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Effects of the emergent macrophyte *Juncus effusus* L. on the chemical composition of interstitial water and bacterial productivity

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Abstract. Release of oxygen from the roots of aquatic macrophytes into anaerobic sediments can affect the quantity of interstitial dissolved organic matter and nutrients that are available to bacteria. Nutrient and dissolved organic carbon (DOC) concentrations were compared between subsurface (interstitial) waters of unvegetated sediments and sediments among stands of the emergent herbaceous macrophyte *Juncus effusus* L. in a lotic wetland ecosystem. Concentrations of inorganic nitrogen (NH_4^+, NO_3^-, and NO_2^-) were greater from sediments of the unvegetated compared to the vegetated zone. DOC concentrations of interstitial waters were greater in sediments of the unvegetated zone both in the winter and spring compared to those from the vegetated zone. Although DOC concentrations in hydrosoils collected from both zones increased from winter to spring, bacterial productivity per mg DOC in spring decreased compared to winter. Greater initial bacterial productivity occurred on DOM collected from the vegetated compared to the unvegetated zone in winter samples (days 1 and 4), with increased bacterial productivity on samples collected from the unvegetated zone at the end of the study (day 20). Bacterial productivity was significantly greater on all sampling days on DOM from vegetated samples compared to unvegetated samples. In nutrient enrichment experiments, bacterial productivity was significantly increased ($p < 0.05$) with phosphorus but not nitrogen only amendments.

Introduction

A defining characteristic of wetlands is the periodic presence of water that creates saturated, anaerobic sediments. Plants that inhabit wetland and aquatic systems must be capable of existing in temporarily or permanently anaerobic sediments. A functional adaptation of aquatic macrophytes to anaerobic sediments is the ability to translocate oxygen to the roots and rhizomes to support belowground respiration. Some of this translocated oxygen is released into the surrounding sediments creating a small aerobic zone

around plant roots (rhizosphere). Release of oxygen into the sediments surrounding the roots can result in small scale changes in the sediment redox potential (Armstrong & Armstrong 1988; Laan et al. 1989; Boon & Sorrell 1991) which can affect the redox state and solubility of biologically important compounds and the concentration of potential phytotoxins. Aquatic macrophytes can affect the concentration of potentially toxic reduced compounds such as ferric iron (Green & Etherington 1977; Roden & Wetzel 1996), hydrogen sulfide (Penhale & Wetzel 1983), and organic acids (Boon & Sorrell 1991) in sediment porewater through the radial release of oxygen from roots into the rhizosphere. Increased concentrations of organic acids and reduced compounds in sediment interstitial water can decrease photosynthesis. Oxygen released by the macrophyte into the rhizosphere can chemically oxidize or facilitate the microbial oxidation of reduced compounds in sediment porewater (Roden & Wetzel 1996) and thus reduce the level of potential phytotoxins and related decrease in photosynthetic rates. Additionally, rhizospheric oxygen release can also affect the solubility and biological availability of compounds such as phosphorus (Moore et al. 1994; Saleque & Kirk 1995).

Interstitial waters of shallow subsurface sediments (<1 m) have been shown to be important to aquatic ecosystem productivity in recent years. Studies have demonstrated that shallow subsurface waters are important in the transport of nutrients and dissolved organic matter (DOM) to riverine, wetland, and lacustrine ecosystems. Although the effects of aquatic macrophytes on nutrient concentrations have been examined, there are few data on the effects of aquatic macrophytes on the concentration and microbial availability on DOM from sediments of aquatic ecosystems. Since macrophyte productivity is seasonal with maximum productivity typically from the late spring through autumn, the impact of macrophytes on the concentration and composition of DOM of interstitial water would be expected to vary seasonally and to interact with other parameters, such as rainfall and UV-photolysis, that also mediate DOM dynamics.

Although studies have examined the bacterial availability and utilization efficiency of DOM from streams (Edwards & Meyer 1986; Servais et al. 1987, 1989), lakes (Tranvik 1988; Markosova 1991; Tulonen et al. 1992), open water marine systems (Bjørnsen & Kuparinen 1991) and subsurface waters (Boissier & Fontvielle 1993; Mann & Wetzel 1995), few studies have examined bacterial growth on DOM from wetland ecosystems (Mann & Wetzel 1995; Bano et al. 1997). Furthermore, few studies have examined the change in DOM concentration (Koepfler et al. 1993) and concomitant shifts in DOM substrate availability as a result of macrophyte rhizosphere interactions. The objective of this study was to evaluate differences in nutri-

ent and DOM concentrations and differences in the biological availability of interstitial dissolved organic matter collected from vegetated and unvegetated zones of a lotic wetland ecosystem. The effects of nutrient additions (nitrogen, phosphorus, and nitrogen plus phosphorus) on the bacterial utilization of interstitial DOM was also examined.

Methods

Bacterial utilization of DOM

To assess the influence of wetland macrophytes on the availability of dissolved organic matter (DOM) as a substrate for wetland bacterial growth, subsurface water was collected from an area of the Talladega Wetland Ecosystem (TWE; Hale County, AL) vegetated by *Juncus effusus* L. and an unvegetated area adjacent to the tussock. Previous studies of *J. effusus* at the TWE (Roden & Wetzel 1996) have determined that there were significant differences in interstitial water chemistry between vegetated and unvegetated zones. Although oxygen release by *J. effusus* into the sediments was not directly measured in the field, laboratory data showed that differences in interstitial water chemistry between vegetated and unvegetated zones resulted from oxygen release into the sediments of the vegetated zone. Therefore, this study was designed to elucidate any difference in the quantity and bacterial availability of DOM from a vegetated and unvegetated zone.

DOM samples were collected from piezometers (2.54 cm diameter) placed 30 cm into the sediments. The well screens on each piezometer, covered with a 10-μm Nitex mesh, extended from 10 to 30 cm below the sediment-water interface (within the *J. effusus* rooting zone). DOM samples for the first bacterial utilization experiments were collected from January 1997 to February 1997 (designated winter) and for the second experiments during June 1997 (designated spring). To ensure that the DOM samples were not contaminated prior to bacterial inoculation, samples were sterile filtered first through precombusted (550 °C, 24 h) Whatman GF/F filters (0.6-μm pore size) and then through autoclaved Millipore GS filters (0.22-μm pore size). Filtration through the Millipore GS filters was conducted in a sterile laminar flow hood (HEPA standards) to eliminate contamination prior to inoculation.

The availability of the DOM, collected from the vegetated and unvegetated zone, as a substrate for bacterial growth was determined by incubating each sample with a natural assemblage of bacteria collected from the TWE. Bacterial productivity was evaluated by the uptake and incorporation of [^{3}H]leucine into bacterial protein (Wetzel & Likens 1991; Kirchman 1993). To determine rates of [^{3}H]leucine incorporation, subsamples of 10 ml were

removed from each inoculated water sample after incubation periods of 1, 4, and 20 days. At each time interval four 10-ml subsamples were removed from each treatment, three replicates for active [^{3}H]leucine incorporation and one killed control (5% formalin) for passive uptake (modified from Wetzel & Likens 1991; Kirchman 1993). [^{3}H]leucine was then added to all four replicates from each treatment to achieve a final concentration of 10 nM. Live samples and controls were incubated in the dark at 20 °C for 0.5-h, with incubations of live samples terminated by the addition of 5% formalin. All samples were treated with 3.25 ml of 15% TCA (5% final concentration) and placed in a hot water bath (90 °C) for 30 minutes. Samples were filtered through Millipore GS filters followed by one rinse with organic-free water (10 ml), two rinses with 5% TCA (3 ml), and two rinses with 80% ethanol (2 ml). Filters were placed into scintillation vials and dissolved with 1 ml of ethyl acetate. Within 24 h, 10 ml of Aquasol-2 Universal LSC Cocktail (Dupont) was added for radioassay on a calibrated Beckman LS 5801 liquid scintillation spectrometer. To correct for differences in bacterial productivity based on differences in DOC concentration, bacterial productivity was divided by DOC concentrations determined (see below) for that time interval to normalize productivity per mg DOC. Thus, direct comparisons between bacterial productivity on porewater DOM from the vegetated and unvegetated zone could be made.

Bacterial inoculum

To maintain similar experimental conditions among bacterial utilization experiments, a standard inoculum was used for all bacterial growth studies. Bacteria for the standard inoculum were collected from the detrital layers of *J. effusus* pools found at the TWE. To establish a parent culture for all bacterial experiments, a modified lake-water solution (Wetzel et al. 1995) was inoculated with the bacteria and grown at 25 °C for 48 h. The bacterial concentrate was added to a glycerol solution and a subsample of the bacterial assemblage (800 μl) was pipetted into sterile cryogenic (Nunc) vials and stored in liquid nitrogen. Prior to each experiment, subsamples of the bacterial assemblage were thawed and added to 150 ml of modified lake-water and grown in the dark at 20 °C for 48 h. The bacterial assemblage was centrifuged at 10,000 rpm for 10 minutes, after the supernatant was decanted, the bacterial pellet was rinsed with a 20 mM MOPS solution (pH 7). This procedure was repeated two more times followed by a final rinse with ultrapure Millipore Q water. After centrifugation the supernatant was decanted and the bacterial pellet was suspended in 10 ml of Millipore Q water with 5 ml added to each experimental flask (4 l total volume for February 1997 experiment and 3.2 l volume for the June 1997 experiment).

Table 1. Chemical composition of interstitial water from vegetated and unvegetated zones at the TWE.

	February 1997		June 1997	
	Unvegetated	Vegetated	Unvegetated	Vegetated
DOC (mg C l^{-1})	35.4	7.2	42.1	18.5
NH_4^+ (μg l^{-1})	1069.4	185.3	1152.7	254.8
NO_3^- (μg l^{-1})	156.7	63.0	118.2	84.7
NO_2^- (μg l^{-1})	7.2	0.0	10.2	2.0

Nutrient amendments to interstitial samples

To evaluate potential nitrogen or phosphorus limitations to bacterial growth on DOM collected from the unvegetated and vegetated zone, nutrient amendments were added to selected treatments prior to bacterial inoculation. Replicated samples of DOM collected either from the vegetated zone or the unvegetated zone received singly or in combination, 100 μg of P l^{-1} as K_2HPO_4 (designated DOM+P), 250 μg N l^{-1} as NH_4NO_3 (designated DOM+N), 100 μg of P l^{-1} and 250 μg of N l^{-1} (designated DOM+NP). Samples from each of the two treatments, not amended with either P or N, served as the control treatments (designated DOM-C). Samples were removed for inorganic nitrogen (N_i) analyses measured as NO_3^-, NO_2^-, and NH_4^+ prior to bacterial inoculation and after 1, 2, 4, and 20 days of incubation (samples collected February 1997). Sample collected in June 1997 were analyzed for initial N_i concentrations of the unamended treatments. All samples for nutrient analyses were frozen prior to analysis on a Lachat QuickChem 8000. Prior to analyses, samples were filtered through Whatman GF/F filters (0.6-μm pore size) after thawing.

Dissolved organic carbon concentration of interstitial samples

Subsurface water samples collected from the vegetated and unvegetated zones were also evaluated for changes in DOC concentration in parallel with bacterial productivity measurements over the 20-day incubation period. DOC samples from treatments were collected prior to bacterial inoculation and after 1, 2, 4, and 20-day incubation periods. For DOC analyses, samples were filtered through pre-rinsed (150 ml organic-free water) Millipore GS filters (0.22-μm pore size) and acidified to pH 2.0 with ultra-pure 2N HCl. DOC concentrations were determined on a Shimadzu TOC5000 Total Organic Carbon Analyzer calibrated against organic standards.

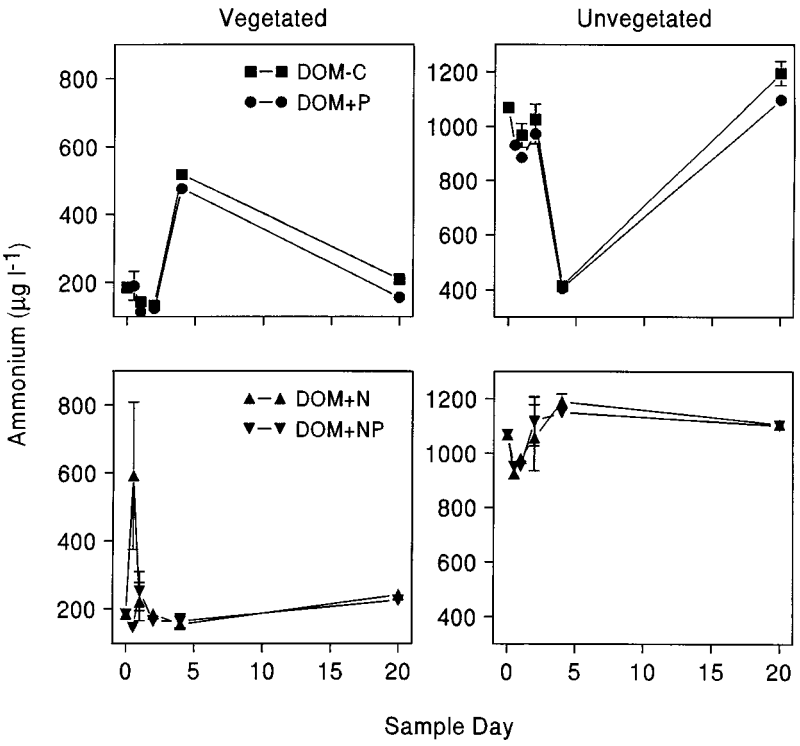

Figure 1. Average NH_4^+ (± 1 SE) concentrations for unamended and nutrient enriched interstitial samples collected in the winter from a vegetated and unvegetated zone at the TWE.

Results

Initial nutrient concentrations of interstitial samples

Initial N_i and DOC concentrations were variable among collection sites (vegetated and unvegetated zone) and times of collection (Table 1). Inorganic nitrogen concentrations of interstitial waters from the unvegetated zone were higher than N_i in those of the vegetated zone. NH_4^+ and NO_2^- concentrations were similar in samples collected from the unvegetated zone, while there was a decrease in NO_3^- concentrations of samples in spring vs winter. In samples collected from the vegetated zone, NO_3^- and NO_2^- concentrations were similar between winter and spring while NH_4^+ concentrations increased during this same period. In both sets of samples (winter and spring), initial DOC concentrations were significantly lower ($p < 0.05$; $n = 3$) in samples collected from the vegetated compared to unvegetated zones. In addition, DOC concentrations increased significantly from winter to spring in samples

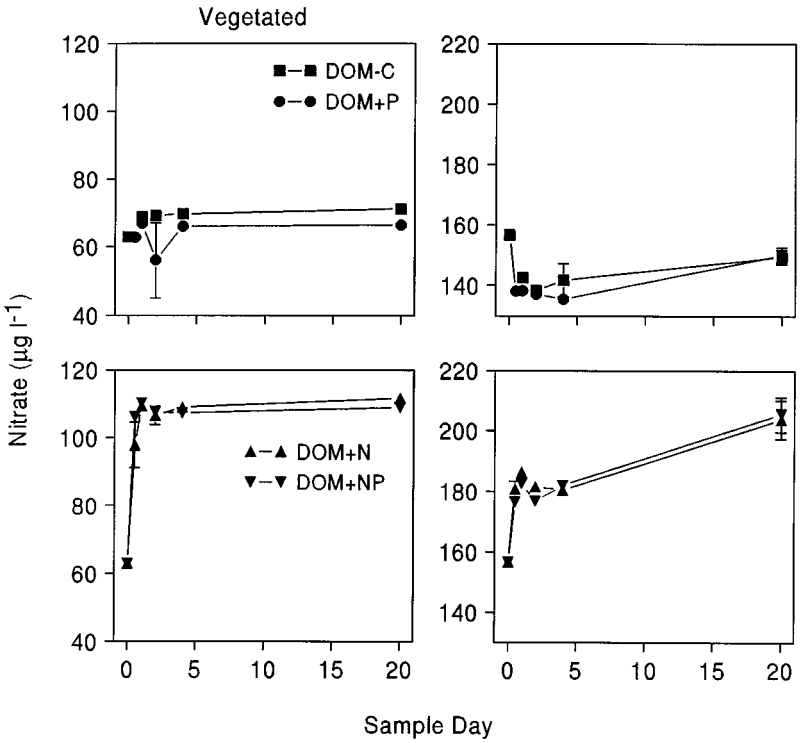

Figure 2. Average NO_3^- (± 1 SE) concentrations for unamended and nutrient enriched interstitial samples collected in the winter from a vegetated (left) and unvegetated (right) zone at TWE.

collected from the vegetated (ca. 2.5 times greater) and unvegetated zones (ca. 1.2 times greater).

Nutrient dynamics during bacterial utilization of interstitial nutrient constituents

Although NH_4^+ concentrations in the first four days of the experiment were variable in subsurface water samples from both the vegetated and unvegetated zones (Figure 1), there was an initial decrease in NH_4^+ concentrations in most samples (day 0 to day 1), particularly in the samples from the unvegetated zone. There were significant increases in NH_4^+ concentrations in the N amended treatments from subsurface waters of the unvegetated zones from day 1 to day 4. Conversely, there was a significant decrease in NH_4^+ concentrations in the DOM and DOM+P treatments in unvegetated samples during the same time period. In samples collected from the vegetated zone, there was an increase in NH_4^+ concentrations from day 1 to 4

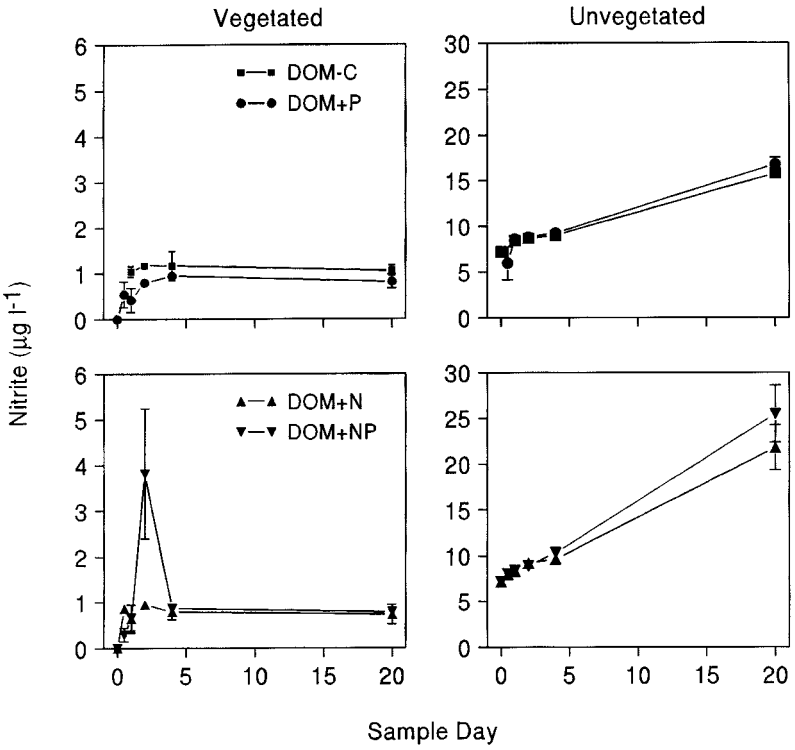

Figure 3. Average NO_2^- (± 1 SE) concentrations for unamended and nutrient enriched interstitial samples collected in the winter from a vegetated and unvegetated zone at TWE.

in the DOM and DOM+P treatments, while there was no significant change in NH_4^+ concentrations in the N amended treatments. On day 20, NH_4^+ concentrations were similar among the four nutrient treatments in samples from the vegetated and unvegetated zones, although final concentrations of NH_4^+ were approximately 5 times greater in interstitial waters from the unvegetated zone. Final NH_4^+ concentrations were similar to initial concentrations among all four nutrient treatments in samples from the vegetated and unvegetated zones.

NO_3^- concentrations increased in interstitial waters from the unvegetated zone in the nitrogen enriched samples (DOM+N and DOM+NP) from day 0 to day 20 (Figure 2). In DOM-C and DOM+P treatments of interstitial samples from the unvegetated zone, NO_3^- concentrations significantly decreased (day 0 to 1) and then did not change significantly through day 20 with final concentrations significantly lower than initial concentrations. NO_3^- concentrations in interstitial waters from the vegetated zone (DOM-C and DOM+P treatments) remained constant from day 0 to day 1, increased from

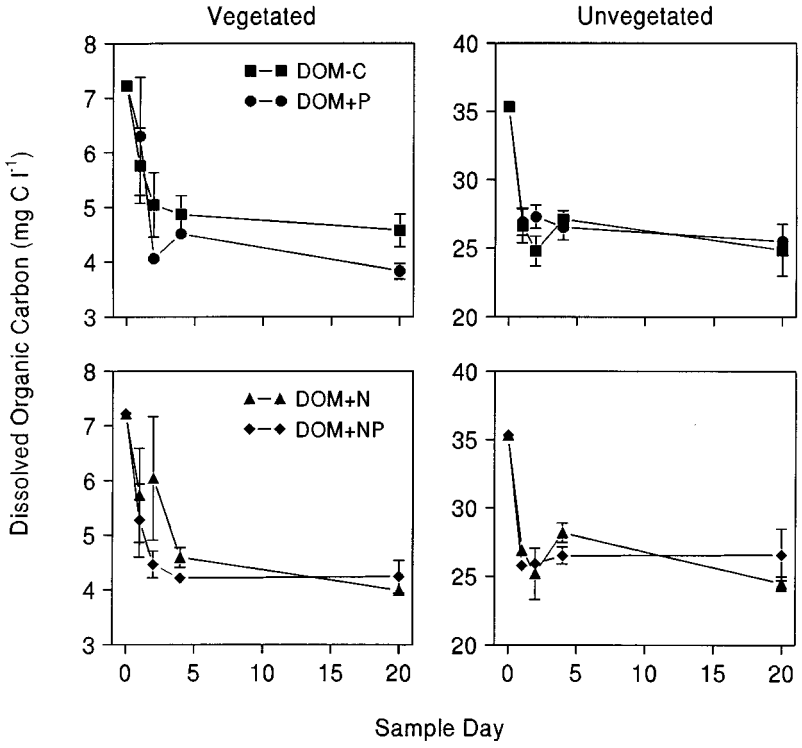

Figure 4. Average DOC (± 1 SE) concentrations for unamended and nutrient enriched interstitial samples collected in the winter from a vegetated and unvegetated zone at the TWE.

day 1 to day 2, and exhibited no significant change in NO_3^- concentrations from day 2 through day 20. In DOM+N and DOM+NP treatments (vegetated samples) a rapid increase occurred in NO_3^- concentrations from day 0 to day 2 with no significant change in NO_3^- concentrations from day 2 through 20. Final NO_3^- concentrations in DOM+N and DOM+NP treatments were significantly greater than initial NO_3^- concentrations and final concentrations in the DOM-C and DOM+P treatments.

NO_2^- concentrations from unvegetated samples were significantly greater (ca. 10 to 15 times greater) throughout the 20-d experiment compared to NO_2^- concentrations in samples from the vegetated zone (Figure 3). A linear increase in NO_2^- concentrations occurred in all four nutrient treatments from day 0 through 20 in interstitial waters from the unvegetated zone. Final NO_2^- concentrations were 3 to 5 times greater than initial concentrations, with significantly higher NO_2^- concentrations in the N-amended treatments. In interstitial waters from the vegetated zone, a rapid increase in NO_2^- concentrations occurred from day 0 to day 2 in all four nutrient treatments, with

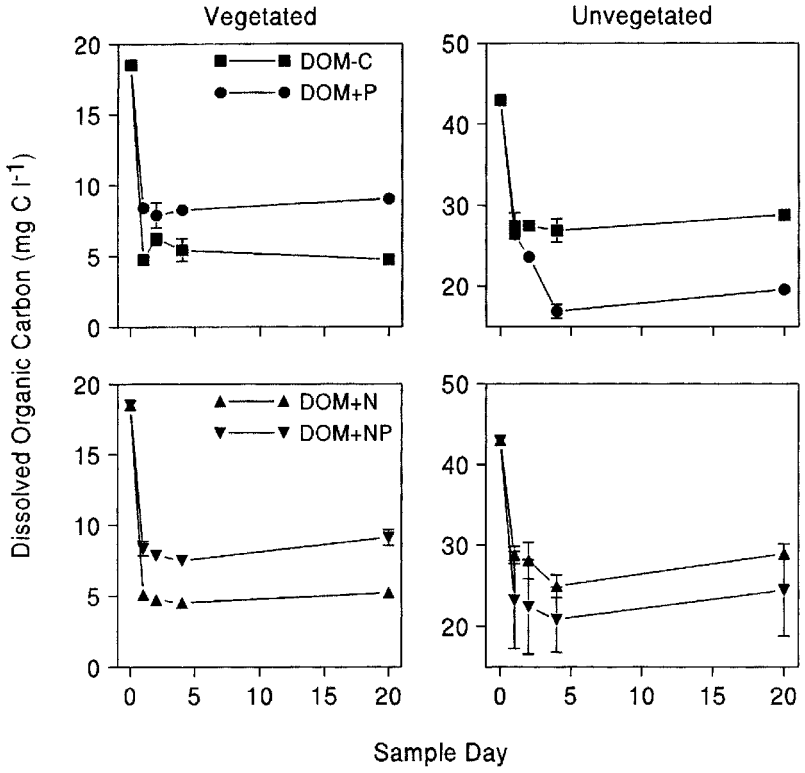

Figure 5. Average DOC (± 1 SE) concentrations for unamended and nutrient enriched interstitial samples collected in the spring from a vegetated and unvegetated zone at the TWE.

generally no significant change in NO_2^- concentrations from day 2 through 20.

Dissolved organic carbon dynamics

In all samples collected in winter and spring from both vegetated and unvegetated zones, DOC concentrations decreased significantly ($p < 0.05$) from initial concentrations through day 4 (Figures 4 and 5). This loss of DOC from day 0 to 4 was greater from the vegetated compared to unvegetated zone (winter and spring samples); in addition, this initial loss of DOC was greater from samples collected in the spring compared to the winter (vegetated and unvegetated samples). DOC concentrations of samples from vegetated and unvegetated zones (winter and spring samples) remained relatively constant with no significant change from day 4 through day 20. In samples collected from the vegetated zone (spring samples), DOC concentrations were significantly higher in treatments with phosphorus additions (DOM+P and

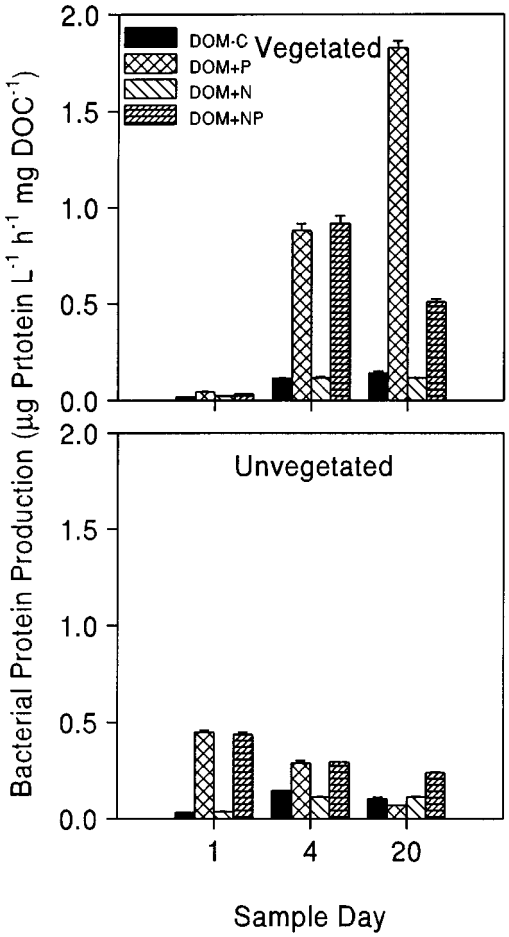

Figure 6. Bacterial protein production (± 1 SE) on unamended and nutrient amended interstitial DOM samples collected in the winter. Samples were collected from a vegetated zone (*Juncus effusus*) and an immediately adjacent unvegetated zone at the TWE.

DOM+NP) than treatments that received no phosphorus additions (DOM-C and DOM+N). In the remaining samples and nutrient treatments, no significant effect of either N or P amendments were seen on DOC dynamics.

Bacterial utilization of interstitial water DOM

In addition to differences in the initial nutrient concentrations and DOM from the two sources and between seasonal collection periods, differences were found in the bacterial utilization of interstitial water DOM. Bacterial productivity on the unamended samples (DOM-C) from the vegetated and

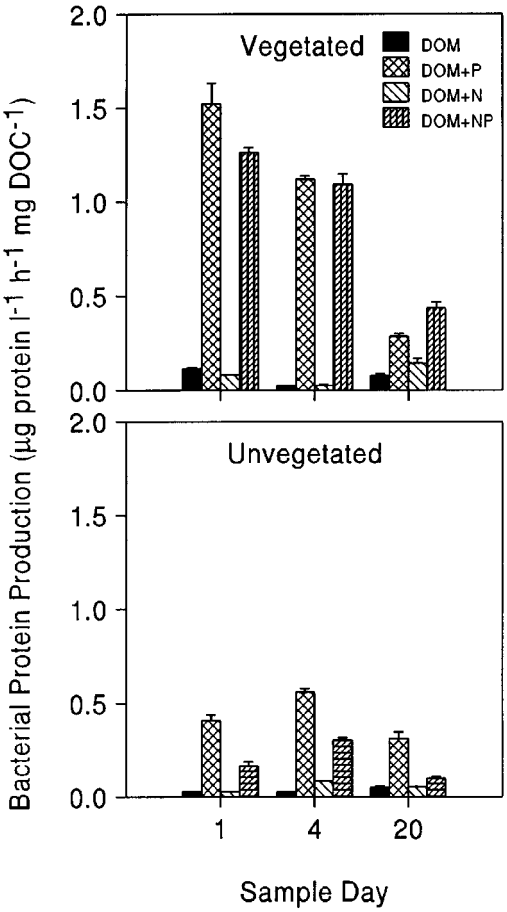

Figure 7. Bacterial protein production (± 1 SE) on unamended and nutrient amended interstitial DOM samples collected in the spring. Samples were collected from a vegetated zone (*Juncus effusus*) and an adjacent unvegetated zone at the TWE.

unvegetated zones in winter showed different patterns of utilization and maximum productivity (Figure 6). Bacterial productivity during the first 4 days of incubation was significantly greater on DOM from the unvegetated zone, while on day 20 bacterial productivity was significantly greater on DOM from the vegetated zone. Bacterial productivity on DOM collected from the vegetated zone significantly increased from day 1 to maximum productivity on day 20. Maximum bacterial productivity on DOM collected from the unvegetated zone was on day 4 followed by significant reductions in bacterial productivity on day 20 with final rates of bacterial productivity significantly greater than on day 1.

In the unamended samples (DOM-C) collected in spring, bacterial productivity was significantly greater on DOM from the vegetated zone on days 1 and 20 compared to the unvegetated zone (Figure 7). On day 4 there was no significant difference in bacterial productivity on DOM from the vegetated and unvegetated zones. In addition to differences in overall rates of bacterial productivity on DOM from the two sources, there were differences in the timing of maximum productivity of the DOM to the wetland bacteria. On DOM from the vegetated zone, bacterial productivity was greatest on day 1 while maximum bacterial productivity on DOM from the unvegetated zone occurred on day 20.

Bacterial productivity was significantly increased with the addition of phosphorus to interstitial DOM (DOM+P and DOM+NP treatments) (Figures 6 and 7). In DOM from the vegetated treatments the addition of phosphorus resulted in a greater increase in bacterial productivity than was seen in DOM+P and DOM+NP treatments on DOM collected from the unvegetated zone. The addition of nitrogen alone did not significantly increase bacterial productivity in DOM collected from either zone and over both collection dates. These data suggest that bacterial growth on interstitial DOM collected from the vegetated and unvegetated zone was limited by the availability of phosphorus.

Disscussion

Previous studies of interstitial water chemistry at the TWE have found significant spatial and temporal differences in N_i (Stanley & Ward 1997) and DOC (Mann & Wetzel 1995) concentrations. In this study, N_i and DOC concentrations were significantly greater from interstitial waters of sediments of unvegetated compared to vegetated zones. The addition of N_i and P did not significantly affect final nutrient concentrations of NH_4^+ relative to control treatments, although patterns of NH_4^+ concentrations during the 20-d experiment were significantly different among the various nutrient treatments. The addition of N_i (DOM+N and DOM+NP) did significantly increase NO_3^- concentrations in samples collected from the vegetated and unvegetated zones. Final NO_2^- concentrations significantly increased from initial to final concentrations in all nutrient treatments of samples collected from the vegetated and unvegetated zones. The addition of N_i resulted in significantly higher NO_2^- concentrations relative to the DOM-C and DOM+P treatments in samples collected from the unvegetated zone. Additionally, N_i and DOC concentrations increased from winter to spring in samples from both the vegetated and the unvegetated zones. Increased DOC (2.6-fold increase), and ammonium (1.4-fold) from winter to spring samples were most conspicuous in samples from

the vegetated zone. Lower initial concentrations of N_i and DOC in samples from the vegetated compared to the unvegetated zone may be attributed to higher rates of utilization by *J. effusus* and increased microbial utilization from organic substrates and oxygen released into the rhizosphere from the macrophytes.

Lower DOC concentrations in interstitial water samples from the vegetated zone contrast with the results of other studies that have compared DOC concentrations between vegetated and unvegetated sediments. Koepfler et al. (1993) found greater DOC concentrations in sediments of marine vegetated beds of *Haloduli wrightii* compared to bare sediments within the *Haloduli* beds and they suggested that higher interstitial DOC in the vegetated beds was a result of greater particulate organic carbon (POC) inputs and higher conversion rates of POC to DOC. At the TWE, the difference in interstitial DOC concentrations between vegetated and unvegetated zones may be a result of differential release of DOC from the roots and rhizomes of the macrophytes or the result of differential utilization rates of interstitial DOC by rhizosphere bacteria.

Although an increase in DOC concentration was observed from winter to spring, the overall microbial availability of the DOM decreased from winter to spring. Although generally higher bacterial productivity was observed on DOM from winter compared to spring samples, initial productivity (day 1) was greater on DOM collected from the vegetated zone in spring compared to winter samples. The difference in microbial availability suggests there are temporal shifts in the relative abundance of labile and recalcitrant compounds in porewater from vegetated and unvegetated zones.

Temporal differences in organic substrate availability were also seen in the nutrient amended treatments. Maximum bacterial productivity occurred at different times based on season and zone of collection, which suggested that the microbial availability of DOC substrates was temporally variable. The increase in bacterial productivity in P treatments on DOM from the vegetated compared to unvegetated zone suggests that DOM from the vegetated zone is more available to bacteria if an adequate nutrient supply were available. These data suggest a strong phosphorus limitation to bacterial growth on porewater collected from both vegetated and unvegetated zones. Bacterial productivity increased approximately 1 to 9 times in phosphorus and nitrogen plus phosphorus treatments. Overall, there was no significant difference in bacterial productivity between the control and N only treatments, which suggests there was no N-limitation to bacteria productivity among any of the treatments. This conclusion is supported by reported high N_i concentrations in the subsurface waters of the TWE (Stanley & Ward 1997).

Wetland macrophytes have been shown to affect substrate utilization rates by bacteria, metabolic pathways of bacterial consortia, interstitial water chemistry, and nutrient availability. The ability of wetland macrophytes to influence interstitial water chemistry is correlated to the release of oxygen from the roots into the surrounding sediments, which facilitates microbial or chemical oxidation of reduced species present in interstitial waters. These data suggest that shallow subsurface waters of wetland hydrosoils need to be carefully analyzed for spatial and temporal variations in DOC and nutrient concentration. Seasonal differences in interstitial water chemistry and differences in relation to the presence or absence of macrophytes can occur, and these differences need to be addressed when examining nutrient and energy flows in wetland ecosystems. These data also suggest that P additions to wetlands can significantly increase initial bacterial productivity on DOC of subsurface waters.

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