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PRIMARY RESEARCH PAPER

Nitrification and denitrification response to varying periods of desiccation and inundation in a western Kansas stream

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Abstract Changing environmental conditions and increased water consumption have transformed many historically perennial stream systems into intermittent systems. Multiple drying and wetting events throughout the year might impact many stream processes including nitrification and denitrification, key components of the nitrogen (N) cycle. During summer 2007, an experimental stream was used to dry and then rewet stream sediments to determine the effects of desiccation and rewetting of stream sediment on nitrification and denitrification potentials. Mean (±SE) nitrification and denitrification rates in sediment not dried (controls) were 0.431 ± 0.017 μg NO_3^-–N/cm^2/h and 0.016 ± 0.002 μg N_2O–N/cm^2/h, respectively. As sediment samples dried, nitrification rates decreased. Rates in sediments dried less than 7 d recovered to levels equal or greater than those in the controls within 1 d of being rewetted. Denitrification rates were not affected by 1 d of drying, but samples dried greater than 1 d experienced reduced rates of denitrification. Denitrification in sediments dried 7 d or less recovered by day seven of being rewetted. Nitrification and denitrification processes failed to fully recover in sediments dried more than 7 d. These results demonstrate that alterations in stream's hydrology can significantly affect N-cycle processes.

Keywords Nitrification · Denitrification · Desiccation

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Introduction

Intermittent streams are common in grassland and arid biomes because of prevailing weather patterns and land/water uses (Dodds et al., 2004). This pattern is certainly relevant in the Great Plains of central North America where drought conditions over the past several decades, coupled with increased groundwater use, have resulted in lowered water tables across the region (Cross & Moss, 1987; Angelo, 1994; Eberle et al., 1998; Gido et al., 2010). This increase in groundwater usage has decreased discharge rates and has dramatically reduced the number of perennial streams in western Kansas (Angelo, 1994; Sophocleuous, 2000; Dodds et al., 2004; Gido

et al., 2010). There is speculation that this drying trend may continue and perhaps expand because drought conditions have been predicted to worsen through the twenty-first century resulting in a 10–30% decrease in runoff in mid-latitude and dry tropical areas worldwide due to global climate change (IPCC, 2007). Aquatic ecologists have long studied the ecology of intermittent streams and the organism inhabitants (primarily macroinvertebrates and fish), but much less in known about the effects of periodic drying on microbial processes, e.g., cycling of nitrogen (N) in these systems.

Biologically available N enters landscapes via several pathways such as microbial N fixation, atmospheric deposition, agricultural inputs, and municipal and industrial waste. Excess N within an ecosystem that is not assimilated is susceptible to export through runoff into streams and rivers or through leaching into groundwater. Recent research has shown that small streams can be major areas for nutrient cycling, decreasing export of N, which potentially decreases eutrophication and hypoxia downstream (Alexander et al., 2000; Peterson et al., 2002; Mulholland et al., 2008). Several inherent characteristics of smaller systems predispose them to relatively high N processing rates. For example, small streams generally have complex channels, shallow water, and long retention times, which increase contact between dissolved nutrients and stream substrates (Bernot & Dodds, 2005). Although most N-cycling processes occur in small streams, the predominant processes which ultimately result in the conversion of N from a biologically to non-biologically available form are nitrification and denitrification.

Nitrification, the chemoautotrophic oxidation of ammonium (NH_4^+), is an aerobic two-step process conducted by relatively few bacterial species that belong to two different functional groups: NH_4^+ oxidizers, which oxidize NH_4^+ to nitrite (NO_2^-) and NO_2^- oxidizers, which oxidize NO_2^- to nitrate (NO_3^-) (Bothe et al., 2000; Konhauser, 2007). Denitrification is the anaerobic reduction of NO_3^-, which is produced via nitrification, and other oxidized N species to dinitrogen gas (N_2). Unlike nitrification, there are multiple orders of bacteria capable of conducting denitrification (Tiedje, 1988). Regulating factors of nitrification include NH_4^+ and dissolved oxygen (DO) availability (Triska et al., 1990; Kemp & Dodds, 2001), and organic carbon quality and availability (Strauss & Dodds, 1997; Strauss & Lamberti, 2000). While regulating factors of denitrification include NO_3^- and DO availability (Nielsen et al., 1990), organic carbon availability (Hedin et al., 1998), and temperature (Andersen, 1977). Changes in water content of substrates and its impacts on nitrification and denitrification have also been examined.

Several studies have also focused on the effects of drying and rewetting on nitrification and denitrification among several different habitats and substrate types. Smith & Parsons (1985) looked at the response of denitrification to desiccated soils, finding increased denitrification rates following re-moistening. Mitchell & Baldwin (1999) measured nitrification and denitrification in desiccated lake sediments, finding nitrification to be non-detectable; however, denitrification was not impacted. While Qiu & McComb (1996) found increased NH_4^+ availability due to mineralization during the drying process and enhanced nitrification rates upon rewetting of dried sediment cores collected from a wetland, due aerobic conditions. Only one study has focused on the desiccation of a lotic system and the impacts on nitrification and denitrification. Cavanaugh et al. (2006) measured nitrification and denitrification rates during and after the intentional water-level draw down in the Upper Mississippi River (UMR), finding decreased nitrification rates due to competition between nitrifiers and macrophytes for NH_4^+ and decreased denitrification due to increased aerobic conditions.

Other studies have found a decrease in bacterial biomass after sediments dried and a subsequent rise in NH_4^+ availability and nitrification upon rewetting (Groffman & Tiedje, 1988; Qiu & McComb, 1996; Mitchell & Baldwin, 1998). The resulting NO_3^- could, in turn, promote denitrification in nearby anaerobic areas (Kern et al., 1996). The findings of both increased nitrification and denitrification might suggest significant reductions in TN for certain systems upon rewetting.

The objectives of this study were to determine how periodic drying of stream sediments affects nitrification and denitrification, and determine how quickly nitrification and denitrification rates return to pre-perturbation levels after rewetting. We hypothesized that nitrification rates would increase in response

aerobic conditions during drying and that NO_3^- would accumulate, thereby stimulating denitrification when sediments rewetted and anaerobic conditions returned. We also predicted that nitrification and denitrification recovery time, after sediments were rewetted, would depend on the time desiccated, based on the assumption that the impact on the microbial communities would be directly proportional to the time dried.

Materials and methods

Site description

This study was conducted at a Fort Hays State University cattle research site on the Saline River in northeastern Ellis County, Kansas (latitude: 39°4′4.97″N; longitude: 99°6′13.73″W). The Saline River falls within the Smoky Hill—Saline River basin and is one of the five major tributaries of the Kansas River. The general land use upstream of the site is mostly ungrazed and grazed rangeland. The Saline River maintains a low base flow (0.10 m^3/s) throughout most of the year; however, during periods of high precipitation, discharge increases rapidly.

Project description

The experimental stream consisted of a fiberglass lined basin ($L \times W \times D = 274$ cm $\times$ 61 cm $\times$ 18 cm). Stream water from the Saline River was supplied to the experimental stream at a rate of 0.75–1.8 l/min via a battery powered peristaltic pump (Master-Flex L/S model # 77200-62, Barnant Co., USA). Stream water was distributed evenly over the experimental stream with a 1.27 cm diameter PVC pipe with holes drilled along its length. The drying table was positioned adjacent to the experimental stream and was constructed to similar dimensions as the experimental stream, with the only variation being holes were drilled into the bottom to facilitate drainage of drying sediments and to drain rain water.

Sediment used in this study was collected from the Saline River adjacent to the experimental stream, and was predominantly a mixture of sand and silt. Approximately 0.065 m^3 of sediment was collected from the stream (only sediment from the top 5 cm was collected), placed into a large container and homogenized before randomly distributing into 252 sample cups ($\sim$250 cm^3). Sample cups consisted of polycarbonate rings (7.6 cm diameter $\times$ 7 cm tall) fitted with 0.5 mm fiberglass mesh on the bottom that limited sediment leakage, but allowed water to drain through the sediment and out of the cups. The sample cups were then placed into the experimental stream for 1 week to acclimate.

After the acclimation period, the 252 sample cups were randomly distributed as follows. Seven sample cups were taken to the laboratory to be analyzed as the initial control, 35 sample cups were left in the experimental stream to act as wet controls, and 210 sample cups were moved to the drying table and allowed to drain dry. The sediment samples placed on the drying table were randomly divided into treatments based on the number of days they were to be dried (1, 3, 7, 14, 21, and 28 d), and within each of those drying treatments they were further divided into treatments based on the number of days they were to be rewetted (0, 1, 3, 7, 14, 21, and 28 d) with five replicates for each combination of treatments.

At each designated treatment interval, five replicates (sample cups) were collected and returned to the laboratory for sediment and N-cycling analyses. Processing of all samples was initiated within 6 h of collection. Sediment properties measured included: percent water, ash free dry mass (AFDM), exchangeable NH_4^+ concentration, and rates of nitrification and denitrification. Water samples were also collected daily from the Saline River and the experimental stream to compare concentrations of NH_4^+, $NO_2^- + NO_3^-$, and soluble reactive phosphorus (SRP) between the actual and experimental streams. Temperature, pH, conductivity, DO, and DO percent saturation were monitored at 15-min intervals throughout the study using Manta multiparameter probes (Eureka Environmental Inc., Austin, TX) placed in both the experimental stream and the Saline River. Multiparameter probe data and water for laboratory analyses were collected in the stream at the point of intake for the experimental stream. Immediately upon arrival to the laboratory, water samples (100 ml) were filtered through dried and pre-weighed filters (Whatman GF/F), preserved with 50 µl of 1 N H_2SO_4, and refrigerated until colorimetric analyses of NH_4^+, $NO_2^- + NO_3^-$, and SRP were conducted. The filter was used for determining total suspended solids (TSS).

TSS in the filtered volume were quantified by drying the filter at 50°C for 24 h and then weighing.

Sediment and water characteristics

Sediment moisture was determined on a 20 cm^3 subsample of the sediment returned to the laboratory by the mass difference measured between wet and dried samples (24 h at 105°C). AFDM was determined by subtracting ash mass (3 h at 500°C) from dry mass. Sediment moisture content and bulk density were calculated following Håkanson & Jansson (1983). Exchangeable NH_4^+ was determined in conjunction with nitrification by measuring NH_4^+ in a potassium chloride (KCl) extract via the phenate method (Solorzano, 1969). Surface water SRP, $NO_2^- + NO_3^-$, and NH_4^+ concentrations were determined by using the standard colorimetric molybdate/ascorbic acid, cadmium reduction, and phenate methods, respectively (APHA, 2005), and using a Turner SP-890 UV–VIS spectrophotometer (Barnstead International, Dubuque, IA).

Nitrification

Nitrification rates were determined by using a modification of the nitrapyrin inhibition method (as described in Strauss et al., 2004). Two slurries for each sediment sample [25 cm^3 sediment and 81 ml filtered surface water or DI water (dry samples)] were incubated aerobically in the dark (3 d) on an orbital shaker table (175 rpm). In each pair of slurries, nitrification was inhibited in one flask by adding 20 µl nitrapyrin/dimethyl-sulfoxide (DMSO) solution (final nitrapyrin concentration in flask = 10 mg/l). In the control flask, 20 µl DMSO without nitrapyrin was added. KCl extraction of NH_4^+ was conducted on a 6 ml sample of each slurry before and after the 3 d incubation period. Ammonium extracts were stored at 4°C until analysis. Ammonium concentration (phenate method) of KCl extracts was measured within 1 week of sample collection and used to calculate gross nitrification rates (Strauss & Lamberti, 2000). Nitrification rates were determined to be the difference between the change of NH_4^+ in the nitrapyrin addition and the change of NH_4^+ in the DMSO control (nitrification rate = $([N_{final} - N_{initial}] - [D_{final} - D_{initial}]$/incubation period). Where N is NH_4^+ concentration in the flask containing nitrapyrin addition and D is the NH_4^+ concentration in the flask containing the DMSO control. The NH_4^+ analysis of the initial samples containing only DMSO was also used as the measure of exchangeable NH_4^+ for that particular sediment sample.

Denitrification

Denitrification in the sediment slurries was determined by using the denitrification enzyme activity (DEA) metric (Groffman et al., 1999; Richardson et al., 2004; Strauss et al., 2006), which is a variation of the commonly used acetylene (C_2H_2) block technique (Sorensen, 1978; Richardson et al., 2004). DEA determines the potential for microorganisms to reduce NO_3^- to N_2 under optimal conditions, and is an indicator for measuring differences in denitrification potential between treatments (Groffman et al., 1999).

Denitrification enzyme activity slurries contained 20 cm^3 sediment, 20 ml unfiltered surface water (or deionized [DI] water for dry samples), and 5 ml DEA solution (final slurry concentrations = 100 mg/l chloramphenicol, 12 mg/l glucose-C, and 14 mg/l potassium nitrate [KNO_3–N]). The antibiotic chloramphenicol inhibits production of additional denitrifying enzymes without killing bacteria or destroying enzymes already present. Glucose provides an energy source and KNO_3 an electron acceptor suitable for denitrification.

Slurries were placed in 237 ml glass canning jars and sealed with standard canning rings and lids equipped with 13 mm butyl septa for gas additions and removal. Jars were evacuated for 5 min using a vacuum pump, and the negative pressure was equalized with chromatographic grade helium (He) gas (99.999% pure) to initiate anaerobic conditions. Atomic absorption grade C_2H_2 (40 cm^3) was then added to the headspace of sealed incubation jars to inhibit nitrous oxide (N_2O) reduction to N_2 gas. Slurries were incubated at room temperatures in the dark on an orbital shaker table (175 rpm) (New Brunswick Scientific C10 Platform Orbital Shaker). At specific intervals (10, 30, 60, and 90 min from the time of C_2H_2 addition) headspace gas samples (10 ml) were extracted from the jars and placed into separate evacuated 10 ml glass serum bottles for later analysis of N_2O concentration. Nitrous oxide concentrations were measured within 1 week of collection on an SRI 8610C gas chromatograph (SRI Instruments, Inc.,

Torrance, CA) equipped with a ^{63}Ni electron capture detector, and argon-5% methane (P5) was used as the carrier gas. The standard curve used to determine sample concentrations was produced using Excaliber 0.95, 10, 100 ppm N_2O gas standards (Linweld Inc., Lincoln, NE). DEA rates were calculated from the linear increase in N_2O concentration throughout the incubation period following the equations in Groffman et al. (1999). Volume/volume concentrations were converted to mass/volume concentrations and adjusted to incorporate the volume of N_2O dissolved in liquid phase at the given pressure and temperature using the ideal gas law and the Bunsen solubility coefficient, respectively.

Data analysis

All statistical analyses were conducted by using SAS statistical software (version 9.1, SAS Institute, Cary, NC). The Shapiro–Wilk test and visual inspection of normal probability plots were used to assess normality of the data sets prior to running parametric tests to look at the relationships among these data. After determining that data sets were distributed normally, a parametric general linear model one-way analysis of variance (ANOVA; *F*-test) was used to identify significant treatment effects. If the overall *F*-test was significant, the LS means procedure was used to determine specific differences among treatment means. In addition, Pearson's correlation coefficients were calculated to explore relationships between nitrification and DEA rates with sediment moisture (%H_2O), exchangeable NH_4^+, and AFDM. All comparisons and correlations were evaluated at $\alpha = 0.05$. The main purpose of the statistical analyses was to determine the effects of desiccation on the major processes (nitrification and denitrification), and then the subsequent recovery of major processes once sediments were re-inundated. An a priori definition of recovery was used, where treatment rates return to or exceed rates measured in the controls.

Results

Experimental stream versus stream

Experimental stream and stream water nutrient chemistry (SRP, NH_4^+, $NO_2^- + NO_3^-$) were similar. However, TSS in the Saline River was consistently higher than the experimental stream (Fig. 1). Multiparameter probe data for all parameters (conductivity, temperature, pH, and DO) exhibited higher values for conductivity and greater diel shifts for temperature, pH, and DO in the experimental stream compared to the Saline River (Fig. 2).

Effect of drying on sediment characteristics

In addition to %H_2O, drying of the sediments also affected exchangeable NH_4^+ concentration (Fig. 3). Percent H_2O decreased to below 5% by 3 d of drying and remained below 5% for the rest of the drying period. In contrast, exchangeable NH_4^+ availability increased over the 28 d drying period, increasing from control sediments (0.112 ± 0.003 μg NH_4^+–N/g dw) to sediments dried 28 d (0.565 ± 0.037 μg NH_4^+–N/g dw). AFDM was variable over the 28 d drying period ranging from 0.020 to 0.038 mg AFDM/cm^3.

Effect of rewetting on sediment characteristics

We examined sediments dried for 28 d prior to rewetting to assess the effect of rewetting on sediment characteristics. As sediments rehydrated, the response was opposite to that of drying for exchangeable NH_4^+; exchangeable NH_4^+ decreased slowly to 0.266 ± 0.023 μg NH_4^+/g dw by the 28th d of rewetting (Fig. 4). There was no definitive correlation between number of days rewet and AFDM.

Effect of drying on nitrification and denitrification

Drying of sediment samples affected rates of nitrification and DEA similarly. For nitrification, as sediments dried there was a significant decline from control rates (0.430 ± 0.017 μg N/cm^2/h) to rates found in sediments dried 1 d (0.108 ± 0.043 μg N/cm^2/h^1) ($F_{(1,10)} = 61.57$; $P < 0.0026$). There were no significant differences found among any of the drying intervals from 1 to 28 d. One day of drying did not change DEA rates from those of the control (0.016 ± 0.002 μg N/cm^2/h), but DEA rates declined sharply to non-detectable levels after 3 d of drying. DEA rates between 3 and 28 d of drying did not differ significantly.

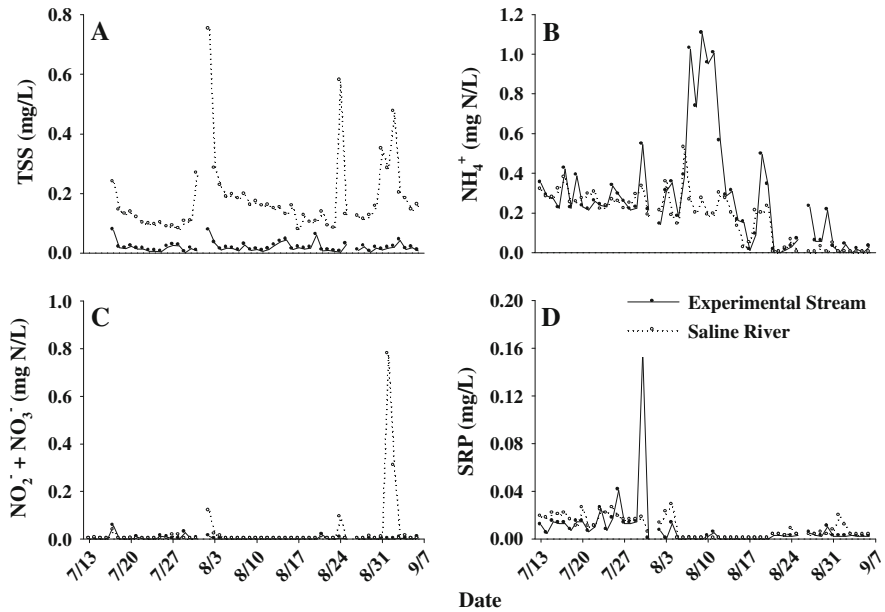

Fig. 1 Total suspended solids (TSS; **A**), and concentrations of NH_4^+ (**B**), $NO_3^- + NO_2^-$ (**C**), and soluble reactive phosphorus (SRP; **D**) measured in the Saline River (*open circle*) and from the experimental stream (*filled circle*) used in this study

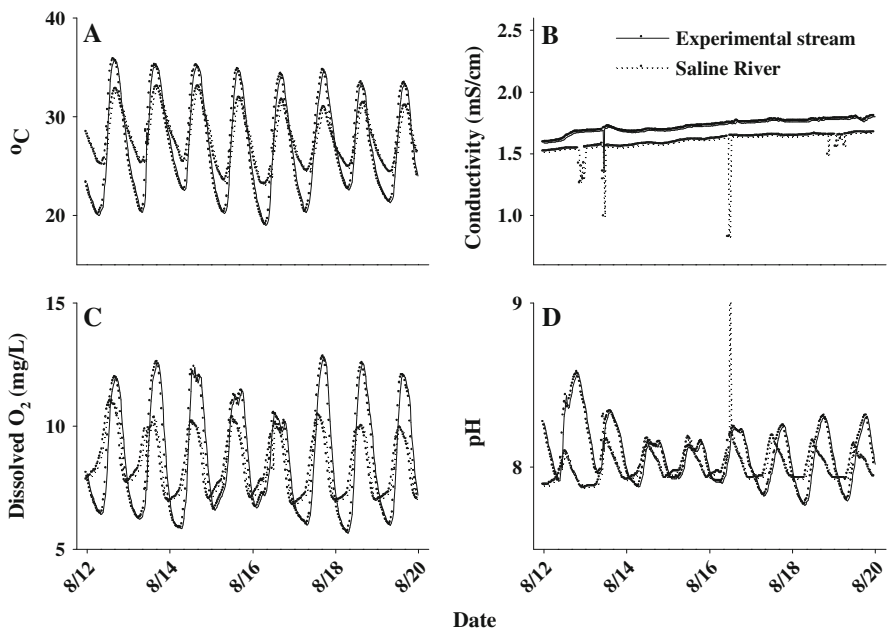

Fig. 2 Temperature (**A**), specific conductivity (**B**), dissolved oxygen (**C**), and pH (**D**) measured in the Saline River (*open circle*) and from the experimental stream (*filled circle*) used in this study. Plots represent a 1 week subset from 11 to 18 August 2007

Effect of rewetting on nitrification and denitrification

Inundation of sediment samples produced varying results between the two processes. Nitrification recovered in sediments dried for 1, 3, 7, and 21 d. However, after rates in each group recovered, the rates declined back below control rates. Rates in sediments dried 14 and 28 d increased toward recovery, but did not reach the initial rate set by the control by the end of the 28 d of rewetting (Fig. 5).

Denitrification enzyme activity rates from rewetting of samples dried for only 1 d were not significantly different than the control with the exception of 21 d rewet which was higher. The sediments dried for 3, 7, and 21 d recovered by 7 d of being rewetted.

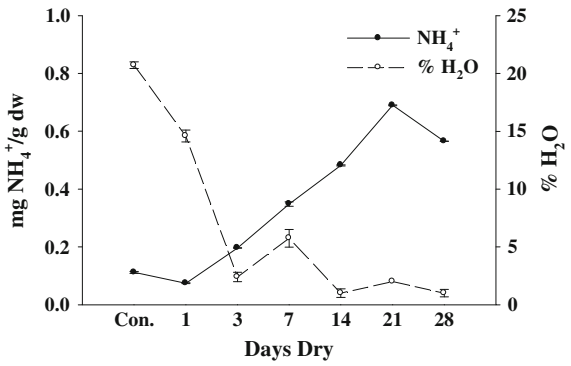

Fig. 3 Sediment exchangeable NH_4^+ and $\%H_2O$ measured within Saline River sediments as they dried. The control indicates sediments that were not dried. *Error bars* = ±1 SE

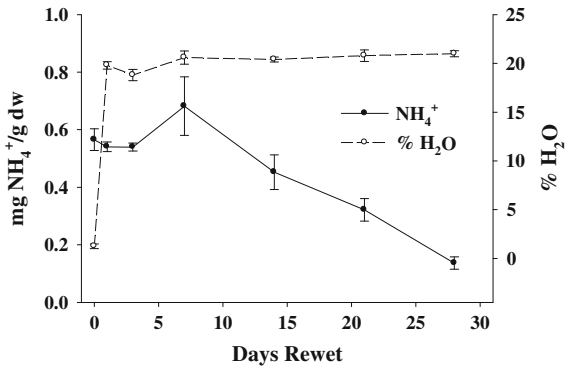

Fig. 4 Sediment exchangeable NH_4^+ and $\%H_2O$ measured in Saline River sediments dried 28 d during rewetting process. *Error bars* = ±1 SE

DEA samples dried 14 and 28 d failed to recover by the 28th d of being rewetted (Fig. 6).

Correlations

As sediment samples dried, both nitrification and DEA rates declined. During this time both nitrification and DEA were positively correlated with $\%H_2O$ ($r = 0.632$, $P < 0.001$; $r = 0.888$, $P < 0.001$, respectively). DEA also was negatively correlated with exchangeable NH_4^+ ($r = -0.684$, $P < 0.001$) and positively correlated with AFDM ($r = 0.506$, $P = 0.002$). During the rewetting process nitrification was negatively correlated with DEA ($r = -0.204$, $P = 0.006$) and DEA was negatively correlated with exchangeable NH_4^+ ($r = -0.512$, $P < 0.001$) (Table 1). No other significant correlations were observed for either process during the rewetting period.

Discussion

Alterations in the physical environment, including water availability, can result in profound changes in the abundance, diversity, and activity of the microbial community (Qiu & McComb, 1996; Mitchell & Baldwin, 1998). Several studies have examined this interaction between hydrological fluctuations on one or both of these N-cycling processes, in habitats including soil (Groffman & Tiedje, 1988), lake sediment (Qiu & McComb, 1996; Mitchell & Baldwin, 1999), floodplains (Kern et al., 1996) and large order streams and backwater areas (Cavanaugh et al., 2006). Although small headwater streams are major areas of nutrient cycling (Alexander et al., 2000; Peterson et al., 2002; Bernot & Dodds, 2005; Mulholland et al., 2008), to our knowledge, no studies examining the impact of desiccation of headwater streams on nitrification and denitrification have been conducted.

In comparison to rates measured in other studies that have used similar methods, our measured mean rate of nitrification (0.430 μg N/cm^2/h for wet controls) was similar to rates measured in two intermittent tallgrass prairie streams (0.22–0.46 μg N/cm^2/h) (Kemp & Dodds, 2002), three agricultural streams from various regions of the United States (0.16–0.44 μg N/cm^2/h) (Duff et al., 2008), and the sandy main channel of the UMR (0.35 μg N/cm^2/h) (Strauss et al., 2004). However, our rate was much higher than those published by Strauss et al. (2002) for streams in northern Wisconsin and the upper peninsula of Michigan (0.015–0.089 μg N/cm^2/h) and Starry et al. (2005) for a small forested headwater stream in North Carolina (0.028–0.081 μg N/cm^2/h). Our DEA control rate (0.016 μg N/cm^2/h) was relatively low compared to rates in similar studies. DEA rates of 0.41–2.02 μg N/cm^2/h were reported for the three agricultural streams in the study by Duff et al. (2008) and 0.178–22.2 μg N/cm^2/h were reported for the UMR (Richardson et al., 2004). The relative magnitude of the process rates we measured was likely a reflection of the availability of nutrients in the stream. The low DEA rates can be explained by the low stream water NO_3^- concentration. Whereas, the higher nitrification rate was a result of the higher stream water NH_4^+ concentration complimenting the NH_4^+ available in the sediment.

During the sediment drying and rewetting process, there are several key changes that occur that might

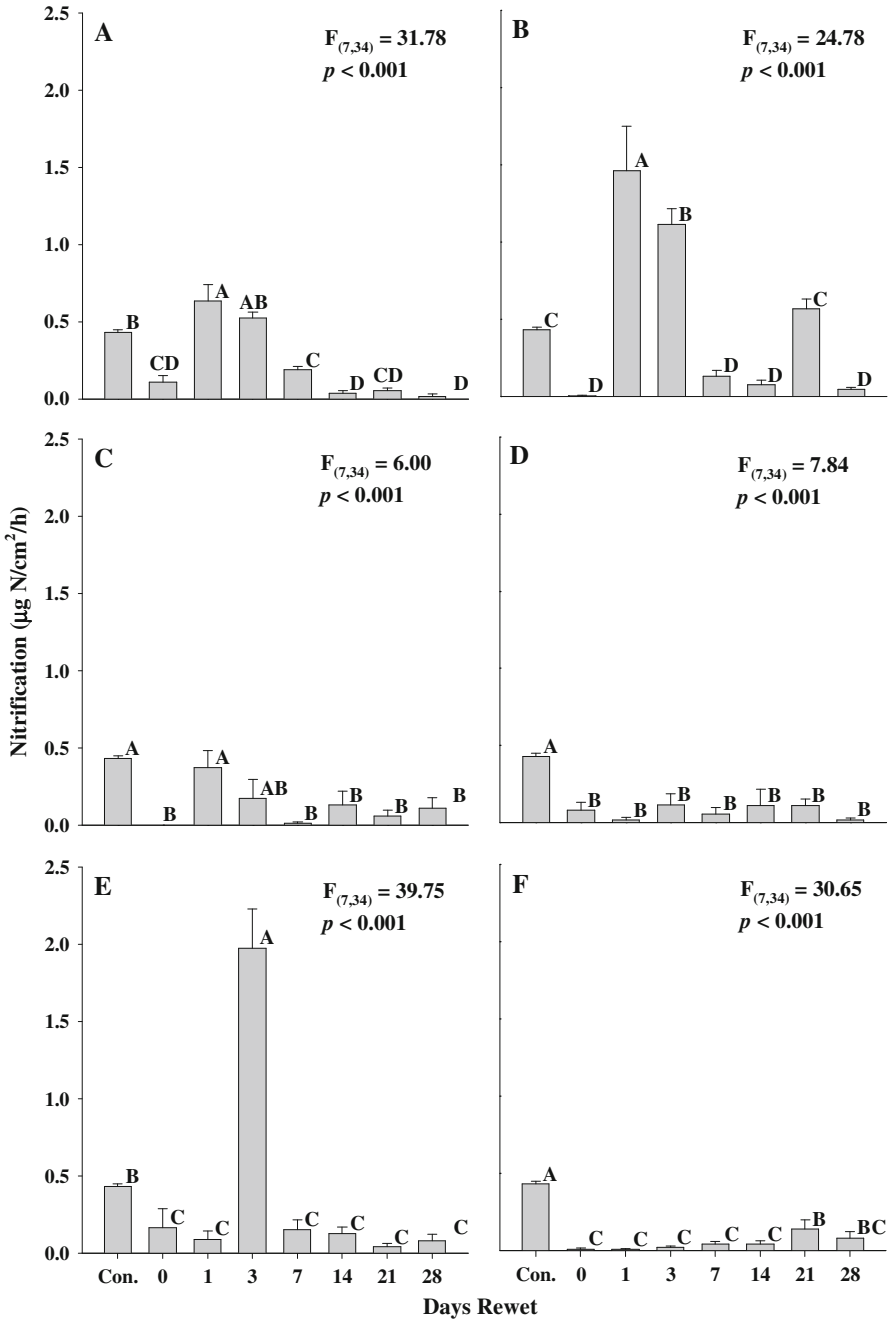

Fig. 5 Nitrification rates measured in Saline River sediments during the rewetting process. The number of days dried is shown in separate panels: 1 (**A**), 3 (**B**), 7 (**C**), 14 (**D**), 21 (**E**), and 28 d (**F**). *F*-test results shown are for the overall one-way ANOVA model. *Different letters* associated with the treatment means (*bars*) signify significant difference ($P < 0.05$; LS means procedure) among the means. *Error bars* = ±1 SE

affect nitrification and DEA potentials. Studies examining dried soil and sediments that were rewetted found increased organic carbon (Kieft et al., 1987; Groffman & Tiedje, 1988) and NH_4^+ (Groffman & Tiedje, 1988; Qiu & McComb, 1996) concentrations upon rewetting, likely due to osmotic lysis of bacterial cells (Kieft et al., 1987; Groffman & Tiedje, 1988; Qiu & McComb, 1994, 1995; Mitchell & Baldwin, 1998; Modini et al., 2002). Although there were no direct measures of bacterial biomass in this study, an increase in exchangeable NH_4^+ was observed as sediments were dried (Fig. 3) as seen by others. It is likely that the increase in exchangeable NH_4^+ was due to the osmotic lysis of bacterial cells

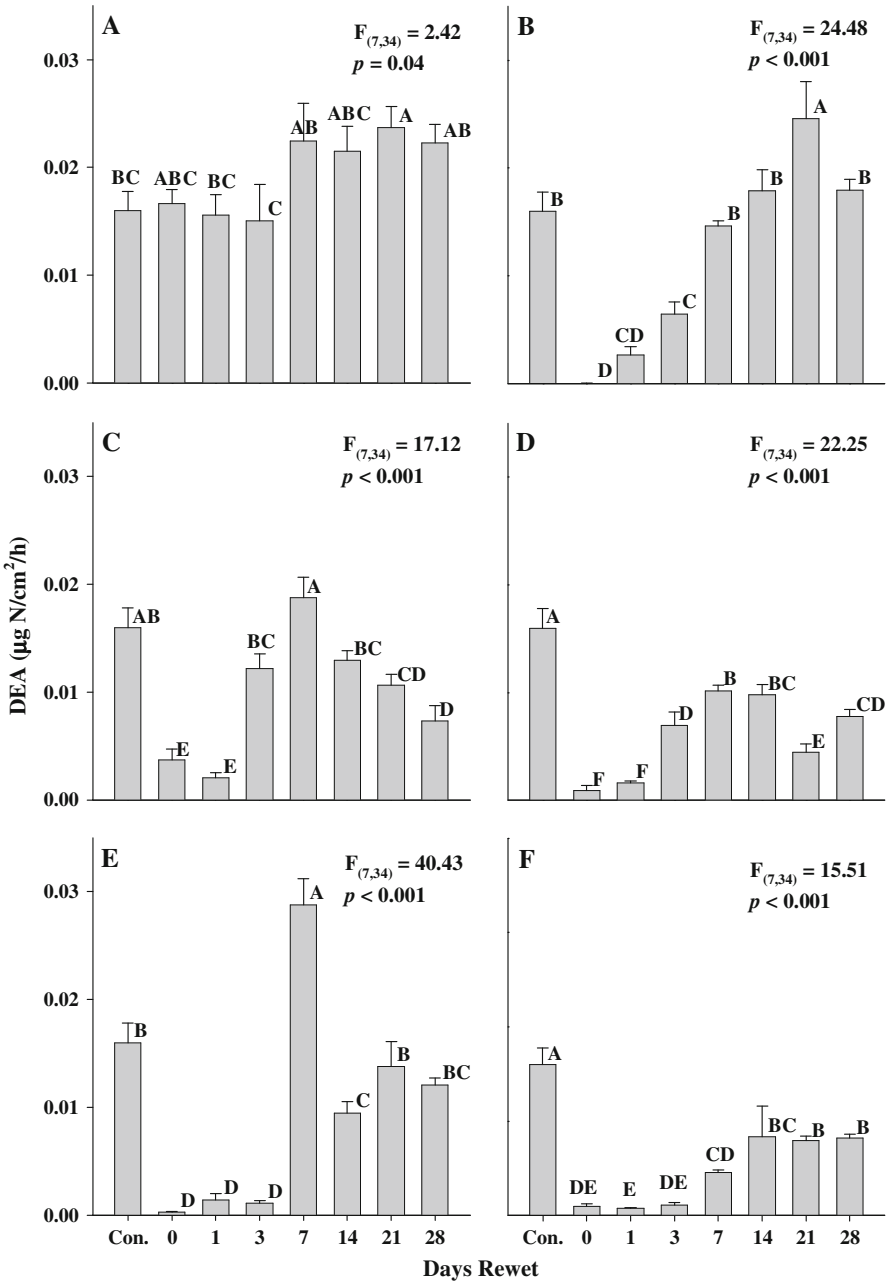

Fig. 6 DEA rates measured in Saline River sediments during the rewetting process. The number of days dried is shown in the separate panels: 1 (**A**), 3 (**B**), 7 (**C**), 14 (**D**), 21 (**E**), and 28 d (**F**). *F*-test results shown are for the overall one-way ANOVA model. *Different letters* associated with the treatment means (*bars*) signify significant difference ($P < 0.05$; LS means procedure) among the means. *Error bars* = ±1 SE

resulting in decreased bacterial biomass, which could possibly affect N processing rates. However, previous studies have found substrate nutrient concentrations and habitat conditions (temperature, O_2, and redox potential) to be more important with respect to microbial processing rates (García-Ruiz et al., 1998; Pattinson et al., 1998; Wall et al., 2005) than bacterial biomass (Jones, 1979; Davidson et al., 1985; Hermansson et al., 2004; Rigobelo & Nahas, 2004).

The drying of sediments likely increases O_2 permeability into the sediment which should favor nitrification over DEA during the initial desiccation period (Mitchell & Baldwin, 1999), which is what we had predicted to occur. However, we found $\%H_2O$ to be the independent variable regulating nitrification and DEA rates during the initial days of drying. After the first day roughly 15% H_2O remained in the sediment cores and at this point nitrification rates

Table 1 Pearson correlations table for nitrification, DEA, and the sediment properties measured in the experimental stream sediments during the drying and rewetting process

	Nitrification	DEA	$\%H_2O$	AFDM	Exc. NH_4^+
All data					
Nitrification	1.0	−0.1164	0.1632	0.1117	−0.1232
	0	0.0870	0.0166	0.1047	0.0700
DEA	–	1.0	0.3890	0.07635	−0.5165
	–	0	<0.0001	0.2684	<0.0001
$\%H_2O$	–	–	1.0	0.1200	−0.20643
	–	–	0	0.0829	0.0023
AFDM	–	–	–	1.0	0.0890
	–	–	–	0	0.1967
Wet data					
Nitrification	1.0	−0.2042	0.0676	0.0978	−0.1240
	0	0.0060	0.3689	0.1965	0.0973
DEA	–	1.0	0.1151	−0.0038	−0.5120
	–	0	0.1249	0.9603	<0.0001
$\%H_2O$	–	–	1.0	−0.0814	−0.1955
	–	–	0	0.2845	0.0087
AFDM	–	–	–	1.0	0.1754
	–	–	–	0	0.0199
Dry data					
Nitrification	1.0	0.5628	0.6323	0.1852	−0.2440
	0	0.0003	<0.0001	0.2796	0.1455
DEA	–	1.0	0.8879	0.5062	−0.6842
	–	0	<0.0001	0.0016	<0.0001
$\%H_2O$	–	–	1.0	0.4748	−0.6165
	–	–	0	0.0040	<0.0001
AFDM	–	–	–	1.0	−0.4188
	–	–	–	0	0.0110

For each variable pair, the upper number is the Pearson correlation coefficient (r) and the lower number is the P-value associated with r

decreased. It was not until the third day of drying and sediment core $\%H_2O$ dropping below 5% that DEA rates declined. This suggests that the denitrifiers present in this system are more diverse and or drought tolerant than the nitrifiers. Although $\%H_2O$ appears to be the regulating factor of N-cycle transformations during drying, O_2 availability was more important during the rewetting process.

Recovery of nitrification rates in other studies has been variable. Increased rates of nitrification were found in lake sediments following re-flooding (Qiu & McComb, 1996) and upon rewetting of dried forest soils (Fierer & Schimel, 2002). Nitrification potential, however, was found to decrease following the end of the intentional drawdown of the UMR (Cavanaugh et al., 2006) and Zaman & Chang (2004) found a 30+ d lag between rewetting and rates returning to normal.

As predicted, we found that sediments dried for a short period of time, 7 d or less, nitrification rates recovered within 1 d of rewetting, followed by a decline to pre-recovery rates (Fig. 5A–C). This pattern is most likely the result of a switch from an aerobic to anaerobic environment in the sediment cores. Although the oxygen content of the cores was not measured at any point throughout the study, findings from DEA measurements supports this hypothesis. Sediments dried for greater than 7 d, although having increased NH_4^+ availability, were unable to recover by 28 d of rewetting. There was one outlier in the group of treatments dried greater than 7 d, the treatment 21 d dry, fully recovered by 3 d of rewetting; this outlier will be discussed in more detail later.

As seen with nitrification rates, there was a lag between rewetting and recovery for DEA rates as

well. Sediments dried 3 and 7 d, recovered within 7 d of rewetting. However, it was not until nitrification rates recovered and then began declining that DEA rates recovered, in the 3 and 7 d dry treatments. In addition, sediments dried only 1 d showed an increase in rates following the decline of nitrification rates. This suggests as nitrification commenced following rewetting of the sediment cores, NH_4^+ and O_2 in the cores were used, producing NO_3^- and an anaerobic environment, creating the appropriate conditions for denitrification to occur. These conditions would have promoted the production of denitrifying enzymes which can persist even after all the NO_3^- is used. The persistence of these enzymes and the NO_3^- source in the DEA solution allowed measured DEA rates to remain relatively stable for several days following recovery. As with nitrification rates, DEA rates also recovered in the 21 d dry treatment only after nitrification rates began to decline, and failed to fully recover in the 14 and 28 d dry treatments.

The recovery of nitrification and DEA rates in sediments dried 21 d was unexpected since both processes failed to recover in sediments dried 14 d. One possible explanation for this is that the 14 d dry treatment could have recovered and then declined sometime between 1 and 3 d of being rewetted and was missed due to the sampling frequency. Evidence for this occurring can be seen in Fig. 6D. Although DEA rates never fully recovered in sediments dried 14 d, the increase in DEA rates seen 3–7 d after rewetting would not have occurred unless nitrification was also occurring. If the recovery of sediments dried 14 d was not detected as suggested, then the 21 d dry treatment would not be an outlier. The same logic could be used to suggest that perhaps some level of nitrification recovery might have also occurred in the 28 d dry treatment.

Sediment drying can cause a loss of microbial biomass and subsequent mineralization of N and C, resulting in increased levels of NH_4^+ in sediments. It was predicted that this increase in NH_4^+ would promote elevated nitrification rates upon re-inundation of sediments, increasing the availability of NO_3^- to denitrifiers. Ammonium did increase in the sediments due to desiccation (Fig. 3); however, much of this was probably lost to the water column upon rewetting, resulting in very little NH_4^+ being converted all the way through to N_2 (Fig. 1B). This increase in NH_4^+ in the water column could potentially be transported downstream to a larger tributary where it would have a lower probability of being processed.

This pulse of NH_4^+ downstream would only be an issue following re-inundation of the stream channel. While the flow of streams in the future is uncertain, some climatic studies suggest the arid conditions of many regions throughout the world will continue or worsen due to decreased precipitation and increased evaporation (National Assessment Synthesis Team, 2001; IPCC, 2007). Clearly, if arid conditions predominate in the future, altered hydrological conditions of the region will not be the only effect. Multiple ecosystem processes, not just nitrification and denitrification, will be severely altered.

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