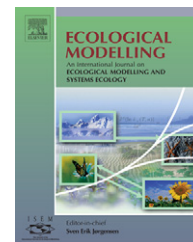


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A novel 2D model of internal O₂ dynamics and H₂S intrusion in seagrasses

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ABSTRACT

Seagrasses provide a physical connection between the water column and sediments by transporting photosynthetic- and seawater-derived oxygen to their roots and rhizomes. In this paper, we present a single-shoot reaction-transport model that incorporates the biological, chemical and physical processes in the water column, seagrass plant, and sediments and that simulates oxygen and hydrogen sulfide dynamics in the system. The model reproduces oxygen and sulfide patterns observed in laboratory manipulations and field measurements of *Thalassia testudinum* and *Zostera marina*. Model results reinforce experimental conclusions that (1) meristem oxygen is tightly coupled to water column oxygen and diel patterns of sunlight, (2) sediment sulfide enters the plant when plant tissues are hypoxic, and (3) internal sulfide is rapidly depleted once oxic seawaters are re-established or with the onset of photosynthesis. Sensitivity analysis further emphasizes that water column oxygen concentration has a strong influence on the minimum oxygen concentration and maximum sulfide concentration in the meristem at night. The model indicates that diffusion is the dominant transport process in the lacunae, though advective mass flow can account for nearly a quarter of oxygen transport during periods of increasing sunlight. In the model, biological sulfide oxidation and plant dissolved organic carbon exudation both play significant roles in determining patterns of sediment oxygen consumption and sulfide intrusion into the plant.

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1. Introduction

The ability of seagrasses to transport oxygen and sustain respiration in the plant's rhizomes and roots is a fundamental adaptation for survival in anoxic marine sediments. Seagrass tissues buried in sediment are susceptible to anoxic stress as surrounding sediments are typically anaerobic and replete in reduced compounds. To thrive in these conditions, seagrasses have evolved intercellular airspace structures, collectively called lacunae, that interconnect leaves, short shoots, rhizomes and roots. Gas-phase diffusion and mass flow in the lacunae facilitate efficient transport of water column and pho-

tosynthetically derived oxygen to below-ground plant organs. Oxygen is then available for root and rhizome respiration, and some aquatic plants leak excess oxygen into the surrounding sediments (Sand-Jensen et al., 1982; Smith et al., 1984; Borum et al., 2005).

Microbes and abiotic reactions quickly consume oxygen in the sediment, and the extent of the aerobic zone around the roots depends on oxygen supply, rates of organic matter remineralization, and both the concentration and reactivity of reduced compounds. In addition to oxygen, seagrass release dissolved organic carbon (DOC) in the sediments, and both seagrass detritus and DOC exudation are signifi-

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cant organic carbon sources to the benthos (Blaabjerg et al., 1998; Holmer et al., 2001; Jones et al., 2003). Kaldy et al. (2006) used isotope-tracer experiments and inverse modeling techniques to estimate that *Thalassia testudinum* exudes 15–30% of its gross primary production (gPP) as labile DOC, a carbon source easily metabolized by sediment bacteria. Thus, seagrasses supply the rhizosphere with both a carbon source as well as the oxidizing agent that drive benthic processes, and the oxic rhizosphere is a site of localized remineralization that regenerates nutrients near the plant (Hemminga, 1998).

In sediments outside the rhizosphere, microbes decompose organic matter using electron acceptors such as nitrate, iron and manganese oxides, and sulfate (Thamdrup et al., 1994). Dissimilatory sulfate reduction is considered a particularly important remineralization pathway in seagrass habitats (Blackburn et al., 1994; Blaabjerg et al., 1998; Holmer et al., 2001). The reaction produces hydrogen sulfide which accumulates in the sediment and can diffuse into the rhizosphere. In areas of the rhizosphere where oxygen and sulfide coexist, bacteria can exploit the redox potential between the two chemical species to drive anabolic reactions (Somero et al., 1989; Jørgensen and Nelson, 2004). Maintaining an oxic rhizosphere is therefore adaptive to the plant as it provides a buffer against reduced metabolites, such as sulfide. Still, if environmental or biological conditions decrease oxygen supply or otherwise result in sulfide accumulation, the extent of the rhizosphere may diminish to the point where sulfide can enter the plant.

Current understanding of oxygen and hydrogen sulfide dynamics in seagrasses is based largely on microsensor measurements in the plant and rhizosphere. Oxic zones have been directly measured in sediments surrounding roots of *Halophilla ovalis* (Connell et al., 1999), *Cymodocea rotundata* (Pedersen et al., 1998) and *Zostera marina* (Frederiksen and Glud, 2006; Jensen et al., 2005) and near *Potamogeton perfoliatus* rhizomes (Caffrey and Kemp, 1991). When maintained in the dark, internal oxygen concentration in seagrasses is related to oxygen concentration in the water column, suggesting water column-derived oxygen supports plant respiration at night (Pedersen et al., 2004; Greve et al., 2003; Borum et al., 2005; Sand-Jensen et al., 2005). Moreover, functional seagrasses in well aerated seawater are able to maintain an oxic rhizosphere, even in darkness (Frederiksen and Glud, 2006; Jensen et al., 2005; Pedersen et al., 1998; Connell et al., 1999). In continuous light, photosynthesis rapidly increases plant oxygen concentration (Greve et al., 2003; Borum et al., 2005; Terrados et al., 1999), and the radial extent of the rhizosphere responds to variations in irradiance and photosynthesis (Jensen et al., 2005; Frederiksen and Glud, 2006). In the absence of light and in sub-oxic waters, seagrasses are susceptible to sulfide intrusion. Borum et al. (2005) and Pedersen et al. (2004) measured sulfide in leaf meristems of *T. testudinum* and *Z. marina* when plants were monitored in darkness and in oxygen deprived waters, and both studies also demonstrated that internal sulfide quickly dissipates with the onset of light and photosynthesis.

Plant–sediment interactions that lead to plant hypoxia and sulfide intrusion have ecosystem-scale consequences. Seagrasses revert to glycolysis and production of fermentation end-products when oxygen conditions no longer support aer-

obic respiration (Smith et al., 1988). If hydrogen sulfide invades the plant and penetrates to metabolically sensitive areas of the plant, it can interfere with mitochondrial electron transport and is generally toxic to aerobic organisms (Raven and Scrimgeour, 1997). Oxygen deprivation and sulfide intrusion likely hamper seagrass growth and decrease survivorship (Holmer and Bondgaard, 2001), particularly if these conditions persist in actively mitotic meristems. Plant hypoxia and sulfide intrusion have been implicated in the *T. testudinum* die-off phenomenon in Florida Bay (Carlson et al., 1994; Zieman et al., 1999) and other seagrass mortality events (Greve et al., 2003).

In this paper, we present a two-dimensional (2D) reaction-transport model that captures the time evolution and interaction of oxygen and hydrogen sulfide in the water column, sediments, and seagrass plant. We first detail the model formulation and demonstrate that the model reproduces important oxygen and sulfide dynamics identified in microelectrode experiments. A diel cycle of oxygen and sulfide is simulated for a *T. testudinum* plant using conditions similar to those found in a healthy seagrass environment in Florida Bay. With this simulation as a baseline, important system-controlling factors are identified through sensitivity analysis. Finally, we discuss the relative significance of advective mass flow to overall mass transport in seagrass lacunae.

2. Model concept

The model domain encompasses the water column and sediment surrounding a single *T. testudinum* ramet composed of four modules: the leaves, short shoot, rhizome and roots (Fig. 1). Seawater oxygen is controlled using a time varying forcing function imposed at the system boundary, and oxygen is produced by plant photosynthesis. In the plant, oxygen travels through the lacunae to support below-ground plant respiration and sediment metabolism in the rhizosphere, i.e., the sediment characterized by enhanced microbial activity surrounding roots and rhizomes. Bacterial carbon respiration drives sediment processes and is fueled by sedimentary organic carbon and DOC released from the below-ground seagrass plant. If oxygen is available, sediment metabolism consumes oxygen. Otherwise sulfate reducing bacteria respire the remaining carbon, and hydrogen sulfide is produced. Where oxygen and sulfide coexist, biologically mediated sulfide oxidation consumes both. Environmental or physiological conditions that stimulate sediment metabolism or decrease oxygen transport lead to increasingly reduced sediments in the plant rhizosphere. Eventually, as sulfide concentrations increase and below-ground plant tissues become hypoxic, sulfide may infiltrate the plant and diffuse to the leaf meristem and other metabolically sensitive areas of the seagrass.

3. Governing equation

We exploit the symmetry of the problem by using a 2D representation of the single ramet system. The plant is further

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