

Nitrogen Retention, Removal, and Saturation in Lotic Ecosystems

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ABSTRACT

Increased nitrogen (N) loading to lotic ecosystems may cause fundamental changes in the ability of streams and rivers to retain or remove N due to the potential for N saturation. Lotic ecosystems will saturate with sustained increases in the N load, but it is unclear at what point saturation will occur. Rates of N transformation in lotic ecosystems will vary depending on the total N load and whether it is an acute or chronic N load. Nitrogen saturation may not occur with only pulsed or short-term increases in N. Overall, saturation of microbial uptake will occur prior to saturation of denitrification of N and denitrification will become saturated prior to nitrification, exacerbating increases in nitrate concentrations and in N export downstream. The rate of N export to downstream ecosystems will increase

proportionally to the N load once saturation occurs. Long term data sets showed that smaller lotic ecosystems have a greater capacity to remove in-stream N loads, relative to larger systems. Thus, denitrification is likely to become less important as a N loss mechanism as the stream size increases. There is a great need for long-term studies of N additions in lotic ecosystems and clear distinctions need to be made between ecosystem responses to short-term or periodic increases in N loading and alterations in ecosystem functions due to chronic N loading.

Key words: nitrogen cycle; lotic ecosystems; nitrogen loading; nitrogen retention; denitrification; primary production; nitrification.

INTRODUCTION

Anthropogenic activities, including fossil fuel burning, watershed disturbance, crop fertilization and wastewater disposal, have increased annual rates of nitrogen (N) loading into freshwater ecosystems 6 to 50 fold, causing global fertilization of continental waters, estuaries and near-coastal marine habitats (Carpenter and others 1998 Townsind and others 2003). There may be both negative direct (for example, methyhemoglobinemia, ammonia toxicity) and indirect (for example, eutrophication, alteration of food webs, non-Hodgkin's lymphoma)

effects of this N loading (Rabalais and others 2002). Nitrogen input into aquatic habitats will increase with an expanding human population and continued growth of resource use rates. Knowledge of how N is transformed and transported within lotic ecosystems will be essential for mitigating the effects of current and future human activities.

The defining feature of lotic ecosystems, unidirectional flow of water, provides the primary physical basis for stream solute studies (for example, nutrient spiraling; Webster and Patten 1979). Watershed biogeochemists have traditionally regarded lotic ecosystems as relatively inert conduits leading from land to sea. However, important biogeochemical reactions (uptake, nitrification, and denitrification) occur during downstream transport, resulting in variations in the percentage of N

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moving downstream (Dent and Grimm 1999; Kemp and Dodds 2001*a*, 2002*a*; Royer and others 2004; Inwood and others *in press*; Bernhardt and others 2004). Biogeochemical reactions associated with stream sediments and other substrata types affect whole-system N cycling, with strong interactions occurring between the surface water, sub-surface water, and hyporheic zones as water moves downstream (Jones and Holmes 1996; Kemp and Dodds 2001*a*, Kemp and Dodds 2002*a*; Schaller and others 2004). Regardless of the amount of N entering streams from terrestrial habitats, any substantial reduction of N moving down stream channels will decrease the impacts of N loading. Previous work has shown that streams and small rivers may influence N export to large rivers due to higher benthic to surface water ratios relative to larger rivers and lakes which result in increased N transformation and cycling rates, consequently decreasing N export (Alexander and others 2000; Peterson and others 2001; Royer and others 2004).

In this paper, we explore how characteristics of the N cycle may influence N transport via flowing waters under variable environmental conditions and N loading scenarios. We first discuss the potential for N saturation in lotic ecosystems relative to terrestrial ecosystems and then mechanisms for retention and removal of N. Next, the components of the N cycle and the factors influencing individual mechanisms of removal and retention are examined. These factors lead to hypotheses on how proportions of N species may change in response to changing process rates when lotic ecosystems are subjected to increased N input. Two general predictions are subsequently tested using long-term data sets. Our overall objectives are to 1) analyze available information on N loading, removal, and retention in lotic ecosystems, 2) propose several hypotheses explaining how lotic ecosystem dynamics will change in response to chronic increases in the N load, and 3) identify future research needs.

NITROGEN SATURATION

Nitrogen loading ranges from chronic to acute. Chronic N loading results from sustained N inputs or frequent recurrence of N inputs over a long period of time. In contrast, acute N loading is a sudden large input of N. Many studies have examined the effects of acute N loading (for example, Bushong and Bachman 1989; Christensen and others 1990; DeLaune and others 1991; Keeney and DeLuca 1993; Kemp and Dodds 2002*a,b*), however, less is known about the influ-

ence of chronic N loading on streams and rivers and whether, or at what point, lotic ecosystems may experience N saturation.

Nitrogen saturation may occur for several reasons: 1) organisms have a finite demand for N because they become limited by other factors when N availability increases; 2) heterotrophic organisms mineralize a greater proportion of the N they take in as their food becomes more N-rich; 3) abiotic adsorption sites become filled. These saturation processes have been documented in terrestrial ecosystems (Kahl and others 1993) although the mechanisms are not specific to terrestrial ecosystems. The question is not do lotic ecosystems saturate with respect to N input, but rather, at what point do they saturate?

Monitoring of N export via streams has been a primary tool to assess terrestrial N saturation (Aber and others 2003). Interestingly, these studies are generally unable to partition retention occurring on land from that occurring in low-order streams. In most headwater streams, nitrate and ammonium are present in low concentrations unless the waters drain from N-saturated terrestrial ecosystems (Galloway and others 2003). The inorganic N that reaches lotic ecosystems in a relatively pristine watershed is usually denitrified or quickly incorporated into biomass (Peterson and others 2001). The major terrestrial flux of inorganic N in undisturbed areas to surface waters may be organic N in the form of detritus or dissolved organic matter washed into the system (Lewis 2002; Perakis and Hedin 2002).

Previous analyses have delineated three general stages of ecosystem response across a gradient of N loading in lotic ecosystems (Stoddard 1994). These stages are characterized by patterns of nitrate concentrations that reflect the relative importance of flux rates within the system. Early stages (designated as "Stage 1" in this paper) are characterized by periodic increases in N export, primarily during periods of high discharge. Middle stages (designated as "Stage 2" in this paper) are characterized by more frequent increases in N export, and late stages (designated as "Stage 3" in this paper) result in continuous high export of N that is directly proportional to discharge. The ranges of N loading across which these stages will occur have been hypothesized to vary depending upon the characteristics of each ecosystem, including surrounding watershed vegetation and soil, size, metabolism, and frequency of scouring. We extend these analyses by examining the response of process rates to these stages of N saturation.

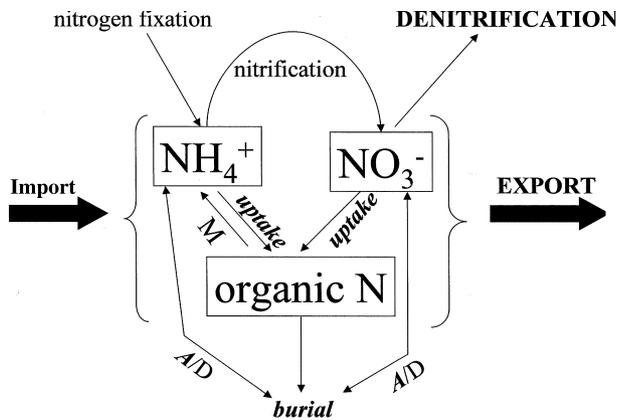


Figure 1. Mechanisms for nitrogen retention and removal in lotic ecosystems. *M*=mineralization; *A*=adsorption; *D*=desorption. Removal mechanisms (denitrification, export) are coded in capital letters and retention mechanisms (adsorption, uptake, burial) are italicized.

NITROGEN RETENTION AND REMOVAL

Nitrogen that enters streams and rivers can be temporarily retained or permanently removed from the ecosystem (Figure 1). Mechanisms for N retention include adsorption, biotic uptake, and burial which stores N temporarily in the sediment and organic matter. Mechanisms for removal include denitrification, harvesting of biomass, ammonia volatilization, and export downstream. All of these retention and removal routes are finite except for N transport, ammonia volatilization, and biomass removal. In most flowing waters, pH is not high enough and ammonia concentrations not great enough for ammonia volatilization to occur at substantial rates, and biomass removal is negligible, so these processes will hereafter be ignored. Because the remaining sub-processes all saturate, N saturation of rivers and streams must occur as N loading increases.

Retention may be a result of storage associated with stream organisms, terrestrial organic material deposited in the stream channel, stream sediments, and hyporheic zones. The length and magnitude of the initial retention period will vary depending on the available capacity in these storage pools. Nitrogen can be retained in terrestrial ecosystems with pulsed or short-term increases in N (Aber and others 1998). Similar responses to short-term increases of N have been observed in lotic ecosystems. For example, many investigators add N in the form of nitrate or ammonium, and measure the downstream disappearance of these compounds to determine nutrient uptake length. The ability of

lotic ecosystems to reduce these spikes of inorganic N to background concentrations indicates a functional capacity to at least temporarily retain N. However, remineralization, desorption, and material transport may allow subsequent downstream movement. Furthermore, in some systems where baseline N concentration is high, uptake of inorganic N from the water column is limited (Dodds and others 2002), a clear indicator of ecosystem N saturation. Large physical structures including wood debris, macrophyte beds and sediments can also increase N retention within lotic ecosystems by reducing water velocity which leads to decreased transport of particulate and dissolved materials (Hyatt and Naiman 2001). Wood debris accumulations have the potential to remain stable for many years. Hyatt and Naiman (2001) demonstrated that although many large pieces of wood in the Queets River channel were less than 50 years old, some were as old as 1440 years, suggesting burial of woody debris and long-term storage can occur in lotic ecosystems and lead to N retention. We expect a similar response to impoundments in larger rivers, also yielding an increase in N retention.

On a broad scale, lotic ecosystems can be categorized as either erosional or depositional with regard to particulate N retention (Dahm and Valett 1996). Erosional systems are typically of higher slope and are subjected to heavier rainfall events and frequent flooding. Short-term N retention may occur in erosional systems during periods without flooding through biotic uptake and/or sedimentation (abiotic adsorption; Triska and others 1989; Dahm and Valett 1996). These systems are able to remove N over long time periods only through denitrification. Thus, factors influencing denitrification rates are of utmost importance when considering long-term N retention and removal efficiency in erosional systems. In contrast, depositional lotic ecosystems are able to both remove N via denitrification and retain N via uptake by organisms or abiotic adsorption followed by sedimentation, yielding higher retention efficiencies relative to erosional systems (Dahm and Valett 1996). In these depositional systems, sediment N can be deposited in the flood plain for centuries or more. Strategies to maximize transient storage, sediment deposition, and denitrification may prove useful in maximizing the retention efficiency in depositional lotic ecosystems.

A key aspect of N retention as influenced by the processes discussed above is the probability that N will be dissolved in the water column. This is be-

cause nutrients in the water column move downstream much more rapidly than those in the particulate phase (Webster and Patten 1979). Thus, biotic properties affecting water column nutrient concentrations are essential to determining N retention. In the next section, we explore factors that influence forms and concentrations of water column N.

FACTORS INFLUENCING NITROGEN CONCENTRATION

Heterotrophic and Autotrophic Uptake

Biofilms (microbial matrix on substrata surfaces) remove nutrients from the water column via uptake, return nutrients to the water column via mineralization, and alter biogeochemical conditions that influence microbial transformation rates. Short-term retention of nutrients via assimilatory uptake in biofilms can be very high as nutrients are intensively recycled within benthic communities (Burns 1998). However, many factors (grazing, sloughing, flood disturbance, light limitation, diffusion) ultimately limit the total amount of N that can be retained in biofilms, regardless of whether they are net autotrophic or heterotrophic.

In ecosystems driven by allochthonous inputs, terrestrial vegetation provides large amounts of carbon-rich, N-poor materials for heterotrophic processing. The stoichiometry (carbon to N ratios of >20 by mass) of this large organic material dictates that N be acquired by the heterotrophic community to grow and exploit carbon. In experiments where leaf litter was excluded, the uptake length for nutrients was longer relative to systems with a natural abundance of litterfall (Webster and others 2000); supporting the idea that at least short-term retention of dissolved N is increased by heterotrophic organisms associated with organic matter. Isotope tracer experiments demonstrate that N turnover rates are greater as C:N of ecosystem compartments increases, suggesting a possible link between stoichiometry and retention (Dodds and others 2004).

Close coupling of primary production, ammonium mineralization, and heterotrophic uptake occurs in many ecosystems and may explain why N concentrations are often found to be moderately stable in the short term (Bushong and Bachman 1989; Webster and others 2000). We hypothesize that short-term retention of N via autotrophic and heterotrophic uptake is less effective with sus-

tained Stage 3 N loading because rates of mineralization ultimately increase with N saturation. Mineralization increases because the relative rate of N mineralization increases as microbial food sources increase in N content (Goldman 1987). The resulting response to chronic loading is an increase in both dissolved inorganic N concentrations and export, as in lakes along a productivity gradient (Cotner and Biddanda 2002). The absolute concentration at which uptake rate becomes saturated can vary both spatially and temporally (Bothwell 1989; Webster and others 2000). Saturation of N uptake is likely to be exacerbated by disturbance of in-stream habitat, which may decrease the heterogeneity of organisms and substrata within the stream, thereby decreasing the ability of the system to handle short periods of increased N loads (Peterson 1985). Heterogeneity is also important because N transformation rates vary significantly with microhabitat (Kemp and Dodds 2002a Schaller and others 2004). Thus, decreasing heterogeneity within the ecosystem may decrease N processing (Dodds and others 2004).

Abiotic Adsorption

Abiotic adsorption has been implicated as an important feature of N retention in soils. Ion exchange binds ammonium to organic and inorganic particles, slowing diffusion and decreasing mobility. Although little N is contained in primary minerals, some clays incorporate N as fixed ammonium which in some soils can represent more than 10% of the total N (Smith and others 1994). Although fixed ammonium release from clay is slow, it may play an important role in determining the availability of N for uptake by organisms (Green and others 1994). The decrease in N availability due to ammonium adsorption is well documented. However, the ability of nitrate to be incorporated into abiotic particles is less well studied although nitrate is generally not retained by ion exchange in sediments and is easily mobilized in water.

Nitrification

Nitrification may be important for N retention for two reasons. First, denitrification often relies on nitrification to provide substrate, so N loss may hinge on nitrification rates. Second, nitrification produces nitrate from ammonium, and nitrate is more easily transported downstream and less likely to be immobilized. Therefore, understanding what controls rates of nitrification, and subsequently denitrification, is crucial to building a mechanistic view of N retention in lotic ecosystems.

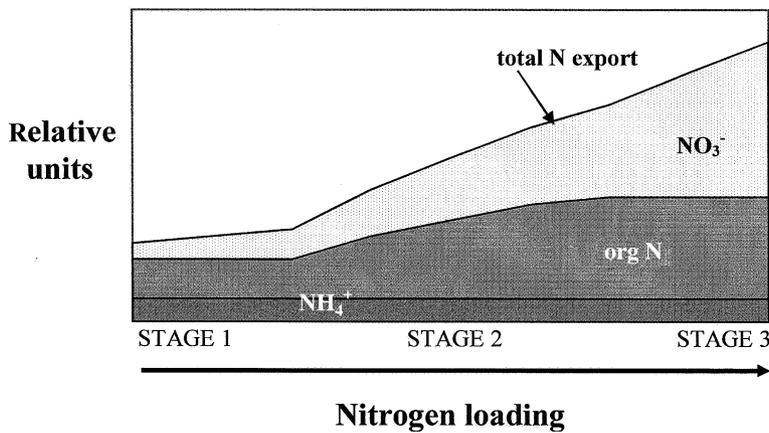


Figure 2. Predicted changes in total nitrogen (N) export, nitrate concentrations (NO_3^-), ammonium concentrations (NH_4^+), and organic nitrogen concentrations (org N) with increasing intensity of chronic N loading in lotic ecosystems.

Nitrification in lotic ecosystems occurs primarily in the oxidized surface of the bottom sediment and only minimally in the overlying water (DeLaune and others 1991; Kemp and Dodds 2001*b*). The efficiency of nitrifying bacteria is highest when dissolved oxygen penetration into the sediment is greatest, and may also depend upon N delivered from the water column (Kemp and Dodds 2001*b*). Stream water nitrate concentrations are correlated with nitrification rates (DeLaune and others 1991; Kemp and Dodds 2002*a*) indicating that in-stream processes, as well as external inputs, can influence stream N concentrations when nutrient concentrations are low.

Nitrification responds linearly to increasing N concentrations (for example, see Peterson and others 2001; Kemp and Dodds 2002*b*). This is logical because oxidation of ammonium and nitrite serve as an energy source for organisms. However, if nitrification rates increase linearly with stream water N concentrations, pH will eventually decrease because nitrification produces hydrogen ions (the magnitude and slope of decrease depending on the buffering capabilities). As the pH decreases, the proportion of free ammonia will also decrease and the proportion of ammonium will increase. Ammonia is thought to be the true substrate for ammonia oxidation, so nitrification rates should decrease at lower values of pH (Strauss and others 2002). If N fertilization also increases primary production, photosynthesis may drive pH high enough during the day that it can offset the self-inhibitory effects of nitrification and lead to a diurnal pattern of increased nitrification rates. This diurnal pattern of nitrification has not been established experimentally to our knowledge.

We predict, given these regulatory factors, that nitrification will increase linearly at low to moderate levels of chronic N loading (Stage 1–2;

Figure 2,3) but become inhibited at higher levels (Stage 2–3) because of low pH and the inhibitory effects of high ammonium, nitrate and nitrite (Anthonisen and others 1976) or other regulatory factors (Strauss and others 2002). Increases in nitrification rates are hypothesized to occur regardless of N species, not only because of higher primary production rates that indirectly stimulate nitrification (An and Joye 2001), but also because of higher substrate availability (Figures 3, 4).

Denitrification

Although increased N loading yields higher denitrification rates in terrestrial ecosystems (Ettema and others 1999), a similar effect is not as clear in lotic ecosystems. For instance, Hill and Lymburner (1998) found that nitrate removal through denitrification decreased as surface flow increased, likely due to the introduction of dissolved oxygen. Thus, in spite of increased nitrate loading associated with increased surface flow, denitrification decreased. The theoretical relationship between nitrate concentrations and denitrification rates can be described by Michaelis-Menten kinetics with denitrification approaching saturation with maximum rates between 100 and 500 $\text{mg N m}^{-2} \text{d}^{-1}$ (for example, Christensen and others 1990; Kemp and Dodds 2002*b* Royer and others 2004). Thus, even in ideal conditions, denitrifiers can only utilize a finite amount of N. Saturation of denitrification in eutrophic lotic ecosystems has previously been demonstrated and may allow for increased rates of ammonium recycling and decreased rates of N removal (Christensen and others 1990).

The amount of N that is denitrified and removed from the ecosystem will depend primarily on the activity of the nitrifying bacterial population when N concentrations are low, the external supply rate of nitrate, and the degree of physical coupling be-

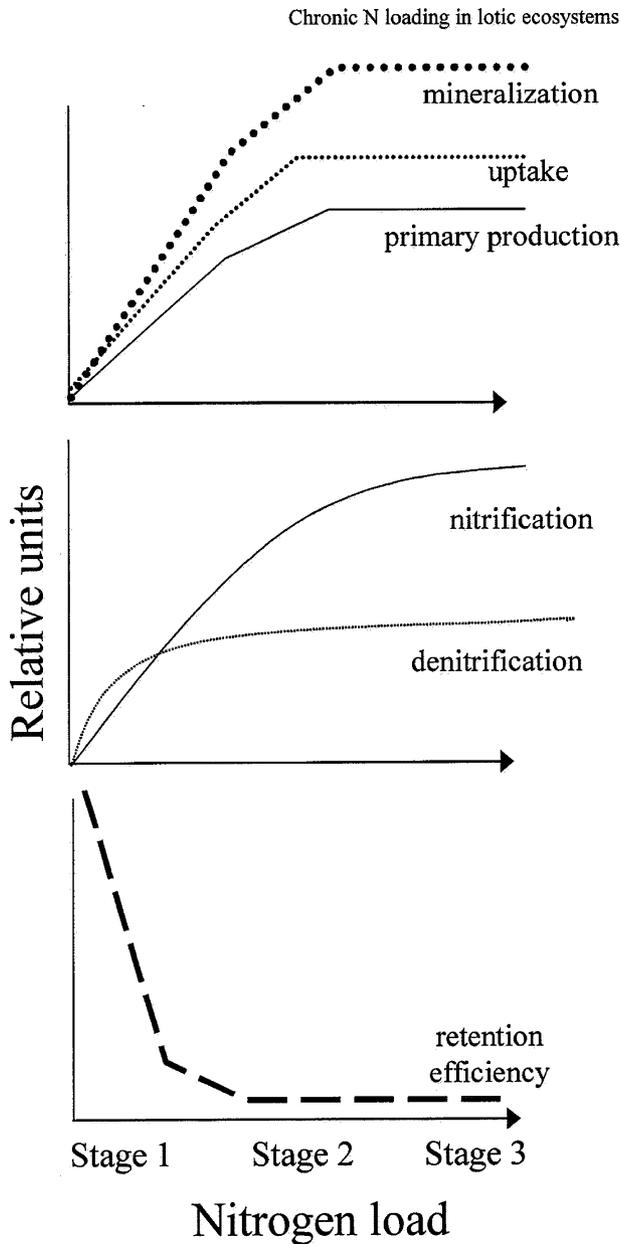


Figure 3. Predicted changes in the rates of nitrogen transformations and retention efficiencies with increasing intensity of chronic nitrogen loading in lotic ecosystems.

tween nitrification and denitrification (DeLaune and others 1991; Kemp and Dodds 2002b) Richardson and others 2004. Additional factors can affect the activity of denitrifying bacteria, including temperature (Andersen 1977), dissolved oxygen concentration (Nielsen and others 1990), and carbon (Hedin and others 1998; Strauss and Lamberti 2000 Inwood and others In press).

The absolute mass of nitrate removed via denitrification is generally greater in downstream

reaches, because the total nitrate inputs are larger (Galloway and others 2003). Denitrification can account for as much as 30–70% of the total input to lotic ecosystems across an entire river system, although the proportion of inputs removed by denitrification in a particular reach (<1 km) is generally quite small (1–20%; Galloway and others 2003; Kemp and Dodds 2002b Royer and others 2004; Inwood and others 2004; Wall and others 2004).

We hypothesize that denitrification rates saturate at lower N concentrations than necessary to saturate nitrification rates (Figure 4) because ammonia provides an energy source for nitrifying bacteria as long as ample dissolved oxygen is present. Dissolved oxygen is usually present in rivers and streams because it can continuously enter the water column from the atmosphere with flow-induced, turbulence-facilitating transfer rates. In contrast, denitrification requires ample nitrate and labile organic carbon, and neither of these enters streams from the atmosphere in substantial amounts. Thus, at moderate N loads (Stage 2), nitrification rates should respond linearly to increasing N concentrations, whereas denitrification rates will become saturated (Figure 4). The higher relative rates of nitrification will tend to exacerbate N transport through systems via increases in nitrate concentrations both from external inputs as well as from changes in internal flux rates. Relative N removal rates via denitrification in lotic ecosystems have previously been demonstrated to be greatest (>50%) when N concentrations are at Stage 2 loading (Kutka and Richards 1997; Downing and others 1999).

WHOLE-SYSTEM RESPONSE TO CHRONIC NITROGEN LOADING

In terrestrial ecosystems, N saturation occurs in a sequence beginning with the fulfillment of vegetational (in most lotic systems microphytobenthos) demand (short-term retention; Stage 1–2) followed by a fulfillment of heterotrophic microbial demand (Stage 2–3; Stoddard 1994). Thus, saturation of retention potential via vegetational uptake will occur prior to saturation of microbial uptake. Once saturation of retention via vegetational demand occurs, the only remaining pathway for removal of N from the ecosystem (other than export) is denitrification. Denitrifiers will saturate at a higher concentration than needed for growth requirements because they require more carbon and N for energy production. In most lotic ecosystems, vegetational demand is minimal be-

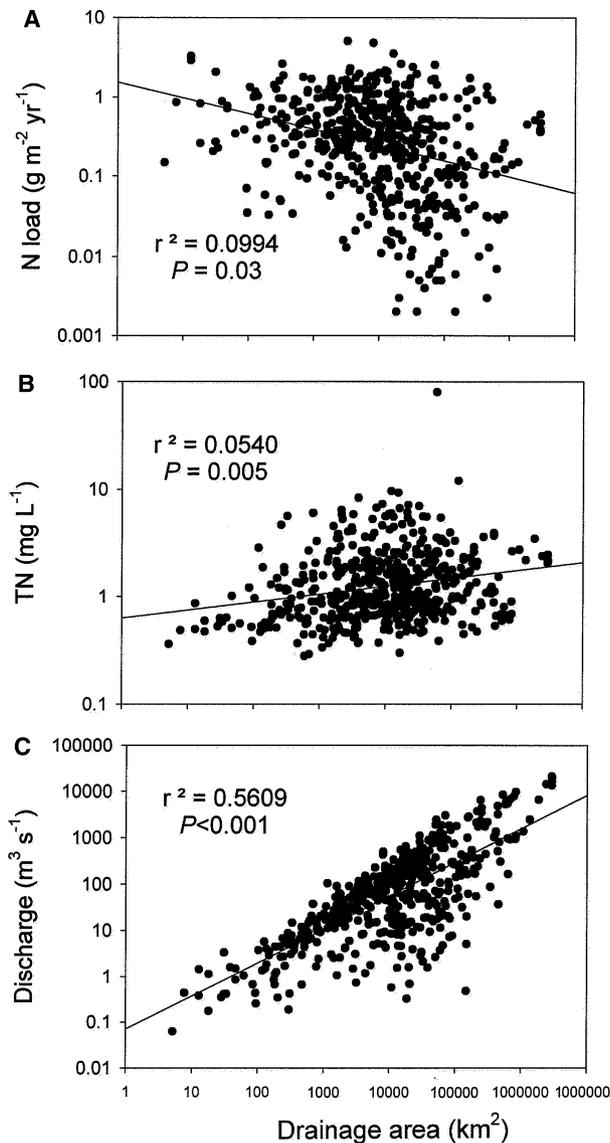


Figure 4. Nitrogen load (A), total nitrogen (TN, B) and discharge (C) as a function of drainage area for lotic ecosystems in the United States. Data courtesy of the United States Geological Survey.

cause a relatively small amount of N is tied up in biomass at any one time (with the exception of macrophyte dominated systems Schaller and others 2004). However, it still is expected that biotic demand for N will be saturated before the potential for denitrification.

With chronic N loading, N export will increase and the rate of increase will be proportional to the load. In addition, we hypothesize that the relative proportions of the forms of N being exported will also change (Figure 2). Increases in the proportion of organic N and nitrate relative to ammonium will occur at low to moderate levels (Stage 1 and 2) of N loading due to increased autotrophic and hetero-

trophic uptake. Increases in organic N will reach a maximal level but nitrate will continue to increase at higher levels (Stage 3) of loading due to saturation of uptake and denitrification rates, but continued mineralization and nitrification. In contrast, carbon to N values will decrease within the stream channel at higher levels of N loading (Stage 2–3), resulting in increased rates of N turnover, decreased time in particulate phase and subsequently greater export (Figure 4).

We developed two general predictions about lotic ecosystem response to chronic N loading that could be tested with available long-term data sets. First, the proportion of nitrate to total N will increase with increased N loading. Second, the total proportion of N entering the stream channel that is retained will be greatest under low N loading scenarios (Stage 1).

Data Analysis

To test our predictions regarding lotic ecosystem response to chronic N loading, we utilized published long-term water chemistry data sets from the United States Geological Survey (USGS). Sites throughout the United States were used, encompassing a range of lotic freshwaters, from first order streams to large rivers (Alexander and others 1996). These data sites included both those in the National Stream Quality Accounting Network (~90% of data, NASQAN) and Hydrologic Benchmark Network (~10% of data stations, HBN). NASQAN sites were chosen at the outlets of major watersheds across the United States to maximize geographic coverage and the HBN sites were chosen specifically as less culturally impacted (generally smaller) watersheds (Alexander and others 1998). For analysis, we compiled all sites with nitrate, ammonium, and total N data for 50 or more sampling dates. The means for each station were obtained, resulting in mean values from 569 stations from a total of 82,578 samples. Samples were distributed fairly evenly across seasons, and the bulk of the data were collected from 1982 to 1987. All data from all years for each station were averaged to lower the amount of variance and allow comparison with the characteristics of the sampling site (watershed area and discharge).

Overall, N export per unit area negatively correlated with drainage area (Figure 5). Given that total N increased significantly with drainage area, and that discharge also increases with drainage area, the absolute load of N increases with larger drainage areas (that is, total mass of N delivered per unit time is simply the discharge multiplied by the concentration). However, discharge increases over 5 orders

of magnitude, drainage area increases over 7 orders of magnitude. Thus, even though concentration and discharge increase with drainage area, the N load per unit area decreases with drainage area (Figure 5). The most parsimonious explanation of this decrease in concentration with increased drainage area is that N load is removed from the water column as the water moves downstream. Alternative explanations, discussed below, include changes in the riparian zone and channel structure. This offers independent verification of the previously suggested idea that smaller rivers have higher retention capacity (Alexander and others 2000). A negative correlation of area-specific N load with drainage area demonstrates the importance of small streams because it implies that N loads from the smaller watersheds are not transferred into the larger watersheds. If rivers were simply pipes, then N export should not vary substantially per unit watershed area. It is worth noting that the trend line of N load is 5 to 10 times higher than the N load reported for relatively pristine watersheds in the United States and elsewhere globally (Lewis 2002).

The relative proportion of dissolved N forms (ammonium, nitrate, organic N) changed with the total N concentration in the water column in accordance to our predictions. Ammonium and organic N were not found to change with total N (data not shown), but the relative proportions of ammonium to nitrate decreased and nitrate to total N increased as predicted (Figure 5) suggesting increased nitrate concentrations and availability with increasing N loads. This, coupled with the general increase in total N with larger watersheds, leads to substantial increases in nitrate being delivered downstream by larger rivers.

Given that smaller streams may be more important to N retention than large, we constructed a simple model to estimate the influence of discharge on percentage of N in the water column that can be denitrified at each individual point in a model river. To construct the model, we assumed that all streams have a total N concentration at each point equal to that of the mean value for lotic ecosystems in the United States as determined from our large database (1.77 mg L^{-1} ; Figure 6). Using this amount of N in the water column, the N load normalized to stream width is given as:

$$\text{N load per meter of stream width} = C * Q/w \quad (1)$$

where: C is nutrient concentration (1.77 mg N L^{-1}), Q is discharge, and w is width (Kemp and Dodds 2002b). We calculated w as a function of discharge using data from Leopold and Maddock (1953).

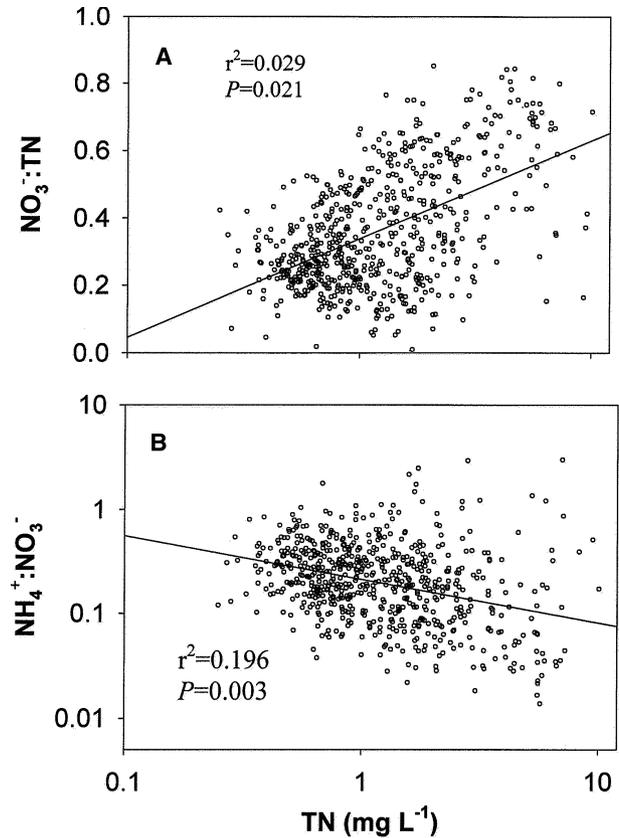


Figure 5. Change in the relative proportions of (A) nitrate (NO_3^-) to total nitrogen (TN), and (B) ammonium (NH_4^+) to nitrate with increasing total nitrogen concentration in lotic ecosystems.

Measurements of discharge and hydrologic characteristics from 113 rivers across the United States were used in the following calculation *where*:

$$w = 17.878 * Q^{0.39175} (r^2 = 0.9118, n = 113) \quad (2)$$

It is important to note that this relationship is conservative because average width of rivers decreases with anthropogenic modification and these data were collected prior to 1953 when fewer rivers were modified.

The proportion of N lost per each meter stream length as a function of denitrification per unit area stream bottom (Kemp and Dodds 2002b) was then calculated for a variety of stream sizes as:

$$\text{Proportion of denitrification} = \frac{\text{denitrification rate}}{\text{nitrate load per meter stream width}} \quad (3)$$

For the denitrification rate, we used the maximum rate of denitrification ($90 \text{ mg N m}^{-2} \text{ d}^{-1}$) found in

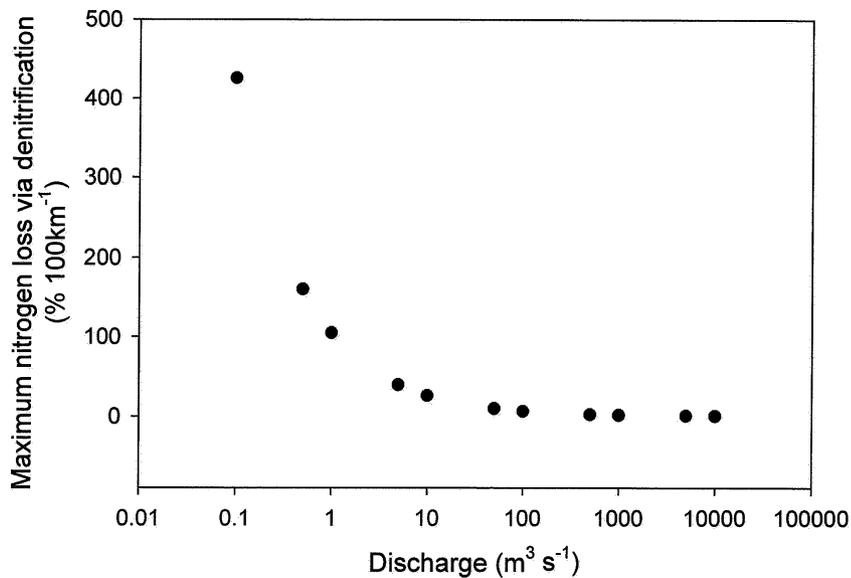


Figure 6. Potential loss of nitrogen via denitrification with increasing discharge. Maximum nitrogen loss derived from equation 3. See text for details.

the literature (see for example, Christensen and others 1990; Chan and Knowles 1979; Nielsen and others 1990; Chatarpaul and others 1980; Baker and Vervier 2004, Böhike and others 2004, Mulholl and others 2004, Gooseff and others 2004, Sheibley and others 2004).

We found smaller lotic ecosystems ($0.1 \text{ m}^3/\text{s}$) have the capacity to remove in-stream N loads at about 4% per kilometer, but this value decreased below 1% per kilometer when discharge exceeded $5 \text{ m}^3/\text{s}$. Negligible amounts of nitrate were lost via denitrification per 100 kilometers when discharge exceeded $100 \text{ m}^3/\text{s}$ (Figure 6). Thus, we expect denitrification to become a much less important N loss mechanism as stream size increases, because of hydrological and physical characteristics of the stream channels. This model provides a mechanistic explanation of the results of Alexander and others (2000) who identified greater amounts of N loss in small rivers and streams than large.

The results of this calculation are mainly related to the fact that there is a maximum rate of denitrification per unit area stream bottom, but that as the water column gets deeper, there is more nitrate per unit area stream bottom to be denitrified. This geometric approach leads to two straightforward conclusions. River channelization reduces sinuosity, effectively decreasing stream length, thus decreasing the probability of nitrate being denitrified. Channelization also can increase mean depth. With a deeper water column, there is less chance for nitrate to be denitrified (that is, there is more nitrate per unit area water column to be denitrified per unit area sediment). Maintaining natural hydrological regimes of large rivers will also de-

crease average depth by increasing connectivity with riparian wetlands. However, even in wetlands, where water depth is generally shallow and hydraulic retention is relatively high, N loading at greater than $0.1 \text{ g m}^{-2} \text{ d}^{-1}$ can saturate retention (Downing and others 1999).

PERSPECTIVE

Nitrogen flux rates and retention efficiencies vary greatly in lotic ecosystems for several reasons. First, the overall ability of a stream to retain N depends on multiple biological, physical and chemical properties that result in maximal and minimal rates being frequently observed within the system. For instance, severe flooding can scour stream channels reducing biotic activity substantially. Additionally, actually measuring N retention in many rivers and streams may be difficult. For example, it is not currently practical to measure actual denitrification rates over the entire stretch of a river (except see Laursen and Seitzinger 2002 Laursen and Seitzinger 2004), many small samples must be incubated, and scaling to the entire river may introduce errors. Characterizing whole system N flux rates will be a central part of describing controls of N retention and the point where chronic N loading exceeds the capacity of any particular system to retain N.

Increased N loading to lotic ecosystems occurs in concert with many other human-induced global changes that are likely to confound the stress placed on freshwater communities. For instance, global warming is hypothesized to increase the severity of droughts and flood (Easterling and others 2000 Bernhard and others 2005), which

may significantly reduce the retention efficiency of lotic ecosystems by decreasing the time between scouring events (impacting retention through uptake). This may exacerbate problems associated with chronic N loading in lotic ecosystems.

There is a great need for long-term studies of N additions in lotic ecosystems as well as attempts to manage increased N loading both by minimizing non-point and point source pollution as well as maximizing N retention and removal within lotic ecosystems. Clear distinctions need to be made between ecosystem responses to short-term or periodic increases in N loading and alterations (that is, drift) in ecosystem functions due to chronic N loading. Although long-term studies need to be implemented, management options need to be designed now to minimize N export from most lotic ecosystems. We are creating a global long-term experiment on the impacts of chronic increased N loading in lotic ecosystems. However, "experiments are weaker" without controls without controls and if current trends continue, we may not have any lotic ecosystems with low levels of N loading for comparisons. The accumulation of N in the environment is a critical problem in our efforts to develop and implement plans for the sustainable management of natural resources. The challenge of N management is to develop strategies that satisfy the food and energy demands of the world's population while also protecting human and ecosystem health.

The most obvious management techniques to control N import into streams is to limit the amount of fertilizer added to the minimum required to produce adequate yields, to minimize runoff from cropland, to treat wastes from animal holding facilities, to treat sewage effluent to remove N, and to lower the amount of atmospheric N loading by controlling N emissions. Several additional management methods that have not been regularly employed may prove to be useful in maximizing N retention and removal in lotic ecosystems. These include: 1) Maximizing substrata heterogeneity within the stream channel and creating backwaters where high rates of N flux can occur (for example, encouraging both nitrification and denitrification). 2) Adding coarse benthic organic matter to alter ecosystem stoichiometry and increase filtration and residence time. Increased carbon to N ratios that come with allochthonous material additions may also lead to slower N turnover in storage compartments, increased N retention, and stimulate denitrification. This could be accomplished by restoring forested riparian zones in low-order streams. 3) Restoring channelized lotic ecosystems that inher-

ently decrease the ability of the system to handle increased N loads. This restoration should include reversion to historical sinuosity, channel complexity, and connectivity to riparian wetlands as well as decreasing meandepth of the water column in the river channel.

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