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Influence of nitrogen on cellulose and lignin mineralization in blackwater and redwater forested wetland soils

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Abstract Microcosms were used to determine the influence of N additions on active bacterial and active fungal biomass, cellulose degradation and lignin degradation at 5, 10 and 15 weeks in soils from blackwater and redwater wetlands in the northern Florida panhandle. Blackwater streams contain a high dissolved organic C concentration which imparts a dark color to the water and contain low concentrations of nutrients. Redwater streams contain high concentrations of suspended clays and inorganic nutrients, such as N and P, compared to blackwater streams. Active bacterial and fungal biomass was determined by direct microscopy; cellulose and lignin degradation were measured radiometrically. The experimental design was a randomized block. Treatments were: soil type (blackwater or redwater forested wetlands) and N additions (soils amended with the equivalent of 0, 200 or 400 kg N ha^{-1} as NH_4NO_3). Redwater soils contained higher concentrations of C, total N, P, K, Ca, Mn, Fe, B and Zn than blackwater soils. After N addition and 15 weeks of incubation, the active bacterial biomass in redwater soils was lower than in blackwater soils; the active bacterial biomass in blackwater soils was lower when 400 kg N ha^{-1}, but not when 200 kg N ha^{-1}, was added. The active fungal biomass in blackwater soils was higher when 400 kg N ha^{-1}, but not when 200 kg N ha^{-1}, was added. The active fungal biomass in redwater wetland soils was lower when 200 kg N ha^{-1}, but not when 400 kg N ha^{-1}, was added. Cellulose and lignin degradation was higher in redwater than in blackwater soils. After 10 and 15 weeks of incubation, the addition of 200 or 400 kg N as NH_4NO_3 ha^{-1} decreased cellulose and lignin degradation in both wetland soils to similar levels. This study indicated that the addition of N may slow organic matter degradation and nutrient mineralization, thereby creating deficiencies of other plant-essential nutrients in wetland forest soils.

Key words Microcosms · Fungal biomass · Cellulose degradation · Lignin · Nitrogen fertilization

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Introduction

The chemical characteristics of forested wetland soils on river floodplains are predominantly controlled by the physiography of the drainage area. Blackwater streams originate in swamps, bogs and marshes, or can drain areas that have nutrient-poor soils (Smock and Gilinsky 1992). The chemical characteristics of blackwater streams, although quite variable, are different from redwater streams in a number of respects. The high organic C concentration imparts a dark color to the water. Concentrations of both dissolved and particle-associated inorganic ions are low because of the absence of readily soluble minerals (Windom et al. 1971; Beck et al. 1974). Redwater streams drain areas that have poorly consolidated soils that are easily eroded (Grissinger et al. 1982; Mulholland and Lenat 1992). Redwater streams contain high concentrations of suspended clays and inorganic nutrients (Beck et al. 1974; Bass and Cox 1985). These streams often have a reddish hue in bright sunlight due to the high concentrations of suspended clay and silt.

Vegetative growth in forest wetland ecosystems are often limited by N and P. Nutrients that are taken up by plants and microbes are supplied through nutrients that are converted to the inorganic form during the litter decomposition process (Koch and Reddy 1992; Cooper and Brush 1993). In the past few decades, intensive agricultural fertilization and inadequate wastewat-

er treatment has contributed to high concentrations of N in surface runoff and groundwater which may cause changes to the soil microbial community and organic matter decomposition. High N concentrations in soils are known to increase soil microbial biomass, lignin and cellulose degradation in forest riparian soils, which may change the rate of nutrient decomposition, nutrient mineralization (Entry and Backman 1995; Entry and Emmingham 1995; Griffiths et al 1997) and ultimately stream chemistry (Windom et al 1971; Johnson 1991; Koch and Reddy 1992).

Previous research suggests that soil N concentrations may be an important factor affecting cellulose and lignin degradation (Freer and Detroy 1982; Leatham and Kirk 1983; Reid 1991; Cromack et al. 1991; Entry and Backman 1995). Since the concentration of lignin in plant material is inversely related to its decomposition rate (Meentmeyer 1978; Berendse et al. 1987; Sinsabaugh et al. 1992), I hypothesized that N additions would alter the active bacterial and fungal biomass and the degradation of ^{14}C-cellulose-labeled lignocellulose and ^{14}C-lignin-labeled lignocellulose in blackwater and redwater forested wetland soils.

Materials and methods

Site descriptions

The top 10 cm of mineral soil was sampled in three blackwater and three redwater forest wetland floodplains in the northern Florida panhandle. The blackwater river floodplains were on the Withlacoohae, Suwannee and Acullia rivers. The Withlacoohae river floodplain was sampled at Blue Springs, Florida (30°30′N, 83°15′W). The site supported a forest consisting of live oak (*Quercus virgiana* Mill.), water oak (*Quercus nigra* L.), sweetgum (*Liquidambar styracifoild* L.) and slash pine (*Pinus ellotti* L.). The Suwannee river floodplain was sampled at Suwannee River State Park, Florida (30°27′N, 83°48′W). The site supported live oak, turkey oak (*Quercus laevis* Walt.), post oak (*Quercus stellata* Wangenh.), blackgum (*Nyssa sylvatica* Walt. Sarg.) and slash pine. The Acullia river floodplain was sampled near Lamont, Florida (30°22′N, 83°44′W). The site supported a forest of bald cypress (*Taxodium distichm* L. Rich), water oak, sweetbay [*Gordonia lasianthus* (L.) Ellis], blackgum. and sweetgum.

The redwater river floodplains were on the Sandy Creek, Chipola and Escambia rivers. The Sandy Creek floodplain was sampled at Ponce de Leon Recreation Area, Florida (30°40′N, 86°00′W). The site supported a forest consisting of blackgum, gum (*Nyssa aquatica* L.), bald cypress, sweetgum and bay [*Gordonia lesianthus* (L.) Ellis]. Most trees were covered with Spanish moss (*Tillandsia usneoides* L.). The Chipola river floodplain was sampled at Florida State Caverns Park, Florida (30°49′N, 85°15′W). The site supported predominantly baldcypress with some blackgum, laurel oak (*Quercus laurifolia* Michx.), swamp oak (*Quercus tyrata* Walt.), and water oak. The Escambia river floodplain was sampled at University of Western Florida wetlands, in Pensacola, Florida (30°30′N, 87°30′W). The site supported a forest of baldcypress, blackgum, water tupelo, swamp oak (*Quercus lyrata* Walt.), water oak and sweetgum trees.

Soil descriptions

The soil on the floodplain of the Withlacoohe river soil was a sandy, siliceous, thermic Arenic Hapludult (Howell and Williams 1990). The A layer was approximately 10 cm thick, dark grey with a fine granular structure and a pH of 5.0. The soil on the floodplain of the Suwannee River soil was a sandy, siliceous, thermic Aquic Hapludult (Howell and Williams 1990). The A layer was dark grey and approximately 18 cm thick. It had a weak, fine granular structure with a pH of 4.8. The soil on the floodplain of the Acullia River soil was a sandy, siliceous, thermic Grossarenic Paleaquult (Howell and Williams 1990). The Ap layer was a dark grey, 18-cm-thick layer with a weak, granular structure and a pH of 5.0.

The soil on the floodplain of the Chipola river was a fine clay, siliceous, non-acid, thermic Typic Fluvaquent (Duffee et al. 1979). The A1 layer was a dark greyish-brown clay-loam, 18 cm thick with a granular structure and a pH of 4.5. The soil on the floodplain of the Sandy creek was a loamy-clay, siliceous, acid, thermic Typic Fluvaquent (Sullivan 1975). The A1 layer was a dark greyish-brown, loamy-clay, approximately 18 cm thick with a pH of 4.8. The soil on the floodplain of the Escambia river was a loamy, siliceous, acid, thermic Typic Fluvaquent (Walker et al. 1960). The A1 layer was a reddish-brown, clay-loam, approximately 12 cm thick with a pH of 4.8.

Sampling procedures

Three soil samples were collected from the top 10 cm of mineral soil in three separate 1-m^2 areas of each soil type on 16 and 17 January 1995. Nine soil samples from each site × N addition were analyzed for cellulose and lignin degradation. Soil was collected and stored in air-tight and moisture-tight plastic freezer bags at 4 °C and at moisture conditions similar to those in the field. Soil was sieved and roots >1 mm diameter were removed. Soil was prepared for microbial testing within 24 h of collection to minimize the effects of storage on microbial activity (West et al. 1986).

Soil chemical analysis

Soil moisture was determined gravimetrically after drying to a constant weight at 104 °C for 24 h. Soil pH was determined with a 1:1 paste of soil:water (McLean 1982). Total C was estimated by dry ashing at 525 °C and assuming C to be equal to 50% of loss on ignition (Nelson and Sommers 1982). Total N was determined using standard microKjeldahl procedures modified for NO_3^- (Bremner and Mulvaney 1982). C:N ratios were calculated by dividing total C by total N. Extractable P, K, Ca, Mg, Mn, Fe, Cu, B and Zn was determined using Mehlich I procedures. A 2-g sample of the top 10 cm of mineral soil was extracted with four aliquots of 0.225 M NH_4OAC plus 0.0005 M diethylenetriaminepentaacetic acid. The soil was shaken for 7 min, centrifuged at 180 rpm min^{-1} and analyzed on a Jarrol Ash 9000 inductively coupled plasma spectrometer (Sims 1989).

Experimental design

The laboratory experiment was arranged in a randomized block (Kirk 1982). Treatments were: (1) type of forested wetland (blackwater or redwater), and (2) the addition of N to the soil which consisted of 0 (control), and the addition of the equivalent of 200 kg N ha^{-1} and 400 kg N ha^{-1} to the top 10 cm of soil. Soil types (sites) were considered as blocking variables. Cellulose and lignin degradation was measured at 5, 10 and 15 weeks and was determined by ^{14}C-CO_2 production from cellulose-labeled lignocellulose or lignin-labeled lignocellulose.

Soil amendments

Three N treatments were based on the amount of N that 15 g soil would receive if 0, 200 or 400 kg N ha^{-1} as NH_4NO_3 was added to the top 10 cm of mineral soil, assuming each soil had a bulk density of 1.0 g cm^{-3}. The measured bulk densities were; Withlacoohae 1.03 g cm^{-3}, Suwannee 1.08 g cm^{-3}, Acullia 1.05 g cm^{-3}, Sandy Creek 0.98 g cm^{-3}, Chipola 1.01 g cm^{-3} and Escambia 0.97 g cm^{-3}. N as NH_4NO_3 was added to all samples on a dry weight basis. The

200 kg N ha^{-1} treatment received 1 ml distilled deionized H_2O containing 0.025 g NH_4NO_3 to 15 g (equivalent dry weight) moist soil and the 400 kg N ha^{-1} treatment received 1 ml distilled deionized H_2O containing 0.050 g NH_4NO_3. Control soils (no additional N) received 1 ml distilled, deionized H_2O.

Microbial biomass measurements

Active bacterial biomass and active fungal biomass were determined for each soil before C additions, and on each treatment after incubation using methods described by Ingham and Klein (1984). A 1.0-g soil sample was diluted in 9 ml of a phosphate buffer (pH 6.0) and shaken at approximately 120 rpm for 5 min. A 1-ml aliquot was removed and stained with 1 ml of a 20 μg ml^{-1} fluorescein diacetate (FDA) solution in a 0.2 M phosphate buffer for 3 min. One milliliter of 1.5% agar in a 0.1 M phosphate buffer, pH 9.5, was added to the FDA suspension. The sample was mixed and an aliquot placed on a microscope slide containing a cavity of known volume (Ingham and Klein 1984). Slides were examined for FDA-stained hyphal length immediately after preparation by epifluorescent microscopy (Stamatiadis et al. 1990). Three fields $slide^{-1}$ were evaluated with phase contrast microscopy for total hyphal length, and three transects were evaluated for FDA-stained (active) hyphal length at × 160 total magnification. Using epifluorescent oil-immersion microscopy, 10 fields $slide^{-1}$ were evaluated to determine numbers and size of fluorescent bacteria (Lodge and Ingham 1991). Bacterial volume from the number of soil bacteria per gram of soil was computed with the assumption that bacterial spheres were 1 μm in diameter (Jenkinson and Ladd 1981). A C to volume conversion factor of 120 μg C mm^{-3} was used for both bacteria and fungi, assuming 1.1 g cm^{-3} wet density, 20% dry matter content, and a C content of the bacterium or fungus of 41% (Jenkinson and Ladd 1981).

Labeling of lignin and cellulose

Phenylalanine is preferentially incorporated into lignin components of actively growing plants (Crawford 1981), while glucose is preferentially incorporated into cellulose components (Crawford and Crawford 1976). Lignin and cellulose were independently labeled with ^{14}C by allowing cut stems of *Populus trichoarpa* L. to absorb phenylalanine ord-[U-^{14}C]-glucose, respectively, as described by (Crawford et al. 1977; Crawford 1981). Plants were allowed to metabolize the ^{14}C-labeled phenylalanine or glucose for 7 days. Bark was removed, the material dried at 60 °C for 7 days and ground to pass a 1.0-mm mesh. The material was then extracted for either lignin or cellulose using methods described in Crawford (1981). The specific activity of the lignin-labeled lignocellulose preparation was 1909 dpm mg^{-1}; the specific activity of the cellulose-labeled lignocellulose preparation was 676 dpm mg^{-1}.

Lignin and cellulose degradation

The influence of N on cellulose and lignin degradation was tested in a microcosm system. There were nine replicates of each treatment for each forested wetland × N addition × soil type. Twenty grams of each soil amended as described above was placed in a 50-ml test tube. One hundred milligrams ^{14}C-cellulose-labeled lignocellulose or 100 mg ^{14}C-lignin-labeled lignocellulose was mixed with each sample. Tubes were then sealed with a rubber stopper with one inlet and one outlet port. Air was passed through soda lime to remove CO_2 and then distilled water at a flow rate of approximately 1660 cm^3 min^{-1}. At 72 h intervals, moist, CO_2–free air was passed into the tube (Edwards 1982). Exit gases containing $^{14}CO_2$ were passed through an air line into a scintillation vial containing 10 ml of 1 M NaOH to trap CO_2. Cellulose and lignin degradation were measured at 5, 10 and 15 weeks of incubation at 20 °C. Blanks were treated as above, but without radio-labeled cellulose or lignin added to the soil to account for background radiation. We ran one blank sample for each set of 27 samples. After incubation, 0.5 ml of the NaOH was removed from each vial and mixed with a 1.0-ml deionized H_2O and 17-ml scintillation cocktail (Bio-Safe II: Research Products International, Mount Prospect, Ill.). Samples were counted for 10 min with a Beckman LS 7500 autoscintillation counter.

Statistical analysis

All dependent variables were tested for normality with univariate procedures. Data were then analyzed by means of two-way ANOVA procedures for a randomized block design with Statistical Analysis Systems (SAS Institute 1996). Residuals were equally distributed with constant variances. All data reported are the sample values minus control values. Differences were judged to be significant at $P = 0.05$, as determined by the least square means test. Correlations were analyzed with N concentration or active bacterial and fungal biomass as dependent (x) variables and cellulose or lignin degradation as independent (y) variables.

Results

Because ANOVAs for all nutrients did not indicate significant differences among sites, only differences among wetland types (blackwater or redwater) and N additions can be discussed (Snedecor and Cochran 1980). Soils in forested wetlands receiving water draining from redwater soils contained higher concentrations of C, total N, P, K, Ca, Mn, Fe, B and Zn (Table 1). Because ANOVAs for active and total fungal and bacterial biomass, as well as cellulose and lignin degradation, did not indicate significant differences among sites, only differences among wetland types (blackwater or redwater) and N additions can be discussed. Active bacterial and active fungal biomass in blackwater and redwater wetland soils were not significantly different prior to incubation and averaged 0.04 and 0.39 μg C g^{-1} soil, respectively. After N addition and 15 weeks of incubation, active bacterial biomass in both redwater soils was lower than in blackwater soils when 400 kg N ha^{-1} was added, but not when 200 kg N ha^{-1} was added. Active fungal biomass in blackwater soils was higher when 400 kg N ha^{-1}, but not when 200 kg N ha^{-1} was added. Active fungal biomass in redwater soils was lower when 200 kg N ha^{-1}, but not when 400 kg N ha^{-1} was added (Table 2).

Table 1 C and nutrient concentrations in the top 10 cm of blackwater and redwater freshwater wetland soils in northern Florida. In *each column*, values followed by the *same letter* are not significantly different as determined by the least square means test ($P \leq 05$)

Soil type	C	N	P	K	Ca	Mg	MR	Fe	Cu	B	Zn
	–%–	g Element kg^{-1} soil									
Blackwater	1.3 b	112 b	8 b	29 b	368 b	39a	6 b	83 b	0.6 a	0.4 b	1.6 b
Redwater	5.9 a	496 a	25 a	61 a	988 a	63 a	33 a	216 a	1.1 a	0.8 a	3.6 a

Table 2 Active bacterial biomass, active fungal biomass, cellulose and lignin degradation in blackwater and redwater river flood plains amended with N. In *each column*, values followed by the *same letter* are not significantly different as determined by the least squares test ($P \leq 0.05$, n-27)

		Microbial biomass[a]		5 Weeks		10 Weeks		15 Weeks	
	N	Bacteria	Fungi	Cellulose	Lignin	Cellulose	Lignin	Cellulose	Lignin
Treatment	kg ha^{-1}[b]	μg C g^{-1} soil				% CO_2 recovered			
Blackwater		3.4 ab	3.9 bc	11.9 b	2.7 b	26.9 c	5.3 c	46.6 c	9.4 c
	200	2.9 bc	4.3 bc	7.7 c	2.4 b	15.2 d	5.1 c	36.6 d	8.7 cd
	400	2.0 c	10.1 a	7.8 c	2.6 b	18.7 d	5.4 c	26.5 d	8.1 d
Redwater	0	4.3 a	4.8 b	19.9 a	5.4 a	42.0 a	10.8 a	71.9 a	17.8 a
	200	2.9 bc	1.6 bc	18.9 a	4.5 a	33.6 b	9.3 b	58 3 b	13.8 b
	400	3.9 ab	4.2 bc	14.9 a	4.6 a	28.8 b	8.8 b	49.9 c	14.3 b

[a] Estimated after 15 weeks of incubation
[b] Top 10 cm of mineral soil assuming a bulk density of 1.0 g cm^{-3}

After 5, 10 and 15 weeks of incubation, cellulose and lignin degradation was higher in redwater than in blackwater wetland soils. After 5 weeks of incubation, the addition of 200 or 400 kg N as NH_4NO_3 ha^{-1} did not influence cellulose or lignin degradation. After 10 and 15 weeks of incubation the addition of 200 or 400 kg N as NH_4NO_3 ha^{-1} decreased both cellulose and lignin degradation. The addition of 400 kg N as NH_4NO_3 ha^{-1} did not suppress cellulose and lignin degradation any more than 200 kg N as NH_4NO_3 ha^{-1}. Active bacterial biomass, active fungal biomass and N addition in incubated soils did not correlate with cellulose degradation in a linear or curvilinear relationship.

Discussion

I found that high N additions in both blackwater and redwater forest wetland soils inhibited both lignin and cellulose degradation in microcosms. In vitro studies have shown that high N concentrations in media inhibit lignin degradation by some white-rot fungi (Freer and Detroy 1982; Leatham and Kirk 1983; Reid 1991). Ander and Erikson (1977) reported that high N concentrations in media increased lignin degradation in some fungi. Barder and Crawford (1981) also found that high N concentrations increased lignin degradation by *Streptomyces badius* in vitro.

Numerous studies have shown that the lignin:N ratio can be used as a predictor of organic matter decomposition rates (Melillo et al. 1982, 1989; McClaugherty et al. 1985; Laishram and Yadara 1988; Aber et al. 1990). Other studies have shown that the lignin:N ratio is only useful for the prediction of organic matter decomposition rates when comparing decomposition of litter types that have similar chemical compositions (Hendrickson 1985; Taylor et al. 1989). Microorganisms require an additional source of energy to decompose lignin (Kirk and Farrell 1987). The C:N ratio is not consistently an accurate predictor of organic matter decomposition because it does not take into account C quality (lignin concentration). Organic matter with similar C:N ratios, such as straw and wood, will decompose at very different rates simply because of differences in C quality. A cellulose:lignin:N ratio of decomposing material would take into account C quantity and quality as well as N concentration. Although further study is necessary, the data presented in this study leads me to conclude that the cellulose:lignin:N ratio may be an accurate, widely adaptable predictor of organic matter decomposition rates in wetland ecosystems as well as upland forests, and warrants further study.

Lignin and cellulose together constitute approximately 60–90% of woody plant tissues, and are thus major factors influencing C turnover rates and nutrient mineralization in forest ecosystems. Fogg (1988) observed that empirical evidence indicated that when N was added to organic material that was comprised of large amounts of hemicellulose or cellulose, decomposition rates increased. In instances where N was added to recalcitrant organic materials that were comprised of large amounts of recalcitrant material, such as lignin, decomposition rates were suppressed. The information collected in this microcosm study leads me to conclude that N additions to blackwater and redwater forested wetlands may increase the cellulose and lignin decomposition rate, which should increase the rate of organic matter decomposition and nutrient mineralization. Increased concentrations of nutrients in soil solution could ultimately be leached into wetland streams and influence stream chemistry.

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