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Regulation of nitrification in aquatic sediments by organic carbon

Abstract—Nitrification, the microbial conversion of ammonium to nitrate, is an important transformation in the aquatic nitrogen cycle, but the factors regulating nitrification rates in freshwater ecosystems are poorly understood. We investigated the effects of organic carbon quantity and quality on nitrification rates in stream sediments. First, we hypothesized that when environmental C : N ratios are high, heterotrophic bacteria are subject to N limitation and will outcompete nitrifying bacteria for available NH_4^+, thereby reducing nitrification rates. In laboratory experiments, organic carbon amendments (30 mg C L^{-1}, as glucose) to stream sediments completely inhibited nitrification with or without addition of NH_4^+ ($P < 0.0001$), whereas amendment with NH_4^+ only (0.75 mg N L^{-1}) increased nitrification by 40% compared with unamended controls ($P < 0.0001$). Carbon amendments also increased microbial respiration rates over controls by 4–6 times. Therefore, organic carbon additions significantly decreased nitrification rates but increased total microbial activity. Second, we hypothesized that carbon of high quality would have a stronger negative effect on nitrification than would carbon of low quality. To stream sediments, we added organic carbon as either glucose (higher quality) or sugar maple leaf extract (lower quality). Nitrification rates were reduced by the addition of either organic carbon source but were more severely inhibited by glucose ($P = 0.001$). Our results suggest that organic carbon is an important regulator of nitrification rates and is of key importance in understanding N dynamics in freshwater ecosystems.

Biological productivity in aquatic ecosystems is highly influenced by the cycling of essential nutrients, especially nitrogen and phosphorus (Vitousek et al. 1997; Carpenter et al. 1998). General attributes of the N cycle have been studied in many aquatic systems, but the factors controlling specific processes within the N cycle remain unclear. For example, nitrification (the oxidation of ammonium, NH_4^+, to nitrate, NO_3^-) probably occurs to some extent in all freshwater ecosystems, but the control of nitrification rates is poorly understood (Hall 1986; Dahm et al. 1998). Because nitrification is central to the accumulation and loss of NO_3^-, the factors regulating nitrification are integral to eutrophication and health concerns related to elevated NO_3^- concentrations in fresh waters.

Despite the potential importance of nitrification, only a few studies have explored the factors regulating this process in streams, and no single set of factors has emerged consistently as the regulator of nitrification rates. Triska et al. (1990) studied nitrification in the hyporheic zone of a California stream and concluded that rates were regulated by the supply of NH_4^+ and oxygen. In Sycamore Creek, Arizona, nitrification rates were positively associated with hyporheic respiration and the mineralization of organic N to NH_4^+ (Jones et al. 1995). In an oligotrophic spring in Oregon, nitrification rates were not correlated with either NH_4^+ or NO_3^- concentrations but were positively correlated with organic carbon content and inversely correlated with redox potential of sediments (Dodds and Jones 1987). Nitrifying bacteria, and nitrification rates in general, may be regulated by many factors including NH_4^+ availability (Triska et al. 1990; Jones et al. 1995; Strauss 1995), pH (Sarathchandra 1978), temperature (Paul and Clark 1989), oxygen concentration (Stenstrom and Poduska 1980; Triska et al. 1990), competition for NH_4^+ (Verhagen and Laanbroek 1991; Strauss and Dodds 1997), and organic carbon availability (Verhagen and Laanbroek 1991; Strauss and Dodds 1997). Among these factors, pH, temperature, and oxygen concentration serve the primary role of defining the physical and chemical environmental conditions that allow nitrification to occur and set the maximum and minimum nitrification potentials. Within these limits, however, the regulation of nitrification rates is not understood.

We investigated the roles of NH_4^+ availability, competition for NH_4^+, and organic carbon availability in determining nitrification rates in stream sediments. These three factors may be intimately linked via the C : N (total organic carbon : total nitrogen) ratio of the available substrate. We hypothesized that when the C : N ratio of the environment is high, heterotrophic bacteria are subject to N limitation and will compete with nitrifiers for available nitrogen (Fig. 1A). Naturally occurring heterotrophic bacteria typically are more abundant and grow faster than nitrifying bacteria (Prosser 1989) and thus should outcompete nitrifying bacteria for available NH_4^+ in N-limited environments. As a result, nitrification rates should decline. Verhagen and Laanbroek (1991) manipulated glucose concentrations in chemostats to test the effects of C : N ratio on a culture containing nitrifying bacteria and one species of heterotrophic bacteria. Their results suggest that nitrification occurs below a critical environmental C : N molar ratio of between 9.6 and 11.6. When the environmental C : N ratio is lower than the critical level, heterotrophic bacteria are not N-limited, nitrifying bacteria are able to compete successfully for NH_4^+, and nitrification occurs. However, an extension of their work is needed to determine whether organic carbon availability and C : N ratios affect nitrification in environmental samples that contain natural carbon sources and intact microbial communities.

Our second hypothesis was that the quality of organic carbon will determine the magnitude of the negative effect of organic carbon on nitrification, provided that the C : N ratio of the environment is high enough to elicit competition for NH_4^+ between nitrifying and heterotrophic bacteria (Fig. 1B). High quality (more easily decomposed) organic carbon should provide a better substrate for heterotrophic activity, which would then increase the demand and competition for inorganic N and reduce nitrification rates. Poor quality (more refractory) organic carbon should have less of an effect on nitrification because lower heterotrophic activity will limit competition for inorganic nitrogen. Thus,

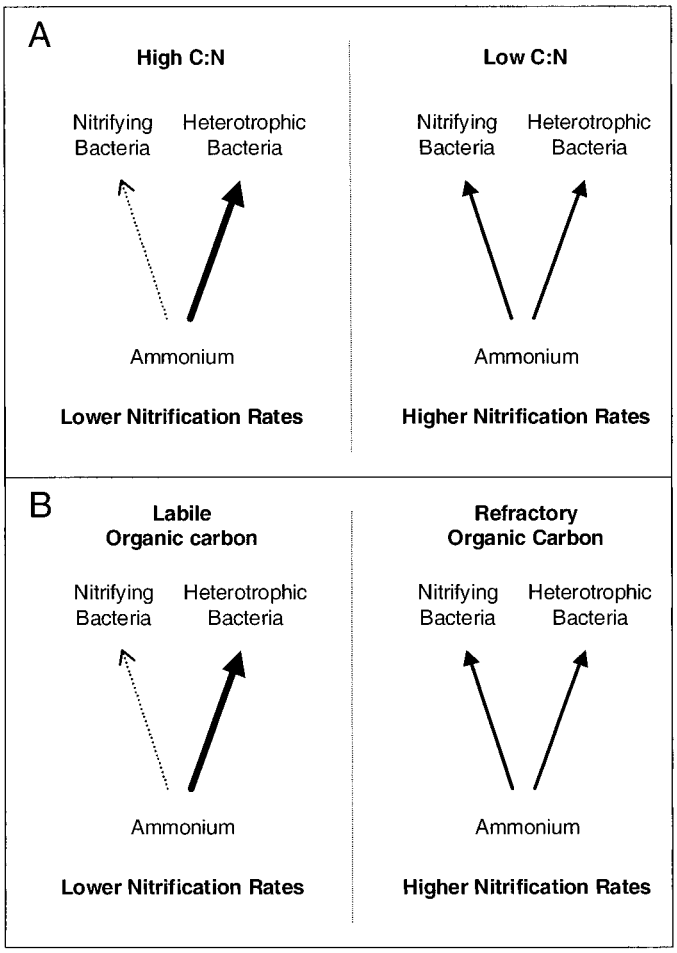

Fig. 1. Schematics of hypotheses describing the effects of C : N ratio and organic carbon quality on nitrification rates. (A) Hypothesis 1: under high environmental C : N ratios, heterotrophic bacteria outcompete nitrifying bacteria for available NH_4^+, resulting in lower nitrification rates; under low environmental C : N ratios nitrifying bacteria do not experience strong competition for available NH_4^+, resulting in higher nitrification rates. (B) Hypothesis 2: when the organic carbon in the environment is mostly labile (easily assimilated by heterotrophic bacteria), the organic carbon present will have a more negative effect on nitrification rates than when the organic carbon is mostly refractory (not easily assimilated by heterotrophic bacteria).

the critical C : N ratio for nitrification (sensu Verhagen and Laanbroek 1991) should vary among systems depending on the quality of the ambient organic carbon. Organic matter quality is often considered to be inversely related to the C : N ratio of the matter, although certain nonnitrogenous carbon compounds also may be very labile (e.g., glucose and acetate) if a separate source of N is present to facilitate decomposition.

In this study, we tested these hypotheses by performing three experiments using stream sediments. The goal of the first two experiments was to measure the responses in nitrification and community respiration rates to changes in C : N ratio. The third experiment was designed to explore the effect of organic carbon quantity and quality on nitrification rates.

Experimental design—Stream sediments and water were collected from Juday Creek, a third-order stream in north central Indiana (41°43.7′N, 86°15.9′W). Juday Creek is a cool-water trout stream (mean discharge, 0.75 $m^3\ s^{-1}$) that flows through an area of mixed land use, including woodland, agriculture, and urbanization (Lamberti and Berg 1995). Surface water inorganic N levels are moderate; biweekly water samples collected from 1996 to 1997 had a mean NH_4^+ concentration of 0.060 mg N L^{-1} (SD = 0.053) and a mean NO_3^- concentration of 1.09 mg N L^{-1} (SD = 0.180). All samples for this study were collected from a woodland reach of the stream. The stream sediments used in the experiments consisted of a sieved (0.64 cm) sand and silt mixture collected from along the stream margin. Total C and N content of sediments was determined from dried (60°C) sediments analyzed on a Carlo Erba CHNS-O analyzer. Preliminary analysis demonstrated that the sand fraction was relatively devoid of organic carbon and N. Thus, to improve the accuracy of C and N measurements, sand (>1 mm) was removed from the sediment via elutriation prior to drying and analysis. Masses of C and N in the sand-free sediment were 124.7 mg C (g sediment dry wt)$^{-1}$ (SD = 13.5) and 6.88 mg N (g sediment dry wt)$^{-1}$ (SD = 0.45), respectively. Mean C : N molar ratio of the sediments was 21.1 (SD = 1.05). Stream water was collected midchannel and was not filtered. Sediments and water were stored on ice or in a refrigerator until experiments were started (always within 24 h of collection).

The first two experiments were designed to test the effects of organic carbon and NH_4^+ availability (i.e., differing C : N ratios) on nitrification rates (experiment 1) and community respiration rates (experiment 2). The experimental design consisted of four treatments: control (no additions), +N (0.75 mg L^{-1} NH_4^+-N added), +C (30 mg L^{-1} glucose-C added), and +N+C (NH_4^+ plus glucose added at above concentrations). Forms added were NH_4Cl and D-glucose. Four replicates of each treatment were used in the first experiment and five replicates in the second experiment.

The third experiment examined the effect of organic carbon quality and quantity on nitrification rates. Two organic carbon sources were used: glucose and leaf leachate. The leachate was made from dried leaves of sugar maple (*Acer saccharum*), an abundant riparian tree along Juday Creek. Recently fallen leaves were collected near the stream and dried at room temperature. Leaves were leached for 24 h in reverse osmosis–treated water at room temperature. To remove bacteria and particulate matter, the leachate was passed sequentially through a series of sieves and filters until it finally passed through a 0.2-μm membrane filter. Organic carbon content of the filtered leachate was determined on a Shimadzu TOC-5000A TOC analyzer. The extract was stored in sterile bottles at 4°C and refiltered (0.2 μm) before use. Treatments (n = 4) were glucose additions of 1, 10, 33, 66, and 109 mg C L^{-1}; leaf leachate additions of 8, 25, 51, 76, 101, and 127 mg C L^{-1}; and a control (no C addition).

Procedures—Gross nitrification rates were measured as the difference in NH_4^+ concentrations between incubations in which nitrification was allowed to occur and those in which nitrification was inhibited with the chemical nitrapyrin (2-chloro-6-[trichloromethyl]-pyridine, Sigma Chemical). Nitrapyrin inhibits the function of the enzyme ammonium monooxygenase and hence inhibits ammonium oxidation. Nitrapyrin does not appear to significantly affect the remaining microbial community because total microbial biomass and microbial respiration rates are not altered (Bauhus et al. 1996). Nitrapyrin, however, does inhibit methanotrophic activity (Roy and Knowles 1995). We elected to use the nitrapyrin method because we wanted to measure the effects of organic carbon on actual (gross) nitrification rather than the net increase in nitrate (net nitrification). Measurement of the latter in natural sediments with a mixed microbial community encompasses the net result of several nitrogen cycle transformations (i.e., denitrification, NO_3^- uptake, and nitrification) instead of strictly nitrification. In addition, several previous studies have used nitrapyrin successfully to measure nitrification rates in aquatic sediments (Hall 1984; Dodds and Jones 1987; Roy and Knowles 1995).

Each nitrification replicate in the experiments consisted of two 125-ml flasks. One flask received a final concentration of 10 mg L^{-1} nitrapyrin dissolved in dimethyl sulfoxide (DMSO) (Powell and Prosser 1985) because nitrapyrin is insoluble in water. The other flask received DMSO only as a control. All flasks contained 34 ml stream sediment and 76 ml stream water. The flasks were covered loosely with aluminum foil and incubated in the dark at 27°C for 72 h on an orbital shaker (175 rpm). Initial and final NH_4^+ concentrations were determined from filtered 1N KCl extracts from each flask using the phenol hypochlorite method (Solorzano 1969). KCl extracts were made by adding 10 ml of 2N KCl to 10 ml of sediment slurry and incubating for 1 h prior to filtration. Preliminary studies demonstrated that KCl extracted filtrates of Juday Creek sediments contain about 1.8× more NH_4^+ than filtrates of nonextracted slurries. Dissolved oxygen (DO) and pH were measured in approximately 50% (randomly selected) of the replicates at the beginning and end of the experiments. Potential nitrification rates over the incubation period were calculated by subtracting the observed change in NH_4^+ in the flasks containing only DMSO from the increase in NH_4^+ in the flasks that contained nitrapyrin plus DMSO. It was assumed that ammonification and heterotrophic NH_4^+ uptake were uninhibited in both sets of flasks. The NH_4^+ increase in the flasks containing nitrapyrin was a result of inhibited NH_4^+ oxidation.

In the second experiment, community respiration was determined by measuring the change in oxygen concentration. Treatments (as described above) were applied to flasks containing 10-ml stream sediment and 100-ml stream water. The samples were incubated in the dark at 27°C for 24 h on an orbital shaker (175 rpm) to allow biota time to adjust to treatments. Following this incubation, the flasks were completely filled with stream water and an initial DO measurement was taken using an Orion DO meter (mean concentration ± SD = 8.18 ± 0.09 mg O_2 L^{-1}). The flasks were sealed, excluding all air bubbles, with a sheet of polyethylene film (0.08 mm thickness). A final dissolved oxygen measurement was taken (range = 3.86 to 7.74 mg O_2 L^{-1}) following a 5-h dark incubation at room temperature (ca. 25°C). Flasks were not shaken during the second incubation. Community respiration was calculated from the change in oxygen concentration during the incubation period and converted into carbon using a respiratory quotient of 0.85 (Bott 1996).

Results of the experiments were analyzed statistically using SAS v. 6.12. One-way analysis of variance was used to analyze the data from the first and second experiments. Tukey's multiple comparison procedure was used to reveal which treatments were significantly different. Analysis of covariance (ANCOVA) was used to analyze the data from the third experiment after organic carbon concentrations were natural log-transformed to linearize the relationship between nitrification and organic carbon.

Effect of C : N ratio—In the first experiment, the mean nitrification rate in the treatment amended with NH_4^+ was significantly higher ($P < 0.0001$) than that for the unamended control (Fig. 2A). The C : N ratio in the control (ca. 21 for sediments) may have been near the critical C : N ratio at which nitrification occurs for this system because nitrification in this treatment was measurable and NH_4^+ additions further increased nitrification. Because the NH_4^+ addition lowered the C : N ratio, competition for NH_4^+ may have diminished, resulting in greater NH_4^+ availability for nitrifiers. Glucose addition significantly inhibited nitrification in the stream sediments with or without NH_4^+ additions ($P < 0.0001$), which reduced nitrification to near zero in both treatments (Fig. 2A). The glucose addition raised the C : N ratio (almost certainly above the critical level), which likely increased competition for NH_4^+ and decreased the amount of NH_4^+ available to nitrifying bacteria, thereby resulting in low nitrification rates. These results are consistent with our first hypothesis and that of Verhagen and Laanbroek (1991) that when environmental conditions are within the physical and chemical constraints required for nitrification, the C : N ratio of the environment is a critical factor regulating nitrification rates in stream sediments.

Several alternative explanations exist for why nitrification rates decreased following the glucose additions. First, glucose could have inhibited nitrification directly through toxicity or by causing the nitrifying bacteria to switch from autotrophic to heterotrophic metabolism. This mechanism is unlikely because glucose additions have no effect on nitrification activity in pure cultures of *Nitrosomonas* (Krummel and Harms 1982). Second, the glucose addition may have caused a pH shift, thereby lowering nitrification rates. The pH in the flasks, however, remained between 6.5 and 7.5, well within the pH range where nitrification occurs, and did not vary significantly among treatments. Third, increased heterotrophic activity within the flasks that received glucose could have caused the contents of the flasks to go anoxic, thereby inhibiting nitrification, which is an obligatory aerobic process. However, shaking the flasks throughout the incubation period maintained adequate dissolved oxygen concentrations in the samples (DO > 7 mg O_2 L^{-1})

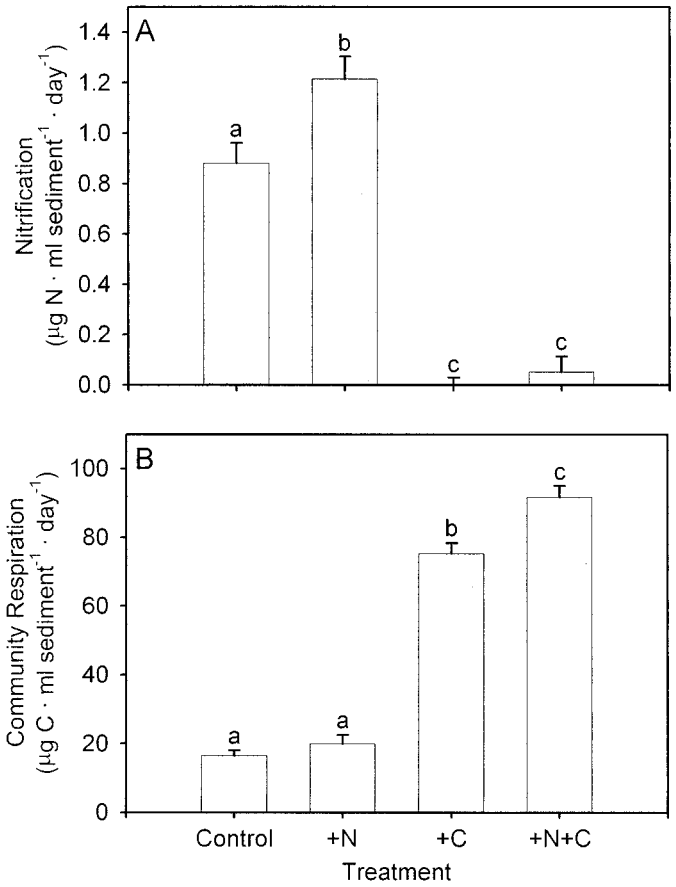

Fig. 2. Responses in (A) nitrification and (B) community respiration in stream sediments amended with glucose and NH_4^+. The four treatments were control (no additions), +N (0.75 mg L^{-1} NH_4^+-N added), +C (30 mg L^{-1} glucose added), and +N+C (NH_4^+ plus glucose added). Error bars = +1 SE. The letters a, b, and c identify treatments that are significantly different (Tukey's $P < 0.05$).

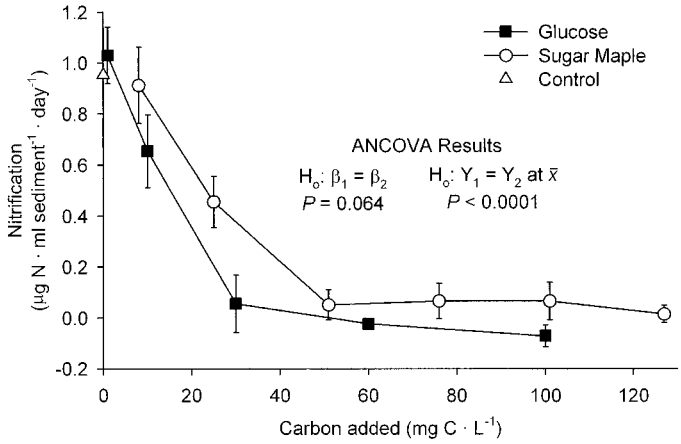

Fig. 3. Effect of added glucose and sugar maple (*Acer saccharum*) leaf leachate on nitrification rates in stream sediments. Error bars = ±1 SE. The open triangle on the *y*-axis represents the control (no carbon addition). $\bar{x}$ refers to the mean ln-transformed concentration of carbon additions and is equal to 30.03 mg C L^{-1}.

for nitrification. Therefore, results from the first experiment are most consistent with the C : N ratio hypothesis.

In the second experiment, glucose additions increased community respiration rates in the stream sediments by 3.8–5.5 times over treatments that received no glucose ($P < 0.0001$, Fig. 2B). Although community respiration includes both autotrophic and heterotrophic respiration, the primary group of organisms positively responding to the added glucose likely was heterotrophic bacteria because they require organic carbon, whereas nitrifiers use CO_2 as a carbon source. Adding glucose increased the C : N ratio, thereby increasing the metabolic need for N in the microbial community and thus competition for available NH_4^+. N limitation of heterotrophic activity also may have occurred in the treatment that received only glucose. Reduction of N limitation would explain why respiration rates were highest for the treatment that received glucose and NH_4^+ additions (Fig. 2B).

Effect of organic carbon quality—In the third experiment, the general nitrification response to the two organic carbon sources was similar in that nitrification rate decreased as carbon concentration increased (Fig. 3). The slopes of the two lines (glucose and leaf leachate) were not significantly different ($P = 0.064$, ANCOVA). However, the nitrification responses for the two organic carbon sources at the mean ln-transformed carbon concentration (30.03 mg C L^{-1}) differed significantly ($P < 0.0001$, ANCOVA). This statistical analysis suggests that although the pattern in nitrification response to the two sources of organic carbon was the same, the magnitude of the response to the two sources differed. Nitrification was inhibited at a lower carbon concentration when glucose was the organic carbon source. The higher quality glucose presumably created conditions that led to stronger competition for NH_4^+ and thereby lower nitrification rates. A larger amount of the leaf leachate was required for the sediments to exhibit the same nitrification response. An alternative explanation for higher nitrification in the leaf leachate treatments could be that the leachate supplied an additional source of NH_4^+ via ammonification. However, in a similar study using leaf leachates from several tree species, we did not observe any relationship between nitrification and N content of leaves (Strauss and Lamberti, unpubl. data). Therefore, these results support our second hypothesis that organic carbon quality can affect nitrification rates.

In the chemostat study by Verhagen and Laanbroek (1991), glucose was used as the carbon source to manipulate C : N ratios and determine critical C : N ratios. Because glucose is a very labile carbon source, it is likely that glucose initiated competition between heterotrophic and nitrifying bacteria at concentrations lower than those for mixed carbon sources typically present in natural systems. Thus, their critical C : N estimate (9.6–11.6) may underestimate the actual critical C : N ratios in most natural systems. In Juday Creek, the sediment C : N was 21.1, well above their laboratory-estimated critical value, and we observed measurable nitrification even without nitrogen amendments. Furthermore,

the variable nitrification response to the two carbon sources suggests that the critical C : N ratio is highly variable depending on the quality (i.e., relative degree of lability) of available organic carbon.

The chemical composition or quality of particulate organic carbon (POC) and dissolved organic carbon (DOC) in aquatic systems varies widely and depends, in part, on its origin. First, the chemical composition of autochthonous organic carbon may differ from allochthonous organic carbon. Newly produced autochthonous organic carbon (e.g., algal exudates) contains a larger fraction of labile, low molecular weight compounds, whereas allochthonous organic carbon has already been processed and decomposed to some degree by the biota, thus removing the most labile compounds (Kaplan and Newbold 1993). Second, the quality of allochthonous organic carbon also may be dependent on the ecosystem from which it originates (Kaplan and Newbold 1993). For example, leaf decomposition rates differ between hardwood and coniferous trees (Webster and Benfield 1986; Maloney and Lamberti 1995) and even among hardwood species (Webster and Benfield 1986; Ostrofsky 1997).

Another possible mechanism explaining the negative effect of organic carbon on nitrification rates is allelopathy, or the direct inhibition of nitrifying bacteria by specific forms of organic carbon. Several terrestrial studies have shown that certain plant-derived organic carbon compounds, including polyphenols, tannins, and monoterpenes, can inhibit nitrification (Baldwin et al. 1983; White 1988; Paavolainen et al. 1998). White (1988) suggested that the mechanism of inhibition for monoterpenes might be similar to that of nitrapyrin. However, monoterpenes can increase respiration rates and may limit nitrification rates by stimulating heterotrophic N immobilization rather than eliciting allelopathy (Bremner and McCarty 1993; Paavolainen et al. 1998). In addition, Purchase (1974) reported minimal inhibition of nitrification when grassland soils were treated with exudates from decaying grass roots, and McCarty et al. (1991) found no significant effect of phenolic acid additions on nitrification in pure cultures of nitrifying bacteria.

Because leaf leachates had a less inhibitory effect on nitrification than did glucose (at similar C concentrations), it is unlikely that allelopathy can explain why the leachate inhibited nitrification. Based on our studies and previous reports, it is difficult to ascertain the true role of allelopathy on nitrification in natural systems. Clearly, additional research is needed to test the effects of several naturally occurring organic carbon sources on nitrifying bacteria in the laboratory and in the field.

Organic carbon abundance is spatially and temporally dynamic in aquatic ecosystems. In streams, high levels of organic carbon often are observed during periods of high discharge, presumably due to flushing of interstitial and soil water organic carbon into the channel (Mulholland and Kuenzler 1979; Thurman 1985). In woodland streams, annual leaf fall is a period in which POC and DOC levels are elevated from inputs of leaf litter and leaf leachates (McDowell and Fisher 1976). Organic carbon concentration also may be high in areas adjacent to submerged leaf packs or woody debris and in the interstitial or hyporheic water of streams (Crocker and Meyer 1987; Fiebig 1995; Tillman 1999). Lakes typically do not show as much variation in DOC as do streams. However, some lakes show annual and seasonal variation, with highest DOC concentrations occurring during wet years and phytoplankton blooms (Serruya et al. 1980; Schindler et al. 1997). Some lakes also exhibit spatial variation in DOC concentration with depth, or proximity to shorelines or point-source inputs (Maier and Swain 1978; Mitamura and Saijo 1981; Wetzel 1983). The trophic status of a lake also can affect DOC concentration. Eutrophic lakes typically have higher DOC concentrations than do oligotrophic lakes (Hama and Handa 1980; Thurman 1985). Such sources of variation in DOC may affect nitrification rates in freshwater ecosystems.

Conclusions—We found that organic carbon inhibited nitrification and that the inhibitory effect was greater when organic carbon quality was higher. Because organic carbon concentrations are spatially and temporally dynamic in aquatic ecosystems, a negative relationship between organic carbon and nitrification may produce spatial and temporal variability in sediment nitrification rates. Therefore, a better understanding of how organic carbon influences nitrification rates may provide insight into how N cycling in freshwater systems is influenced by natural or anthropogenic changes in organic carbon dynamics.

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References

BALDWIN, I. T., R. K. OLSON, AND W. A. REINERS. 1983. Protein binding phenolics and the inhibition of nitrification in subalpine balsam fir soils. Soil Biol. Biochem. **15:** 419–423.

BAUHUS, J., A. C. MEYER, AND R. BRUMME. 1996. Effect of the inhibitors nitrapyrin and sodium chlorate on nitrification and N_2O formation in an acid forest soil. Biol. Fert. Soils **22:** 318–325.

BOTT, T. L. 1996. Primary productivity and community respiration, p. 533–556. *In* F. R. Hauer and G. A. Lamberti [eds.], Methods in stream ecology. Academic.

BREMNER, J. M., AND G. W. MCCARTY. 1993. Inhibition of nitrification in soil by allelochemicals derived from plants and plant residues, p. 181–218. *In* J.-M. Bollag and G. Stotzky [eds.], Soil biochemistry. Vol. 5. Marcel Dekker.

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CARPENTER, S. R., N. F. CARACO, D. L. CORRELL, R. W. HOWARTH, A. N. SHARPLEY, AND V. H. SMITH. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol. Appl. **8:** 559–568.

CROCKER, M. T., AND J. L. MEYER. 1987. Interstitial dissolved organic carbon in sediments of a southern Appalachian headwater stream. J. N. Am. Benthol. Soc. **6:** 159–167.

DAHM, C. N., N. B. GRIMM, P. MARMONIER, H. M. VALETT, AND P. VERVIER. 1998. Nutrient dynamics at the interface between surface waters and groundwaters. Freshw. Biol. **40:** 427–451.

DODDS, W. K., AND R. D. JONES. 1987. Potential rates of nitrification and denitrification in an oligotrophic freshwater sediment system. Microb. Ecol. **14:** 91–100.

FIEBIG, D. M. 1995. Groundwater discharge and its contribution of dissolved organic carbon to an upland stream. Arch. Hydrobiol. **134:** 129–155.

HALL, G. H. 1984. Measurement of nitrification rates in lake sediments: Comparison of the nitrification inhibitors nitrapyrin and allylthiourea. Microb. Ecol. **10:** 25–36.

———. 1986. Nitrification in lakes, p. 127–156. *In* J. I. Prosser [ed.], Nitrification. IRL.

HAMA, T., AND N. HANDA. 1980. Molecular weight distribution and characterization of dissolved organic matter from lake waters. Arch. Hydrobiol. **90:** 106–120.

JONES, J. B., S. G. FISHER, AND N. B. GRIMM. 1995. Nitrification in the hyporheic zone of a desert stream ecosystem. J. N. Am. Benthol. Soc. **14:** 249–258.

KAPLAN, L. A., AND J. D. NEWBOLD. 1993. Biogeochemistry of dissolved organic carbon entering streams, p. 139–165. *In* T. E. Ford [ed.], Aquatic microbiology: An ecological approach. Blackwell.

KRUMMEL, A., AND H. HARMS. 1982. Effect of organic matter on growth and cell yield of ammonia-oxidizing bacteria. Arch. Microbiol. **133:** 50–54.

LAMBERTI, G. A., AND M. B. BERG. 1995. Invertebrates and other benthic features as indicators of environmental change in Juday Creek, Indiana. Nat. Areas J. **15:** 249–258.

MAIER, W. J., AND W. R. SWAIN. 1978. Organic carbon—a nonspecific water quality indicator for Lake Superior. Water Res. **12:** 523–529.

MALONEY, D. C., AND G. A. LAMBERTI. 1995. Rapid decomposition of summer-input leaves in a northern Michigan stream. Am. Midl. Nat. **133:** 184–195.

MCCARTY, G. W., J. M. BREMNER, AND E. L. SCHMIDT. 1991. Effects of phenolic acids on ammonia oxidation by terrestrial autotrophic nitrifying organisms. FEMS Microbiol. Ecol. **85:** 345–450.

MCDOWELL, W. H., AND S. G. FISHER. 1976. Autumnal processing of dissolved organic matter in a small woodland stream ecosystem. Ecology **57:** 561–569.

MITAMURA, O., AND Y. SAIJO. 1981. Studies on the seasonal changes of dissolved organic carbon, nitrogen, phosphorus, and urea concentrations in Lake Biwa. Arch. Hydrobiol. **91:** 1–14.

MULHOLLAND, P. J., AND E. J. KUENZLER. 1979. Organic carbon transport from upland and forested wetland watersheds. Limnol. Oceanogr. **24:** 960–966.

OSTROFSKY, M. L. 1997. Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. J. N. Am. Benthol. Soc. **16:** 750–759.

PAAVOLAINEN, L., V. KITUNEN, AND A. SMOLANDER. 1998. Inhibition of nitrification in forest soil by monoterpenes. Plant Soil **205:** 147–154.

PAUL, E. A., AND F. E. CLARK. 1989. Soil microbiology and biochemistry. Academic.

POWELL, S. J., AND J. I. PROSSER. 1985. The effect of nitrapyrin and chloropicolinic acid on ammonium oxidation by *Nitrosomonas europaea*. FEMS Microbiol. Lett. **28:** 51–54.

PROSSER, J. I. 1989. Autotrophic nitrification in bacteria. Adv. Microb. Physiol. **30:** 125–181.

PURCHASE, B. S. 1974. Evaluation of the claim that grass root exudates inhibit nitrification. Plant Soil **41:** 527–539.

ROY, R., AND R. KNOWLES. 1995. Differential inhibition by allylsulfide of nitrification and methane oxidation in freshwater sediment. Appl. Environ. Microbiol. **61:** 4278–4283.

SARATHCHANDRA, S. U. 1978. Nitrification activities and the changes in the populations of nitrifying bacteria in soil perfused at two different H-ion concentrations. Plant Soil **50:** 99–111.

SCHINDLER, D. W., P. J. CURTIS, S. E. BAYLEY, B. R. PARKER, K. G. BEATY, AND M. P. STAINTON. 1997. Climate-induced changes in the dissolved organic carbon budgets of boreal lakes. Biogeochem. **36:** 9–28.

SERRUYA, C., M. GOPHEN, AND U. POLLINGHER. 1980. Lake Kinneret: Carbon flow patterns and ecosystem management. Arch. Hydrobiol. **88:** 265–302.

SOLORZANO, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. **14:** 799–801.

STENSTROM, M. K., AND R. A. PODUSKA. 1980. The effect of dissolved oxygen concentration on nitrification. Water Res. **14:** 643–649.

STRAUSS, E. A. 1995. Protozoa-bacteria interactions in subsurface sediments and the subsequent effects on nitrification. MS Thesis. Kansas State Univ.

———, AND W. K. DODDS. 1997. Influence of protozoa and nutrient availability on nitrification rates in subsurface sediments. Microb. Ecol. **34:** 155–165.

THURMAN, E. M. 1985. Organic geochemistry of natural waters. Nijhoff/Junk.

TILLMAN, D. 1999. The influence of surface water–groundwater interactions on sediment organic matter dynamics in a second-order Michigan stream. Ph.D. thesis. Univ. Notre Dame.

TRISKA, F. J., J. H. DUFF, AND R. J. AVANZINO. 1990. Influence of exchange flow between the channel and hyporheic zone on nitrate production in a small mountain stream. Can. J. Fish. Aquat. Sci. **47:** 2099–2111.

VERHAGEN, F. J. M., AND H. J. LAANBROEK. 1991. Competition for ammonium between nitrifying and heterotrophic bacteria in dual energy-limited chemostats. Appl. Environ. Microbiol. **57:** 3255–3263.

VITOUSEK, P. M., AND OTHERS. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. Ecol. Appl. **7:** 737–750.

WEBSTER, J. R., AND E. F. BENFIELD. 1986. Vascular plant breakdown in freshwater ecosystems. Annu. Rev. Ecol. Syst. **17:** 567–594.

WETZEL, R. G. 1983. Limnology. 2nd ed. Saunders College.

WHITE, C. S. 1988. Nitrification inhibition by monoterpenoids: Theoretical mode of action based on molecular structures. Ecology **69:** 1631–1633.

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