–13% of estimated TDN input. Similarly, DON loss amounted to only 5% of total N input to an old Adirondack spruce-fir stand (Friedland and Miller 1999), and 5%–20% of input to nine northern New England watersheds (Campbell and others 2000). A large fraction of N inputs to unpolluted or preindustrial systems may be exported as DON, but DON export is unlikely to substantially offset elevated atmospheric N inputs due to human activities.

Nitrogen Retention, Succession, and Nitrogen Saturation

In this region of moderate, chronic N deposition, plant and microbial demand appear to substantially affect DIN losses and overall N retention. Models of ecosystem N retention predict lower net ecosystem production and demand for N in old-growth watersheds. In the present study, we found that old-growth watersheds had higher NO_3^- -N losses than comparable forests disturbed 80–110 years ago. While old-growth forests appear to be relatively sensitive indicators of N saturation (Stoddard 1994; Hedin and others 1995; Goodale and Aber forthcoming), they retained at least 65% of N inputs, far from the zero net retention theorized for late-successional old-growth systems (Vitousek and Reiners 1975) and for late-stage N-saturated systems (Agren and Bosatta 1988; Aber and others 1989). Our methods easily could have underestimated stream N flux by several tenths of a $\text{kg ha}^{-1} \text{ y}^{-1}$, but these errors would have had little effect on esti-

mates of watershed N retention. Had dry and cloud-water N inputs been fully included, estimates of N retention would have been substantially higher. Even Ammonoosuc Brook, with three-quarters of its watershed covered by rock and alpine tundra, retained at least 60% of N inputs, as calculated from liberal estimates of N export (see Results) and conservative estimates of N inputs ($14 \text{ kg N ha}^{-1} \text{ y}^{-1}$, assuming no cloud deposition).

Why was N retention so high? A related study of plots on a subset of these and similar watersheds indicated that net nitrification does occur in these acid soils, producing $20\text{--}65 \text{ kg NO}_3^- \text{-N ha}^{-1} \text{ y}^{-1}$ (Goodale and Aber forthcoming). Mean above-ground biomass on the old-growth plots (260 mg ha^{-1}) exceeded that on the 80–110-year-old plots (190 mg ha^{-1}), suggesting that N could have still been accumulating in biomass on the disturbed watersheds. If we assume biomass accumulation rates of approximately $1\text{--}2 \text{ Mg ha}^{-1} \text{ y}^{-1}$ and a woody N concentration of 0.3% (Whittaker and others 1979), net plant uptake could have accounted for approximately $3\text{--}6 \text{ kg N ha}^{-1} \text{ y}^{-1}$ on the disturbed watersheds. However, plant accumulation alone is not sufficient to explain the high N retention (Table 3), and it is unlikely to have been a significant N sink on the old-growth watersheds. Old-growth forest soils could have been accumulating N even if the vegetation was not (for example, Sollins and others 1980). Rates of N_2O loss in upland forest soils at HBEF and Harvard Forest are quite low, even after disturbance or fertilization (under $0.4 \text{ kg N ha}^{-1} \text{ y}^{-1}$) (Bowden and Bormann 1986; Bowden and others 1991; Magill and others 1997). However, in southern New England, Groffman and Hanson (1997) measured $1\text{--}4 \text{ kg N ha}^{-1} \text{ y}^{-1}$ of N_2O loss in moderately well-drained soils and up to $136 \text{ kg N ha}^{-1} \text{ y}^{-1}$ in poorly drained soils. Together, accumulation of N in plant and soil organic matter and unmeasured gaseous losses may explain the large difference between atmospheric N inputs and stream export, although the magnitude of gaseous losses of N (as NO , N_2O , and N_2) are highly uncertain.

Interannual climate variability could also partially explain the high N retention and generally low NO_3^- -N concentrations across all watersheds. At HBEF W6, there has been no significant trend in N deposition over the past 3 decades (Likens and Bormann 1995), and yet retention of inorganic N has varied erratically from less than 20% of bulk N inputs in the early 1970s to over 80% in the mid-1980s (Pardo and others 1995) and 90% in the mid-1990s (Hornbeck and others 1997; Campbell and others 2000). Similar declines in stream

NO_3^- -N loss have been observed elsewhere in the WMNF (Goodale 1999; Aber and Driscoll 1997). Model estimates suggest that climate variability and its relative effects on microbial N mineralization and plant uptake can explain much of the observed interannual variation in N retention at HBEF W6 (Aber and Driscoll 1997). The generally high N retention observed in this study may be due to particular climate factors in 1996–97 that favored biotic N retention over NO_3^- -N loss.

Understanding the cause of the perceived high N retention is important. If it is due to unmeasured gaseous loss of N, hydrologic N export may remain low while production of N_2O , a greenhouse gas, increases. If it is due to a large capacity for N accumulation in soils (for example, Magill and others 1997), ecosystems may require several decades to reach late-stage N saturation. If it is due to climate variability, periodic episodes of high NO_3^- -N loss may occur much sooner. Although stream export of DON may have largely balanced N inputs during the preindustrial era, losses of DON are not likely to offset the N inputs received in anthropogenic N deposition.

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