

Microtopographic variability in plant distribution and biogeochemistry in a brackish-marsh system

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ABSTRACT: Microtopography is often observed and studied in plant communities where environmental conditions limit distribution, for example in desert and peatland ecosystems. Brackish marshes, relatively poorly studied despite their importance in many coastal areas, frequently display similar fine-scale variability. In these systems, limits to plant distribution derive from the combination of flooding and salinity fluctuations. We examined the relationship between spatial variability of vegetation and biogeochemical features of sediment in a brackish tidal ecosystem in 2 adjacent *Spartina* spp. marshes of differing hydrology and vegetation distribution. The first, a low-elevation, interior marsh, was frequently flooded and poorly drained, and it exhibited distinct hummock/hollow topography. The plant distribution was reflected in patchy sediment biogeochemical features at the same scale. The second marsh, on a well-drained, elevated streamside bank, contained homogeneous vegetation cover and relatively uniform sediment chemistry. The formation of the hummock/hollow topography in the interior marsh appeared to be controlled by the plants, as they maximized growth in a high-stress, variable environment. The plants favorably modified discrete patches of these environments to such a degree that the hummock sediment biogeochemistry was very similar to that of the higher-elevation homogeneous marsh. The microtopography of this interior brackish marsh strongly resembles that of other stress-impacted ecosystems.

KEY WORDS: Hummock/hollow topography · Ecosystem engineering · Spatial variability · Patchiness · Marsh sediment · Microsite heterogeneity

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INTRODUCTION

Microtopographic variation is a common spatial feature (of 10⁻¹ to 10 m² scale) that has been well-studied in terrestrial habitats. Arid shrub systems exhibit microtopography; these 'islands of fertility' are associated with patchiness of soil chemical and physical features (Jackson & Caldwell 1993, Schlesinger et al. 1996). Similar patterns also develop in savannah systems (Augustine 2003) and in grasslands (Rietkerk et al. 2000). In Mid-Eastern nebkhas, shrubs trap wind-borne sediment, forming persistent hillocks with elevated fine particles and increased organic carbon and nitrogen at the edges, where higher moisture may accelerate decomposition (El-Bana et al. 2002). Many

authors attribute this microscale heterogeneity to macrophyte-generated accumulation of inorganic and organic matter and of nutrients, although Jackson & Caldwell (1993) emphasize the response of plants to underlying variability.

In deserts, the scale of heterogeneity of shrub 'islands' is that of the individual plants (e.g. *Larrea tridentata*). In grassland ecosystems, microtopographic habitat heterogeneity is found on the scale of clonal grass tufts (Schlesinger et al. 1996, Rietkerk et al. 2000). In general, microtopographic variation scales with the size of the vegetation in systems dominated by macrophytes (Huenneke & Sharitz 1986, Kleb 1999).

Persistent microtopography is also found in wetlands in the form of elevated hummocks and low hollows.

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Such systems include peatlands (Malmer & Wallen 1999, Branfireun 2004), forested wetlands (Huenneke & Sharitz 1986), and even subtidal seagrass beds (Herbert & Morse 2003). For each of these, sediment biogeochemical variability has been shown to coincide with vegetational patterns. As with terrestrial systems, the scale of the spatial variability may also reflect that of the dominant plant species (e.g. Huenneke & Sharitz 1986).

Tidal marshes exhibit both mesoscale (10 to 1000 m²) and microtopographic variability. These dynamic systems display well-defined spatial variability related to age (Tyler & Ziemann 1999) and to geomorphological features such as distance from tidal creeks and elevation (Bertness & Ellison 1987, Gardner et al. 1988). This mesoscale topography may develop along hydrological or salinity gradients, which largely determine soil chemical conditions. Variability at finer spatial scales in marshes is also common, often resulting from disturbance (Fischer et al. 2000). Fire, grazing, wrack deposition, treefall, and flooding may all generate discrete patches in wetlands (e.g. Bertness & Ellison 1987, White & Howes 1994, Berg et al. 1997, Stoeckel & Miller-Goodman 2001, McLaren & Jefferies 2004). On longer time scales, submergence via sea-level rise generates ponding, peat degradation, and vegetation losses that may produce spatial heterogeneity (De-laune et al. 1994, Hartig et al. 2002).

In addition to responses to disturbance, tidal marshes may contain microtopography that represents more steady-state environmental conditions, persisting over many years and over a substantial spatial extent, as found in other wetlands. St. Omer (2003) found spatial variability in soil constituents associated with microsite differences in plant species distribution in a California salt marsh. In brackish marshes, distinct microtopographic vegetational relief has been noted by several authors, yet it is poorly understood, particularly as it relates to sediment biogeochemical features. In these systems, clonal plant species form clumps, elevated (5 to 10 cm; Windham 1999, Posey et al. 2003) above adjacent bare, unconsolidated sediments. Hummock/hollow topography has been described for *Spartina patens* marshes (New Jersey, Windham 1999; Louisiana, R. Twilley pers. comm.), for mesohaline marshes dominated by *Phragmites australis* and *Sp. alterniflora* on Chesapeake Bay (Posey et al. 2003) and the Hudson River (Montalto et al. 2006), and for a tidal freshwater/oligohaline marsh dominated by *Peltandra virginica* (Yozzo & Smith 1995).

Brackish-marsh microtopographic variability is found in interior-marsh areas remote from tidal creeks (Windham 1999, Montalto et al. 2006). These interior marshes receive reduced sediment inputs and more limited tidal flushing. Interior marshes are commonly

characterized as having reduced productivity, largely due to elevated stressors such as H₂S and sediment anoxia (Mendelssohn & Morris 2000).

In this study, we investigated microtopographic variability in vegetation cover and sediment biogeochemistry within a mesohaline brackish marsh. We studied 2 adjacent regions of different elevation and hydrological regime: the elevated streamside bank-marsh area, and the low, frequently flooded, interior-marsh area. Distinct microtopography was present only at the interior site. We hypothesized that variability in the sediment biogeochemistry would reflect the spatial variability of the vegetation in that marsh. Our premise was that the plants maintained a more favorable sedimentary environment within the hummocks, much as plants in deserts and other terrestrial ecosystems create favorable microhabitats that enhance their survival.

MATERIALS AND METHODS

Study sites. The 2 marsh sites studied are on the eastern shore of Chesapeake Bay, Maryland, US, located on Monie Creek (38° 13' N, 75° 51' W), a tributary of Monie Bay, in the National Estuarine Research Reserve System (Fig. 1). The first site was within the elevated bank-marsh adjacent to the creek, and the second was within the low, interior marsh, approximately 100 m inland from the creek. The interior marsh receives semidiurnal tidal flooding, whereas

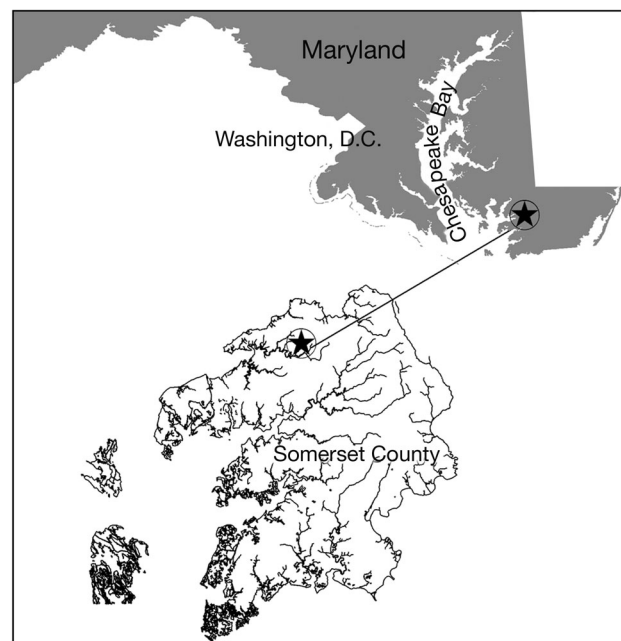


Fig. 1. Study site, showing sampling marsh (*Spartina* spp.) area (★) above Monie Creek, Chesapeake Bay

the bank marsh is usually flooded only on spring tides. Sampling was conducted between late July and early August of 2000.

The bank marsh was dominated by *Spartina cynosuroides* (L.) Roth, with some *S. alterniflora* Loisel., and the interior marsh site was almost monotypic *S. alterniflora*. The vegetation of the interior marsh displayed a hummock/hollow distribution, with the bare hollows devoid of both above- and below-ground plant material. The margins of the hummocks were abrupt, with a clear edge defining the transition between the exposed mud of the hollows and the elevated clumps of the hummocks.

We randomly selected 5 sampling sites within each marsh. For each site, elevation was measured at the microtopographic scale, and porewater and solid phase samples were collected. Hummock topography was delineated for the 5 sites within the interior marsh.

Elevation and microtopographic measurements. Hummock height was determined as the difference between the hummock and hollow elevations. In the bank marsh, where there were no well-defined unvegetated areas, measurements were made within and between culms. We measured elevation using a water level (accurate to ± 0.25 cm) with an arbitrary reference point to allow comparison of elevation between the 2 marsh sites as well as between microsites.

For the interior marsh, the scale of microtopographic relief was assessed using a 2 m² rectangular PVC quadrat, which was divided into a 4 × 8 (32 cell) grid. Hummock boundaries within the quadrat were outlined on graph paper for each of the 5 randomly chosen sampling sites. These plots were digitized, and analyzed through overlaying 5 grid templates from 0.04 to 1.0 m² using ARC/INFO GIS. The data of each of the plots from the GIS (Geographic Information System) analysis were then used to produce a variogram of percent vegetation cover.

Sediment porewater collection and analysis. Porewater was sampled at the peak of the growing season (late July) in 2000 for dissolved, soluble, reactive phosphorus (SRP), NH₄⁺, ΣH₂S and Fe²⁺. These represent the bioavailable forms of the 2 most important nutrients in the marsh (N and P) and of 2 primary indicators of biogeochemical processes related to anoxia (ΣH₂S and Fe²⁺). At each marsh, porewater was collected at the 5 previously established sampling sites for each of 2 microsites, 'vegetated' and 'bare.' In the bank marsh, where plant cover was homogeneous and no unvegetated areas were present, vegetated and bare samples were taken beneath and between culms, respectively. In the interior marsh, which was topographically heterogeneous, hummocks and hollows represented the vegetated and bare sampling sites,

respectively. Modified Hesslein (1976) diffusion equilibrators (Stribling et al. 1998) were used to collect porewater in 5 circular chambers (4 cm diam.) centered at depths encompassing the active root zone: 3, 8, 13, 18, and 23 cm. The equilibrators were deployed for 10 d, then sampled immediately upon retrieval.

For determination of ΣH₂S, water was drawn from the chamber through a 0.45 μm filter directly into diamine sulfide reagent (Cline 1969) for colorimetric analysis. The remainder of the sample was divided into filtered aliquots and stored frozen prior to analysis. Measurement of SRP and NH₄⁺ used the ascorbic acid method and the indophenol method, respectively (Parsons et al. 1984). Dissolved Fe²⁺ concentrations were determined according to Gibbs (1979). This method measures total dissolved Fe; we presumed most of the Fe in the porewater to be Fe²⁺.

A 2-level design of vegetated and bare sediments was used to assess the microtopographic variability. Continuous sampling along a transect to establish a semi-variogram of sediment characteristics would appear to be more precise, but the scale of the marsh hummocks combined with that of the sampling devices (larger sediment cores and equilibrator-derived porewater) would have made such sampling too destructive and created interference between samples. In addition, no gradient of plant cover was visibly evident from center to margin of the hummocks.

In addition to comparison of microsite sediment porewater within each marsh, we further evaluated the effect of vegetation on the sediment biogeochemistry by comparing porewater concentrations between the 2 marshes, focusing in particular on comparison of the bank-marsh sediments with those of the interior hummocks. Experimental design for this mesoscale analysis was the same as for the microsite comparison.

Solid-phase sediment sampling and analysis. Sediments were collected from both marshes in early August 2000 using a McAuley corer (Bricker 1989) for acid-extractable Mn and Fe, total P, N and C, and inorganic P. These were chosen for their potential to reflect dynamic biogeochemical transformations. Of the randomly chosen sampling sites at each marsh, 4 were cored in pairs (vegetated and bare sediments). Cores were sectioned at 2.5 cm intervals to a depth of 25 cm, then at 5 cm intervals to 50 cm. Sediments were dried at 60°C for 5 d and then ground with a mortar and pestle.

Sediment C and N were determined using a Control Equipment CHN analyzer (Exeter Analytical); total and inorganic P were measured on ashed and unashed samples, respectively, using 1 N HCl extraction (Aspila et al. 1976) and colorimetric analysis. Solid-phase Fe and Mn were measured using flame atomic-absorption

spectrophotometry on the unashed sediment acid-extraction (Leventhal & Taylor 1990).

Statistical analysis. Statistical analysis of porewater and solid-phase profiles was performed using a mixed model, univariate, repeated-measures analysis (Statistical Analysis System 2001). The estimation method was restricted maximum likelihood (REML), with depth as the within-unit factor and microsite (vegetated or bare) as the between-unit factor for the microsite comparison. For the mesoscale comparison, topographic position (bank or interior) and microsite (vegetated or bare) were the between-unit factors.

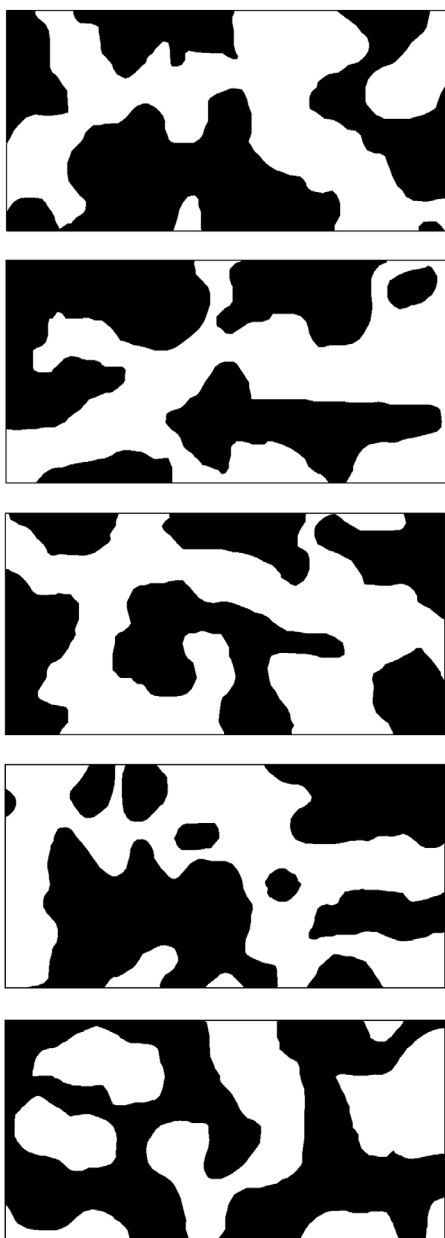


Fig. 2. *Spartina* spp. marsh. Digitized image of the five 2 m² interior-marsh sampling sites (hummocks in black)

RESULTS

Sediment elevation and scale of variability of plant cover

Hummocks in the interior marsh covered approximately 40% of the surface, with the remainder completely unvegetated (Fig. 2). The variance of percent vegetation cover reached an asymptote at 0.64 m². The mean \pm SE elevation of hummocks above hollows was 7.2 \pm 0.8 cm (ANOVA; $F_{1,8} = 7.66$, $p = 0.02$; Fig. 3). There was a larger mesoscale elevation difference: the mean sediment elevation at the bank was 15.7 cm above the mean elevation of the hummocks in the interior marsh. No topographic relief was measurable between the vegetated and interculm sediments of the bank marsh.

Porewater chemistry

Depth-averaged porewater ion concentrations were of similar magnitude to measurements from other brackish systems (Chambers et al. 2002, Windham & Ehrenfeld 2003). Few authors have examined porewater profiles of these ions in mesohaline marshes.

Microscale spatial variability

Biogeochemical spatial variability was pronounced in the interior marsh. There were significantly ($p < 0.05$) higher concentrations of $\Sigma\text{H}_2\text{S}$ and NH_4^+ in the hollow sediments compared with the hummocks, and spatial variability was present for SRP and Fe^{2+} also (Table 1, Fig. 4).

In many cases, the profiles converged or diverged near 13 cm, upholding visual observation of this depth as the limit of the active root zone (Fig. 4). Lower

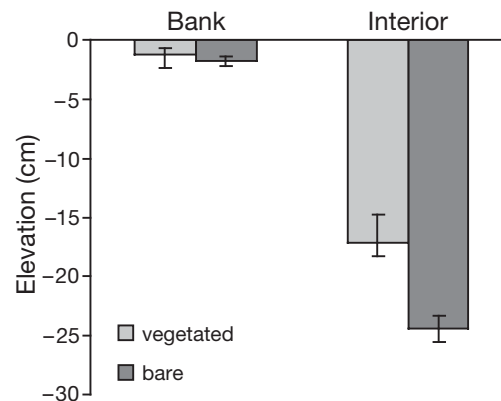


Fig. 3. *Spartina* spp. marsh. Mean elevations of vegetated and bare sediments of the 2 marshes, based on randomly chosen reference value

Table 1. *Spartina* spp. marsh. Between-microsite analysis of porewater Fe²⁺, NH₄⁺, SRP (soluble reactive phosphorus) and ΣH₂S depth profiles in the interior marsh (non-significant [ns] comparisons omitted). Depths shown are those for which post-hoc comparisons were significant (p < 0.05)

Ion	p (depth × microsite) (F _{4,7})	p (microsite) (F _{1,7})	Depth (cm)
Fe ²⁺	0.0145 (6.16)	ns	3, 8
NH ₄ ⁺	0.0314 (4.63)	ns	
SRP	0.0148 (6.12)	ns	
ΣH ₂ S	ns	0.0270 (7.30)	

concentrations of the reduced forms ΣH₂S and NH₄⁺ in the upper sediments reflected oxidation by plant roots in that region. The SRP hummock profiles indicated depletion within the root zone (probably resulting from plant uptake and adsorption to iron oxyhydroxide minerals) and higher concentrations at depth (where anoxic conditions release soluble SRP). In contrast, SRP concentrations in the hollow porewater changed little with depth (Fig. 4c).

For all 4 porewater constituents sampled, there were no significant differences between vegetated and interculm profiles in the bank-marsh sediments. This elevated portion of the marsh was virtually homogeneous spatially both in plant distribution and in porewater chemistry.

Topographic scale (mesoscale) variability

The effect of microtopography on sediment porewater in this brackish-marsh system is especially well-illustrated through a mesoscale comparison of the interior with the bank-marsh microsite types (Table 2, Fig. 4). The bare (interior hollow and bank interculm) porewater profiles were significantly different, either by topographic position (bank or interior), or by depth × topographic position interaction, or both, for all ions. However, there were no significant differences detected between the vegetated (interior hummock and bank beneath-culm) porewater profiles for ΣH₂S, SRP and NH₄⁺. In fact, the interior-marsh hummock profiles for ammonium were almost identical to those of the bank marsh, and the hummock sulfide profiles more closely resembled those of the bank marsh than they did those of the surrounding hollows (Fig. 4). For most porewater ions, therefore, the presence of vegetation was more important than topographic position, and the hummocks were associated with a biogeochemical environment similar to that of the bank sediments.

Porewater ΣH₂S and NH₄⁺ concentrations were elevated in the interior hollow sediments compared with

Table 2. *Spartina* spp. marsh. Comparison of vegetated (hummock or interculm) and bare (hollow or beneath-culm) porewater (PW) profiles for Fe²⁺, NH₄⁺, SRP, and ΣH₂S. Depths shown are those for which post-hoc comparisons were significant (p < 0.05). No significant differences were found for NH₄⁺, SRP, or ΣH₂S in vegetated profile comparisons

Microsite	PW ion	p (depth × site) (F _{4,7})	p (site) (F _{1,7})	Depth (cm)
Vegetated	Fe ²⁺	ns	0.0187 (6.16)	8, 13
Bare	Fe ²⁺	<0.0001 (153.12)	<0.0001 (62.50)	8, 13
Bare	NH ₄ ⁺	ns	0.0255 (7.99)	All
Bare	SRP	0.0006 (20.55)	ns	
Bare	ΣH ₂ S	ns	0.0007 (32.76)	All

those of the bank marsh (Fig. 4), as expected for ions in the redox sequence within such a poorly flushed region. However, the pattern for reduced Fe²⁺ was almost the opposite; bank-marsh Fe²⁺ concentrations were higher than for the interior porewater above 18 cm depth (Fig. 4). A topographic-scale pattern of elevated creekbank Fe relative to low-marsh sediments has also

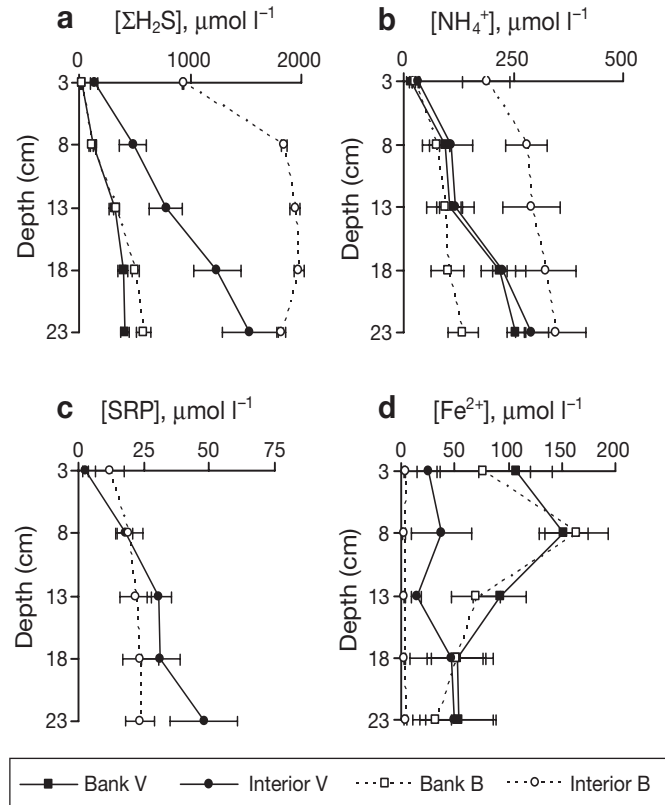


Fig. 4. *Spartina* spp. marsh. Mean ± 1 SE depth profiles for interior and bank vegetated (V) and bare (B) microsite porewater. (a) ΣH₂S, (b) NH₄⁺, (c) SRP, and (d) Fe²⁺. For the bank marsh, sampling was done (V) beneath and (B) between culms within the homogeneous plant community. Bank-marsh profiles for SRP (not significantly different) have been omitted for clarity; their concentrations were similar to those in the interior marsh

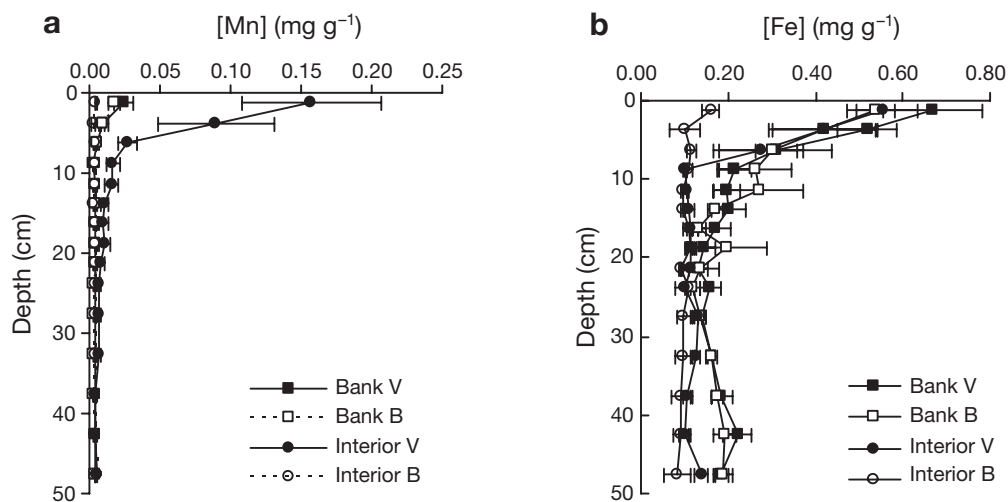


Fig. 5. *Spartina* spp. marsh. Mean \pm 1 SE depth profiles of solid-phase acid-extractable (a) Mn and (b) Fe for interior and bank vegetated (V) and bare (B) sediments

Table 3. *Spartina* spp. marsh. Between-microsite analysis of solid-phase Fe, Mn, TP (total P) and N profiles in the interior marsh. Depths shown are those (except for Mn) for which post-hoc comparisons were significant ($p < 0.05$). For the bank marsh, only TP showed a significant ($p = 0.04$; $F_{14,84} = 1.85$) depth \times microsite interaction

Element	p (depth \times microsite) ($F_{14,84}$)	p (microsite) ($F_{1,6}$)	Depth (cm)
Fe	0.0003 (3.32)	0.0476 (6.17)	1, 3, 21
Mn	0.0719 (1.69)	ns	11, 13, 18, 21, 27
TP	0.0004 (3.29)	ns	1, 3
N	0.0326 (1.94)	ns	1, 21

been noted in tidal freshwater marshes (Chambers & Odum 1990, Bryner 2000). This phenomenon may be indirectly related to the enhanced ability of the plants to oxidize upper sediments in the more favorable bank-marsh habitat. Rapid precipitation of oxidized Fe that is delivered to the rhizosphere as Fe^{2+} via porewater advection would result in a region of enhanced Fe(III) concentration, with tidally driven cycling between Fe^{2+} and Fe(III) oxides producing elevated porewater Fe^{2+} profiles. We observed Fe(III) oxides within the bank-marsh equilibrator chambers when they were sampled at low tide, indicating re-oxidation of the porewater Fe^{2+} within the chambers. Sediment Fe profiles support the hypothesis of increased Fe pools within the rhizosphere (see Fig. 5 and next section).

Solid-phase sediment minerals

As with porewater, sediments in the bank marsh were homogeneous with respect to solid-phase mine-

erals, with the exception of a depth \times microsite interaction ($p = 0.04$) for total P (Table 3). In contrast, in the interior marsh, microscale variability in solid-phase constituents was significant for Fe, total P and N. For these, as with porewater, the variability was limited to the upper, root-zone segments. No microsite differences were found for C in the interior marsh, however. Percent C in both marshes was relatively high (mean over all depths = 10.3% in the bank marsh, 10.8% in the interior). Perhaps the low tidal energy in the interior marsh results in retention of fine organic particulates, offsetting the absence of vegetation in the hollows. Posey et al. (2003) found no difference in percent organic matter between microsites in either *Phragmites australis* or *Spartina alterniflora* communities of a Chesapeake Bay marsh.

In the interior marsh, hummock sediment Fe concentrations were substantially higher than in the hollows, as appeared to be the case for Mn also (Fig. 5). Significant differences in near-surface solid-phase Mn between interior hummocks (mean \pm SE 0.157 ± 0.049 mg g^{-1}) and hollows (0.0045 ± 0.0008 mg g^{-1}) were not detected, although post-hoc comparisons found significant differences for 5 depths (Table 3). It is likely that the highly reducing environment of the interior sediments facilitates mobility of Fe and Mn and their subsequent precipitation and concentration around the oxidizing plant roots in the hummocks (Mendelssohn & Postek 1982).

DISCUSSION

This study demonstrates that microscale spatial variability of brackish-marsh vegetation reflects variability in sediment biogeochemical features at the same

scale. The microtopographic variability was also of approximately the same scale as the height of the dominant plant species, as has been found for many systems (Huenneke & Sharitz 1986, Schlesinger et al. 1996, Windham 1999, Rietkerk et al. 2000).

Microtopographic variability may result from the actions of the plants themselves, or it may arise as plants respond to underlying sediment heterogeneity through spatial distribution. In studies of other ecosystems, correlation between the spatial distribution of sediment biogeochemistry and of vegetation is often presented as evidence for creation of soil heterogeneity by plants (Schlesinger et al. 1996, Rietkerk et al. 2000). However, Huenneke & Sharitz (1986) described swamp microtopography as arising from such features as woody debris or treefall mounds, and Jackson & Caldwell (1996) also noted that plants may respond to pre-existing variability.

In this study, the marsh exhibited no evidence of a pre-existing microtopographic variability. On the other hand, the enhancement of spatial variability in the upper, root-zone sediments, which was exhibited by both porewater and solid-phase constituents, supports the role of plants as creating this variability through root oxidation and other processes. Further evidence of the plants' ability to create favorable microhabitats within more stressful brackish-marsh environments was found in the biogeochemical similarity between the vegetated sediments of the bank and interior marshes, despite the interior marsh's lower elevation and its location remote from tidal flushing.

There is ample evidence for modification of sediment biogeochemistry by marsh plants. *Spartina alterniflora* has been shown to affect sediment oxidation, redox potential (Howes et al. 1981), and sulfate reduction rates (Howes et al. 1986, Hines et al. 1989). Hsieh & Yang (1997) demonstrated that *Juncus roemerianus* roots significantly influenced Fe and S sediment dynamics. Madureira et al. (1997) described strong effects of vegetation on sediment sulfur chemistry in a Tagus (Portugal) *S. maritima* salt marsh, although vegetated and unvegetated sediments in their study were more widely separated than in the present study.

In the hummock/hollow interior of this brackish marsh, the hummocks represent the outcome of 'ecosystem engineering' (Jones et al. 1994) by marsh vegetation. Plants increase elevation through sediment trapping and organic matter accumulation, and they alter sediment chemistry through root oxidation. Increased elevation adds to the potential for sediment oxidation. A positive feedback is established whereby plant productivity, and consequently the ability to promote accretion and to oxidize sediments, increases. Sparse plant distribution in the interior marsh results in unvegetated hollows. The plants may be unable to ex-

pand to a uniform distribution, given the need to allocate plant resources to managing the sediment chemical environment. As Schlesinger et al. (1996) described for desert 'islands of fertility', plants become more resistant and better able to survive in the local environment. Windham (1999) further credited hummock-forming root morphology in *Spartina patens* as enhancing the plants' competitive ability in the face of invasion by *Phragmites australis*.

Van Breemen & Finzi (1998) provided examples of a number of ecosystems in which plants create environmental changes that facilitate survival, creating positive plant-soil feedbacks. In particular, they emphasized changes in nutrient availability, and in other constituents directly related to plant survival, as evidence for the plant-to-soil direction of the relationship. Distinguishing between nutrients and elements unrelated to plant success can point to whether soil characteristics are responsible for plant patchiness or vice versa. In systems where nutrient availability is not the most important factor for plant success, other limiting resources underlie heterogeneity of plant distribution (Schlesinger et al. 1996, Rietkerk et al. 2000). Rietkerk et al. (2000) showed that when soil moisture was scarce in a semi-arid West African ecosystem, its availability matched vegetation heterogeneity, and when moisture was adequate, soil organic matter and NH_4^+ availability became more important in determining the spatial variability in distribution of perennial grasses. They concluded that these spatial patterns were a result of positive effects of vegetation on the soils, and not of pre-existing microtopography.

In this study, solid-phase N showed no microtopographic heterogeneity, whereas indicators of sediment anoxia, such as $\Sigma\text{H}_2\text{S}$ and NH_4^+ , were negatively associated with vegetative cover. This is to be expected in an environment in which sediment oxidation is more likely to limit productivity than nutrient availability, as is well-documented for wetlands (e.g. DeLaune et al. 1983, Bradley & Morris 1990). For this marsh, then, the plant-soil environmental change centers on reduction of anoxic conditions and of the associated inorganic ions ammonium and sulfide.

Temporal variability superimposed on spatial variability may amplify microtopographic differences in sediment chemistry. The differences we measured between hummock and hollow porewater constituents may have underestimated the extent of spatial variability for reduced substances such as $\Sigma\text{H}_2\text{S}$, NH_4^+ and Fe^{2+} . For the submerged aquatic plant *Zostera marina*, diurnal fluctuations of considerable magnitude have been measured in sediment H_2S and Fe^{2+} (Hebert & Morse 2003), based on cycles of peak photosynthetic activity and root oxidation. Such variation also occurs in intertidal marsh sediments. For example, pH has

been demonstrated to change by as much as 2 U on a diurnal cycle in a Virginia marsh (Wolaver et al. 1986). Sediment oxidation by plants during periods of maximum photosynthesis could produce heterogeneity in concentrations of reduced substances not detectable with equilibrators, which integrate porewater signals over several days.

The relatively common occurrence of microtopographic variability in brackish tidal wetlands highlights the necessity for appropriately scaling sampling design. Where this is not done (as Branfireun [2004] concluded from a study of peatland spatial variability), the location of sampling can substantially affect conclusions drawn from wetland studies. Primary productivity estimates based on biomass harvest, the determination of sediment chemical constituents, and virtually all wetland assessments are subject to considerable error, depending on the scale of sampling. In heterogeneous systems, observation of reduced productivity on an aerial basis may result as much from the substantial area of unvegetated hollows as from reduced production by plants within the hummocks. Characterizations of sediment–plant interactions in spatially variable systems must also be based on sampling each from the same topographic microsite.

Tidal marsh hummock/hollow microtopography appears to be restricted to regions of brackish systems remote from effective tidal flushing, and it may be useful as a visual indicator of sediment condition. This feature merits further investigation, in part because of the large geographic extent of brackish wetlands. They comprise 73% of the areal coverage of tidal marshes in the Chesapeake Bay system (Stevenson et al. 1985) and are widespread in (e.g.) the Camargue and other regions of the Mediterranean, in Mississippi Delta marshes, in boreal marsh systems, and in SE Australia (Adam 1990). More extensive documentation of the extent of this spatial patterning within brackish wetlands would contribute to our understanding of the functioning of these wetlands in the landscape.

In conclusion, this study has documented microtopographic variability in both vegetation distribution and sediment chemistry within a brackish-marsh system. Hummock/hollow patterning reflected the relatively stressful and variable environmental conditions of the interior marsh compared with the more favorable environment of the bank marsh, where plant distribution was homogeneous. The association of sediment biogeochemistry with heterogeneity of plant cover has received only limited attention for tidal marshes. Although such complex interactions have been extensively described for ecosystems from deserts to peatlands, even in these, there is rarely the opportunity to compare biogeochemical features associated with heterogeneous vegetation with those of adjacent ho-

mogeneous areas, as the present study has done. In addition to identifying differences between hummock and hollow sediments, we found a strong resemblance of sediment biogeochemical features beneath hummocks to those of the homogeneous marsh.

The microtopographic relief of interior, brackish marshes is a notable example of the effects of plant–soil feedback. Plants modified elevation and sediment chemistry within the frequently flooded interior marsh to produce a growing environment that, albeit limited to discrete patches, closely resembled that of the elevated bank marsh.

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