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Nitrogen retention in wetlands, lakes and rivers

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Abstract

As human activities continue to alter the global nitrogen cycle, the ability to predict the impact of increased nitrogen loading to freshwater systems is becoming more and more important. Nitrogen retention is of particular interest because it is through its combined processes (denitrification, nitrogen sedimentation and uptake by aquatic plants) that local and downstream nitrogen concentrations are reduced. Here, we compare the magnitude of nitrogen retention and its components in wetlands, lakes and rivers. We show that wetlands retain the highest proportion of total nitrogen loading, followed by lakes and then rivers. The differences in the proportion of N retained among systems is explained almost entirely by differences in water discharge. Denitrification is the primary mechanism of nitrogen retention, followed by nitrogen sedimentation and uptake by aquatic plants.

Introduction

During the last century, human activities have dramatically changed the global nitrogen cycle. Practices such as agricultural fertilization, fossil fuel combustion and the clearing and conversion of land have dramatically increased the supply of nitrogen to freshwaters (Jansson et al., 1994a; Vitousek et al., 1997; Moffat, 1998). Elevated concentrations of nitrogen in freshwater are of concern for several reasons. Nitrogen plays a prominent role in the eutrophication of aquatic systems (Moffat, 1998). Increasing nitrate (NO_3^-) concentrations are of particular concern because of associated human health risks (e.g. Focht & Verstraete, 1977). Finally, nitrate is known to contribute to lake acidification (Kelly et al., 1990). Given the negative impact of increasing nitrogen loads, the mechanisms by which freshwater systems can reduce local and downstream nitrogen concentrations are becoming increasingly important.

Nitrogen retention is the difference between N inputs and N outputs to a given freshwater system. Three processes contribute to nitrogen retention: denitrification, sedimentation and uptake by aquatic plants. Denitrification is the process whereby facultative anaerobic bacteria produce N_2 or N_2O gas by using nitrate (NO_3^-) or nitrite (NO_2^-) as terminal electron acceptors (Knowles, 1982). Denitrifying bacteria release N_2 into the atmosphere thereby permanently removing it from aquatic systems. Nitrogen is also retained when particulate matter becomes incorporated into the sediment. Lastly, macrophytes influence nitrogen cycling by taking up and storing nitrogen in their shoots and roots during the growing season (Hill, 1986).

Despite the importance of nitrogen dynamics, there have been no comparisons of the magnitude of nitrogen retention and its components among freshwater systems. By identifying which systems retain nitrogen most efficiently, management strategies can utilize natural retention capacities more effectively (Jansson et al., 1994a). For example, wetlands are increasingly being used to protect aquatic systems against N-rich wastewaters (Mitsch & Gosselink, 1993). A comparison of the components of nitrogen retention also has the potential to yield predictions useful for lake management. Denitrification is particularly important as it results in a permanent removal of nitrogen from fresh-

Table 1. Sources of total nitrogen loading and retention data (Figures 1 and 2). * Indicates that water discharge data was not available

	Site	Location	Source
Lakes	Blue Chalk	Canada	Molot & Dillon (1993)
	Chub	Canada	"
	Crosson	Canada	"
	Dickie	Canada	"
	Harp	Canada	"
	Plastic	Canada	"
	Red Chalk	Canada	"
	*Okeechobee	U.S.A.	Messer & Brezonik (1983)
	Bryup Langsø	Denmark	Andersen (1974)
	Kvind	Denmark	"
	Kul	Denmark	"
	Salten Lang	Denmark	"
	Halle	Denmark	"
	Stigsholm	Denmark	"
	Kvie	Denmark	Olsen & Andersen (1994)
	Søbygård	Denmark	Jensen et al. (1992)
	Vallentuna	Sweden	Ahlgren et al. (1994)
	Norrviken	Sweden	"
	*Hallwilersee	Switzerland	"
	*Pfäffikersee	Switzerland	"
	*Kinneret	Israel	Smith et al. (1989)
	Baldegg	Switzerland	Mengis et al. (1997)
	Zugg	Switzerland	"
Wetlands	Harp 4-Beaver pond	Canada	Devito et al. (1989)
	Plastic-Conifer swamp	Canada	"
	Paint -Sedge fen	Canada	"
	Clermont Plot L	USA	Knight et al. (1993)
	Clermont Plot M	U.S.A.	"
	Clermont Plot H	U.S.A.	"
	Pottsburg Creek Swamp	U.S.A.	"
	Eastern Service Area1	U.S.A.	"
	Cypress Domes	U.S.A.	"
	Reedy Creek WTS1	U.S.A.	"
	Reedy Creek OFWTS	U.S.A.	"
	Ironbridge	U.S.A.	"
	Boot	U.S.A.	"
	Apalachicola	U.S.A.	"
	Boggy Gut	U.S.A.	"
	Central Slough	U.S.A.	"
	Bear Bay	U.S.A.	"
	Hurtsboro	U.S.A.	"
	Hamilton	U.S.A.	"
	*Marcell Forest Bog	U.S.A.	Verry & Timmons (1982)
	*Tarr River Floodplain	U.S.A.	Brinson et al. (1984)
	*Rabis Baek Riparian Zone	Denmark	Dørge (1994)
	*Syvbaek	Denmark	"
Rivers	Gjern River	Denmark	Svendsen & Kronvang (1993)
	Swift’s Brook	Canada	Kaushik et al. (1975)
	River Raan	Sweden	Jansson (1994b)
	Potomac River	U.S.A.	Seitzinger (1986)
	Great Ouse	England	Owens et al. (1972)
	River Trent	England	"

water. The relative importance of this mechanism, therefore, will determine whether observed nitrogen retention is a long term or seasonal sink.

To address these issues, we examine differences in nitrogen retention among wetlands, lakes and rivers. We further assess the mechanisms of nitrogen retention and their relative importance. Finally, we relate these findings to their impact on ecosystem processes.

Methods

Nitrogen retention

It has been well established that nitrogen retention increases with nitrogen loading in aquatic systems (Jensen et al., 1990; Gale et al., 1993; Jansson et al., 1994a; Windolf et al., 1996). A study by Fleischer & Stibe (1991) found that nitrogen loading was an excellent predictor (r^2 = 0.94, $p<0.05$, n=50) of nitrogen retention in lakes, rivers and wetlands in Europe. Differences in this relationship among these three types of waterbodies have, however, been largely unexplored. An among systems comparison of nitrogen retention would be useful to identify differences in nitrogen removal capacity and efficiency. To this end, total nitrogen (TN) retention and loading data were compiled from the literature for 23 wetlands, 23 lakes and 5 rivers in North America and Europe (Table 1). All data were taken from mass balance studies in which nitrogen retention was calculated by subtracting total nitrogen (TN) outputs (g m^{-2} yr^{-1}) from TN inputs (g m^{-2} yr^{-1}). Due to the characteristically high water discharge rates (m^3 s^{-1}) of rivers, the nitrogen loads of these systems were dramatically higher than those of wetlands and lakes. To facilitate comparison among systems, nitrogen load and retention were standardized by dividing by the discharge. Discharge was not available for seven sites (Table 1).

Components of N retention

There are three components to nitrogen retention: uptake by vegetation, sedimentation and denitrification. It has generally been assumed that denitrification is responsible for most nitrogen retention in freshwaters (Seitzinger, 1988; Jensen et al., 1990; Svendsen & Kronvang, 1993). Studies quantifying the proportion of retention accounted for by denitrification are, however, relatively rare and almost exclusively restricted to lakes. To determine the importance of denitrification relative to the two other retention processes, we analyze data from TN mass balance studies of lakes in Europe and North America (Table 2). Lakes were the only waterbodies for which both sedimentation and denitrification rates were readily available. In these studies, net nitrogen sedimentation was calculated using sediment cores and nitrogen uptake by vegetation was assumed to be negligible over the long term.

Table 2. Sources of denitrification and nitrogen sedimentation data (Figure 3)

Lake	Location	Source
Blue Chalk	Canada	Molot & Dillon (1993)
Chub	Canada	"
Crosson	Canada	"
Dickie	Canada	"
Harp	Canada	"
Plastic	Canada	"
Red Chalk	Canada	"
Okeechobee	Florida	Messer & Brezonik (1983)
Bryup Lang	Denmark	Andersen (1974)
Kvind	Denmark	"
Kul	Denmark	"
Salten Lang	Denmark	"
Halle	Denmark	"
Stigsholm	Denmark	"
Kvie	Denmark	Olsen & Andersen (1994)
Søbygård	Denmark	Jensen et al. (1992)
Vallentuna	Sweden	Ahlgren et al. (1994)
Norrviken	Sweden	"
Aegerisee	Switzerland	Vollenweider (1971)
Hallwilersee	Switzerland	"
Kinneret	Israel	Smith et al. (1989)
Baldegg	Switzerland	Mengis et al. (1997)
Zugg	Switzerland	"

Results

Nitrogen retention

Total nitrogen loading is an excellent predictor of TN retention for wetlands and lakes (Table 3, Figure 1). An ANCOVA showed that, on average, wetlands retain approximately twice as much TN as lakes for a given N load ($p<0.001$). The relationship between TN loading and retention was not significant for rivers (Table 3), presumably because the large differences among their discharge results in a highly variable TN loading and water residence time. Regression analysis

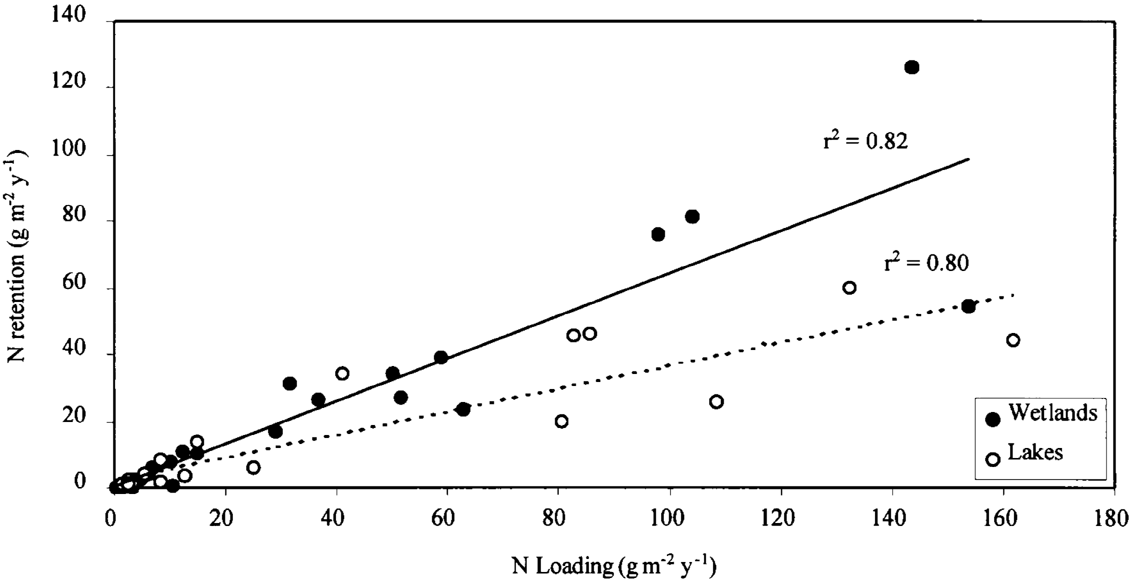

Figure 1. Nitrogen retention as a function of nitrogen loading in wetlands and lakes.

Table 3. Regression equations describing the relationship between nitrogen retention (y) and load (x) in wetlands, lakes and rivers

	n	Regression equation	r^2	SEE	*p*
Wetlands	23	$y = 0.42 + 0.64x$	0.82	13.8	<0.001
Lakes	23	$y = 2.53 + 0.34x$	0.80	8.3	<0.001
Rivers	5	$y = 145.6 + 0.02x$	0.10	206.0	>0.050
Wetlands, lakes and rivers	43	$y = (10^{(1.00(\log(x/\text{water discharge}))-0.39)})/(\text{water discharge})$	0.92	0.4	<0.001

indicates that, on average, wetlands retain 64% of the TN loading, lakes 34% and rivers 2%. Average water discharge was 0.1 m^3 s^{-1}, 0.7 m^3 s^{-1} and 18.6 m^3 s^{-1} in wetlands, lakes and rivers, respectively. ANCOVA shows that after standardization to water discharge, the relationship between TN loading and retention is extremely strong (Table 3, Figure 2). Furthermore, there is no longer a significant difference among wetlands, lakes and rivers in the proportion of N retained (Figure 2).

Components of N retention

Denitrification was more effective than nitrogen sedimentation in preventing nitrogen from being exported downstream (paired ANOVA, $p<0.005$) (Figure 3). Both components of nitrogen retention were significantly related to N load (Figure 3). Calculation of the mean percentage contributed by denitrification and sedimentation to total nitrogen retention in lake systems indicates that, on average, denitrification accounted for 63% of the TN retention while sedimentation was responsible for 37%.

Discussion

N retention

For a given TN load, wetlands retain almost twice the amount of nitrogen as lakes (Figure 1, Table 3). In general, the proportion of N retained by rivers is minimal. Once differences in water discharge have been taken into consideration, however, there are no longer significant differences in the nitrogen retention capacities of wetlands, lakes and rivers (Figure 2).

The principle reason why water discharge affects the percentage of nitrogen loading retained is that discharge serves as surrogate measure for water residence time. Water residence time (or renewal rate) is defined here as the ratio of discharge to volume of the system (Mitsch & Gosselink, 1986). The greater

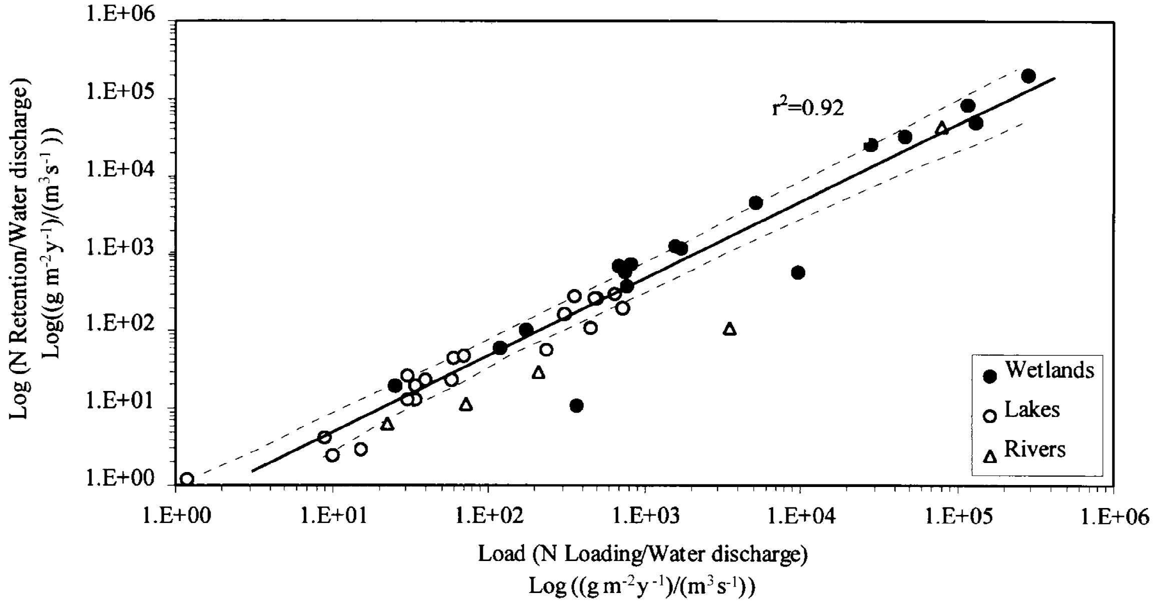

Figure 2. Log nitrogen retention standardized for water discharge as a function of log nitrogen loading standardized for water discharge in wetlands, lakes and rivers. Dotted lines indicate the 95% confidence interval about the mean.

the discharge, the shorter the time it will take for a water body to completely flush (Abrahamsson & Håkanson, 1998). Lower discharge rates (and longer water residence times) provide greater opportunities for sediment-water contact, thereby promoting retention processes such denitrification and sedimentation (Nichols, 1983; Svendsen & Kronvang, 1993; Hammer & Knight, 1994; Windolf et al., 1996; Sand-Jensen, 1998). Increased water residence times in wetlands are due, in part, to the dense stands of aquatic plants that characterize these ecosystems (Brix, 1997; Eriksson & Weisner, 1997; Benoy & Kalff, 1999). Aquatic plants increase nitrogen retention through vegetative uptake and provide favorable conditions for sedimentation and denitrification (Howard-Williams, 1983; Reddy et al., 1989; Brix, 1997; Benoy and Kalff, 1999). The importance of water residence time to nitrogen retention is supported by the strong, positive relationship observed between the two variables in Danish lakes (r^2=0.79, p<0.05, n=16) (Windolf et al., 1996).

Nitrogen retention in freshwater has a significant impact on ecosystem processes and the importance of nitrogen as a limiting nutrient in aquatic systems is increasingly recognized (Elser et al., 1990; Downing & McCauley, 1992). Low N:P loading ratios are characteristic of waste-water and runoff from disturbed catchments (Nichols, 1983; Downing & McCauley, 1992). The receiving waters, therefore, are more likely to be nitrogen limited. Nutrient rich systems characterized by nitrogen limitation commonly have noxious blooms of blue-green algae, resulting in fish kills, beach closures and increased water treatment costs (Downing & McCauley, 1992; Findlay et al., 1994).

Components of N retention

In the lakes examined, denitrification was the primary mechanism of nitrogen retention (Figure 3). A review of 69 shallow, Danish lakes similarly found denitrification to account for the majority (77%) of TN removal (Jensen et al, 1990). Available evidence from other freshwaters supports the conclusion that denitrification is the primary mechanism by which N is retained. Denitrification has been observed to be an order of magnitude larger than sedimentation in both experimental and natural wetlands (Brinson et al., 1984; Van Oostrom, 1995). In the Danish River, Gjern å, denitrification was calculated to exceed sedimentation on an annual basis by a factor of 2–3 (Svendsen & Kronvang, 1993). In general, the proportion of TN retention accounted for by denitrification in rivers must be higher than in lakes. River turbulence is sufficiently high that typically little or no sediment accumulates relative to wetlands and lakes (Ryder & Pesendorfer,

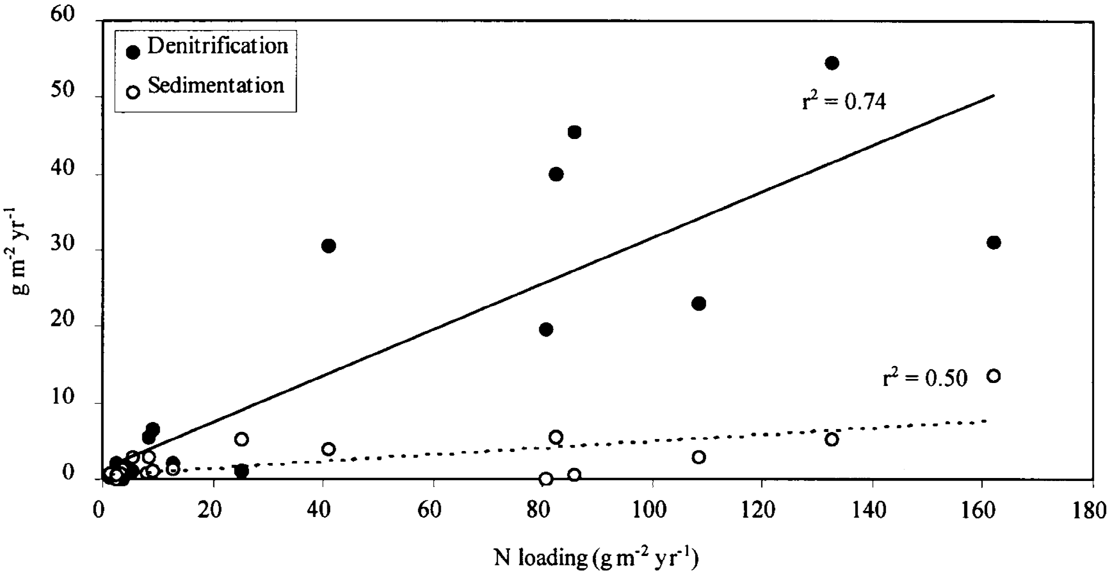

Figure 3. Lake denitrification and nitrogen sedimentation as a function of nitrogen loading.

1989). Furthermore, in agricultural areas, rivers tend to receive higher proportions of their TN loading as nitrate, which is not subject to significant sedimentation (Jansson et al., 1994a).

The importance of denitrification in freshwaters has implications beyond the process of nitrogen retention. Denitrifying bacteria play an important role in the carbon cycle of aquatic systems by oxidizing organic matter. Wherever NO_3^- is present in concentrations similar to those of dissolved oxygen, denitrification will contribute significantly to the carbon mineralization budget (Andersen, 1977; Christensen et al., 1990). Up to 50% of the carbon mineralized in eutrophic freshwaters has been attributed to denitrifier activity (Andersen et al., 1977). Denitrification can also buffer against lake acidification by reducing nitric acid concentrations (Rudd et al., 1990). With increasing nitric acid additions, denitrification rates have been observed to increase dramatically, whereas other nitrogen retention processes remained the same (Rudd et al., 1990).

Studies of TN retention in freshwaters usually overlook uptake and retention by aquatic plants. This has been justified by the assumption that macrophytes represent a small and temporary nitrogen sink (Nichols, 1983; Reddy & D’Angelo, 1994). While studies calculating nitrogen retention in lakes do not normally take macrophytes into account, TN budgets of rivers and wetlands occasionally do. Such studies provide important information as to the relative importance of vegetative uptake as a retention mechanism. Macrophyte uptake was calculated to be an order of magnitude lower than other nitrogen retention processes in a lowland Danish river (Svendsen & Kronvang, 1993). Uptake of nitrogen by benthic algae and macrophytes accounted for only 15% of nitrate removal from Duffin Creek, Ontario (Hill, 1979). Researchers studying nitrogen dynamics in a New Zealand stream concluded that, in the long-term, stream channel vegetation acted primarily to modify nitrogen export rather than retain it (Cooper & Cooke, 1984). In wetlands, the relative importance of vegetative uptake also appears to be small. Removal by denitrification (3.0–3.3 g N m^{-2} d^{-1}) was far greater than either sedimentation (0.16–0.27 g N m^{-2} d^{-1}) or plant uptake (0.19–0.33 g N m^{-2} d^{-1}) in three experimental New Zealand wetlands (Van Oostrom, 1995). In a natural floodplain swamp, uptake of nitrogen by vegetation (0.32 g m^{-2} d^{-1}) was small in comparison with retention by denitrification (1.3 g m^{-2} d^{-1}) and sedimentation (0.64 g m^{-2} d^{-1}) (Brinson et al., 1984). It is evident that while the importance of vegetative assimilation varies, it tends to be minor compared to other nitrogen retention processes.

Despite the relatively small contribution of macrophyte uptake as a nitrogen retention mechanism, aquatic plants also affect nitrogen cycling indirectly. By retaining N during the growing season, aquatic plants can influence the growth of phytoplankton by sequestering nitrogen during the period when it is in highest demand. Nutrient assimilation by macrophytes also affects sedimentation rates by contributing particulate matter to sediments during their senescence (Hill, 1986). Aquatic plants increase sedimentation rates by decreasing water velocity and increasing water retention time (Howard-Williams, 1985; Brix, 1997; Eriksson & Weisner, 1997; Benoy & Kalff, 1999). Finally, macrophytes create an ideal environment for denitrification by increasing the supply of potentially limiting organic carbon and nitrate to denitrifying bacteria (Reddy et al., 1989; Weisner et al., 1994; Brix, 1997). The presence of aquatic plants, therefore, has a significant indirect impact on nitrogen retention in rivers, lakes and wetlands.

Conclusion

As nitrogen loading to freshwater systems increases as a result of human activities, the ability to predict the resulting impact is becoming more and more important. Wetlands retain the highest proportion of total nitrogen loading, followed by lakes and then distantly, by rivers. The observed differences in retention capacity are explained almost entirely by differences in water discharge. The low retention capacities of rivers are of particular concern, because these systems are often subject to high nitrogen loading from agricultural drainage basins and point source loading from urban areas. This also allows them to serve as major sources of nitrogen to downstream lakes and wetlands. The problem has surely been exacerbated by the canalization of rivers and the draining of wetlands for agricultural and other purposes, preventing them from serving as major sites of denitrification.

Our findings show that denitrification is the principal mechanism of nitrogen retention. The majority of nitrogen retained in freshwaters, therefore, will be permanently removed through release of N_2 into the atmosphere. Although nitrogen sedimentation and uptake by aquatic plants are responsible for a smaller proportion of N retention, these processes significantly contribute, both directly and indirectly, to nitrogen cycling in freshwaters.

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