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Centimeter-scale patterns in dissolved oxygen and nitrification rates in a prairie stream

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Abstract. Dissolved oxygen (O_2) was measured with microelectrodes in shallow subsurface microsites in a prairie stream and related to rates of nitrification determined in the laboratory using the nitrapyrin method. Substrata sampled included diatom mats, leaves and wood (coarse benthic organic matter, CBOM), filamentous green algae, bryophytes, and fine benthic organic matter (FBOM). Significant differences in O_2 concentrations were found among the substrata, with anoxic zones occurring primarily in FBOM from deep pool sediments and CBOM from litter accumulations. Filamentous green algae and bryophytes had average O_2 concentrations near saturation and intermediate rates of nitrification. Diatom mats had the highest concentrations of O_2 (up to several times saturation) and the highest rates of nitrification. In the summer, O_2 concentrations were above saturation in epilithon and filamentous green algal mats. Nitrification rates were highest in epilithon and filamentous green algae samples taken in the spring and autumn. A significant positive relationship between nitrification rates and O_2 concentration was observed in all seasons except summer. These data suggest that O_2 concentration could control nitrification in prairie streams.

Key words: nitrification, microelectrodes, O_2 concentration, N cycling, algae, streams, tallgrass prairie.

Nitrification is the predominant source of nitrate (NO_3^-) in most ecosystems (DeLaune et al. 1991, Henriksen et al. 1993, Gilbert et al. 1997). Several factors that influence nitrification in aquatic systems include temperature, substrate availability, pH, and dissolved oxygen (O_2) concentrations (e.g., Henriksen et al. 1993, Strauss and Dodds 1997). Of particular importance are ammonium (NH_4^+) availability and O_2 concentration, which are the substrates necessary for nitrification to occur (Dahm et al. 1987, Binnerup et al. 1992, Rysgaard et al. 1994). Spatial and temporal variation of O_2 and NH_4^+ thus could significantly influence rates of nitrification at the whole-stream and substratum levels.

In situ measurements in streams have shown that O_2 concentrations vary over small spatial scales (<1 mm, Revsbech and Jørgensen 1986, Dodds 1991), and that such small-scale variation in the benthos is common (Revsbech et al. 1981, Eichem et al. 1993, Dodds et al. 1996a, Bott et al. 1997). However, sites rarely are sampled extensively without bias or across seasons and, therefore, the distribution of microscale anoxia and supersaturation is not known in most environments.

Microscale anoxic zones can provide nutrients to overlying waters and abundance of such zones may be related to productivity of stream ecosystems (Dahm et al. 1987). Reduced forms of N (e.g., NH_4^+) predominate in anoxic habitats, and oxic habitats in close proximity to anoxic zones thus receive a diffusive flux of NH_4^+. Therefore, stream nitrification rates could depend upon the relative abundance of oxic and anoxic zones. The objective of our study was to compare spatial and temporal variations in O_2 concentrations and nitrification rates in various substrata for a prairie stream. We also calculated instream rates of nitrification for each substratum to allow comparison with other studies.

Methods

Study site characteristics

The Konza Prairie Biological Station (KPBS) is located ~10 km southeast of Manhattan, Kansas, in the Flint Hills region of the Great Plains. This area includes Kings Creek, an intensively studied stream draining pristine tallgrass prairie (Gray and Dodds 1999, Gray et al. 1999, Oviatt 1999, Dodds et al. 2000, Kemp and Dodds 2001). We selected for study a 200-m reach of a 2nd-order intermittent stream characterized by low NH_4^+ concentrations and little riparian cover (Table 1; watershed N04D; Kemp and Dodds 2001). Measurements were taken seasonally beginning in the winter of 1998 and

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TABLE 1. Summary of site measurements during each sampling period. SRP = soluble reactive P, DOC = dissolved organic C. – = data not available.

	Spring	Summer	Autumn	Winter
NO_3^--N (μg/L)	2.2	6.0	22.2	1.7
NH_4^+-N (μg/L)	4.1	3.9	3.9	3.1
SRP (μg/L)	—	3.7	2.9	1.0
DOC (mg/L)	0.99	0.34	1.35	1.11
Water temperature (°C)	12.5	17.1	12.9	6.5
pH	7.3	7.3	7.3	7.3
Water column O_2 (mg/L)	11.5	9.7	9.7	12.0
Mean depth (m)	0.27	0.13	0.22	0.17
Discharge (L/s)	37.6	40.4	36.5	21.0

extending to the autumn (4 sampling periods: February, May, August, November).

Determination of biomass

Biomass of each substratum within the stream reach was determined seasonally. Detailed methods are described by Dodds et al. (2000). Six replicate samples within the stream reach were collected randomly with a 313 cm^2 stovepipe corer. All small wood and leaves (coarse benthic organic matter, CBOM) were carefully removed from the isolated stream bottom; fine benthic organic matter (FBOM) was then agitated and a known volume collected. Suspended particulate organic matter (SPOM) was sampled by collecting and filtering 1 L of stream water at 6 different locations in the stream reach. Epilithon (EP) was sampled by scrubbing and washing all material within a 174 cm^2 area from replicate rocks. Six separate randomly selected samples of bryophytes (BRY) and filamentous green algae (FG) were collected by harvesting all material within a 1 m^2 quadrat. The collected materials of FBOM, SPOM, and EP were filtered onto preweighed Whatman GF/F filters. Biomass was determined for each substratum as the mass after drying at 60°C for >48 h.

O_2 profiles

Cathode-type O_2 microelectrodes (Revsbech and Jørgensen 1986) were used to measure O_2 concentrations. The electrodes were glass coated and had a gold-plated platinum wire tip 10 μm in diameter. They were not sensitive to water velocity and could be used without stirring (i.e., within benthic substrata). The sensing tip of the electrode was placed inside a 16 mm gauge hypodermic needle and held flush with the bevel of the needle with epoxy to avoid breakage during field measurements. Line transects across the channel were established every 30 m within the reach and each transect was divided into 10 equal points at which O_2 concentration was measured. The electrodes were calibrated using open water at the atmosphere–water interface and anoxic mud. Calibration was conducted prior to each line transect and reassessed several times during each transect by measurement of water-column O_2. Care was taken not to allow the O_2 electrode to leave the water when moving from point to point to avoid breaking polarity and changing calibration parameters. Water-column O_2 concentrations were also measured at each transect using a conventional YSI O_2 meter. Profiles of O_2 were recorded with every mm of depth up to the maximum depth possible. Comparisons among substrata were made at a depth of 1 cm or at the maximum depth the probe could be inserted before hitting rock.

Nitrification rates

Three paired replicate samples of each substratum type were taken to determine nitrification rates associated with EP, FG, FBOM, CBOM, BRY, and SPOM from the open water column. Approximately 50 cm^3 of the substratum were placed into each incubation vessel along with 150 mL of stream water (200 mL of stream water for analysis of SPOM). Nitrapyrin (2-chloro-6-[trichloromethyl]-pyridine, SIGMA Chemical Co., St. Louis, Missouri, 10 mg/L final concentration) dissolved in 10 μL dimethyl sulfide (DMSO) were added into 3 of the replicate

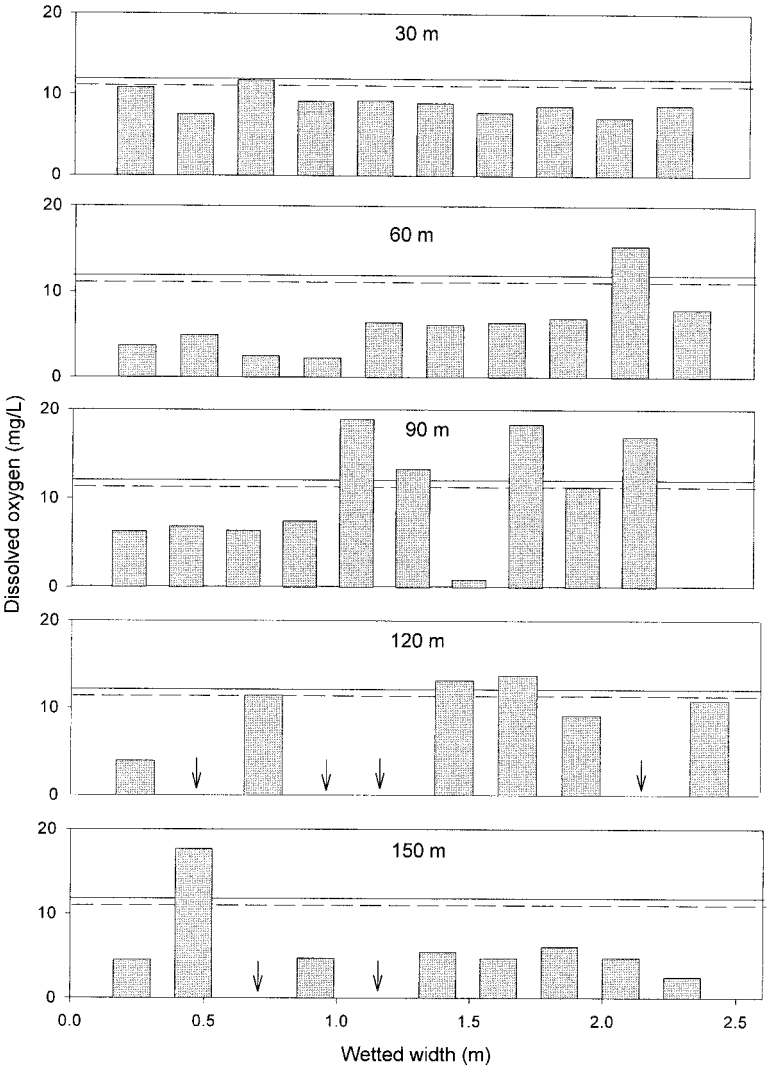

FIG. 1. Representative line transects in the spring showing the variability of dissolved oxygen (O_2) concentrations at 1 cm below the sediment–water interface. Transects were established every 30 m within the reach. The solid line represents water-column O_2 concentrations; the dotted line represents concentration of O_2 saturation at the measured temperature. Arrows indicate anoxic sites.

samples and 10 μL of DMSO were added into the 3 other samples as the control treatment (Powell and Prosser 1985, Strauss 2000, Strauss and Lamberti 2000). Each sample was then incubated on a shaker (175 rpm) for 1 wk at ambient stream temperatures. The duration of the incubation was determined in 3 experiments, using all substrata, with varying incubation times (4, 7, and 10 d). One-week incubations consistently provided the best results (i.e., shorter incubations did not allow for detection of nitrification in all samples and longer incubations led to a plateau in the NH_4^+ concentrations and decreased rate estimates because of uptake and transformation). Following incubation, samples were extracted by adding 5 mL of 1N potassium chloride (KCl) to each sample and incubating on a shaker (175 rpm) for 30 min. The filtered extracts were analyzed for NH_4^+ using the phenol-hypochlorite method (Solarzano 1969). The standards were made using a matrix of DMSO, KCl, and deionized water in appropriate pro-

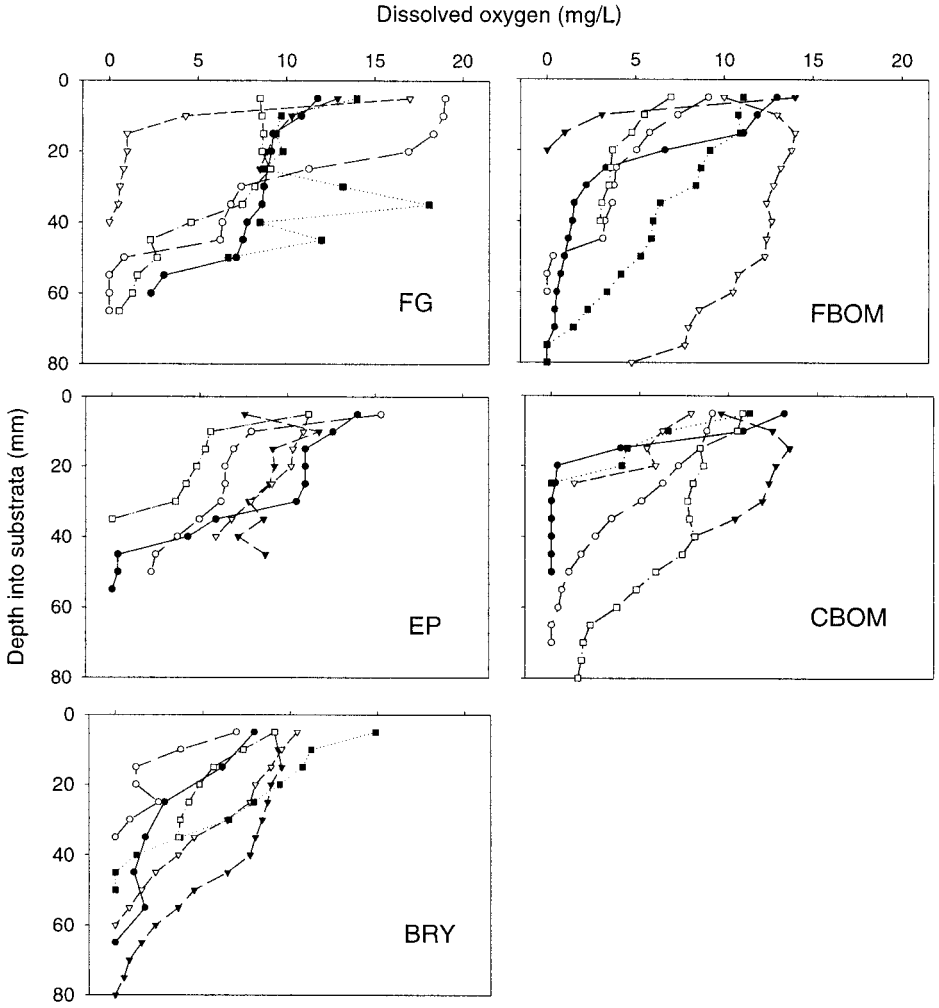

FIG. 2. The first 6 dissolved oxygen (O_2) profiles measured in each substratum in the spring, demonstrating the variability in slope and depth of O_2 penetration into the substrata. Different symbols indicate separate profiles. Substrata abbreviations: BRY = bryophytes, CBOM = coarse benthic organic matter, FBOM = fine benthic organic matter, FG = filamentous green algae, EP = epilithic diatoms.

portions. Nitrification was calculated as the difference in NH_4^+ between the incubations with and without (control) nitrapyrin and subsequently divided by the dry mass of the substratum and the number of days incubated.

Statistics

A 2-way analysis of variance (ANOVA) was used to detect differences in nitrification rates among substrata and seasons. Repeated measures ANOVA was used for all O_2 comparisons. Pairwise comparisons were made using the nonparametric Student-Newman-Keuls test. Linear regression analyses of the relationships between O_2 concentration and nitrification rate for individual substrata, averaged across all samples, were performed. An α-level of 0.05 was used for all analyses.

Results

Oxygen concentrations varied considerably across the stream channel in sites that were sep-

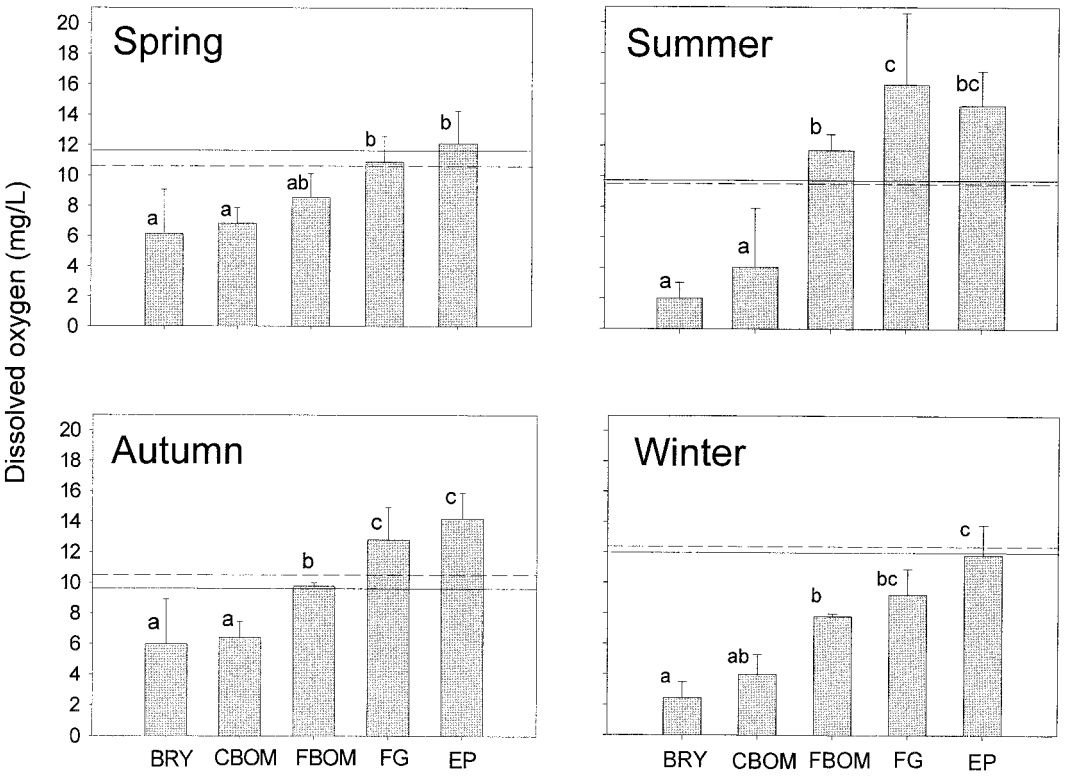

FIG. 3. Average seasonal dissolved oxygen (O_2) concentrations (+1 SE) for different substrata at 1 cm depth into the substrata. Different letters indicate significantly different values (ANOVA, $p < 0.001$). The solid line represents water-column O_2 concentrations; the dotted line represents concentration of O_2 saturation at the measured temperature. Substrata abbreviations: BRY = bryophytes, CBOM = coarse benthic organic matter, FBOM = fine benthic organic matter, FG = filamentous green algae, EP = epilithic diatoms. n ranged from 4 to 16 depending on the abundance of the substratum in each season.

arated by only 10 to 20 cm (Fig. 1). Several line transects (average cross-channel width of 2.25 m) contained both anoxic patches and O_2 supersaturated patches in spring. All other seasons demonstrated similar variability in O_2 concentrations, and no significant seasonal differences occurred in the number of oxic or anoxic patches within the reach (ANOVA, $p > 0.10$). Profiles of O_2 also varied considerably both within and among the substrata types (Fig. 2). When all substrata were combined, the change in O_2 with depth ranged from a 20 mg/L decrease in 1 cm to maintenance of O_2 saturation at a depth of 10 cm.

Seasonal variability in O_2 concentration depended on the substratum type (Fig. 3). EP, FG, and FBOM had consistently higher O_2 concentrations (frequently above saturation) than BRY and CBOM. The greatest range in mean O_2 concentrations associated with different substrata (0–21 mg/L) was observed in the summer, whereas the smallest range (2–13 mg/L) occurred in spring. For all seasons, O_2 concentration differed, albeit weakly, among substratum types (ANOVA, $p = 0.094$), and there was no significant interaction between season and substratum (ANOVA, $p = 0.44$).

Across all seasons, nitrification rates were highly variable with over 10-fold differences among substratum types (ANOVA, $p = 0.048$, Fig. 4). In general, FG, EP, and FBOM had high nitrification rates, whereas BRY and CBOM had lower rates. The lowest nitrification activity was associated with SPOM in the water column during all seasons. CBOM had 2 to 3 times higher nitrification rates in the summer and winter than in the spring and autumn (ANOVA, $p < 0.001$). EP had lower nitrification rates in the

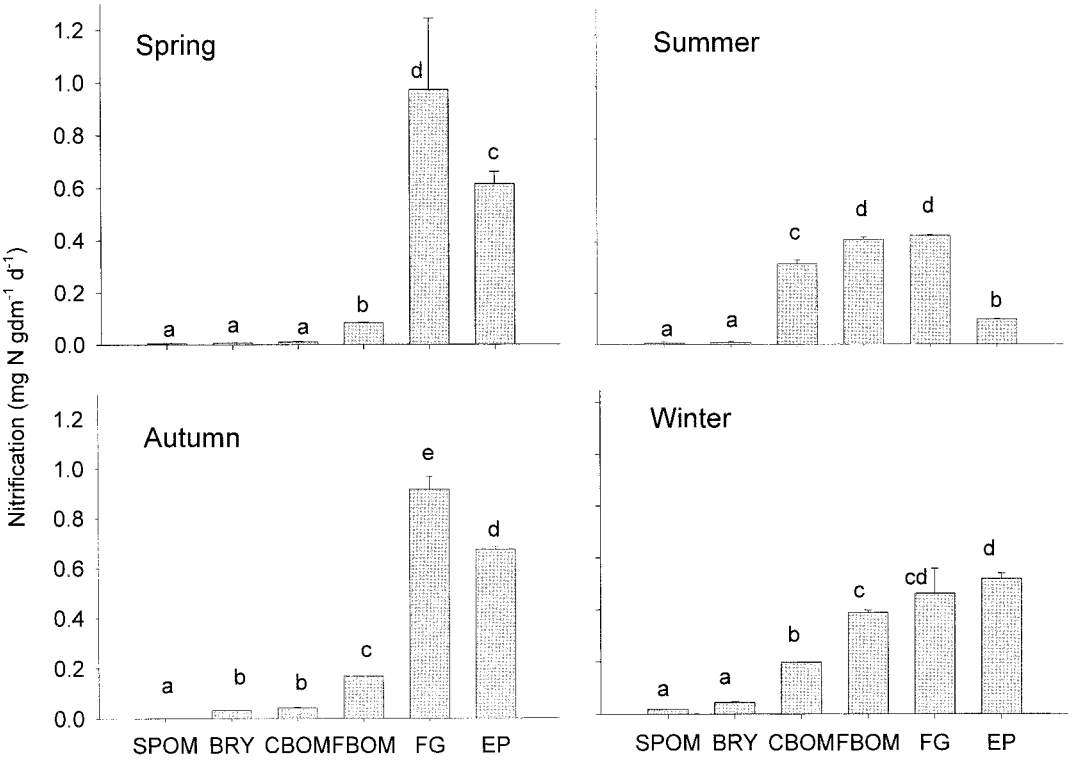

FIG. 4. Average seasonal nitrification rates for different substrata (+1 SE). Different letters indicate significantly different values (ANOVA, $p < 0.001$). Substrata abbreviations: SPOM = suspended particulate organic matter, BRY = bryophytes, CBOM = coarse benthic organic matter, FBOM = fine benthic organic matter, FG = filamentous green algae, EP = epilithic diatoms. $n = 3$ for all bars.

summer (ANOVA, $p < 0.001$) relative to other seasons. A weak interaction between season and substratum type was found (ANOVA, $p = 0.10$). The greatest range of mean nitrification rates among substrata was observed in spring (0–1.2 mg N gdm^{-1} d^{-1}), and the lowest range was observed in summer (0–0.4 mg N gdm^{-1} d^{-1}).

O_2 concentrations and nitrification rates were significantly and positively correlated in spring ($p < 0.001$), autumn ($p < 0.001$), and winter ($p < 0.001$), but not in the summer ($p > 0.10$; Fig. 5). Analysis of whole-stream nitrification rates indicated that the highest rates occurred in the autumn and the lowest rates occurred in the winter (Table 2). EP and FBOM were the major contributors to whole-stream nitrification, with EP having highest nitrification rates in spring and fall, and FBOM having highest rates in summer and winter.

Discussion

O_2 concentration

O_2 concentrations in the riverbed of a prairie stream were highly variable, even over small spatial scales. Numerous researchers (e.g., Carlton and Wetzel 1987, Dodds and Jones 1987, Dodds 1991, Eichem et al. 1993, Rysgaard et al. 1994) have also documented microscale spatial variability of O_2 concentrations. This variability has been associated with organic substrata on spatial scales as small as a leaf rib (Eichem et al. 1993). Such small-scale variability allows for formation of steep redox gradients, thereby affecting N cycling rates. In the absence of such microscale variation in O_2 concentrations, some substrata (e.g., CBOM) may lack nitrifiers because there is not enough O_2 for nitrification to occur.

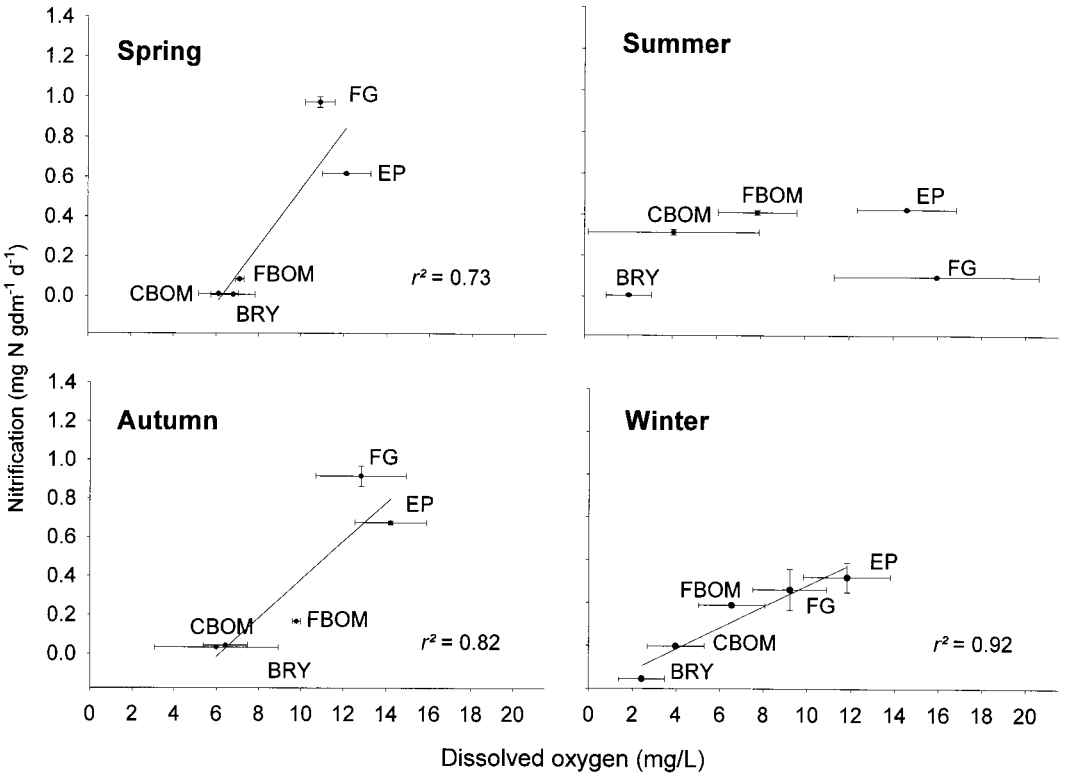

FIG. 5. Seasonal relationships between nitrification rate and dissolved oxygen (O_2) concentration (±1 SE). Substrata abbreviations: SPOM = suspended particulate organic matter, BRY = bryophytes, CBOM = coarse benthic organic matter, FBOM = fine benthic organic matter, FG = filamentous green algae, EP = epilithic diatoms. Error bars cannot be seen when they are smaller than symbols.

TABLE 2. Biomass within the stream channel and weighted nitrification rates for each substratum for every sampling period. Substrata abbreviations: FG = filamentous green algae, FBOM = fine benthic organic matter, CBOM = coarse benthic organic matter, BRY = bryophytes, SPOM = suspended particulate organic matter, EP = epilithic diatoms.

	Spring	Summer	Autumn	Winter
Biomass (g/m^2):				
FG	2.7	9.0	6.2	8.6
FBOM	240	192	68	87
CBOM	4	11	29	15
BRY	29	29	34	40
SPOM	2.2	4.2	6.0	5.1
EP	83	168	162	49
Whole-stream nitrification (mg NH_4^+ m^{-2} d^{-1}):				
FG	2.63	3.81	5.68	3.97
FBOM	20.0	78.5	11.4	33.8
CBOM	0.04	3.45	1.22	2.94
BRY	0.17	0.20	1.11	1.72
SPOM	0.01	0.02	0.01	0.09
EP	51.1	16.3	109.4	25.4
Whole stream	74	102	129	68

The high variability of O_2 at small spatial scales observed in this study (Figs 1, 2) indicates that subhabitats for organisms will vary spatially across distances of decimeters or less. For example, nitrifiers require O_2 to obtain energy and their activity is correlated with O_2 measured in the field over most seasons (Fig. 5). The greatest rates of nitrification were associated with high O_2 concentrations that were found in actively photosynthesizing primary producers. The lowest nitrification rates were associated with CBOM in which anoxic zones were more abundant. This result was consistent in every season except for summer (Fig. 5).

Rysgaard et al. (1994) demonstrated that nitrification was stimulated by increasing O_2 concentrations to a threshold of 100% atmospheric saturation. Above this threshold, nitrification rates began to decline, probably because nitrifiers were inhibited by the supersaturated O_2 concentrations. This finding is consistent with our results, showing that substrata with O_2 concentrations exceeding saturation in the summer had nitrification rates that did not increase with O_2 concentration as in other seasons (Fig. 5). The lack of a significant relationship with O_2 concentration in the summer also may indicate that other factors regulating nitrification (e.g., NH_4^+ availability, temperature, pH) become increasingly important.

Nitrification rates

Comparison of nitrification rates (calculated per unit area using biomass estimates; Table 3) for Kings Creek and other aquatic habitats showed that the lowest rates of nitrification typically occurred within the water column, whereas the highest rates of nitrification usually occurred within the substrata. Rates within the substrata varied depending upon what was being sampled: the highest recorded rates occurred in EP in our study (0.51 g N m^{-2} d^{-1}) and in sediments near a spring source of an oligotrophic pond (0.38 g N m^{-2} d^{-1}). The lowest rates associated with the benthos occurred in litter packs (0.00191 g N m^{-2} d^{-1}, CBOM in our study).

Several explanations are possible for the correlation between O_2 concentrations and nitrification rates. Microbial activity increases with increased flow rates because of a greater inward transport of O_2, which promotes higher rates of metabolism and processing (Eichem et al. 1993, Dodds et al. 1996b). Other researchers (Dodds and Jones 1987, Rysgaard et al. 1994) have demonstrated that nitrification efficiency is highest when O_2 penetration into the sediment is greatest. Under these conditions, microbial uptake and nitrification rates are maximized. Thus, there is little NH_4^+ export from the sediments even though advective transport is greater.

The consistently high nitrification rates in specific substrata demonstrated in this study were probably not caused entirely by O_2 availability and degree of transport. Organic carbon (Strauss and Dodds 1997, Strauss 2000, Strauss and Lamberti 2000); temperature; NH_4^+ (Rasmussen and Jørgensen 1992, Strauss and Lamberti 2000); and pH (Strauss 2000) all affect nitrification rates in conjunction with O_2 concentration. Regulation of nitrification by multiple factors may explain why the rates are highest in the spring and autumn primarily in FG and EP but decrease in the winter and summer when O_2 is available but other factors (e.g., temperature) are more extreme and may inhibit nitrifiers (Figs 4, 5).

In conclusion, O_2 concentrations likely regulate nitrification to some degree. Because O_2 concentration is highly dependent upon local rates of photosynthesis, respiration, and advective transport, O_2 concentrations vary over small spatial scales in this stream and others. Our data demonstrated that O_2 concentration covaried with nitrification rates. Thus, the absolute rate and spatial distribution of nitrification likely are controlled partly by microscale variations in O_2 concentration. The extent of O_2 regulation probably depends on a variety of other factors including NH_4^+ availability, temperature, and pH. More research is needed to determine the interactions of these factors in regulating nitrification rates both at the microsite and whole-stream scales.

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TABLE 3. Nitrification rates reported in the literature from various aquatic habitats for a variety of substrata. Rates from our study are averaged across all seasons.

Substratum	Site	Method	Nitrification rate (g N m^{-2} d^{-1})	Reference
Sediments				
Epilithon	Konza Prairie, Kansas	Nitrapyrin	0.51	This study
Fine benthic organic matter	Konza Prairie, Kansas	Nitrapyrin	0.0036	This study
Filamentous green algae	Konza Prairie, Kansas	Nitrapyrin	0.0402	This study
Coarse benthic organic matter	Konza Prairie, Kansas	Nitrapyrin	0.00191	This study
Sediments	Alaska Coast	Nitrapyrin	0.004–0.011	Henriksen et al. 1993
Sediments containing bivalves	Bering Strait	Nitrapyrin	0.014–0.017	Henriksen et al. 1993
Sediments containing amphipods	Bering Strait	Nitrapyrin	0.008–0.025	Henriksen et al. 1993
Estuarine sediments	Denmark	$[NH_4^+]$ before and after C_2H_2 blockage	0.006	Binnerup et al. 1992
Oigotrophic freshwater sediment	Mare's Egg Spring, Oregon	Inhibited CO oxidation	0.04	Dodds and Jones 1987
Under *Nostoc*	Mare's Egg Spring, Oregon	Inhibited CO oxidation	0.035	Dodds and Jones 1987
Near spring source	Mare's Egg Spring, Oregon	Inhibited CO oxidation	0.38	Dodds and Jones 1987
Oligotrophic freshwater sediment	Mare's Egg Spring, Oregon	Inhibited CO oxidation	0.25	Dodds and Jones 1987
Sediment–water interface	Calcasieu River, Louisiana	Change in NO_3^-	0.060–0.15	DeLaune et al. 1991
Open water				
Open water	Mare's Egg Spring, Oregon	Inhibited CO oxidation	0.037	Dodds and Jones 1987
Open water	Calcasieu River, Louisiana	Change in NO_3^-	0.007–0.044	DeLaune et al. 1991
Suspended particulate organic matter	Konza Prairie, Kansas	Nitrapyrin	0.000032	This study

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