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ECOSYSTEMS

SHORT COMMUNICATIONS

Control of Nitrogen Loss from Forested Watersheds by Soil Carbon:Nitrogen Ratio and Tree Species Composition

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ABSTRACT

Leaching losses of nitrate from forests can have potentially serious consequences for soils and receiving waters. In this study, based on extensive sampling of forested watersheds in the Catskill Mountains of New York State, we examine the relationships among stream chemistry, the properties of the forest floor, and the tree species composition of watersheds. We report the first evidence from North America that nitrate export from forested watersheds is strongly influenced by the carbon:nitrogen (C:N) ratio of the watershed soils. We also show that variation in soil C:N ratio is associated with variation in tree species composition. This implies that N retention and release in forested watersheds is regulated at least in part by tree species composition and that changes in species composition caused by introduced pests, climate change, or forest management could affect the capacity of a forest ecosystem to retain atmospherically deposited N.

Key words: carbon; nitrogen; watershed; nitrate leaching; tree species; soils; *Acer saccharum; Quercus rubra.*

INTRODUCTION

Export of nitrogen (N) from forested watersheds has become an important research area and public policy issue in recent years because N leaching can strip nutrients from forest soils, acidify streams, and cause eutrophication in estuaries and coastal waters (Vitousek and others 1997; Fenn and others 1998; Murdoch and Stoddard 1992). Nitrogen losses from forested watersheds can be quite variable, and the variation has been ascribed to many causes, including differences in atmospheric N inputs (Stoddard 1994; Dise and Wright 1995), geology (Holloway and others 1998), hydrology (Creed and Band 1998), and forest history (Vitousek 1977; Goodale and others 2000). The N cycle in forests is complex, and controls on N losses from watersheds with mature forest vegetation are not well understood. In recently disturbed forests, N export may be elevated immediately after the disturbance, due to the reduction in plant uptake, and later suppressed during the vigorous regrowth of young plants due to rapid N uptake in plant tissue (Vitousek 1977; Likens and others 1970). In mature temperate forests, however, most of the N deposited on the ecosystem is retained in the soil, not in the plants (Nadelhoffer and others 1999), and NO_3^- leaching is related to rates of soil N transformations (Van Miegroet and others 1992; Williard and others 1997). For these ecosystems, the controls on watershed N export reside largely in the soil–microbe–root complex that

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regulates litter decomposition and the accumulation of carbon (C) and N in soil organic matter. Previous studies in European forests have shown that soil C:N ratio is inversely related to forest NO_3^- leaching, after taking into account differing atmospheric deposition regimes (Gunderson and others 1998; Dise and others 1998; Emmett and others 1998); however, these studies were done primarily in coniferous forests, some of which receive very high rates of atmospheric N deposition (up to 80 kg N $ha^{-1}y^{-1}$). In contrast, most of the mid-Atlantic and northeastern United States is dominated by deciduous forests that receive low or moderate levels of N deposition (less than 15 kg N $ha^{-1}y^{-1}$).

In the Catskill Mountains of southeastern New York State, our survey of 39 streams draining small, forested watersheds showed a 17-fold range of NO_3^- concentration (Lovett and others 2000). All of these watersheds are vegetated almost entirely by unmanaged forest, so the variation in NO_3^- concentration was not a result of differences in current land use. Dissolved organic N concentrations were much less variable and ammonium concentrations were very low, so NO_3^- explained more than 96% of the variation in total dissolved N concentration among streams. Because water discharge per unit of watershed area is relatively constant within this area, variation in mean N concentration in stream water is a good index of variation in N export among watersheds (Lovett and others 2000). Our estimates of N input and export from these watersheds indicate that N retention (deposition minus export) ranges from about 49% to 90% of the atmospheric N deposition (Lovett and others 2000). Previous work indicated that variation in stream water N concentration among watersheds in this area was probably not due to variation in atmospheric deposition, topography, in-stream N retention, or groundwater input to streams (Lovett and others 2000; West and others 2001). In this study, we examine the relationship between stream water concentration in Catskill streams and characteristics of watershed soils and forests.

SITE AND METHODS

Study Area

Our research took place in the Catskill Mountains, an area of about 5000 km^2 with several ranges of mountains (peak elevations, 1100–1274 m) separated by deeply incised valleys and underlain by shales and sandstones of Devonian age (Stoddard and Murdoch 1991). The climate is moist and cool, with a mean annual temperature of 4.3°C and mean annual precipitation of 153 cm at a station located at 808 m elevation near Slide Mountain in the central Catskills (Lovett and others 2000). Soils in the Catskills are predominantly acidic inceptisols, generally shallow, stony, and well-drained (Stoddard and Murdoch 1991; Lovett and others 2000). Atmospheric N deposition (wet + dry) is about 11 kg N $ha^{-1}y^{-1}$ (Lovett and Rueth 1999). Forests are predominantly of the northern hardwood association dominated by sugar maple (*Acer saccharum* Marsh), American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britt.), with oak-dominated forests (especially northern red oak, *Quercus rubra* L.) near the larger river valleys and limited areas of spruce–fir vegetation on some of the higher peaks (Lovett and others 2000). Symbiotic N-fixing trees are not a significant component of the forest. Most of the land used in this study is part of the New York State Catskill Forest Preserve, which was first designated in 1885 and has been continually augmented ever since. Forested lands in the preserve are not harvested, fertilized, or otherwise managed. The Catskill region is the principal source of water for New York City.

Methods

We have measured stream water chemistry approximately quarterly since 1994 in 39 watersheds in the Catskills (Lovett and others 2000). The NO_3^- concentrations used in this analysis are means of sampling from 1994 to 1999, including the 1994–97 data in Lovett and others (2000) and extending the data set to 1999 using the same methods. After sampling the stream water in precleaned polyethylene bottles, the sample was returned to the laboratory and four drops of chloroform were added per 100 ml of sample as a preservative. The samples were then stored at 4°C until analysis could be performed. Nitrate concentrations were measured with a Dionex 2000 ion chromatograph (Dionex Corporation, Sunnyvale, California, USA).

We sampled the vegetation and soils in 13 of these watersheds, ranging from 63 to 476 ha in area. The watersheds were Windham Ridge, Mill Brook, Winnisook, Buttermilk Falls, Pecoy, BWS6, Halcott, Tonshi, Grog Kill, Black, Kittle, Myrtle, and Becker Hollow. More information about these watersheds, including more solute concentrations and watershed topographic characteristics, can be found in Lovett and others (2000). Vegetation and soil were sampled in 725 plots (6 × 30 m) in the 13 watersheds, for an average of 55 plots per watershed. The plots were clustered, with five plots representing a roughly 1-ha area, which we call a "stand." The 145 stands were distributed in a stratified random design such that stands were distributed among watersheds in proportion to the watershed area and within watersheds in proportion to the area in elevational zones. Trees greater than 10 cm dbh were measured in each plot, and a sample of organic horizon (Oe + Oa layers) soil was taken. Basal area (at breast height) was calculated by species assuming a circular bole cross section. The vegetation data from the five plots in a stand were averaged, and the five soil samples were composited before analysis of C and N concentration (on a Carlo-Erba NA 1500 element analyzer, Carlo Erba Strumetazione, Milan, Italy). This yielded a data set of 145 stands with mean vegetation and soil C:N data.

Forest history information for each stand was obtained using a Geographic Information System by plotting the location of each stand (measured with a global positioning system (GPS) unit in the field) on a digital version of the Catskill forest history map published by Kudish (2000). The forest history classifications used by Kudish are based on extensive field observations and searches of local land-use records. The forest history categories present in the watersheds that we studied were as follows: old growth (forest that has not been harvested or burned), second growth (forest that shows evidence of harvest), burned (forest with a confirmed record of forest fire), and pasture (forest that was formerly pastureland).

Statistical analysis was done with the SAS statistical package (SAS Institute, Cary, NC, USA) using the procedures REG (for regression analysis), ANOVA (for analysis of variance) and GLM (for general linear model analysis). In the stepwise regression, variables were entered and removed at $P = 0.15$, and statistical significance was assessed at $P < 0.05$.

RESULTS AND DISCUSSION

Using stepwise regression, we found that the C:N ratio in organic horizon soils was the only significant predictor of mean annual stream NO_3^- concentration among a suite of independent variables, including the basal area of all major tree species and topographic variables such as minimum and maximum elevation, slope, area, and stream length. Soil C:N explained 57% of the variance in mean annual stream NO_3^-, and the two variables were inversely related (Figure 1). Soil C:N was also the best single-variable predictor of NO_3^- concentration in both the summer (June–September) and winter (December–March) periods (r^2 values of 0.60 and 0.46, respectively). This result implies that organic soil C:N controls NO_3^- export and retention in these watersheds, or that some other factor controls both soil C:N and NO_3^- export. The former explanation is likely because a high soil C:N ratio produces a strong demand for N by heterotrophic soil microbes, leaving less N available for nitrification and subsequent NO_3^- leaching (VanMiegroet and others 1992; Riha and others 1986). Strong negative associations between soil C:N and nitrification rate have been observed in both hardwood and coniferous forests in the northeastern United States (McNulty and others 1991; Lovett and Rueth 1999; Goodale and Aber 2001; Ollinger and others 2002).

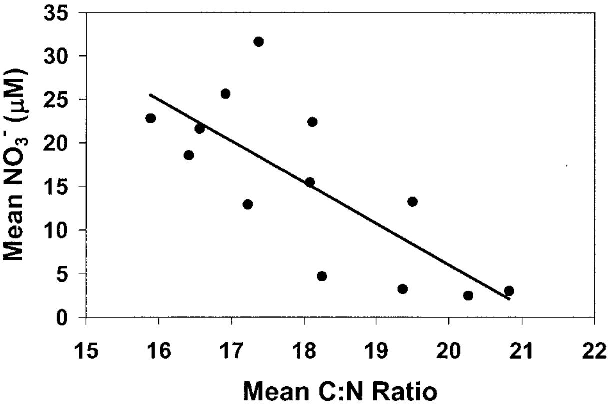

Figure 1. Mean stream NO_3^- concentration versus mean C:N ratio in organic horizon of watershed soils. The points represent the 13 watersheds. The line is the best fit regression line ($y = -4.741x + 100.81$, $r^2 = 0.57$, $P = 0.0027$)

This is the first evidence, to our knowledge, of the relationship between stream NO_3^- loss and soil C:N ratio in the forested watersheds of North America. This finding leads us to ask what controls soil C:N in the forested watersheds we studied. In our 13-watershed data set, the variable most strongly associated with mean soil C:N was mean basal area of sugar maple (inverse relationship, $r^2 = 0.57$, $P = 0.003$). However, a much more powerful analysis can be done on our stand-level data set ($n = 145$), which includes vegetation, soil C:N, elevation, and forest history information for each stand we sampled. In this data set, the variables that explained the most variance in soil C:N (using stepwise linear regression) were the basal areas of sugar maple and red oak (Figure 2); variables of secondary importance were the basal areas of red maple (*Acer rubrum*) and white ash (*Fraxinus americana*). These four vegetation variables were the only significant variables in the stepwise regression analysis; together they explained 40% of the variation in soil C:N ($P < 0.0001$). The partial r^2 for each variable

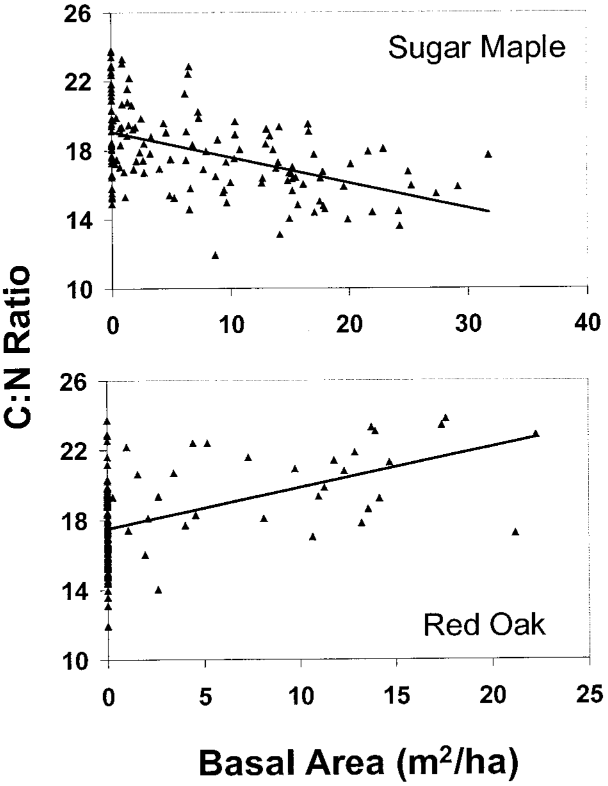

Figure 2. Organic horizon C:N ratio versus basal area of sugar maple ($r^2 = 0.22$, $P < 0.0001$) and red oak ($r^2 = 0.20$, $P < 0.0001$) in mixed-species stands.

was: sugar maple, 0.22; red oak, 0.12; red maple, 0.03; and white ash, 0.02. All variables were significant at $P < 0.05$. Sugar maple and white ash basal areas were inversely related to C:N, whereas red oak and red maple were positively related to C:N. Given that soil C:N is inversely related to stream NO_3^- concentration (Figure 1), this finding suggests that forests with a higher abundance of sugar maple and white ash should leach relatively more NO_3^-, whereas forests with more red oak or red maple should leach less. These results are consistent with other reports on the relative rates of nitrification and nitrate leaching associated with these species (Finzi and others 1998; Lovett and Rueth 1999; Lewis and Likens 2000; Christ and others 2002; Venterea and others in press), except that in one study red maple produced relatively high nitrification rates in the soil (Finzi and others 1998).

Although our analysis shows correlation rather than causation, it seems quite likely that tree species composition can control soil C:N, especially in the organic horizons. Trees vary markedly in litter chemistry, and this variation can cause different rates of litter decomposition and C and N storage in soils (Melillo and others 1982; Son and Gower 1992; Hattenschwiler and Vitousek 2000). Other candidates for control of soil C:N include atmospheric N deposition, climate, forest history, and, in some cases, geology. Atmospheric deposition and climate vary markedly with elevation in the Catskill Mountains (Lovett and others 1999; Weathers and others 2000; Kudish 2000), but in our data set the relationship between soil C:N ratio and elevation was very weak, albeit statistically significant ($P < 0.05$, $r^2 = 0.05$, $n = 145$). Elevation was not a significant term in multiple regression models that also included vegetation variables, suggesting that the influence of elevation on C:N is primarily due to its influence on tree species composition. Interestingly, in an intensive study of one of these Catskill watersheds, Lawrence and others (2000) found that while atmospheric N deposition increased with elevation, stream water NO_3^- concentration decreased with elevation. This effect was attributed to the presence of different vegetation and soils at higher elevations.

Because forest history and species composition are interrelated, their effects can be difficult to distinguish. Nonetheless, our stand data do not show any significant direct effect of forest history on soil C:N ratio. Forest history was not statistically significant either in an analysis of variance (ANOVA) using forest history alone or in a general linear model (GLM) using forest history as a categorical variable and the basal area of the four tree species as continuous variables. The two most common forest history classifications for our stands, second growth ($n = 91$) and old growth ($n = 26$), differ in mean C:N ratio by less than 0.4%. The classification "second growth" is admittedly crude, encompassing a range of prior harvesting practices and times, but these data do not suggest any effect on C:N ratio resulting directly from forest history. This result differs from studies in New Hampshire that reported strong effects of forest history on N cycling, but also noted that it was difficult to disentangle the influences of forest history and species composition (Goodale and Aber 2001; Ollinger and others 2002). The differences between the Catskills and New Hampshire may have to do with differences in the intensity of past disturbances or the identity of the tree species involved. Forest history almost certainly has an indirect influence on soil C:N because forests subject to disturbance can differ in species composition from old-growth forests, and these changes in species composition can be reflected in soil C:N. In addition to forest history, patterns of tree species composition can be influenced by a number of factors, including bedrock chemistry, soil texture, climate, and tree dispersal dynamics.

In some areas, watershed NO_3^- export has been related to geological sources of N from weathering of N-bearing sedimentary rocks (Holloway and others 1998). This additional source of N would presumably also influence the soil C:N ratio (Dahlgren 1994). However, the central Catskills area that was the site of this study has relatively homogeneous bedrock mineralogy (Stoddard and Murdoch 1991), although the N concentration of the rocks has not been reported. Moreover, in our stand-level data set, the range of stand C:N ratios within most watersheds was greater than the range of mean values among watersheds, suggesting variation on a scale smaller than would be expected from differences in bedrock geology but appropriate for the scale of tree species heterogeneity.

It has been argued that in-stream retention or processing of N is a major factor influencing stream NO_3^- concentrations in a variety of ecosystems in North America (Peterson and others 2001). However, the Catskill headwater streams that we studied are steep, rocky, and frequently shaded by overhanging trees, conditions that tend to reduce in-stream N retention. There is a strong 1:1 correspondence between groundwater seep and stream NO_3^- concentrations in these Catskill watersheds, indicating that NO_3^- concentrations are set before the water enters the stream (West and others 2001).

The fact that stream NO_3^- concentrations in our 13-watershed data set were more strongly associated with soil C:N ratios than with vegetation composition suggests to us that organic horizon C:N ratio is a good integrating variable that simplifies some of the multivariate complexity of tree species composition. Combined with the data from conifer forests in Europe (Gundersen and others 1998; Dise and others 1998), these results suggest that the C:N ratio is a broadly applicable and very useful indicator of the propensity for NO_3^- leaching from forests.

Our data indicate that vegetation plays a strong role in controlling soil C:N and thereby influencing watershed N retention and loss in the Catskill region. We expect this result to be generally applicable to forests elsewhere in the temperate zone that are heterogeneous in vegetation. However, two important points are worth bearing in mind. First, N cycling and leaching loss depend on the interactions among a suite of potentially important variables, including atmospheric deposition, hydrology, geology, vegetation, forest age and history, and climate. In any given study region, a large relative range in one of those variables may cause it to dominate the mix and mask the influence of the others. We believe that contradictory reports in the literature on which factors control forest losses and retention of N can be explained by differences among study regions in the relative ranges of this suite of potential controlling factors. Second, the factors that control the spatial variation in N loss, as discussed in this paper, are not necessarily the same ones that control the temporal variation. Some factors, such as bedrock geology, are essentially unchanging on ecological time scales; whereas others, such as forest age, are certain to change. In the Catskill region, we believe that the main control on spatial variation of NO_3^- loss is the vegetation composition, but controls on temporal variation in the next few decades will include changes in climate (Murdoch and others 1998) and N deposition (Murdoch and Stoddard 1992), as well as changes in species composition.

There are several important implications to our finding that forest composition influences soil C:N and watershed N export in our region. First, watershed managers must take the species composition of their watersheds into account when evaluating the likely consequences of continued N deposition on water quality. For instance, our results indicate that the leaching of N in drainage water and the resultant effects on acidification and eutrophication are likely to be more severe in sugar maple–dominated forests than in red oak–dominated forests. Second, factors that change the species composition of a forest may also change its capacity to retain N from atmospheric deposition. These factors include disease and pest outbreaks, selective harvest, and climate change. In the Catskills, there has been a marked change in species composition over the last 50 years as an introduced pest has decimated the population of beech (formerly the dominant tree of the region), permitting sugar maple to become dominant (McIntosh 1962). In the future, the populations of sugar maple may succumb to acid deposition (Driscoll and others 2001), climate change (Iverson and Prasad 1998), or a new introduced pest (USDA 1999); and it is unclear what the next dominant species will be, or how it will affect N losses. Finally, in recent years, much attention has been paid to the extent to which individual species influence ecosystem function (Chapin and others 1997; Hobbie 1992; Wedin and Tilman 1990), and these results provide a compelling example of how tree species can affect important ecosystem characteristics and processes at the both the stand and watershed scales.

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