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# Effect of dissolved organic carbon quality on microbial decomposition and nitrification rates in stream sediments

ERIC A. STRAUSS and GARY A. LAMBERTI
*Department of Biological Sciences, University of Notre Dame, Notre Dame, IN, U.S.A*

## SUMMARY

1. Microbial decomposition of dissolved organic carbon (DOC) contributes to overall stream metabolism and can influence many processes in the nitrogen cycle, including nitrification. Little is known, however, about the relative decomposition rates of different DOC sources and their subsequent effect on nitrification.
2. In this study, labile fraction and overall microbial decomposition of DOC were measured for leaf leachates from 18 temperate forest tree species. Between 61 and 82% (mean, 75%) of the DOC was metabolized in 24 days. Significant differences among leachates were found for labile fraction rates ($P < 0.0001$) but not for overall rates ($P = 0.088$).
3. Nitrification rates in stream sediments were determined after addition of 10 mg C $L^{-1}$ of each leachate. Nitrification rates ranged from below detection to 0.49 μg N mL sediment$^{-1}$ day$^{-1}$ and were significantly correlated with two independent measures of leachate DOC quality, overall microbial decomposition rate ($r = -0.594$, $P = 0.0093$) and specific ultraviolet absorbance ($r = 0.469$, $P = 0.0497$). Both correlations suggest that nitrification rates were lower in the presence of higher quality carbon.
4. Nitrification rates in sediments also were measured after additions of four leachates and glucose at three carbon concentrations (10, 30, and 50 mg C $L^{-1}$). For all carbon sources, nitrification rates decreased as carbon concentration increased. Glucose and white pine leachate most strongly depressed nitrification. Glucose likely increased the metabolism of heterotrophic bacteria, which then out-competed nitrifying bacteria for $NH_4^+$. White pine leachate probably increased heterotrophic metabolism and directly inhibited nitrification by allelopathy.

*Keywords*: dissolved organic carbon (DOC) quality, leaf leachates, microbial decomposition, nitrification, nutrient cycling, stream

## Introduction

Metabolism in stream ecosystems often is dependent on inputs of allochthonous organic matter (Fisher & Likens, 1972; Vannote *et al*., 1980). Direct input and lateral blow-in of forest litter, especially leaves, can account for a substantial portion of the total carbon budget of streams (Webster, Wallace & Benfield, 1995). Because of the importance of leaves to stream metabolism, many studies have focused on determining species-specific processing rates or understanding the factors influencing those rates in stream ecosystems (e.g. Webster & Benfield, 1986; Maloney & Lamberti, 1995). Considerably less is known about how microbial decomposition rates of dissolved organic carbon (DOC) leached from leaves differ among tree species.

Dissolved organic carbon enters streams through several pathways including overland flow, flushing of soil water, groundwater inputs, autochthonous inputs from algal exudates, and direct leaching from litter after it enters the stream (Kaplan & Newbold, 1993;

Correspondence and present address: Eric A. Strauss, U.S. Geological Survey, Upper Midwest Environmental Sciences Center, 2630 Fanta Reed Road, La Crosse WI 54603 USA.
E-mail: eric_strauss@usgs.gov

Meyer, Wallace & Eggert, 1998). Regardless of the entry pathway, the original source of much of the DOC that eventually enters a stream is leached leaf litter. Dissolved organic carbon leached from leaves likely varies in *quality* (defined here as ease of microbial decomposition) depending on the molecular weight and chemical structure of soluble compounds in the leaf tissue (Thurman, 1985). For instance, Ostrofsky (1993) reported high variability in the concentration of total phenolics and condensed tannins in the leaves from 48 species of deciduous trees.

Certain transformations in the nitrogen cycle (e.g. denitrification, ammonification and nitrification) are tightly coupled with each other and influenced by organic carbon availability and metabolism. Denitrification (reduction of $NO_3^-$, $NO_2^-$, NO, or $N_2O$ to $N_2$) is a heterotrophic process and can be limited by the availability of organic carbon in some aquatic environments (Seitzinger, 1988). Nitrogen mineralization or ammonification (release of $NH_4^+$ from processed organic matter) is controlled by the C : N ratio of the environment; under high C : N conditions nitrogen is mostly sequestered in microbial biomass and under low C : N conditions a net flux of $NH_4^+$ occurs into the environment (Schlesinger, 1997). Nitrification (chemoautotrophic oxidation of $NH_4^+$ to $NO_3^-$) also is indirectly influenced by organic carbon availability. We demonstrated previously that both glucose and sugar maple leaf leachate inhibited nitrification (Strauss & Lamberti, 2000). We proposed that under high C : N ratios, heterotrophic bacteria out-compete the less abundant and slower-growing nitrifying bacteria for available $NH_4^+$, thereby reducing nitrification rates. In the current study, we examined whether the magnitude of nitrification also responded to variation in carbon quality.

If the C : N ratio is high enough to promote competition for $NH_4^+$ between nitrifying and heterotrophic bacteria (Strauss & Lamberti, 2000), then the quality of organic carbon may influence nitrification. Higher quality organic carbon should provide a better substrate for heterotrophic metabolism, which would then increase the demand and competition for $NH_4^+$ and reduce nitrification rates. Poorer quality organic carbon should affect nitrification less because lower heterotrophic activity will moderate competition for $NH_4^+$. An alternative mechanism to explain the negative effect of some DOC on nitrification is allelopathy, the direct inhibition of nitrification primarily through inactivation of the enzyme ammonia monooxygenase. For example, White (1988) attributed low nitrification in coniferous forest soils to allelopathy by monoterpenes leached from pine litter. We tested this carbon quality hypothesis using a two-step approach. First, we measured microbial decomposition rates on DOC leached from leaves of 18 temperate forest tree species. Secondly, we determined the relative effect of organic carbon quality (using leaf leachates) on nitrification rates in stream sediments.

## Methods

### *Sample collection and processing*

Stream water and sediments used in our experiments were collected from Juday Creek, a third-order cool-water stream (mean discharge, 0.75 $m^3\ s^{-1}$) located in northcentral Indiana, U.S.A. (N 41°43.7′, W 86°15.9′). Juday Creek flows through areas of mixed land use, including woodland, agriculture, and urbanization (Lamberti & Berg, 1995). In 1996–97, mean surface water SRP, $NH_4^+$, and $NO_3^-$ concentrations were 27 μg P $L^{-1}$ (SD = 24), 60 μg N $L^{-1}$ (SD = 53) and 1.09 mg N $L^{-1}$ (SD = 0.18), respectively (Strauss & Lamberti, 2000). The mean DOC concentration in August 1998 was 6.57 mg C $L^{-1}$ (SD = 1.47).

All samples for this study were collected from a woodland reach of the stream. The stream sediments used in the experiments were collected from along the stream margin and consisted primarily of a sand-silt mixture that was sieved (0.64 cm) to remove larger stones and debris. Stream water was collected mid-channel and was not filtered. Sediments and water were stored on ice or in the refrigerator until experiments were started (always within 24 h of collection).

Organic carbon was obtained by making leaf extracts from 18 species of trees: eastern white pine (*Pinus strobus*), bitternut hickory (*Carya cordiformis*), shagbark hickory (*C. ovata*), eastern cottonwood (*Populus deltoides*), American beech (*Fagus grandifolia*), white oak (*Quercus alba*), chinkapin oak (*Q. muehlenbergii*), northern red oak (*Q. rubra*), black oak (*Q. velutina*), American elm (*Ulmus americana*), white mulberry (*Morus alba*), tuliptree (*Liriodendron tulipifera*), American sycamore (*Platanus occidentalis*), black cherry (*Prunus serotina*), eastern redbud (*Cercis canadensis*), sugar maple (*Acer saccharum*), silver maple (*A. saccharinum*) and red maple (*A. rubrum*). Recently

fallen leaves were collected from forested areas near Juday Creek, dried at room temperature and ground into coarse fragments. Leachates were extracted from the leaf fragments for 24 h in reverse osmosis-treated (RO) water at room temperature (*c*. 23 °C). Bacteria and particulate matter were removed by drawing the extracts sequentially through a series of sieves and filters until they finally passed through a 0.2-μm membrane filter. The extracts were stored in sterile bottles at 4 °C and re-filtered (0.2 μm) before use. Dissolved organic carbon concentrations of the filtered extracts were determined on a Shimadzu TOC-5000 A analyser (Shimadzu Scientific Instruments, Columbia, MD, U.S.A.).

### *Decomposition and leachate DOC quality*

We used two independent methods to measure the quality of the 18 leaf leachates as microbial carbon sources. First, quality was determined directly by quantifying microbial decomposition of the different leachates during laboratory incubations. Aliquots of each leachate were added to replicate ($n = 4$) 250-mL flasks containing unfiltered stream water and 1 mL of stream sediment inoculum. Total initial liquid volume in each flask was 200 mL with a final carbon amendment concentration of 35 (± 4) mg C $L^{-1}$. Flasks were loosely covered with aluminum foil and stored in the dark at room temperature (*c*. 23 °C). On days 0, 2, 4, 6, 14 and 24, a 20-mL subsample was removed from each flask, filtered (ashed Whatman GF/F), and analysed for DOC concentration as described above. Rates of microbial decomposition ($k$) were calculated for two DOC fractions of each leachate: (1) decomposition of the labile fraction was calculated from DOC concentration ($C$) loss through time ($t$) during the first 6 days of the study; and (2) overall decomposition was calculated from the entire 24-day incubation. Decomposition of the labile component was calculated using the traditional exponential decay model ($C_t = C_0\ e^{-kt}$). Overall decomposition was calculated using a similar model ($t$ was ln-transformed rather than $C$): $C_t = -k(\ln t + 1) + C_0$. We elected to use the new model to calculate the overall decomposition rate because it provided a much better fit to the data (mean $r^2$ values were 0.64 and 0.81 for the traditional and new models, respectively).

Secondly, physical and chemical properties of DOC were assessed with UV spectroscopy to further characterize the quality of the leaf leachates. Specific ultraviolet absorbance (SUVA) is highly related to percent aromaticity ($r^2 = 0.84$–$0.90$) and molecular weight ($r^2 = 0.66$–$0.97$) of dissolved organic matter (Chin, Aiken & O'Loughlin, 1994; Ravichandran *et al*., 1998), and thus serves as a reasonable surrogate for organic carbon quality. Specific ultraviolet absorbance was determined on each leachate by dividing its UV absorbance at 254 nm (measured on a Spectronic Genesys 2 spectrophotometer (Thermospectronic, Rochester, NY, U.S.A.), 1 cm path length) by its DOC concentration (Ravichandran *et al*., 1998).

### *Nitrification experiments*

Nitrification rates for stream sediments were measured in two different experiments after exposure to different leaf leachates. In the first experiment, nitrification rates were determined in the presence of each of the 18 leaf leachates at a constant C amendment (10 mg C $L^{-1}$) and for a control (no $C$ amendment). For each leachate, nitrification measurements were not replicated because the purpose of this experiment was to determine solely how well nitrification rates correlated with microbial decomposition and SUVA. The second experiment explored the nitrification response to four leaf leachates (chinkapin oak, eastern cottonwood, eastern white pine and white oak) and glucose at three levels of C amendment (10, 30, and 50 mg C $L^{-1}$), where each level and a control (no C added) was replicated six times. The goal of this experiment was to determine the interactive effects of C quality and quantity on nitrification.

In both experiments, nitrification rates were determined during laboratory incubations using the nitrapyrin method as modified by Strauss & Lamberti (2000). Nitrapyrin [2-chloro-6-(trichloromethyl)-pyridine] inhibits the function of the enzyme ammonia monooxygenase and thereby prevent nitrification. Each nitrification replicate consisted of two 125-mL flasks. Each flask contained 25 mL of stream sediment and 85 mL of C-amended stream water. Nitrification was inhibited in one flask with the addition of 10 mg $L^{-1}$ (final conc.) nitrapyrin, dissolved in dimethyl sulfoxide (DMSO). The other flask received only DMSO as a control. The flasks were covered loosely with aluminum foil and incubated in the dark at 27 °C for 72 h on an orbital shaker (175 r.p.m.). Initial and final $NH_4^+$ concentrations were determined

on filtered 1-N KCl extracts from each flask using the phenol hypochlorite method (Solorzano, 1969). Dissolved oxygen (DO) and pH were checked in approximately 50% (randomly selected) of the flasks at the beginning and end of the experiments to ensure proper environmental conditions for nitrification, an aerobic circumneutral process. DO concentrations in both experiments (data pooled) ranged from 7.1 to 7.8 mg $L^{-1}$ with a mean of 7.5; pH ranged from 7.7 to 8.4 with a mean of 8.3. 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. Initial $NH_4^+$ concentrations in the flasks were similar for both experiments (mean = 0.06 mg N $L^{-1}$, SD = 0.04).

### *Statistical analysis*

Statistical analyses were performed with SAS version 6.12. One-way analysis of variance (ANOVA) was used to compare mean decomposition rates of the leaf leachates. Tukey's multiple comparison test was used to determine where significant differences among leaf leachates resided. Pearson correlations were used to determine if significant linear relationships existed between nitrification rate and the two measures of organic carbon quality, microbial decomposition and SUVA. Analysis of covariance (ANCOVA) was used to analyse the experiment on the interactive effects of carbon quality and quantity on nitrification. The covariate, organic carbon concentration, was natural log-transformed to linearize the relationship between nitrification and organic carbon concentration.

## Results

### *Microbial decomposition*

In general, leachate decomposition followed a logarithmic decay pattern (Fig. 1), as is typically observed in leaf litter decomposition studies (reviewed by Webster & Benfield, 1986). For most leachates, DOC concentration declined rapidly during the first 6 days of decomposition, followed by little change in DOC concentration through day 24. On average, 75% of the DOC from each leachate was metabolized during the experiment. Presumably, the more labile carbon compounds were metabolized first, thereby accounting for the initial rapid decrease in DOC concentration. Decomposition rates of the labile fraction ranged from 0.05 to 0.26 ln (mg C $L^{-1}$) $days^{-1}$ (Fig. 2A). Differences in labile DOC decomposition rates among the leachates were significant ($P < 0.0001$) with the highest rates observed for eastern redbud and black cherry and the lowest rates seen in American elm, white mulberry and chinkapin oak. As the availability of labile compounds diminished, slower decomposition of the more refractory compounds likely ensued, resulting in a slower decline in DOC concentration. Overall microbial decomposition rates for the different leachates ranged from 7.0 to 9.7 mg C $L^{-1}$ ln $days^{-1}$ (Fig. 2B), but differences among leachates were not significant ($P = 0.088$).

### *Nitrification experiments*

Addition of leaf leachates to stream sediment and water resulted in nitrification rates that ranged from below detection (for red oak and tuliptree) to 0.49 μg N mL $sediment^{-1}$ $day^{-1}$ (for sugar maple) (Fig. 2C). Nitrification rates did not significantly correlate with labile DOC decomposition, but did significantly correlate with the other two surrogates of organic carbon quality (Fig. 3): overall microbial decomposition ($r = -0.594$, $P = 0.0093$) and SUVA ($r = 0.469$, $P = 0.0497$). Both correlations suggest that nitrification rates were lower in the presence of high quality organic carbon.

In the experiment where nitrification was determined after exposure to five carbon sources at three carbon concentrations, the nitrification rate consistently decreased as carbon concentration increased (Fig. 4). The slopes of the five regressions were not significantly different ($P = 0.2502$, ANCOVA). However, the nitrification responses for the five organic carbon sources at the mean ln-transformed carbon concentration (24.7 mg C $L^{-1}$) differed significantly ($P = 0.0043$, ANCOVA). White oak leachate differed significantly from glucose and white pine leachate ($P < 0.05$, Tukey's test). Therefore, the pattern of the nitrification response to organic carbon was similar among carbon sources, but the magnitude of the response was dependent on the specific type of organic carbon.

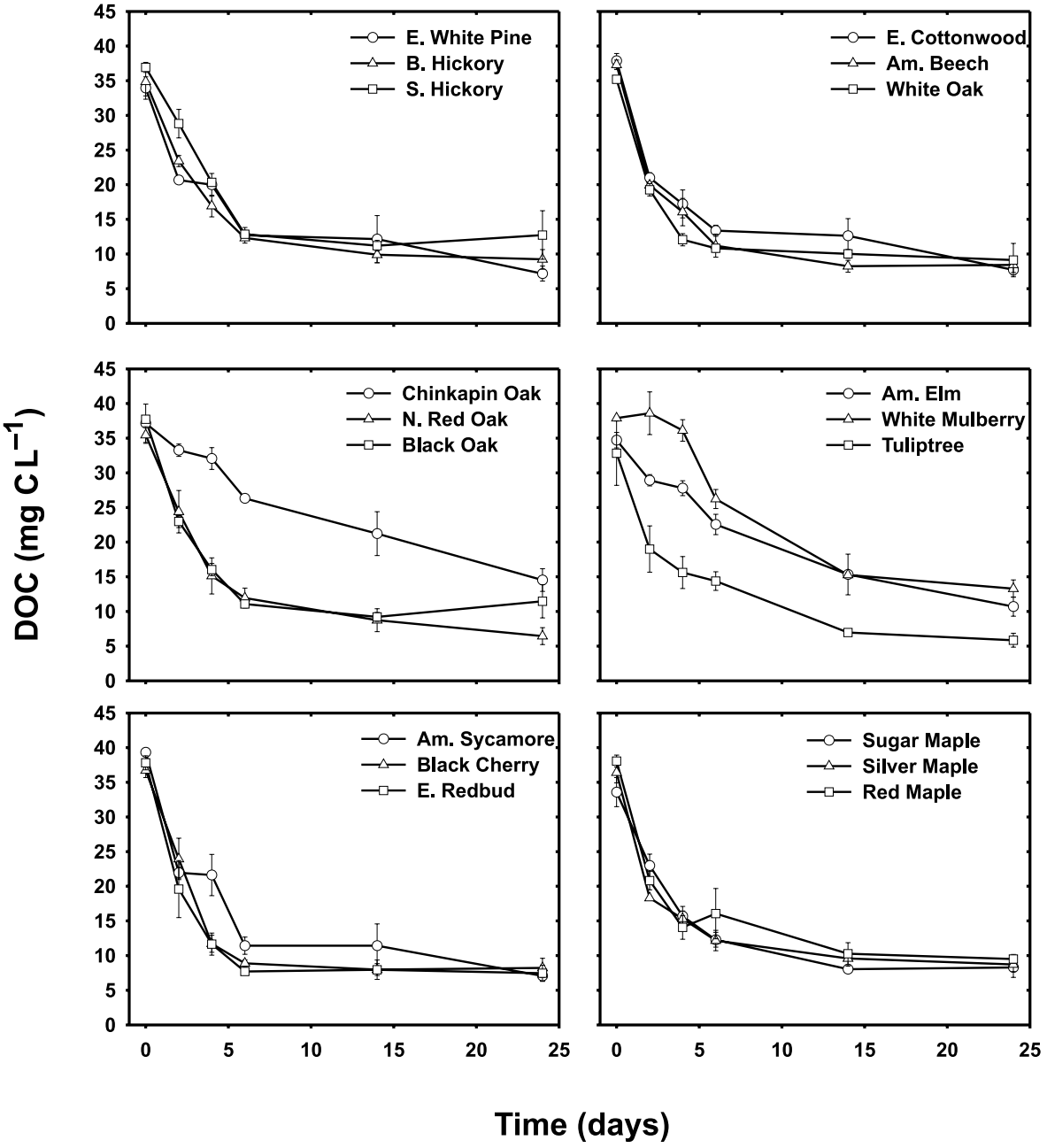


**Fig. 1** Reduction in dissolved organic carbon (DOC) concentration through time for 18 leaf leachates incubated in stream water and sediments. Incubations ($n = 4$ per leachate) were conducted in darkness at room temperature (*c.* 23 °C). Error bars = ± SE.

## Discussion

### *Microbial decomposition of leaf leachates*

Most studies of leaf breakdown or processing consist of monitoring loss of leaf mass over time. Such studies do not measure decomposition *per se* because they cannot distinguish between physical (particularly leaching and fragmentation) and biological mechanisms of breakdown (Suberkropp, 1998). Decomposition is the process of assimilation and subsequent mineralization (conversion to $CO_2$). After leaves enter a stream, 10–30% of the initial dry mass typically is lost to leaching within the first few days (Petersen & Cummins, 1974). In essence, we

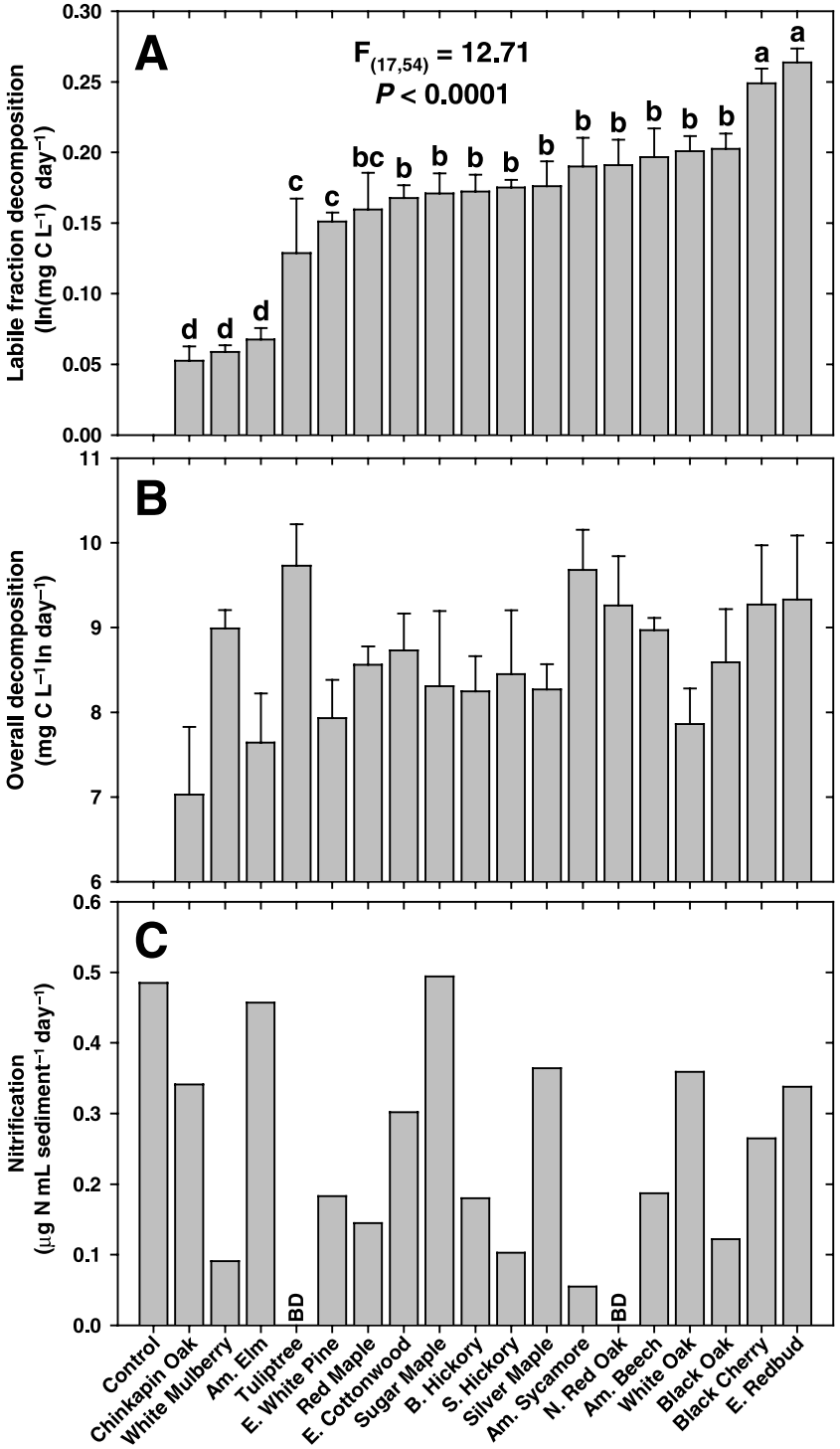


**Fig. 2** Decomposition of dissolved organic carbon (DOC) in 18 leaf leachates: (A) microbial decomposition rate of labile DOC; (B) overall microbial decomposition; and (C) nitrification rate in stream sediments after addition of 18 leaf leachates. Labile fraction and overall decomposition rates ($k$) were determined from the loss of DOC over time using the equations $C_t = C_0\, e^{-kt}$ and $C_t = -k\,(\ln t + 1) + C_0$, respectively. Error bars = ± SE. Nitrification responses were determined after a single DOC addition of 10 mg C $L^{-1}$ of each leachate except for the control, which had no carbon added. BD = below detection.

measured (in a controlled environment) the decomposition rate of DOC that would have leached from leaves directly entering a stream. We assumed that the primary mechanism for DOC loss was assimilation and mineralization. Chemical adsorption of organic molecules to sediment particles could account for some initial DOC loss, but this loss was assumed to be constant among leachates. In general, adsorption occurs more rapidly than microbial uptake, but microbial activity is much more effective

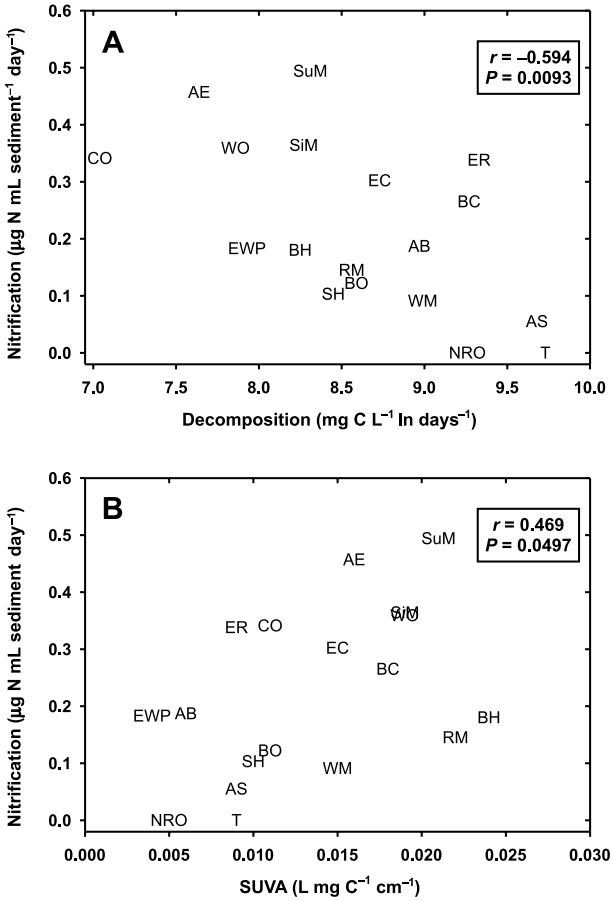


**Fig. 3** Linear correlations (Pearson's *r*) of nitrification with two independent measures of organic carbon quality: (A) overall microbial decomposition rates of leaf leachates and nitrification, and (B) specific ultraviolet absorbance (SUVA) values of leaf leachates and nitrification. Nitrification rates are the same as in Fig. 2B and the symbols are the common name initials for the tree species (see Fig. 1) used to make the leaf leachate.

at removal and degradation of total DOC (Dahm, 1981).

We compared our leachate decomposition rates with leaf litter processing rates obtained from published literature, using Spearman rank correlations on a species-specific basis. Leaf processing rates reported by Ostrofsky (1997) included 14 of our 18 species and were not significantly correlated with our overall ($r = 0.22$, $P = 0.46$, $n = 14$) or our labile fraction ($r = -0.05$, $P = 0.87$, $n = 14$) leachate decomposition rates. A review by Webster *et al*. (1995) of leaf processing contained nine matching species (when multiple rates for a single species were reported, the values were averaged), which again were not significantly correlated with overall ($r = 0.13$, $P = 0.73$, $n = 9$) or labile fraction ($r = -0.48$, $P = 0.19$, $n = 9$) leachate decomposition. The low correlations suggest that DOC leached from leaves may not decompose at rates comparable with processing rates of intact leaves. For example, the DOC leached from a leaf species that is processed quickly does not necessarily decompose quickly. This finding could be an important consideration when evaluating the relative role of different litter leachate inputs to the carbon metabolism of a stream or other aquatic habitat.

A large proportion of the DOC in some streams (small forested streams in particular) originates from leached leaf litter. In a small New Hampshire, U.S.A., stream, nearly 17% of the litter mass that entered the stream was released as DOC within 3 days and contributed 42% of the total DOC in the stream (McDowell & Fisher, 1976). Several streams in the southern Appalachian Mountains are reported to obtain 18–37% of stream water DOC from litter leachates (Tate & Meyer, 1983; Meyer *et al*., 1998). However, discerning the relative contributions of various leaf species to the DOC pool and their subsequent role in carbon cycling has received little attention. Our study suggests that DOC decomposition rates differ among DOC sources, especially for the labile fractions. Leachates containing a large fraction of labile compounds that are decomposed quickly should have a more profound effect on local carbon metabolism than those containing mostly refractory compounds. Alternatively, persistent compounds may be important 'exports' to downstream communities.

### *Effect of DOC quality and allelopathy on nitrification*

Organic carbon can negatively affect nitrification in soils (Rice & Pancholy, 1973; Paavolainen, Kitunen & Smolander, 1998), but such inhibition has not been studied in aquatic systems. In a previous study, we demonstrated with laboratory experiments that nitrification in sediments was reduced by additions of glucose or sugar maple leaf leachate (Strauss & Lamberti, 2000). In the current study, we expanded on our earlier work by quantifying the effect of 18 DOC sources (leaf leachates) on nitrification. We observed highly variable responses in nitrification rates to different leachates. For example, sugar maple leachate elicited virtually no change in nitrification whereas red oak and tuliptree leachates resulted in

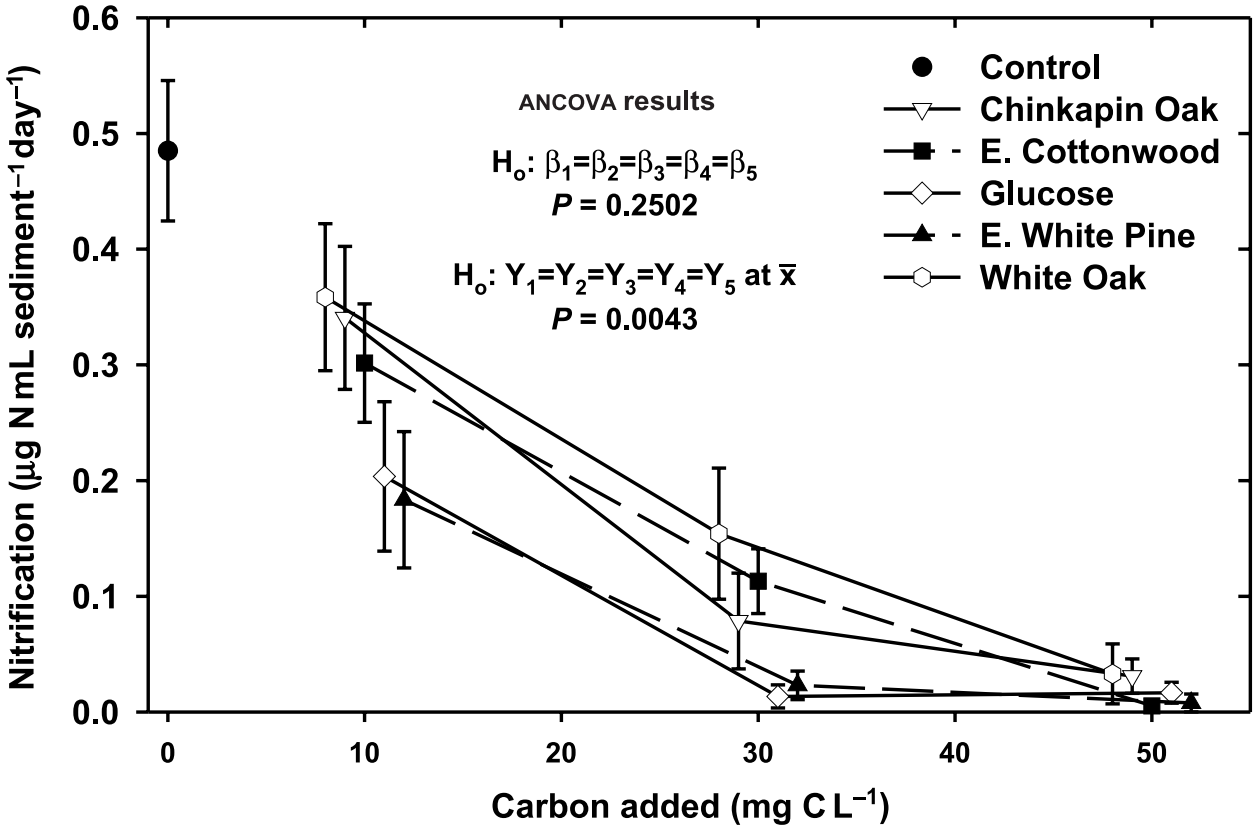


**Fig. 4** Effect of glucose and four leaf leachates on nitrification rates in stream sediments. Error bars = ± 1 SE. The solid circle represents the control (no carbon addition). $\bar{x}$ refers to the mean ln concentration of carbon additions (24.7 mg C $L^{-1}$). Symbols are slightly offset from actual horizontal positions (10, 30 and 50 mg C $L^{-1}$) to show error associated with each point.

nearly 100% inhibition of nitrification. If the mechanism responsible for the decrease in nitrification was DOC concentration alone, then the nitrification response should have been the same for all leachates because the carbon additions were kept constant (10 mg C $L^{-1}$). Thus, the variable nitrification responses suggest that unique characteristics inherent to each leachate can affect nitrification differently. It is possible that N mineralized from the leachates affected nitrification. However, the significant correlations between nitrification rate and DOC quality (i.e. overall microbial decomposition rate and SUVA values) suggest that DOC quality is at least partially responsible for variation in nitrification. However, alternative explanations must be considered.

Allelopathy is another mechanism commonly invoked for terrestrial systems to explain the negative relationship between nitrification and organic carbon. Rice & Pancholy (1973) attributed reduced nitrification in late successional stages of a tallgrass prairie, an oak forest, and an oak-pine forest in Oklahoma to allelopathy from phenolics and tannins. In a ponderosa pine forest, low nitrification rates were attributed to direct inhibition from monoterpenes leached from pine litter (White, 1986). White (1988) further speculated that the mode of action by monoterpenes was similar to that of nitrapyrin (i.e. inhibition of the $NH_4^+$ oxidation enzyme, ammonium monooxygenase). In a review of nitrification–allelopathy relationships in soils, Bremner & McCarty (1993) proposed an alternative mechanism by arguing that the presence of phenolics, tannins and monoterpenes initiates heterotrophic immobilization of $NH_4^+$, which results in decreased availability of $NH_4^+$ for nitrifying bacteria and thus lower nitrification rates. A recent soil study in a Norway spruce forest supports this argument because increased microbial respiration and decreased nitrification were observed after additions of monoterpenes (Paavolainen *et al.*, 1998). However, another study provided strong evidence for

allelopathic suppression of nitrification because additions of redwood monoterpenes decreased nitrification in pure cultures of *Nitrosomonas europea* (Ward *et al*., 1997). Inhibition of nitrification in pure cultures of nitrifying bacteria eliminates the possibility of heterotrophic competition. Furthermore, glucose has no effect on nitrification activity in pure cultures of *Nitrosomonas* (Krummel & Harms, 1982). Overall, the significance of allelopathy in regulating nitrification remains uncertain.

In our experiment in which nitrification was measured after additions of four leaf leachates and glucose at three carbon concentrations, we demonstrated that DOC source and quantity both were important in influencing nitrification rates. An unexpected result from this experiment was the similar nitrification response to the glucose and white pine DOC additions. Glucose is generally considered a very labile carbon source, whereas pine is considered a poorer carbon source. The fact that both DOC sources resulted in similar nitrification rates is inconsistent with both the heterotrophic competition hypothesis and the allelopathy hypothesis. If carbon quality alone was responsible for variable nitrification responses to DOC additions (heterotrophic competition hypothesis), we should have seen much lower nitrification rates in the treatments that received glucose than those receiving white pine leachate. If chemical inhibition alone was responsible for variable nitrification responses to DOC additions (allelopathy hypothesis), we should have seen much lower nitrification rates in the treatments that received the white pine leachate (because of high monoterpene concentration) than those receiving glucose. Our results suggest that both mechanisms function concurrently at suppressing nitrification: (1) high quality carbon induces competition between heterotrophic and nitrifying bacteria for $NH_4^+$ and (2) some functionality of nitrifying bacteria is hindered via direct allelopathy from certain compounds in litter leachate.

Although *in situ* evidence for a negative relationship between nitrification and organic carbon in aquatic systems is still lacking, our laboratory study suggests that the potential for such a relationship exists. Because leaf leachates constitute an important carbon source for forested streams, and likely for other aquatic ecosystems as well, relationships between organic carbon and nitrification may have important implications for nitrogen cycling in these ecosystems.

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