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A Comparison of Sediment Microbial Communities Associated with *Phragmites australis* and *Spartina alterniflora* in Two Brackish Wetlands of New Jersey

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ABSTRACT: The extensive spread of *Phragmites australis* throughout brackish marshes on the East Coast of the United States is a major factor governing management and restoration decisions because it is assumed that biogeochemical functions are altered by the invasion. Microbial activity is important in providing wetland biogeochemical functions such as carbon and nitrogen cycling, but there is little known about sediment microbial communities in *Phragmites* marshes. Microbial populations associated with invasive *Phragmites* vegetation and with native salt marsh cordgrass, *Spartina alterniflora,* may differ in the relative abundance of microbial taxa (community structure) and in the ability of this biota to decompose organic substrates (community biogeochemical function). This study compares sediment microbial communities associated with *Phragmites* and *Spartina* vegetation in an undisturbed brackish marsh near Tuckerton, New Jersey (MUL), and in a brackish marsh in the anthropogenically affected Hackensack Meadowlands (SMC). We use phospholipid fatty acid (PLFA) analysis and enzymatic activity to profile sediment microbial communities associated with both plants in each site. Sediment analyses include bulk density, total organic matter, and root biomass. PLFA profiles indicate that the microbial communities differ between sites with the undisturbed site exhibiting greater fatty acid richness (62 PLFA recovered from MUL versus 38 from SMC). Activity of the 5 enzymes analyzed (β-glucosidase, acid phosphatase, chitobiase, and 2 oxidases) was higher in the undisturbed site. Differences between vegetation species as measured by Principal Components Analysis were significantly greater at the undisturbed MUL site than at SMC, and patterns of enzyme activity and PLFAs did not correspond to patterns of root biomass. We suggest that in natural wetland sediments, macrophyte rhizosphere effects influence the community composition of sediment microbial populations. Physical and chemical site disturbances may impose limits on these rhizosphere effects, decreasing sediment microbial diversity and potentially, microbial biogeochemical functions.

Introduction

The increasing dominance of *Phragmites australis* (Cav.) Trin. ex. Steud. (hereafter *Phragmites*) in brackish estuarine marshes has been a cause of major concern, and has sparked extensive and expensive efforts to restore *Spartina* species to these marshes (Meyerson et al. 2000; Rooth and Stevenson 2000; Rice et al. 2000). Restoration efforts are often justified in terms of lost or altered biogeochemical functions associated with *Phragmites* invasions. While these restoration efforts have stimulated many studies of the comparative ability of *Phragmites* and *Spartina* to support vertebrate and invertebrate faunas (Weinstein and Balletto 1999; Wainwright et al. 2000; Weis and Weis 2000), little attention has been paid to the microbial biota of the sediments. This biota is critical to the performance of biogeochemical functions, including the storage or emission of carbon (Brix et al. 1992), nitrogen cycling (Windham in press), and the biodegradation of toxic compounds (Alder et al. 1993; Adriaens and Vogel 1995; Haggblom et al. 2000).

In this study we compare microbial community structure and biogeochemical functional capacity in *Phragmites* and *Spartina alterniflora* Loisel (hereafter *Spartina*) sediments from disturbed and undisturbed sites to determine whether plant species and anthropogenic disturbances alter the microbial component of the marsh ecosystem. We hypothesized that because the root systems of *Phragmites* and *Spartina* differ substantially in morphology (size and relative abundance of rhizomes and roots), total biomass, spatial distribution, and the mechanisms of oxygen transport and radial oxygen loss (Valiela et al. 1976; Howes et al. 1981; Armstrong et al. 1996; Grosse et al. 1996; Windham 2001), the microbiota associated with their rhizospheres would differ in both community composition and biogeochemical functions.

Evidence, primarily from studies of upland soils, has clearly shown that microbial community com-

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position and biogeochemical functions respond to changes in the plant community (Westover et al. 1997; Grayston et al. 1998; Ehrenfeld 2001). A number of studies using metabolic profiles, phospholipid fatty acid composition, and DNA analysis have demonstrated that microbial community structure differs in rhizosphere soils of different co-occurring plant species (Borga et al. 1994; Westover et al. 1997; Grayston et al. 1998). While these studies used upland plants, several studies of wetland macrophytes have shown that these species also affect the microbial populations in their rhizospheres (Ludemann et al. 2000; Piceno and Lovell 2000; Bergholz et al. 2001; Lovell et al. 2001). For example, diazotroph (nitrogen-fixing) populations differ in composition and abundance between *Spartina* rhizospheres and the rhizospheres of other plants or root-free bulk soils (Gandy and Yoch 1988; Piceno et al. 1999). If the sediment microbiota of coastal wetlands are sensitive to the species identity of the macrophyte community, then changes in species composition, such as *Phragmites* invasions or the reestablishment of *Spartina* in *Phragmites*-dominated sites, may alter this biota potentially affecting the biogeochemical functions they perform.

Microbial communities are also affected by the presence of contaminants. Toxic compounds can affect the relative abundance and activity of different microbial species, and the use of these contaminants as carbon sources by competent microbes may select for a particular microbial community composition (Wolfaardt et al. 1994; Moller et al. 1997; Karthikeyan et al. 1999).

This study uses two methods to compare the biogeochemical functions and community structure of the sediment microbiota under *Phragmites* and *Spartina* in both contaminated and uncontaminated brackish marshes. Measurements of extracellular enzyme activity provide an index of microbial ability to carry out key processes that provide biogeochemical functions (Sinsabaugh 1994; Sinsabaugh and Moorhead 1994; Sinsabaugh et al. 1993). This enzyme activity has proven sensitive to environment disturbance (Nannipieri et al. 1990; Dick and Tabatabai 1993). Comparison of enzyme activities among soils is commonly used in upland systems to provide insight into the relative biogeochemical capacity of the soil microbiota to carry out decomposition and nutrient cycling functions (Sinsabaugh 1994). Enzyme activities have also been used in a small number of studies to investigate the biodegradative function of constructed wetlands (Kang et al. 1998; Shackle et al. 2000).

The structure of a sediment microbial community can be examined by looking at the set of phospholipid fatty acids (PLFAs) in the sediments. PLFAs are key components of microbial cell membranes, and because different groups of microorganisms produce unique types and suites of fatty acids, the structure of the microbial community can be examined by looking at the set of PLFAs extractable from a sediment sample (Borga et al. 1994; White et al. 1996; Haggblom et al. 2000). Used in conjunction with each other, these techniques can provide insight into the effects of different plant species on sediment microbial communities. We used these techniques to test the hypotheses that sediment microbial communities are different below *Phragmites* and *Spartina* vegetation, and these differences are consistently observed at different sites.

Methods

Adjacent populations of *Phragmites* and *Spartina* were located on Saw Mill Creek in the Hackensack Meadowlands, New Jersey (40°46′N, 74°06′W; referred to as SMC), and on an unnamed tidal creek of the Mullica River, west of the Garden State Parkway about 7 km from the river mouth (39°33′N, 74°28′W; referred to as MUL). Saw Mill Creek has had a lengthy history of disturbances from the presence of a variety of industrial and regional contaminants such as heavy metals, chlorinated hydrocarbons, polycyclic hydrocarbons, and other toxic compounds (Kennish 1992), as well as numerous physical disturbances such as ditching and tidal obstruction (Quinn 1997). SMC waters are brackish (salinities of 12–18‰, Bart personal communication). Heavy metal concentrations in the water column are well above background. Median concentrations measured over a 5-yr period (1994–1999) were 25.9 $\mu g\ l^{-1}$ Cd, 18.5 $\mu g\ l^{-1}$ Cr, 28.9 $\mu g\ l^{-1}$ Cu, and 151 $\mu g\ l^{-1}$ Pb (New Jersey Meadowlands Commission unpublished data). Water column metal concentrations, in turn, affect SMC sediment metal concentrations (105 $\mu g\ g^{-1}$ Cu, 205 $\mu g\ g^{-1}$ Zn, 156 $\mu g\ g^{-1}$ Cr, 2.8 $\mu g\ g^{-1}$ Hg, and 176 $\mu g\ g^{-1}$ Pb [Weis personal communication]). The SMC marsh is located between the eastern and western branches of the New Jersey Turnpike, and bounded on the north and south by major road and railroad corridors. In contrast, the MUL site is bounded on the inland side by the largest protected watershed in the northeast (the Pinelands National Reserve), and is part of the Jacques Cousteau National Estuarine Research Reserve on the seaward side; there is virtually no industrial activity within the watershed. The MUL study area is also brackish, with salinities of about 18‰.

At both sites, transects 12 m in length, parallel to the main surface water channel, were established starting at a randomly chosen point within monospecific populations of each species. Three

plots, each 4 m^2, were marked at 2-m intervals along the transect. Three replicate sediment cores extending to 70-cm depth were randomly extracted within each plot using a Russian peat corer (Aquatic Research Instruments) during July–August 2001. All cores were extracted within 2 h of low tide, and wrapped in gas-impermeable Saran wrap for transport to the laboratory, where they were divided into 10-cm subsections. Each of these sections was subsampled for moisture content (gravimetric analysis), organic matter content (loss-on-ignition at 500°C), and bulk density (using a 1 cm deep × 1 cm diam ring pushed into the core section, dried, and then weighed). Two additional sets of subsamples were taken from the 0–10, 30–40, and 60–70 cm subsections. Subsamples were processed immediately for enzyme activities or frozen at −20°C for later PLFA analysis as described below.

Root and rhizome biomass was determined from samples obtained by excavating soil blocks within each of the plots. This method was used because preliminary sampling at SMC suggested that the peat corer was not adequately sampling larger rhizomes. At SMC, rectangular blocks (15 × 44 × 10 cm) were excavated using a metal frame to define the block. Aboveground vegetation was clipped to the marsh surface, and the frame inserted into the sediments to a depth of 10 cm using a sharp knife and a shovel to cut the root mat, and then to remove the intact block. At MUL a circular metal frame (8.5 × 11 cm) was used. Blocks were transported to the laboratory where sediments were washed from the roots and rhizomes. Because of the large mass of material and the interwoven nature of different root sizes and status, no attempt was made to separate live and dead roots or rhizomes. Washed biomass was dried at 70°C to constant weight.

Phospholipid Fatty Acid Analysis

The method of PLFA analysis described by White et al. (1979) was slightly modified. Samples were thawed and dewatered by centrifuging, and duplicate subsamples were run for each extraction. Fatty acids were extracted using a single-phase chloroform:methanol:0.05 M phosphate buffer (pH 7.5) solvent. The concentrated chloroform extract was separated into lipid fractions on a silicic acid column using the method of King et al. (1977). The phospholipid fraction was eluted with methanol, saponified, and methylated according to protocols for the Microbial Identification System (MIDI 1995). The MIDI Sherlock Microbial Identification System (MIS, Microbial ID, Newark, Delaware) was used to identify individual fatty acid methyl esters based on their gas chromatograph (GC) retention time. Individual fatty acids were quantified as a percentage of the total fatty acids recovered from the sample. Fatty acids contributing < 1% of the total amount extracted from each sample or observed in only one sample were eliminated from the data set, leaving 41 fatty acids for statistical analysis.

Enzyme Analysis

Using the methods of Sinsabaugh et al. (1993), the activity of 5 extracellular enzymes related to carbon (C), nitrogen (N), phosphorus (P), and soil organic matter (SOM) cycling were measured. β-glucosidase (E.C. 3.2.1.21), an enzyme important in degradation of carbohydrates, was used as an indicator of C cycling potential. β-*N*-acetylglucosaminidase (E.C. 3.2.1.30), commonly known as chitobiase, is involved in degradation of the N-containing fungal cell wall compound acetylglucosamine, and was used as the N-related enzyme. Acid phosphatase (E.C. 3.1.3.2), an enzyme necessary for the degradation of P containing organic molecules, was used as an indicator of P cycling potential. Two enzymes active in the degradation of complex organic substrates, phenol oxidase (E.C. 1.10.3.2 and E.C. 1.14.18.1) and peroxidase (E.C. 1.11.1.7) were used as indicators of SOM cycling. The substrates used for β-glucosidase, chitobiase, and acid phosphatase were *p*-nitrophenol (*p*NP) derivatives that release *p*NP when hydrolyzed, which is then analyzed spectrophotometrically. Substrates (10 mM) were each dissolved in 50 mM acetate buffer (pH 5) and added to a sediment slurry. Two ml of slurry were incubated with 2 ml of each substrate at 20°C for the time specified for each enzyme. Enzyme and sediment controls were run simultaneously. After incubation the samples were centrifuged and 1 ml of the supernatant was then added to 0.2 ml of 1 N NaOH followed by the addition of deionized H_2O. Absorbance was measured on a spectrophotometer (Spectronic Instruments) at 410 nm and enzyme activity expressed as μM substrate g^{-1} h^{-1}. The same procedure was used to measure phenol oxidase and peroxidase activity using L-DOPA as the substrate. Two ml of sediment slurry were mixed with 2 ml of substrate (plus 0.2 ml of 0.03% H_2O_2 for peroxidase) and incubated 30 min at 20°C. Enzyme and sediment controls were run simultaneously. Samples were centrifuged at 2,500 RPM for 10 min and the supernatant directly used to measure absorbance at 460 nm. Enzyme activity is expressed as μM substrate g^{-1} h^{-1}. The peroxidase assay includes the addition of H_2O_2, and measures the sum of phenol and peroxidase activity. Peroxidase activity alone was obtained by subtracting phenol oxidase results from the peroxidase total results.

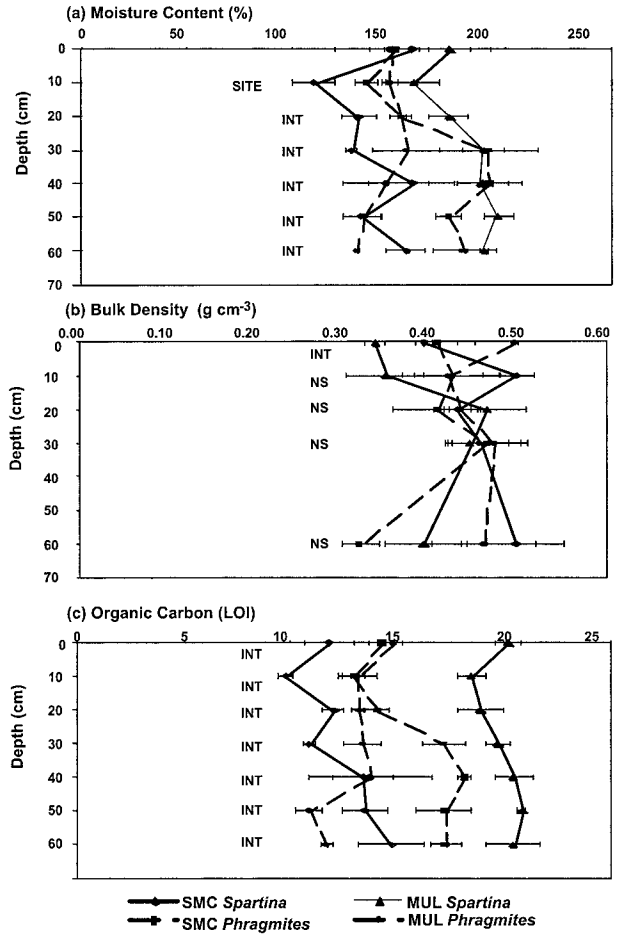

Fig. 1. Sediment characteristics through the profile. (A) gravimetric moisture content, (B) bulk density, and (C) organic matter (as percent loss-on-ignition). The results of two-way analyses of variance are given as the name of the significant factor in the ANOVA (Site, Species, or Int for interaction).

Statistical Analysis

Sediment characteristics, including root biomass, were analyzed using two-factor analyses of variance (ANOVA; SITE factor: MUL versus SMC, and SPECIES factor: *Phragmites* and *Spartina*, n = 3 for each site-species combination). Two-way ANOVAs were also applied to the data from each enzyme and each fatty acid. Contrast analysis was used to compare vegetation effects within each site. Principal components analyses were used to examine patterns among the four site-species combinations based on the multivariate sets of enzyme activities and fatty acids.

Results

Sediment characteristics were different between the sites (Fig. 1), although the quantitative differences among the site-species combinations for all of the variables were small. In most cases, ANOVA revealed significant interactions between sites and species, and contrast analyses demonstrated different relationship between the species at the two sites. Sediment moisture beneath *Phragmites* was higher than beneath *Spartina* in SMC, but the opposite pattern was found at MUL (Fig. 1a). The bulk density of surface sediments under *Spartina* was lower than under *Phragmites* in MUL but not SMC, but few other differences were found lower in the profile (Fig. 1b). Organic matter (Fig. 1c) was consistently higher under *Spartina* than under *Phragmites* at MUL, but the opposite was observed at the SMC site. The absolute difference between the sites is again relatively small (particularly for the two *Phragmites* populations).

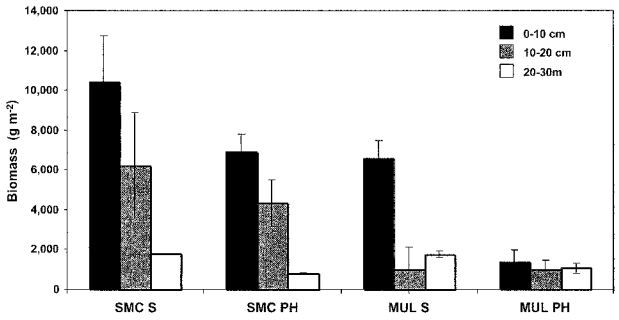

Fig. 2. Total root and rhizome biomass in excavated sediment blocks for the top 30 cm of sediment.

Total root and rhizome biomass in the top 10 cm was higher under *Spartina* than under *Phragmites* at both sites, and root biomass was generally higher at the disturbed SMC site than the undisturbed MUL site (Fig. 2; species factor in two-way ANOVA $F_{1,11} = 9.407$, $p < 0.01$, site factor $F_{1,11} = 11.11$, $p < 0.01$). No significant differences in root biomass were found for the lower layers.

Patterns of extracellular enzyme activity varied with both the species and the site (Fig. 3). In most cases two-way ANOVA showed that the pattern of differences between the species depended on the

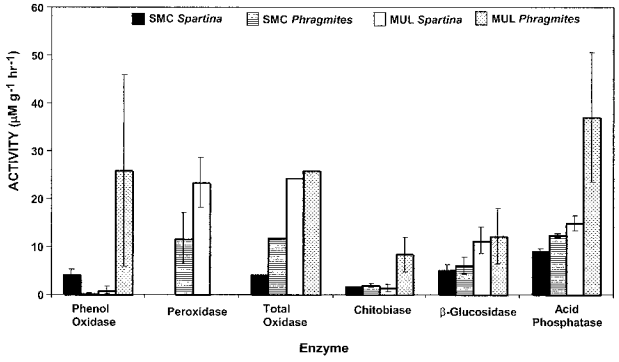

Fig. 3. Activities (μM g soil^{-1} h^{-1}) of extracellular enzymes of the two species at each site, for three sediment depths.

TABLE 1. Patterns of significance in two-way analyses of variance and 1 df contrasts of site and species effects on extracellular enzyme activities, for each of three sediment depths (Top = 0–10 cm, Middle = 30–40 cm, Bottom = 60–70 cm). P = *Phragmites*, S = *Spartina*. Letters (a,b,c) indicate significance level of the overall 2-way ANOVA, and numbers (1,2,3) indicate significance of 1 df contrasts comparing species within each site. Int = Interaction factor ^{a,1} $p < 0.05$, ^{b,2} $p = 0.01$, ^{c,3} = $p < 0.001$; "P = S" indicates no significant difference in 1 df contrasts.

Enzyme	Site	Top	Middle	Bottom
Phenoxidase		Int^{c}	Int^{c}	Int^{c}
	MUL	P > S^{3}	P > S^{3}	P > S^{3}
	SMC	S = P	S > P^{3}	S > P^{3}
Peroxidase		Int^{c}	Site^{c}	Int^{b}
	MUL	S > P^{3}	S = P	S > P^{3}
	SMC	P > S^{3}	S = P	P > S^{3}
Chitobiase		Int^{b}	Int^{a}	Int^{b}
	MUL	P > S^{3}	P > S^{3}	P > S^{3}
	SMC	P = S	P = S	P > S^{3}
β-Glucosidase		Site^{a} (M > S)	Int^{b}	Site^{a}
	MUL	P = S	S > P^{3}	S > P^{3}
	SMC	P = S	S = P	S = P
Acid phosphatase		Site^{b} (M > S)	Site^{b} (M > S)	Site^{b} (M > S)
	MUL	P > S^{3}	P = S	P > S^{1}
	SMC	P = S	P = S	P > S^{1}

site (Table 1). Phenol oxidase activities were higher under *Phragmites* than *Spartina* at MUL, but the opposite pattern was observed at SMC. Conversely, peroxidase, the other enzyme implicated in the degradation of lignin, humics, and other complex substrates, was higher under *Spartina* than *Phragmites* at MUL. Chitobiase had low levels of activity at all sites, but significantly different patterns at the two sites were found (*Phragmites* sediments showed greater activity than did *Spartina* sediments at MUL but not SMC). β-glucosidase showed higher surface sediment activity under both species at MUL than at SMC, but higher activity under *Spartina* than under *Phragmites* lower in the profile. Acid phosphatase activity was especially high in surface sediments under *Phragmites* at MUL, and all sediment samples from MUL exhibited higher activity than the corresponding sediments from SMC (Fig. 3). Contrast analyses (Table 1) showed that differences between the species were commonly observed for most enzymes at most depths in MUL, but more rarely in SMC.

Principal components analysis using the 5 enzymes at the 4 site-species combinations (Fig. 4a) indicated that while the two species were separable at each site, this difference was greater at MUL than at SMC. At SMC both species clustered close together; at MUL the two sets of samples clustered farther apart. There was no tendency for the two populations of each species to be found in adjacent areas of the ordination space.

The distribution of phospholipid fatty acids for each of the site-species combinations (Fig. 5) suggests small differences between species and sites. Of the 41 fatty acids retained for analysis, 7 were found only at MUL but only one was found exclusively at SMC. At MUL, 7 fatty acids were found only under *Phragmites* but not *Spartina*, whereas at SMC, only one fatty acid was restricted to *Phragmites* sediments. Ubiquitous fatty acids contributed a higher percentage to the total fatty acids extracted from SMC sediments than from MUL sediments. These patterns suggest a less diverse microbial population with less difference between the species at SMC than at MUL. Two-way ANOVAs for each of the PLFAs (Table 2) show that for about half the fatty acids there were no significant differences among samples; for the remaining fatty acids, interaction effects were predominant. In only a few cases, in surface and deep sediment layers, were differences among species uniformly seen at the two sites. Contrast analysis indicates species differences are significant at MUL, but not at SMC.

PLFA principal components analysis (Fig. 4b) indicates ordination separation is much greater between species at MUL than at SMC, a similar finding to that observed with enzyme activities. Only in the MUL-*Phragmites* samples were there significant differences with depth (the mid-layer samples differed from the top and bottom layers), so the samples from the three depths were lumped together in the analysis. The *Phragmites* and *Spartina* samples from the SMC samples co-occur in the ordination space; in contrast, the species from the MUL samples are clearly separated, primarily along the first ordination axis. Interestingly, the *Spartina* samples from MUL overlap the area of the ordination space occupied by the SMC samples.

Discussion

The data suggest that the differentiation of sediment microbial communities beneath plant species in brackish marshes is contingent on qualities associated with the individual sites. Patterns of dif-

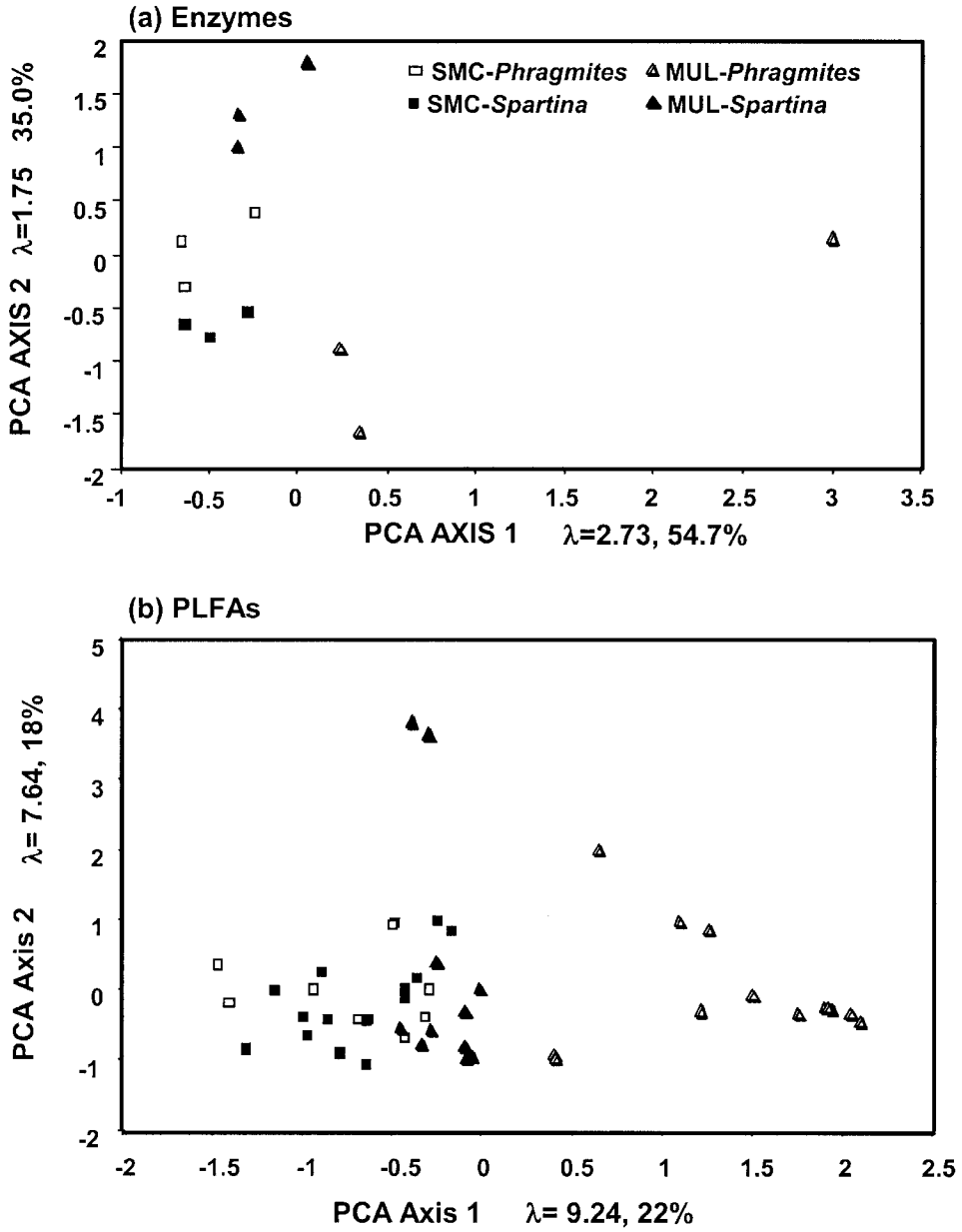

Fig. 4. Principal components ordination diagrams for (a) enzyme activities and (b) aggregate PLFA variables. For each diagram, the eigenvalue and the percent of variation explained are given along each axis.

ference between descriptors of the microbiota observed at the undisturbed MUL site were more frequently statistically significant than at SMC, and were often opposite in direction to those occurring at the heavily disturbed SMC site. These patterns of difference between species within each site do not clearly correspond to the relatively small differences in physical conditions between sites.

The undisturbed MUL site generally had higher levels of enzyme activity with greater variation in activity between plant species than did the SMC marsh. Soil enzyme activities have been interpreted to be indices of microbial biomass, microbial activity, and the ecological health of soils and sediments (Nannipieri et al. 1990; Dick and Tabatabai 1993; Ajwa et al. 1999). Although individual enzyme activities may not always correlate with other measures of soil quality or microbial activity (Frankenberger and Dick 1983), assessments based on the aggregate activities of several enzymes have proven

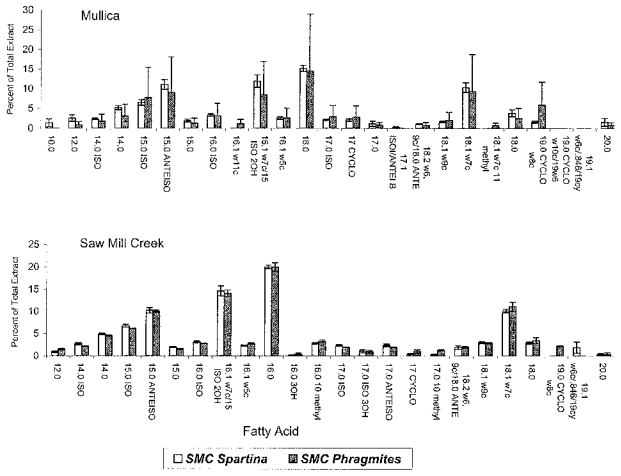

Fig. 5. Relative amounts (as percentages of the total fatty acid extract) of 25 most common PLFAs isolated from surface sediments in the four sets of samples.

useful in comparing sites with different land uses and histories of disturbance (Frankenberger and Dick 1983; Nannipieri et al. 1990). The consistent pattern of lower enzyme activities at SMC, found across many of the enzyme assays (5 enzymes at each of 3 depths under each species), suggests that microbial function in general may be lower at the Hackensack site than in the undisturbed MUL site.

Some studies have found that enzyme activities are correlated with soil organic matter content (Waldrop et al. 2000), but other studies have not found this to be case (Eivazi and Bayan 1996). The pattern of enzyme activities we observed did not necessarily correspond to the patterns of organic matter in the sediment samples. For example, peroxidase activities at MUL are higher under *Spartina* than *Phragmites* (Table 1), despite the opposite pattern of organic matter content (Fig. 1c). The differences we observed in SMC may also reflect the disturbed and contaminated nature of the sediments. In a variety of studies, Dick and Tabatabai (1993) found that enzyme activities are sensitive to metal contamination; Kuperman and Carreiro (1997) found a 10-to-50-fold reduction in enzyme activity, which paralleled increases in heavy metal concentrations.

The results of this study were contrary to expectation in several ways. At SMC, the disturbed site, the root biomasses were considerably higher than those reported in the literature (*Spartina* > 10,000 g m^{-2} versus 3,300–5,000 g m^{-2} [Valiela et al. 1976]; *Phragmites* ~6,500 g m^{-2} versus 1,400 g m^{-2} [Windham 2001]); in contrast, the biomasses recorded at the MUL site were within these reported ranges from other areas (*Spartina* ~6,500 g m^{-2}, *Phragmites* ~1,600 g m^{-2}). We do not know if this finding is a result of our sampling a large sediment block rather than smaller sediment cores or a result of morphological effects of anthropogenic impacts. While the individual rhizomes of *Phragmites* are much larger than the *Spartina* rhizomes, each supports a smaller number of roots, and the rhizomes are less densely packed within the surface sediments than are the *Spartina* root-rhizome systems. This pattern was particularly marked at SMC, where the *Spartina* occurred as tussocks separated by sparsely vegetated or bare mud; at MUL, the *Spartina* formed a more typical uniform lawn. The tussocks had notably dense root-rhizome mats, compared with the other sampling locations.

TABLE 2. Number of significant factors of each factor in 2-way analyses of variance of site and species effects for the phospholipid fatty acids in the surface sediments.

Depth	Site	Species	Interaction	None
0–10 cm	6	3	13	18
30–40 cm	7	0	7	23
60–70 cm	8	4	8	19

Another surprising find was that the comparison of microbial structure and function did not correspond to the amounts of root biomass in the sediments. Although enzyme activities were higher in most cases at MUL, root biomasses were lower at this site, particularly in the surface horizons. In addition, there was a larger contrast in root biomass between *Spartina* and *Phragmites* at MUL than at SMC, but the patterns of enzyme activity and PLFA occurrences did not correspond to these patterns of root biomass. These results suggest that microbial community structure and function are not simply and directly driven by the quantities of roots in the sediments.

Differences in microbial communities were found to be markedly different between the two sites. We had expected that the differences in oxygenation mechanisms employed by the two plant species (Venturi-enhanced convective airflow in *Phragmites* [Armstrong et al. 1996] versus convection-enhanced diffusive flow in *Spartina* [Hwang and Morris 1991; Howes and Teal 1994]) would result in different levels of rhizosphere oxygenation, providing conditions that select for different rhizosphere microbial communities. Microbial populations were significantly different between plant species at the MUL site but not at the SMC site.

In upland soils, differences in microbial community structure and biogeochemical function are frequently observed beneath different plant species (Grayston et al. 1998; Waldrop et al. 2000; Kourtev et al. in press). These differences are thought to correspond to differences in root bio-

mass, root distribution, root exudation, plant growth characteristics, and litter chemistry (Hobbie 1992; Binkley and Giardina 1998; Ehrenfeld 2001). It is surprising to find that significant differences in enzyme activity and fatty acid profiles were found at the MUL site but not at the SMC site. We offer four possible non-mutually exclusive explanations for the species-specific microbial effects observed in sediments at these two sites.

First, it may be that the stressful and specialized conditions of highly disturbed anaerobic soils impose controls on microbial community structure and biogeochemical function that make the more subtle effects of variations in plant species relatively unimportant. Second, despite the difference in root oxygenation mechanism, there may be equally low oxygen loss to the sediments from the roots, if most or all of the transported oxygen is used by the root tissues (Howes and Teal 1994; Brix et al. 1996; Armstrong et al. 2000). If there is no difference in the redox status of the SMC rhizoplanes and rhizospheres of the two species, differences in the microbiota would be less likely to occur. Third, root-derived C is thought to be the major feature generating differences in the microbiota, as suggested for upland soils (Garland 1996; Grayston et al. 1998); however, in the marsh peats, there is a large amount of C available in the salt marsh sediments, and this C may render the plant-derived C of minor importance to the microbiota.

Finally, the higher enzyme activities and larger number of fatty acids recovered from the MUL sediments (total of 62) versus the SMC sediments (total of 38) suggest that the history of contamination and physical disturbance in the Meadowlands has had a direct effect on microbially-mediated biogeochemical processes through a diminution of microbial abundance, activity, and diversity. Without more specific data on contaminant loads and comparative studies within the Meadowlands district, this remains speculation. There are abundant data in the microbiological literature showing that stress due to contamination and disturbance can reduce enzyme activity and microbial diversity (Dick and Tabatabai 1993; Kuperman and Carreiro 1997). The large difference in environmental history of the two sites may have overwhelmed the effects of the two plant species, contributing to the conclusion that brackish marsh microbial communities are primarily affected by the nature of the site. In highly disturbed systems, site-specific variables may be of greater importance in determining microbial community composition than the macrophytes species forming the plant cover. Our results indicate that root-mediated effects on microbial communities appear to be impacted in wetland sediments of disturbed systems. There is a notable lack of studies using these analytical techniques in other wetland soils, and so there is a clear need for additional work to test these hypotheses.

Acknowledgments

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