Published July 18, 2014

Inorganic Nitrogen Retention by Watersheds at Fernow Experimental Forest and Coweeta Hydrologic Laboratory

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Because elevated N loading can impair both terrestrial and aquatic ecosystems, understanding the abiotic and biotic controls over retention and export of dissolved inorganic N (DIN) is crucial. Long-term research has been conducted on experimental watersheds at two U.S. Forest Service experimental forests in the Appalachian region: Fernow Experimental Forest (FEF) in West Virginia and Coweeta Hydrologic Laboratory (CHL) in North Carolina. While similar in vegetation and research history, FEF and CHL differ in climate, historic DIN deposition, and soils. We evaluated long-term patterns of DIN inputs and exports from three watersheds at each location with similar treatments including clear-cut harvest, conversion to conifer plantation (Norway spruce [*Picea abies* (L.) H. Karst.] at FEF and white pine [*Pinus strobus* L.] at CHL), as well as reference watersheds. We examined DIN export and retention in these watersheds, comparing treated and reference watersheds within each experimental forest and comparing similarly treated watersheds between the experimental forests. Despite current similar levels of N deposition, stream water DIN concentrations and exports were generally greater at FEF by almost an order of magnitude. We found differences between FEF and CHL in stream DIN concentrations, watershed export, and retention of DIN inputs not only in the untreated reference watersheds but also in the watersheds with similar disturbance treatment. We hypothesize that these differences are the result of site and vegetation differences as well as site history including long-term patterns of DIN deposition. We document the switch from biogeochemical to hydrologic controls that occurred when N availability exceeded N immobilization, due to either N deposition or biological N inputs.

Abbreviations: CHL, Coweeta Hydrologic Laboratory; DIN, dissolved inorganic nitrogen; FEF, Fernow Experimental Forest.

Nitrogen loading is a critical ecosystem issue that can lead to impairment of terrestrial and aquatic ecosystems from mountainous headwater catchments to coastal waters (e.g., Seitzinger et al., 2005). Much work has been done on N cycling processes and fluxes in forested watersheds, using either a biogeochemical (e.g., Likens and Bormann, 1995; Lovett et al., 2004) or hydrologic (e.g., Creed et al., 1996; Ocampo et al., 2006a, 2006b) approach; however, it has proven difficult to identify specific mechanisms responsible for the variability in dissolved inorganic N (DIN = NO_3 + NH_4) export among watersheds or even within individual watersheds with time (e.g., Gilliam et al., 2001; Campbell et al., 2004; Bernhardt et al., 2005; Christopher et al., 2008; Kelly et al., 2011; Argerich et al., 2013). Linkages have been made between levels of atmospheric N deposition

This work was presented at the 12th North American Forest Soils Conference, Whitefish, MT, 16–20 June 2013, in the Forest Change Dynamics and Climate Change session.
Soil Sci. Soc. Am. J.
doi:10.2136/sssaj2013.11.0463nafsc
Received 1 Nov. 2013.
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and DIN export in forested watersheds of the eastern United States (Eshleman et al., 2013), but deposition generally explains <50% of the variation in surface water DIN export (Aber et al., 2003), suggesting that other processes are critical. Understanding the role of disturbance in regulating DIN export from watersheds is also important.

It has been well documented that major disturbances in forested watersheds, particularly clear-cutting, result in increased annual stream flows and N losses (Bormann and Likens, 1979; Swank and Webster, 2014), at least in the short term. This has been attributed to increased N cycling rates due to increased soil water content and elevated soil temperatures, along with decreased plant N uptake, which results in greater N export. These responses have been documented for treatments that impact only a portion of the watershed, and recovery periods can range from a few years to decades (Reinhart et al., 1963; Hornbeck et al., 1993; Jones and Post, 2004). Watershed treatments that result in changes in tree species composition can also alter hydrologic processes (Hornbeck et al., 1993; Adams and Kochenderfer, 2007; Ford et al., 2011). Research has shown that conifers generally use more water than hardwoods due to higher annual transpiration demand (Kochenderfer and Lee, 1973) and greater interception of precipitation, especially during the dormant season (Helvey, 1967; Vose and Swank, 1992). Nutrient cycling rates and patterns also differ between hardwoods and conifers due to differences in total leaf area, seasonality of photosynthesis, nutrient requirements, leaf chemistry, and decomposition rates (Johnson and Lindberg, 1992).

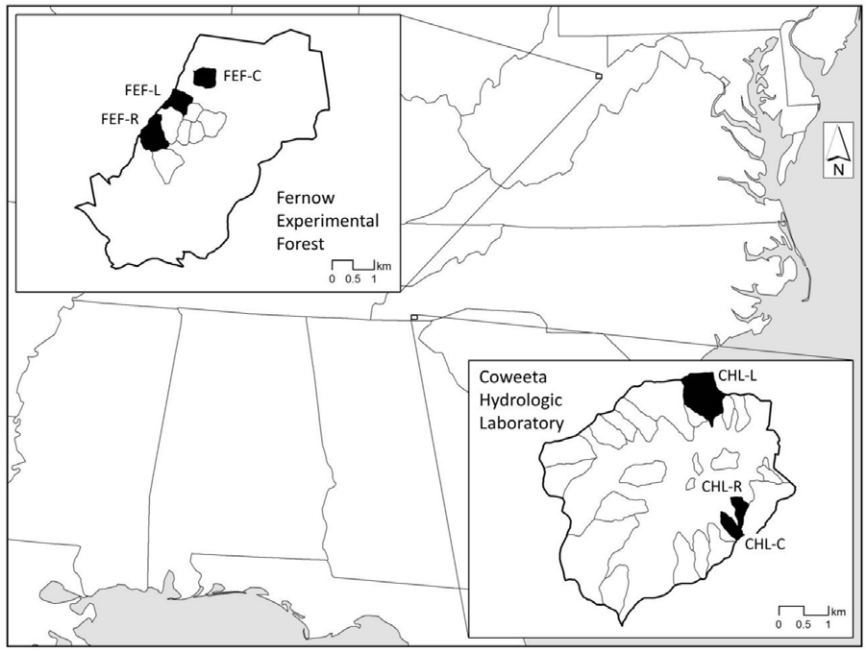

Fig. 1. Locations of the Fernow Experimental Forest and Coweeta Hydrologic Laboratory.

We used data from long-term watershed experiments at two U.S. Forest Service experimental forest sites in the Appalachian Mountains to examine changes in N exports and N retention in response to treatment across decadal time scales. We used data from the Coweeta Hydrologic Laboratory (CHL) in North Carolina and the Fernow Experimental Forest (FEF) in West Virginia (Fig. 1; Table 1).

Our objective was to evaluate the influence of disturbance on inorganic N ($NO_3 + NH_4$) cycling regulation using similarly treated watersheds in FEF and CHL. We were particularly focused on evaluating the role of N inputs and hydrology in regulating DIN export and retention within forested watersheds vs. the role of biological processes. At each location, we compared long-term trends of inorganic N deposition inputs and stream water exports in watersheds that were untreated (reference watersheds), converted to a conifer plantation, or clear-cut harvested. Based on previous research, we expected that the untreated reference watersheds would generally retain N. We also expected that conversion from hardwoods to conifers would result in increased N retention and decreased N flux to stream water, while clear-cut harvesting would increase N flux in stream water, resulting in decreased retention. We expected that these responses would differ between FEF and CHL due to climate and site history differences.

MATERIALS AND METHODS

Site Description

Fernow Experimental Forest is located in the central Appalachian Mountains of northeastern West Virginia. Elevation ranges from 533 to 1112 m. Mean annual precipitation is about 150 cm and mean annual temperature is 8.9°C. The parent material underlying the experimental watersheds is sandstone and shale. Soils are mesic Typic Dystrudepts and average 1 m in depth. The FEF was heavily logged early in the 20th century, and current vegetation is aggrading mixed mesophytic hardwoods (Kochenderfer, 2006). Atmospheric inorganic N deposition averages 8.1 kg N ha^{-1} yr^{-1} and has been measured since 1978. In this study, we examined Watersheds 4 (FEF-R), 7 (FEF-L), and 6 (FEF-C), which represent reference, logged by clear-cut harvest methods, and conversion to Norway spruce plantation (planted in 1973). Both FEF-L and FEF-C were kept free of regrowth using herbicides for four growing seasons (regeneration started in 1970) following clear-cutting (Adams and Kochenderfer, 2014).

Coweeta Hydrologic Laboratory is located in the southern Appalachian Mountains of southwestern North Carolina. Elevation ranges from 679 to 1592 m. Mean annual precipitation is about 200 cm and mean annual temperature is 12.6°C. Parent materials are metamorphosed granitic schist and gneiss. Dominant hillslope soils are mesic Typic Dystrochrepts or Hapludults. Riparian and high-elevation soils are mesic Typic Haplumbrepts. Soil depths average 1 m and are underlain by

Table 1. Characteristics of six study watersheds from the Fernow Experimental Forest and Coweeta Hydrologic Laboratory.

Watershed characteristic	Fernow Experimental Forest (FEF)			Coweeta Hydrologic Laboratory (CHL)		
	Reference FEF-R (Watershed 4)	Logged FEF-L (Watershed 7)	Spruce FEF-C (Watershed 6)	Reference CHL-R (Watershed 18)	Logged CHL-L (Watershed 7)	White pine CHL-C (Watershed 17)
Vegetation and history	mesic mixed hardwoods, undisturbed since 1910	mesic mixed hardwoods, logged 1963–1967	Norway spruce, planted 1973	mixed oak–cove hardwoods, undisturbed since 1927	mixed hardwoods, logged 1977	white pine, planted 1956
N deposition, kg N ha^{-1} yr^{-1}	8.1	–	–	5.9	5.4	5.9
Soils	Inceptisols	Inceptisols	Inceptisols	Ultisols and Inceptisols	Ultisols and Inceptisols	Ultisols and Inceptisols
C/N ratio	20	16	20	25	24	20
Bulk density	1.0	1.0	0.9	0.85	0.9	0.85
pH†	3.95	3.90	3.75	4.03	4.34	5.02
Watershed area, ha	38.7	24.2	22.3	13	61	13
Aspect	east–southeast	east	south	northwest	south	northwest
Avg. precipitation, cm yr^{-1}	148	142	143	196	181	201
Avg. discharge, cm yr^{-1}	64 (1951–2007)	86 (1957–2007)	54 (1957–2007)	97 (1936–2009)	106 (1936–2009)	97 (1936–2009)
Stream NO_3 conc., μg N L^{-1}	840 (2004–2006)	1200 (2004–2006)	20 (2004–2006)	11 (2000–2009)	102 (2000–2009)	155 (2000–2009)
Dissolved inorganic N export, kg N ha^{-1} yr^{-1}	6.2 (2006–2010)	10.3 (2006–2010)	4.3 2006–2010	0.10 (2002–2007)	1.5 (2008–2009)	1.1 (2008–2009)

† FEF and CHL-C pH is in water; all other CHL pHs are measured in 0.01 mol L^{-1} $CaCl_2$.

a saprolite layer up to 5 m deep. The CHL was logged in the 1920s, and current vegetation communities include mixed oak hardwood, northern hardwoods, cove hardwoods, and xeric mixed oak and pine. Atmospheric inorganic N deposition averages 5.7 kg N ha^{-1} yr^{-1} and has been measured since 1972. In this study, we examined Watersheds 18 (CHL-R), 7 (CHL-L), and 17 (CHL-C), which represent reference, logged using clear-cut harvest methods (1977), and conversion to white pine plantation in 1956. Watershed CHL-C was cut repeatedly as part of a water yield experiment for 15 yr, with no product removal, before white pine establishment. During the drought of 1999 to 2002, 1% of the basal area in CHL-C was impacted by a southern pine beetle outbreak (Kloeppel et al., 2003).

Flux Calculations and Data Analysis

Precipitation input for each watershed was calculated using established relationships between specific watershed locations and individual or multiple rain gauges (Swift et al., 1988; Adams et al., 1994). Bulk precipitation samples were collected weekly for chemical analysis. For FEF, National Atmospheric Deposition Program precipitation chemistry data (nadp.sws.uiuc.edu/sites/siteinfo.asp?net=NTN&id=WV18) were used; for CHL, we used data from samples analyzed on site. Precipitation inorganic N inputs are total inorganic N because these samples were not filtered before chemical analysis. Stream discharge for each watershed was measured using sharp-crested 90 or 120° V-notch weirs with continuous flow level recorders; weekly stream grab samples were collected above the weir for chemical analysis. Nitrogen analyses were conducted using established methods (Brown et al., 2009; Edwards and Wood, 1993). We examined inputs and export in Fernow and Coweeta watersheds using long-term annual data from each site. For more detail on flux estimations, see Adams et al. (2006) and Swank and Waide (1988). We tested for increasing or decreasing trends in flow-weighted average annual concentrations, annual precipitation, annual stream discharge, annual N fluxes (export and input), and export/input ratios for each watershed using a Mann–Kendall nonparametric test for trend analysis (Helsel and Hirsch, 2002; Helsel et al., 2006). We also looked for relationships between variables using linear regression. We used $\alpha = 0.05$ for statistical significance and $\alpha = 0.10$ for marginal significance.

RESULTS

Trends in Hydrology and Deposition

No significant trend in annual precipitation amount was detected at either site (Fig. 2 and 3; $P > 0.05$), but there has been significant interannual variability, with multiyear patterns that are perhaps related to the North Atlantic Oscillation (Hurrell, 1995; Hurrell and Deser, 2009). Patterns of stream discharge reflect those of precipitation (Fig. 2 and 3), and at both sites discharge from the conifer watershed was consistently the lowest. At FEF, discharge from the conifer watershed has significantly decreased with time ($\tau = -0.368$, $P = 0.008$), and at CHL, discharge from all three watersheds has significantly decreased (CHL-R: $\tau = -0.233$, $P = 0.035$; CHL-C: $\tau = -0.228$, $P = 0.042$; CHL-L: $\tau = -0.231$, $P = 0.040$).

Current N deposition levels at FEF and CHL are now approximately equal, despite large historic differences (Fig. 4). The inorganic N concentration in precipitation at FEF has historically been very high, among some of the highest levels in the

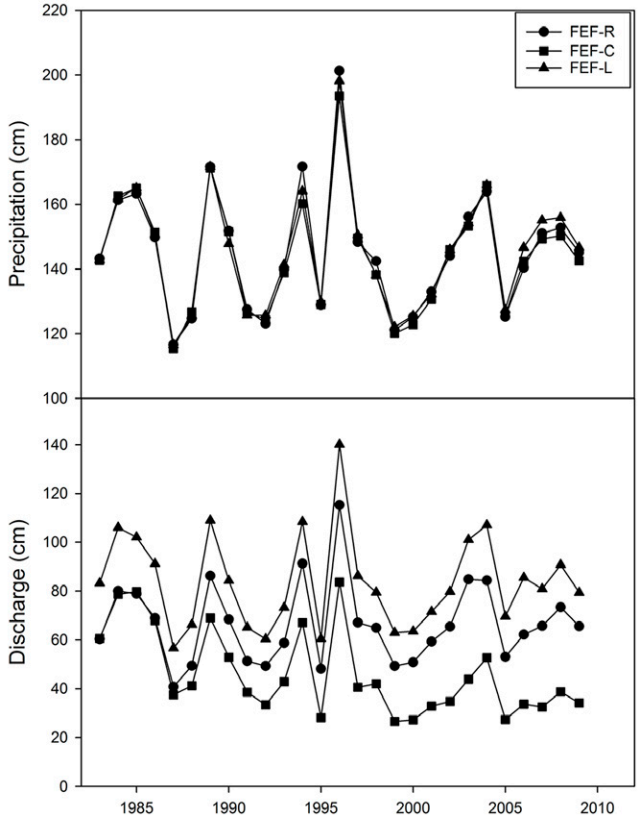

Fig. 2. Precipitation and discharge at the three watersheds at the Fernow Experimental Forest (FEF).

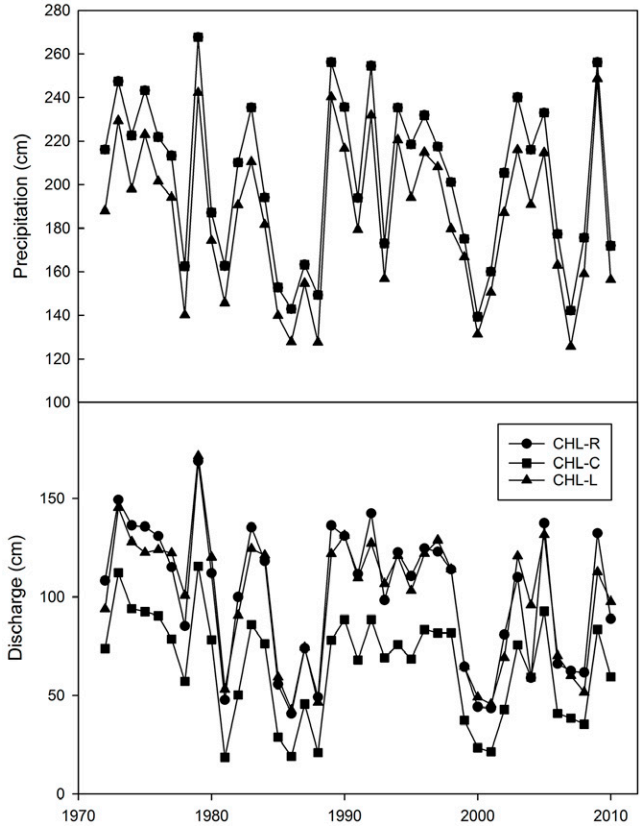

Fig. 3. Precipitation and discharge at the three watersheds at Coweeta Hydrologic Laboratory (CHL).

eastern United States (Adams et al., 2003), but has declined significantly since 1979 (Fig. 4; $\tau = -0.61$, $P < 0.001$). At CHL there was a significant increase in inorganic N concentration from 1972 to 1988 ($\tau = -0.244$, $P = 0.028$), but since about 1990 the trend has not been significant. Until about 2005, N concentrations in deposition were greater at FEF than CHL, but more recent levels are strikingly similar. We see the same general trends for annual N input (kg N ha^{-1} yr^{-1})—N deposition has significantly decreased at FEF ($\tau = -0.504$, $P < 0.001$), and at CHL N deposition has increased during the period of record ($\tau = 0.26$, $P = 0.020$) but has significantly decreased since 1988 ($\tau = -0.431$, $P = 0.004$). Since 1983, N deposition has generally been higher at CHL than FEF as a result of similar DIN concentrations and greater total precipitation.

Stream Water Trends

Mean annual stream water DIN concentrations are generally much higher at FEF than at CHL (Fig. 5; note different scales on *y* axis). At FEF, stream water DIN concentrations from FEF-R have averaged about 60 μmol L^{-1}, and about 80 μmol L^{-1} from FEF-L, and neither watershed has shown a significant trend ($P > 0.05$). Since 1983, DIN concentrations in stream water from FEF-C have declined from 40 μmol L^{-1} to near zero ($\tau = -0.603$, $P < 0.001$). At CHL, the average annual DIN concentration in CHL-R has been increasing significantly ($\tau = 0.497$, $P < 0.001$) but is still generally <3 μmol L^{-1}. In CHL-C, the average annual DIN concentration has been higher, around 12 μmol L^{-1}, highly variable, and without any significant trend ($P > 0.05$). Before logging, DIN in CHL-L was similar to reference levels, but since logging there has been a significant increase ($\tau = 0.528$, $P < 0.001$), although with variability.

Patterns of DIN export from most of the watersheds reflect the patterns of concentration and discharge (Fig. 6). There are no trends in DIN export from FEF-R and FEF-L ($P > 0.05$), but exports are highly variable. Both watersheds show the same pattern of increases and decreases in DIN exports but at different magnitudes. Because of low DIN concentration and low discharge, DIN export from FEF-C declined to near zero in some years ($\tau = -0.606$, $P < 0.001$). At CHL, export from CHL-R has increased slightly, but this trend is only marginally significant ($\tau = 0.211$, $P = 0.061$). Dissolved inorganic N export from CHL-C has been high, with no significant trend ($P > 0.10$) but with variability reflecting the precipitation–discharge pattern seen in Fig. 3. Export from CHL-L was very low before logging but has increased significantly since then ($\tau = 0.394$, $P < 0.001$) and has become highly synchronous with CHL-C. When we calculated export as a percentage of input (Fig. 7), annual N export from FEF-L was >100%, with export exceeding input, and this percentage increased with time ($\tau = 0.379$, $P = 0.006$). For FEF-R, this percentage has also increased with time ($\tau = 0.442$, $P = 0.001$) and in 2009 was approaching 100%. In contrast, most DIN input has been retained on FEF-C and the percentage of input that is exported has declined during the period of this study ($\tau = -0.557$, $P < 0.001$).

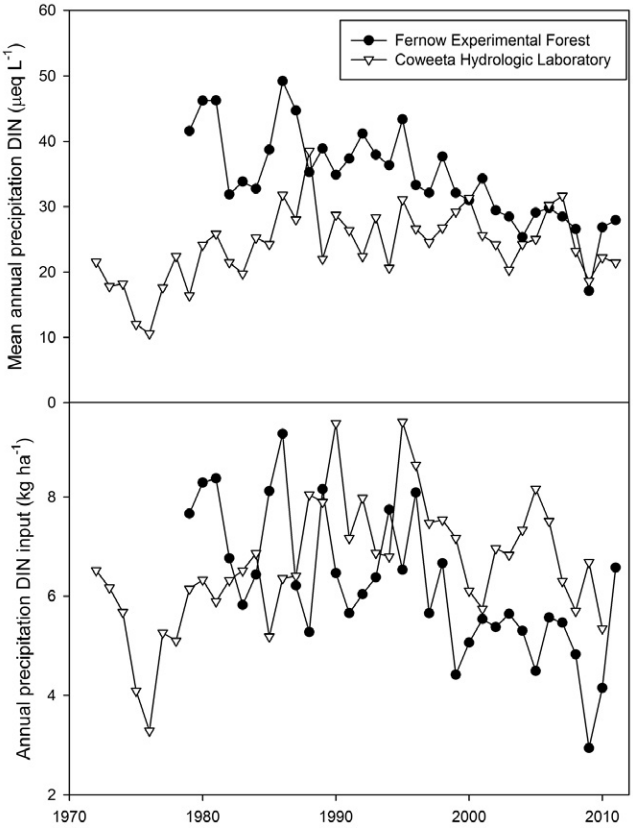

Fig. 4. Mean annual concentration of dissolved inorganic N (DIN) in precipitation (top) and DIN input in precipitation (bottom) at the Fernow Experimental Forest and Coweeta Hydrologic Laboratory. For DIN, 1 μeq L^{-1} = 1 μmol L^{-1}.

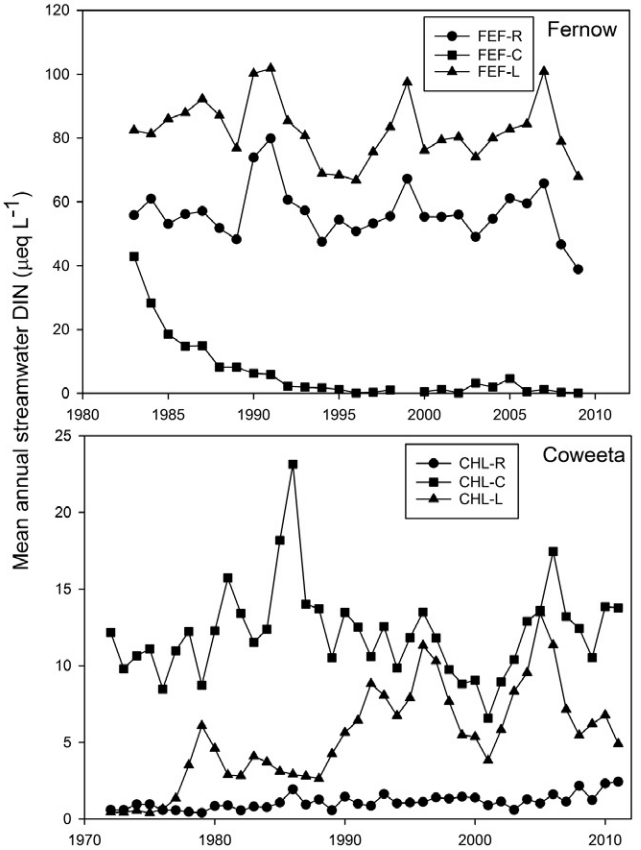

Fig. 5. Mean annual dissolved inorganic N (DIN) concentration in streams draining the six watersheds at the Fernow Experimental Forest (top) and Coweeta Hydrologic Laboratory (bottom). For DIN, 1 μeq L^{-1} = 1 μmol L^{-1}.

In general, CHL watersheds retain much more DIN (Fig. 7) than FEF. Generally, <3% of input DIN is exported from CHL-R, and there has been no significant trend with time ($P > 0.10$). Watershed CHL-C has much lower retention, with export sometimes exceeding 20% of input; however, the retention percentage has been significantly decreasing with time ($\tau = -0.325$, $P = 0.004$). The export percentage from CWT-L has increased with time ($\tau = 0.412$, $P < 0.001$). Since about 1990, patterns of DIN export for CWT-L and CWT-C have become highly synchronous.

DISCUSSION

Our results suggest that many forested watersheds show signs of N limitation (high N retention), but as soil N availability increases there is a switch from biological to hydrologic control of DIN export. This idea builds on two fundamental aspects of the N saturation hypothesis proposed by Aber et al. (1989). First, annual DIN export does not depend on the N input that year but rather on the long-term accumulation of available DIN in the soil. Second, available DIN comes not just from atmospheric deposition but also from internal biological processes, especially in response to watershed disturbance (e.g., Swank and Vose, 1997). As a result of disturbance such as logging, biological N mineralization by vegetation, soils, and in-stream processes may exceed N immobilization in the watershed. These processes are illustrated by what has happened in watersheds at the FEF and CHL.

The Coweeta reference watershed (CHL-R) shows evidence of N limitation and is highly retentive (Fig. 7), with annual DIN export of about 2% of annual input. During the period of this study, export was not significantly related to annual precipitation (Fig. 8; $r^2 = 0.04$, $P = 0.22$) or the annual average DIN concentration in precipitation (Fig. 9; $r^2 = 0.09$, $P = 0.06$). This suggests that despite the multiple disturbances that occurred historically (pre-1930 logging, chestnut [*Castanea dentata* (Marshall) Borkh.] death, and atmospheric deposition), CHL-R still has a large capacity for inorganic N retention and would not be described as N saturated. Most of this N probably remains bound in vegetation and refractory organic compounds in the soil organic matter. Efficient retention of DIN was also true for the CHL logged watershed (CHL-L) in 1972 to 1975, before logging (Fig. 7).

However, this efficient retention of N in reference watersheds at CHL has been declining (Swank and Vose, 1997; Argerich et al., 2013). Stream water DIN concentration, export, and the export/input ratio in CHL-R have all significantly increased during the period of this study (Fig. 5, 6, and 7) despite the decrease in N deposition. One possible explanation for this trend is forest maturation (e.g., Vitousek and Reiners, 1975), older forests generally being less retentive of N than younger

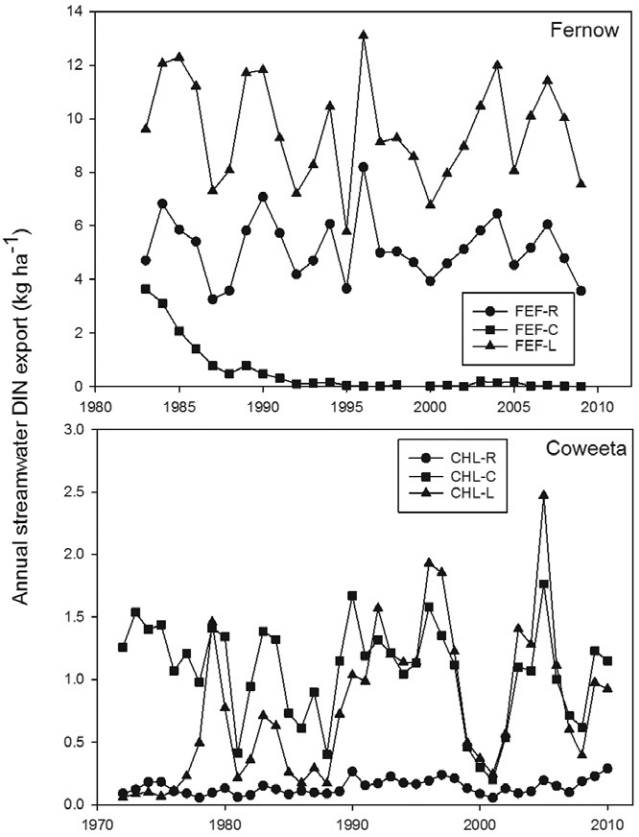

Fig. 6. Mean annual dissolved inorganic N (DIN) export from streams draining the six watersheds at the Fernow Experimental Forest (top) and Coweeta Hydrologic Laboratory (bottom). For DIN, 1 μeq L^{-1} = 1 μmol L^{-1}.

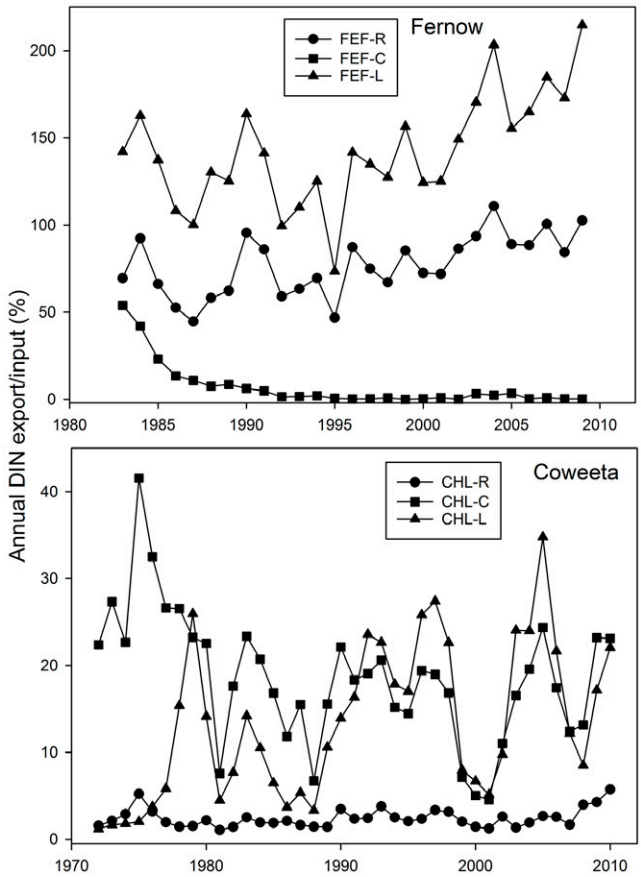

Fig. 7. Ratio of annual dissolved inorganic N (DIN) export to input for the six watersheds at the Fernow Experimental Forest (top) and Coweeta Hydrologic Laboratory (bottom).

stands. Also, the increasing concentration could be due to decreasing discharge, but this would not explain increasing export. It is possible that increasing annual air temperature (Laseter et al., 2012) may be accelerating soil N mineralization (Knoepp and Swank, 1997) and thereby increasing the available DIN pool (Brookshire et al., 2011). There is also evidence that high-elevation, reference watersheds at CHL are showing symptoms congruent with the initial stages of N saturation (Swank and Vose, 1997; Knoepp et al., 2008; Argerich et al., 2013), reflecting greater N deposition at higher elevations.

The conifer plantation at CHL (CHL-C) has exhibited high stream DIN concentrations and export (Fig. 5, 6, and 7) since measurements were begun in 1972. The amount of export and the export/input ratio have both been well above reference levels and highly variable. During the period of study, export was significantly related to both annual precipitation amount (Fig. 8; $r^2 = 0.31$, $P < 0.001$) and the annual average DIN concentration of precipitation (Fig. 9; $r^2 = 0.54$, $P < 0.001$). However, instead of DIN export being higher when the precipitation DIN concentration was high, as observed by Eshleman et al. (2013), it was lower (Fig. 9). This is strong evidence of that annual DIN export and atmospheric input are uncoupled. While atmospheric DIN input has been declining since 1980, total inputs (consisting of atmospheric input plus mineralization) may still exceed uptake and export, resulting in a continued accumulation of available DIN and increasing export. Before white pine establishment in 1956, the watershed was part of a water yield experiment. It was clear-cut in 1942 (no products were removed), and sprouts were cut annually from 1947 to 1955 to maintain a vegetation-free watershed. This treatment was evident in a 1990 study by Knoepp and Swank (1997; Knoepp, unpublished data, 2005) when the soil total C concentration in all soil horizons on CHL-C was greater than that found on the reference watershed. Measurements in 2005 found that the C/N ratio of CHL-C A horizon soils was 20, compared with 25 for CHL-R (Knoepp, unpublished data, 2005), suggesting more rapid N cycling in CHL-C. The combination of soil organic matter accumulation and decreased water movement through the watershed due to species conversion (Ford et al., 2011) has resulted in changes in N cycling patterns compared with the reference watershed.

Following logging in 1977, DIN export from CHL-L switched from biological to hydrological control within about 4 yr (Fig. 6). Around this time, patterns of export and the export/input ratio became closely coincident with those of CHL-C (Fig. 6 and 7). From 1978 through 2010, the export/input ratio of CHL-L was significantly related to annual precipitation (Fig. 8; $r^2 = 0.35$, $P < 0.001$) but only weakly related to the annual average DIN concentration of precipitation (Fig. 9; $r^2 = 0.11$, $P < 0.0.06$). Our interpretation of these data is that a combination of increased availability from logging (min-

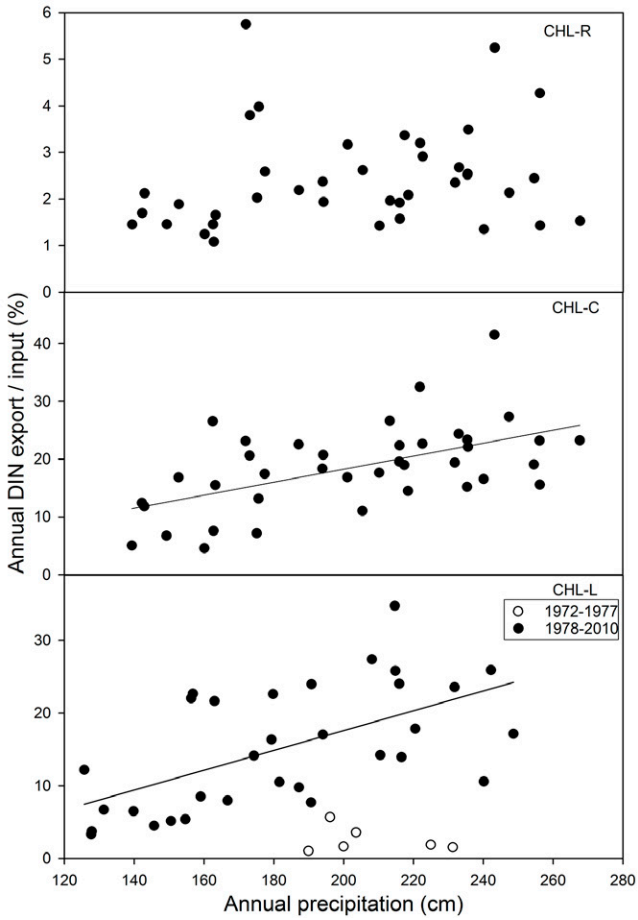

Fig. 8. Relationships between the ratio of annual dissolved inorganic N (DIN) export to input and annual precipitation for watersheds at Coweeta Hydrologic Laboratory. Lines represent statistically significant regressions. For Watershed CHL-L, the regression line is for 1978 to 2010 data only. Watershed CHL-C: slope = 0.122, intercept = –4.21; Watershed CHL-L: slope = 0.136, intercept = –9.67.

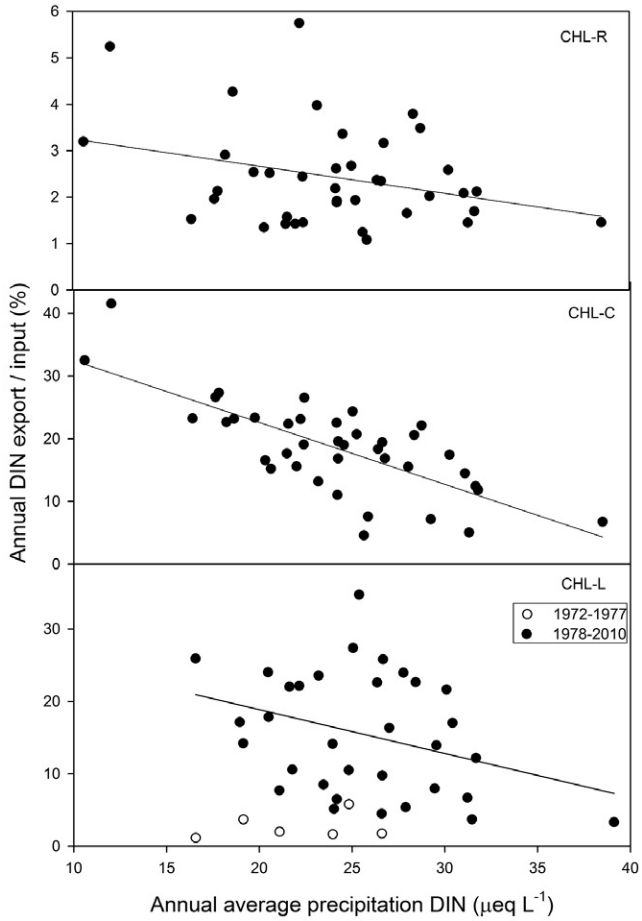

Fig. 9. Relationships between the ratio of annual dissolved inorganic N (DIN) export to input and the annual average concentration of DIN in precipitation for watersheds at Coweeta Hydrologic Laboratory. Lines represent statistically significant regressions. For Watershed CHL-L, the regression line is for 1978 to 2010 data only. Watershed CHL-R: slope = –0.058, intercept = 3.84; Watershed CHL-C: slope = –0.987, intercept = 42.3; Watershed CHL-L: slope = –0.606, intercept = 31.0. For DIN, 1 μeq L^{-1} = 1 μmol L^{-1}.

eralization of logging residue, reduced vegetation uptake of N for several years, low heterotrophic immobilization because of low leaf fall) and increased N inputs (continued atmospheric N input, input from N_2–fixing associates of black locust (*Robinia pseudoacacia* L.), and later the mineralization of high-N black locust trees as most black locust trees died from stem borer infection, Boring et al., 2014) contributed to an accumulation of available DIN that exceeded and continues to exceed uptake, creating conditions or symptoms of N saturation.

It is likely that the large input of N from the N_2–fixing symbionts of black locust ultimately resulted in N saturation. Mortality of the black locust due to stem borer infestation began 15 to 20 yr after clear-cutting, resulting in increased root inputs along with a reduction in N_2 fixation. However, the high rates of N mineralization that resulted following harvest continued through at least 1999 (Knoepp et al., 2014). Knoepp et al. (2014) hypothesized that this pattern of high soil N availability and stream N export resulted from the large N inputs and the change in species composition following harvest (Boring et al., 2014). In the first few years after logging, the stand on CHL-L contained almost 40% black locust, which later declined to only slightly more than 10% (Elliott and Vose, 2011). Boring et al. (1988) estimated that N_2 fixation by black locust in areas that were 100% black locust ranged from 48 kg N ha^{-1} yr^{-1} 4 yr after clear-cut harvesting to 75 kg N ha^{-1} yr^{-1} 17 yr after clear-cutting, and declining to 33 kg N ha^{-1} yr^{-1} after 28 yr. These numbers represent N inputs in areas of 100% black locust, and they estimated that the average contribution across a whole watershed is likely to be lower, around 10 kg N ha^{-1} yr^{-1} (Boring et al., 1988). At this level of N_2 fixation, over the course of the first 20 yr, the approximate lifespan of a black locust tree, total N inputs to CHL-L would equal around 200 kg N ha^{-1}.

The patterns of DIN export at the FEF have been very different from those at Coweeta, but they also support our mechanistic interpretation. The long history of high levels of acidic deposition to the FEF resulted in its early recognition as one of the best examples of an N-saturated forest ecosystem in the United States (Stoddard, 1994; Peterjohn et al., 1996; Fenn et al., 1998). For both the logged (FEF-L) and reference (FEF-R) watersheds, annual DIN export has been very high (Fig. 6). Annual DIN export from FEF-L has usually exceeded annual

input, and this has also been true for FEF-R in some years (Fig. 7). Campbell et al. (2004) documented that retention of N by FEF-R was the lowest of 24 forested reference watersheds across the eastern United States. Peterjohn (unpublished data, 2013) estimated N deposition for FEF during the last 100 yr to be about 250 kg N ha^{-1} more than the stand might have received at preindustrial deposition levels. While DIN input has been declining since about 1980 (Fig. 4), export has remained high so that the ratio of export to input has continued to increase for FEF-L and FEF-R (Fig. 6 and 7). For both FEF-R and FEF-L, the export/input ratio is weakly related to precipitation amount (Fig. 10; FEF-R: $r^2 = 0.11$, $P = 0.096$; FEF-L: $r^2 = 0.12$, $P = 0.081$), and the export/input ratio was significantly correlated with the DIN concentration of precipitation (Fig. 11; FEF-R: $r^2 = 0.70$, $P < 0.001$; FEF-L: $r^2 = 0.76$, $P < 0.001$). However, as with CHL-C, the relationship with the DIN concentration of precipitation is negative (Fig. 11). Therefore, while inorganic N deposition has been declining, historically high total inputs (deposition plus mineralization) have created conditions of high N availability, which still exceeds uptake and export. This and other evidence suggest that forests at FEF are not N limited, but growth may be limited by other factors, including P (Adams et al., 2006; Gress et al., 2007).

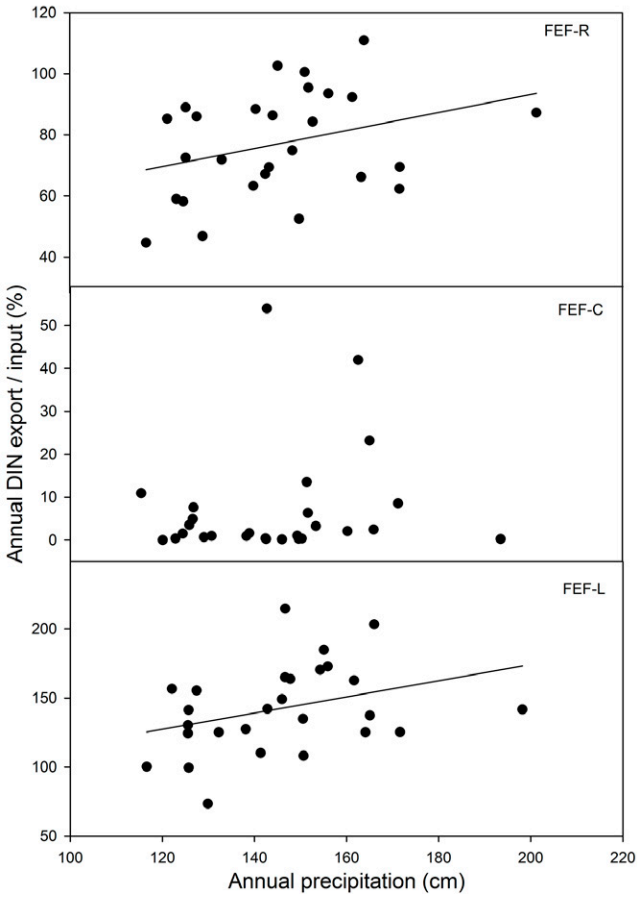

Fig. 10. Relationships between the ratio of annual dissolved inorganic N (DIN) export to input and annual precipitation for watersheds at the Fernow Experimental Forest. Lines represent statistically significant regressions. Watershed FEF-R: slope = 0.295, intercept = 34.2; Watershed FEF-L: slope = 0.586, intercept = 57.0.

For FEF-C, DIN export has declined to near zero in the last 30 yr (Fig. 6). This is quite different from the other FEF watersheds and from the CHL-C watersheds. Nitrate concentration in the FEF-C stream has been and continues to be very low (Adams et al., 2003; Adams and Kochenderfer, 2014). Also, dissolved organic N exports measured during 2007 to 2009 were quite low (mean value of 0.477 kg N ha^{-1} yr^{-1}; C.N. Kelly, unpublished data, 2009), suggesting that very little N is making it to the stream in either form. Nitrogen is apparently being immobilized in the plant biomass and soil organic matter, and there is evidence that the forest floor is aggrading (Kelly et al., 2011). This could be due to inputs of low-quality spruce litter, which is more resistant to decomposition than hardwood leaf litter. In addition, soil acidification may limit nitrification (Kelly et al., 2011), and abiotic immobilization of DIN may be an important factor (Davidson et al., 2003). Finally, annual stream flow has been significantly reduced on the FEF-C watershed (Fig. 2; Adams and Kochenderfer, 2007), which would indicate that even if N were available, there would be little water to export it from the watershed.

The results from the two conifer plantations illustrate how differences in internal processes can override the effects of N

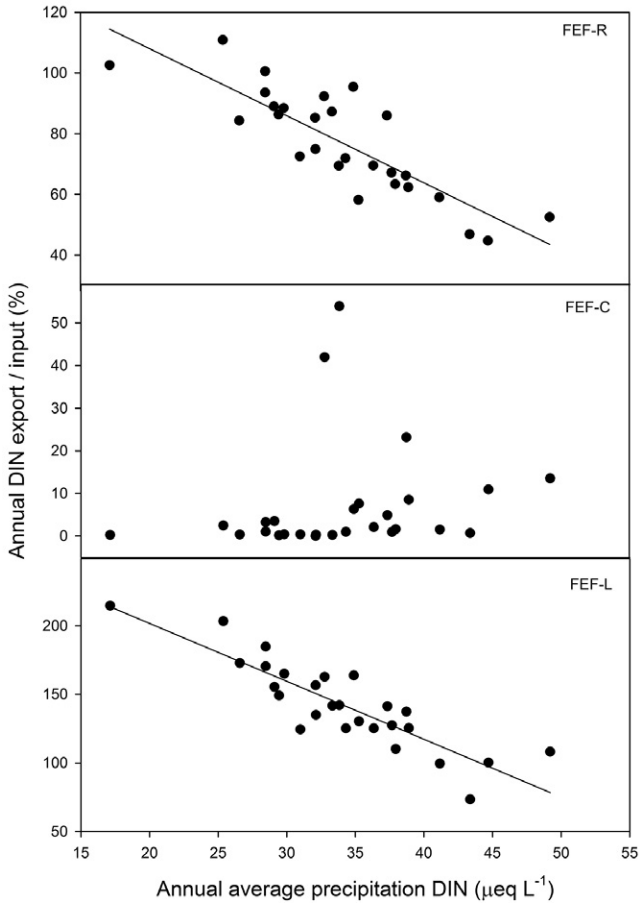

Fig. 11. Relationships between the ratio of annual dissolved inorganic N (DIN) export to input and the annual average concentration of DIN in precipitation for watersheds at the Fernow Experimental Forest. Lines represent statistically significant regressions. Watershed FEF-R: slope = −2.21, intercept = 152; Watershed FEF-L: slope = −4.22, intercept = 286. For DIN, 1 μeq L^{-1} = 1 μmol L^{-1}.

deposition. Both conifer plantations were treated similarly: clear-cut, several years of regrowth control, and conifer planting. But at the FEF, the logging was commercial and trees were removed, whereas at Coweeta, trees were clear-felled and there was no product removal. The resulting N dynamics were very different. At Coweeta, it is apparent that mineralization of soil organic matter has generated a large pool of available DIN that is exported in direct proportion to water moving through the watershed. At Fernow, mineralization rates are very low and there is essentially no available DIN to be exported.

Examining the impacts of similarly treated watersheds at the Fernow Experimental Forest and Coweeta Hydrologic Laboratory on inorganic N export and retention illuminates the importance of long-term measurements for understanding the regulation of N cycling in forest ecosystems and their response to disturbance. The legacy effect of historic DIN deposition is a major factor in predicting watershed N retention and export, results supported by the recent review of Johnson and Turner (2014). However, by including disturbed watersheds in our study, it has become evident that processes within a watershed may have much greater effects on N export than N deposition. Within the reference watershed at Coweeta, biological immobilization is sufficient to retain most N deposition and DIN export remains under biological control, but at Fernow, due to the historically high DIN deposition, accumulated N now exceeds immobilization processes, resulting in hydrologic regulation of DIN export.

The idea of a switch from biogeochemical (limiting source) to hydrologic (i.e., transport) control of DIN has been expressed elsewhere. For example, Ocampo et al. (2006a) and Basu et al. (2010) described switching between hydrologic and biogeochemical control of nutrient export at event, seasonal, and interannual scales. However, we are evaluating this switch in mechanistic regulation over much longer, decadal time scales. Thompson et al. (2011) described some catchments as exhibiting chemostatic regulation of chemicals where there is large storage of the chemical. In these cases, export was hydrologically controlled. However, they found that chemicals with rapid reaction rates (e.g., important biological nutrients) showed considerably more variability not related to hydrology. In their study, NO_3 export was variable, which is similar to what we found. We assume that undisturbed forest watersheds are highly DIN retentive and export is biologically controlled, but accumulation of available N beyond what can be biologically or perhaps abiotically immobilized can switch the regulation of DIN export to hydrologic control.

This excess N may come from atmospheric deposition, fertilization, N_2 fixation, a disturbance that increases N mineralization, or probably a combination of these processes. Methods of determining available soil N are used as indices of N status, yet they may not represent all sources of N (e.g., Knoepp et al., 2014). For instance, the DIN available for export may be present much deeper in the soil profile than is typically sampled or in coarse fragments, which are also not usually sampled (Smaill et al., 2014). Also, the DIN that is exported to the stream may come from a fairly small area of the watershed, perhaps due to DIN accumulation in near-stream zones (e.g., Duncan et al., 2013). A better understanding of how and where to measure available soil N would greatly improve our understanding of the processes regulating N retention and export from forest ecosystems.

Our study examined long-term patterns of N inputs, exports, and net N retention in reference and managed watersheds in two experimental forests, giving us the opportunity to investigate sites showing both N limitation and N saturation. Data suggest that in N-limited sites, watershed N retention is regulated by internal biological controls on soil N availability. On the other hand, in N-saturated sites, N export is directly related to abiotic properties, such as rainfall amount and watershed hydrology. The availability of long-term data as well as the inclusion of sites with high historic N deposition allowed us to document the switch from biogeochemical to hydrologic controls that occurred when N availability exceeded N immobilization, due to either N deposition or biological N inputs.

ACKNOWLEDGMENTS

We thank Bobbie Niederlehner for help with the statistical analyses. Many of the ideas in this paper resulted from discussions with Durrell Scott, Stephen Schoenholtz, Jeb Barrett, Kevin McGuire, Brian Strahm, Sheila Christopher, and Charley Kelly. This study was partially supported by NSF Grants DEB0218001 and DEB0823293 to the Coweeta LTER program at the University of Georgia and DEB0417678 and DEB1019522 for the Fernow LTREB project through West Virginia University.

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