A novel 2D model of internal $O_2$ dynamics and $H_2S$ intrusion in seagrasses

Harlan L. Miller III*, Christof Meile, Adrian B. Burd

Marine Sciences Department, University of Georgia, Athens, GA 30602, USA

A R T I C L E   I N F O

Article history:
Received 13 August 2006
Received in revised form
24 February 2007
Accepted 2 March 2007
Published on line 6 April 2007

Keywords:
Thalassia testudinum
Zostera marina
Reaction-transport models
Hydrogen sulfide
Oxygen
Biological sulfide oxidation
Root aeration
Sulfide intrusion

A B S T R A C T

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.

© 2007 Elsevier B.V. All rights reserved.

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 photosynthetically 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-
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 Halophila 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 aerobic 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
Fig. 1 – Conceptual model for oxygen and hydrogen sulfide transport in seagrasses. Transport and reactive processes are followed throughout the water column, seagrass plant, and sediment system. Diel forcing functions—$E_{\text{PAR}}$: photosynthetically active radiation, $f_{\text{O}_2}$: water column oxygen concentration, $T$: temperature, and $S$: salinity (held constant). Rates—$P$: photosynthesis, $R_p$: plant respiration, $R_C$: carbon respiration profile in sediments, and $R_{\text{Sox}}$: biological sulfide oxidation. DOC and POC denote dissolved and particulate organic carbon. Original Thalassia testudinum line drawing from Tomlinson and Vargo (1966).

simplified to a single T. testudinum leaf, oriented edgewise, and the fraction of below-ground tissues supported by one leaf (Fig. 2). Mass conservation is described by,

$$\phi(x, y) \frac{\partial C_i}{\partial t} = \nabla [\phi(x, y)D_i(x, y)\nabla (\alpha_i(x, y) C_i)]$$

$$- \frac{\partial}{\partial y} [v(y)C_i] + \phi(x, y) \sum R,$$

where $C_i$ represents either oxygen or hydrogen sulfide concentrations ($\mu$M), $\phi$ is porosity, set to 0.8 in sediments and 1 otherwise (Carlson et al., 1994), $D_i$ are solute-specific diffusion coefficients, $\alpha_i$ is a solubility factor acting at the lacunal phase-transition boundary and 1 elsewhere, $v$ denotes advective velocities in the lacunae, and $\sum R$ represents the sum of all reaction rates (including photosynthesis) acting on solute $i$. Thus, change in concentration with time depends on diffusion, advection in lacunae, and net reaction.

3.1. Diffusion

Diffusion coefficients reflect the physical characteristics and biological structure in the model domain. Diffusion in seawater varies from a turbulent, well-mixed zone to an unstirred boundary layer near plant and sediment surfaces (Table 1), and diffusion coefficients in sediment porewaters ($D^*_i$) are corrected for tortuosity using $D^*_i = D_i^\text{(aq)}/(1 - 2 \ln(\phi))$ (Boudreau, 1997). In the plant, diffusion coefficients are based on T. testudinum anatomy and morphology (Tables 2 and 3) and follow the general resistance circuit for seagrasses proposed in Larkum et al. (1989). Within the lacunae, we use the relationships given in Sorrell and Dromgoole (1987) and Larkum et al. (1989) to account for differences in diffusion coefficients between internode chambers and nodal diaphragms.

The structure of the below-ground organs is a complex three-dimensional network. This is simulated in the model by calculating a modified, area weighted, diffusion coefficient ($D_i^*$) such that the 3D fluxes are conserved in the 2D model. The model flux, $F_m$, across the 2D exchange area, $A_m$, is equivalent to the combined fluxes across the plant–sediment interfaces.
The epidermis of the three subterranean plant modules (ss: short shoot, rz: rhizome, rt: root, and s: sediment): i.e., the epidermis of the three subterranean plant modules

\[ A_{ss}(y)F_{ss}(y) = -D_{ss}A_{ss} \frac{\partial C_i}{\partial x} \bigg|_{ss-s} \]
\[ - D_{rz}A_{rz} \frac{\partial C_i}{\partial x} \bigg|_{rz-s} - D_{rt}A_{rt} \frac{\partial C_i}{\partial x} \bigg|_{rt-s} \]

In Eq. (2), diffusion coefficients are estimated for each module's epidermis (Table 1), and surface area profiles \( A_{ss}(y) \), \( A_{rz}(y) \) and \( A_{rt}(y) \) are related to corresponding biomass profiles by assuming that each module has a cylindrical morphology (Table 3). The short shoot is distributed evenly over its depth in the sediments, and rhizome and root biomass profiles are modeled using Gamma distribution functions (Fig. 2). Assuming that the modeled plant–sediment concentration gradient is representative for all below-ground modules, then the flux evaluated at the plant–sediment interface \( p \rightarrow s \) is,

\[ F_{ss}(y) = -D'(y) \frac{\partial C_i}{\partial x} \bigg|_{p-s}. \]

### Table 1 – Diffusion coefficients (m² s⁻¹)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>( D_v )</td>
<td>Vapor phase</td>
<td>( 9.7 \times 10^{-5} )</td>
<td>1</td>
</tr>
<tr>
<td>( D_{H2O} )</td>
<td>( \mathrm{O}_2 ) in aequous solution</td>
<td>( 1.98 \times 10^{-9} )</td>
<td>1</td>
</tr>
<tr>
<td>( D_{H2S} )</td>
<td>( \mathrm{H}_2\mathrm{S} ) in aequous solution</td>
<td>( 1.72 \times 10^{-9} )</td>
<td>2</td>
</tr>
<tr>
<td>( D_s )</td>
<td>Eddy diffusivity in mixed seawater</td>
<td>( 1.0 \times 10^{-5} )</td>
<td>3</td>
</tr>
<tr>
<td>( D_{syt} )</td>
<td>Cytoplasm</td>
<td>( D_{syt} )</td>
<td>4</td>
</tr>
<tr>
<td>( D_m )</td>
<td>Cell plasma membrane</td>
<td>( 1.0 \times 10^{-12} )</td>
<td>1</td>
</tr>
<tr>
<td>( D_w )</td>
<td>Cell wall</td>
<td>( 4.0 \times 10^{-10} )</td>
<td>1</td>
</tr>
<tr>
<td>( D_c )</td>
<td>Leaf cuticle</td>
<td>( 5.0 \times 10^{-12} )</td>
<td>1</td>
</tr>
<tr>
<td>( D_{chl} )</td>
<td>Chloroplast envelope (two layers)</td>
<td>( 5.0 \times 10^{-11} )</td>
<td>1</td>
</tr>
<tr>
<td>( D_{thy} )</td>
<td>Thylakoid membrane</td>
<td>( 5.0 \times 10^{-11} )</td>
<td>1</td>
</tr>
<tr>
<td>( D_{lw} )</td>
<td>Lacunae cell wall</td>
<td>( 2.0 \times 10^{-11} )</td>
<td>1</td>
</tr>
<tr>
<td>( D_{ho} )</td>
<td>Leaf outside cell wall</td>
<td>( 1.3 \times 10^{-10} )</td>
<td>1</td>
</tr>
<tr>
<td>( D_{exo} )</td>
<td>Leaf sheath outside cell wall</td>
<td>( 1.0 \times 10^{-12} )</td>
<td>U</td>
</tr>
<tr>
<td>( D_{rzo} )</td>
<td>Rhizome outside cell wall</td>
<td>( 1.0 \times 10^{-12} )</td>
<td>U</td>
</tr>
<tr>
<td>( D_{rto} )</td>
<td>Root outside cell wall</td>
<td>( 2.0 \times 10^{-11} )</td>
<td>U</td>
</tr>
</tbody>
</table>

Oxygen and hydrogen sulfide diffusion coefficients are distinct in aequous solution, otherwise they are assumed constant and equal in air, mixed seawater, and within the seagrass plant. Diffusion coefficients within Thalassia testudinum are derived from seagrass resistance estimates in Larkum et al. (1989) and cell structure dimensions (Table 2). Sources: (1) Larkum et al. (1989), (2) Boudreau (1997), (3) Ackerman and Okubo (1993), (4) Nobel (1999), and (U) user imposed.

### Table 2 – T. testudinum anatomy

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Value</th>
<th>Units</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>( X_e )</td>
<td>Epidermis cell thickness</td>
<td>28</td>
<td>μm</td>
<td>1</td>
</tr>
<tr>
<td>( Y_e )</td>
<td>Epidermis cell height</td>
<td>25</td>
<td>μm</td>
<td>1</td>
</tr>
<tr>
<td>( X_h )</td>
<td>Hypodermis cell thickness</td>
<td>40</td>
<td>μm</td>
<td>1</td>
</tr>
<tr>
<td>( Y_h )</td>
<td>Hypodermis cell height</td>
<td>50</td>
<td>μm</td>
<td>1</td>
</tr>
<tr>
<td>( X_c )</td>
<td>Leaf cuticle thickness</td>
<td>1</td>
<td>μm</td>
<td>1</td>
</tr>
<tr>
<td>( X_{sw} )</td>
<td>Leaf outside wall thickness</td>
<td>1</td>
<td>μm</td>
<td>U</td>
</tr>
<tr>
<td>( X_{cw} )</td>
<td>Plant cell wall thickness</td>
<td>1</td>
<td>μm</td>
<td>1</td>
</tr>
<tr>
<td>( X_m )</td>
<td>Plant membrane thickness</td>
<td>50</td>
<td>nm</td>
<td>2</td>
</tr>
<tr>
<td>( X_{chy} )</td>
<td>Chloroplast membrane thickness</td>
<td>5</td>
<td>nm</td>
<td>2</td>
</tr>
<tr>
<td>( X_{lw} )</td>
<td>Lacunae cell wall thickness</td>
<td>1</td>
<td>μm</td>
<td>U</td>
</tr>
<tr>
<td>( Y_l )</td>
<td>Lacunae internode length</td>
<td>200</td>
<td>μm</td>
<td>1</td>
</tr>
<tr>
<td>( Y_d )</td>
<td>Lacunae diaphragm length</td>
<td>10</td>
<td>μm</td>
<td>1</td>
</tr>
<tr>
<td>( f_p )</td>
<td>Diaphragm pore radius</td>
<td>0.5</td>
<td>μm</td>
<td>3</td>
</tr>
<tr>
<td>( P_{dia} )</td>
<td>Diaphragm pore spacing</td>
<td>0.2</td>
<td>pores μm⁻¹</td>
<td>3</td>
</tr>
<tr>
<td>( X_{swe} )</td>
<td>Leaf sheath outside cell wall</td>
<td>1</td>
<td>μm</td>
<td>U</td>
</tr>
<tr>
<td>( X_{swe} )</td>
<td>Short shoot outside cell wall</td>
<td>1</td>
<td>μm</td>
<td>U</td>
</tr>
<tr>
<td>( X_{swe} )</td>
<td>Rhizome outside cell wall</td>
<td>1</td>
<td>μm</td>
<td>U</td>
</tr>
<tr>
<td>( X_{rwe} )</td>
<td>Root outside cell wall</td>
<td>1</td>
<td>μm</td>
<td>U</td>
</tr>
<tr>
<td>( X_{swe} )</td>
<td>Below-ground outside cell wall</td>
<td>2</td>
<td>μm</td>
<td>U</td>
</tr>
<tr>
<td>( N_c )</td>
<td>Number of cortex cells</td>
<td>2</td>
<td>—</td>
<td>U</td>
</tr>
</tbody>
</table>

Sources: (1) Tomlinson (1972), (2) Nobel (1999), (3) Roberts and McComb (1984), and (U) user imposed.
The solubility factor,

\[
K_{\text{H}(y)} = B_{0}(y) - P_{T}(y).
\]  

(5)

where Bunsen coefficients, \( B_{i} \), are functions of temperature (T) and salinity (S) and \( P_{T} \) is total pressure (kPa) in the lacunae. \( P_{T} \) is the sum of hydrostatic pressure and constituent gas partial pressures, including nitrogen, argon and carbon dioxide gases, which are held constant at atmospheric partial pressures (Colt, 1984).

Oxygen and sulfide partial pressures in the lacunae are calculated from internal concentrations using the ideal gas law. \( B_{0_{2}} \) is calculated from the formula in Colt (1984), whereas \( B_{H_{2}S} \) is given by

\[
B_{H_{2}S}(T, S) = \frac{e^{(-k_{S}S)^{T}}}{H(T)} \cdot U(\rho).
\]  

(6)

where \( H(T) \) is Henry’s solubility constant in pure water (Carroll and Mather, 1989), \( k_{S} \) the sulfide salting coefficient (Millero, 1986), and \( U(\rho) \) is the density-dependent unit conversion factor to \( \mu M_{\text{aq}} \cdot \mu M_{\text{g}}^{-1} \cdot \text{kPa}^{-1} \). Density, \( \rho \), is determined using the 1980 International equation of State (Millero and Poisson, 1981).

### 3.3. Advection

Advective transport is restricted to the vertical direction within the lacunae, and velocities are calculated as

\[
v(y) = \frac{\Delta P_{T}(y)}{Re_{v}}.
\]  

(7)

where \( \Delta P_{T}(y) \) are the spatial differences in total gas pressure. \( Re_{v} \) is the average flow resistance and is derived from the Hagen-Poiseuille equation (Olson and Shelstad, 1987; Sorrell and Dromgoole, 1988), modified to include flow through...
internodes, diaphragm pores, and multiple lacunae (Table 2),

\[
R_{\text{EV}} = \left( \frac{\delta_{\text{lac}}}{\pi r^2_{\text{lac}}} + \frac{\delta_{\text{d}}}{N_p \pi r^2_{\text{d}}} \right) \frac{8n A_{\text{lac}}}{\pi N_{\text{lac}}},
\]

where \( N_p = \pi r^2_{\text{lac}} P_{\text{lac}} \) is the number of diaphragm pores, \( N_{\text{lac}} = Z/2r_{\text{lac}} \) the number of lacunal tubes, and \( \delta \) is the temperature dependent dynamic viscosity in air calculated at 50% relative humidity (Rasmussen, 1997). \( r_{\text{lac}} \) is the lacunal radius and \( r_{\text{d}} \) is the diaphragm pore radius. The relative length contributions of internodes and diaphragms within a \( \Delta Y \) step are denoted as \( \delta_{\text{lac}} \) and \( \delta_{\text{d}} \), respectively, and \( A_{\text{lac}} \) is the cross-sectional area of transport.

3.4. Reactions

Seagrass photosynthesis occurs in the leaf epidermis and is modeled using a Jassby-Platt relationship (Fourqurean and Zieman, 1991). Respiration consumes oxygen at all non-lacunae locations within the plant, and respiration rates vary between leaf, short shoot, rhizome and root modules (Table 4). Biomass-specific \( T. \ testudinum \) metabolic rates are based on measurements in Fourqurean and Zieman (1991). Leaf biomass is derived from ramet density (Hall et al., 1999) while short shoot, rhizome and root biomasses are proportional to the relative contribution of each to total biomass (Fourqurean and Zieman, 1991). Plant respiration rates are calculated at each computational grid node using equations in Table 4 and 5. Respiration temperature dependency is included as an Arrhenius function (Burd and Dunton, 2001), and a Monod formulation constrains respiration at low oxygen concentrations (Table 5).

Bacterial carbon respiration drives sediment metabolism and results in either oxygen consumption or hydrogen sulfide production (Table 5). Metabolic rates driven by the sedimentation of organic matter decline exponentially with sediment depth (Wang and Van Cappellen, 1996), and rate constants are calibrated such that modeled oxygen and sulfide profiles approximate measured profiles in seagrass bare areas (Borum et al., 2005). Bare area concentration profiles were used as an approximation of the local sediment processes that occur without the seagrass plant.

Microbial respiration in the sediment is also supported by seagrass-derived carbon. Sediment respiration of seagrass carbon is implemented assuming the plant releases a constant percentage of its daily gPP as DOC. This integrated rate is distributed with depth proportionally to the profile of diffusive exchange, \( D^*(y) \) in Eq. (4), across the plant–sediment boundary. Carbon respiration decreases exponentially with distance from the plant (Table 5), and the calculation assumes that DOC is completely metabolized by sediment bacteria. Thus, total carbon respiration at each sediment location is the sum of the vertical (i.e., sedimentary organic carbon) and horizontal (i.e., plant organic carbon) rate decay functions. If sediment oxygen is not sufficient to account for the imposed respiration rate, sulfate reduction is implied and hydrogen sulfide produced.

Hydrogen sulfide oxidation is implemented as:

\[
\text{H}_2\text{S} + 2\text{O}_2 \rightarrow \text{SO}_4^{2-} + 2\text{H}^+
\]

where the reaction rate depends on oxygen and sulfide concentrations. The reaction is implemented as a Monod formulation (Table 5), and the rate constant is calibrated such that measured oxygen and sulfide trends are reproduced. Since the calibrated reaction rate is much greater than the rate expected from the spontaneous reaction between oxygen and sulfide (Millero, 1986), the reaction is interpreted as biologically mediated sulfide oxidation (Jørgensen and Nelson, 2004).

3.4.1. Temporal environmental forcing functions

Oxygen concentration in the water column is imposed at the domain boundary using time-series data measured in a dense, albeit healthy, seagrass bed near Rabbit Key in Florida Bay (Borum et al., 2005). Diel oxygen forcing functions are formed from regression of oxygen data to a periodic function,

\[
f_{O_2}(t) = m + a \sin \left( \frac{2\pi (t - \phi)}{24} - \frac{\phi}{2} \right),
\]

where parameters \( m, a, \) and \( \phi \) are determined using a Levenberg-Marquardt algorithm (Press et al., 1992), and \( t \) is time in hours.

Irradiance is modeled as photosynthetically active radiation \( (E_{PAR}(t)) \) incident at the leaf surface. First, clear-sky irradiance is simulated at the sea-surface using a PAR model based on latitude and day number (Iqbal, 1983). The model assumes a flat sea and accounts for reflection and refraction at the air–sea interface (Kirk, 1994). Irradiance penetration to the top of the seagrass canopy is calculated using Beer’s Law and an imposed water column attenuation coefficient (canopy depth 0.5 m; \( k_d = 0.2 \text{m}^{-1} \)). Light along the leaf diminishes with a canopy-specific attenuation coefficient, which varies with ramet density as measured in \( T. \ testudinum \) seagrass beds (Enriquez and Fantoja-Reyes, 2005).

3.5. Numerics

Equation (1) is solved using an alternating-direction-implicit (ADI) method (Press et al., 1992), and the implementation was tested by simulating steady heat flow in a rectangular plate (Carslaw and Jaeger, 1986). Grid nodes exist at every \( \Delta Y \), but the x dimension is separated into two regions: (1) water and sediment with \( \Delta X = 1000 \mu\text{m} \), but the x dimension is separated into two regions: (1) water and sediment with \( \Delta X = 1000 \mu\text{m} \) and (2) a higher resolution \( \Delta X = 10 \mu\text{m} \) plant region which extends 500 \( \mu\text{m} \) from the plant boundary into the sediment. Diffusion coefficients, such as those calculated in Eq. (4) or defined in Table 1, are imposed at a 1 \( \mu\text{m} \times 1 \mu\text{m} \) resolution throughout the model domain (Fig. 3). Nodal effective diffusion coefficients are then calculated using parallel and series circuit analogies (Fig. 3). Computational time is reduced by considering the symmetry of the system (Fig. 2). At each time step oxygen and hydrogen sulfide concentrations are calculated sequentially, with rates determined from previous time step concentrations. The advection term is solved using an upwind scheme (Press et al., 1992; Boudreau, 1997).

Initial concentrations in the seagrass and water column are set to seawater saturation values while initial sediment
concentration profiles are obtained from

$$\frac{\partial}{\partial y} \left( \phi(y) D_y(y) \frac{\partial \phi(y)}{\partial y} \right) + \phi(y) \sum R, \quad (11)$$

in the absence of the plant. Oxygen concentration calculated using Eq. (10) is imposed on the top boundary while hydrogen sulfide is maintained at zero at this boundary. The remaining three system boundaries are defined as Neumann conditions (Fig. 2).

### 4. Results

#### 4.1. Oxygen and sulfide dynamics in seagrasses

The model was validated by comparing simulation results to in situ and in vitro oxygen and hydrogen sulfide microelectrode measurements in the literature. To evaluate how well the model reproduces diel oxygen and sulfide dynamics, we first devised a simulation using environmental settings similar to conditions in a dense *T. testudinum* seagrass bed near Rabbit Key, Florida Bay. In this population, Borum et al. (2005) measured oxygen content in the water column and in three

| Table 4 – *T. testudinum* and sediment metabolic variables and constants |
|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| Variable                   | Description                | Value | Units | Source |
| Plant                       | Maximum photosynthesis     | 321   | μmol O2 gdw h^{-1} | 1 |
| $P_m$                       | Saturation irradiance      | 426   | μmol photons m^{-2} s^{-1} | 1 |
| $\sigma$                    | Ramet density              | 1233  | ramets m^{-2} | 2 |
| $R_p$                       | Plant respiration          |       | μM O2 h^{-1} | D |
| $R_l$                       | Leaf respiration           | -13.9 | μmol O2 gdw h^{-1} | 1 |
| $R_s$                       | Shoot respiration          | -3.4  | μmol O2 gdw h^{-1} | 1 |
| $R_z$                       | Rhizome respiration        | -1.7  | μmol O2 gdw h^{-1} | 1 |
| $R_r$                       | Root respiration           | -8.6  | μmol O2 gdw h^{-1} | 1 |
| $M_m$                       | Meristem respiration multiplier | 2     |            | U |

| Sediment                   | C respiration rate at Ys = 0 | 16    | μM C h^{-1} | C, 3 |
| $Y_s$                      | Depth in sediment           | cm    |            | U   |
| $\beta_y$                  | C respiration decay term    | 0.52  | cm^{-1}    | C, 3 |
| $R_{C(D)x}^{(0)}$           | C respiration rate at Xs = 0 |       | μM C h^{-1} | D |
| $Q^l$                      | Plant DOC respiration in sediment | | μmol h^{-1} | D |
| $\rho_x$                   | C respiration decay term = $-\ln(0.01/dx)$ | | μm^{-1} | D |
| $X_s$                      | Distance from plant boundary| μm    |            | D   |
| $P_{DOC}$                  | Percent gPP released in sediment | 20    | %       | C, 4 |
| $\delta_x$                | 1% C respiration distance | 1 cm  |            | U   |

| Common                     | Volume PDE node            | 6.4 × 10^{-8} | L   | U |
| $V_n$                      | Biological sulfide oxidation constant | $M_{ox}k_{ox1}k_{ox2}$ | | |
| $k_{ox}$                   | Oxidation multiplier       | 5 × 10^{3}   | μM h^{-1} | D |
| $k_{ox}(t, S)$             | Abiotic sulfide oxidation constant | 1.7 × 10^{-4} | μM h^{-1} | 5 |
| $k_{O_2}$                  | Oxidation O2 Monod constant | 50 μM | | U |
| $k_{HS}$                   | Oxidation H2S Monod constant | 20 μM | | U |
| $k_C$                      | C respiration Monod constant | 20 μM O2 | | 3 |

### Sources:


<table>
<thead>
<tr>
<th>Table 5 – Plant and sediment reaction equations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reaction</td>
</tr>
<tr>
<td>Plant oxygen reactions</td>
</tr>
<tr>
<td>Plant sulfide reaction</td>
</tr>
<tr>
<td>Total sediment carbon metabolism</td>
</tr>
<tr>
<td>Sediment oxygen reactions</td>
</tr>
<tr>
<td>Sediment sulfide reactions</td>
</tr>
</tbody>
</table>
Fig. 3 – Calculation of diffusion coefficients defined every $1 \, \mu m \times 1 \, \mu m$ (points) into effective diffusivity at half node intervals ($\times$) using series and parallel circuit analogies (Armstrong, 1979; Larkum et al., 1989; Press et al., 1992). Open circles denote PDE nodes. Lengths $l_i = l_j = 1 \, \mu m$, and $D_{ij}$ are the diffusion coefficients defined in Table 1 and Eq. (4) for the $1 \, \mu m$ grid.

replicate $T. testudinum$ meristems over a day/night cycle. In the simulation, water column oxygen was calculated using a smooth sine function with amplitude and period parameterized from field measurements (Eq. (10), Fig. 4A). Irradiance incident at the top of the seagrass canopy was modeled using a PAR irradiance model and assuming that oxygen measurements were made in late October (C. Madden, pers. comm). Other environmental and plant parameters were either estimated or determined from literature values (Tables 2–4). The simulation was started from initial conditions and run for 30 days to establish a representative sediment environment and regular daily cycles. Meristem oxygen on day 30 was then compared to measured values of the simulation (Fig. 4B). The model clearly responded to irradiance with meristem oxygen concentrations decreasing in the afternoon and increasing in the morning to nearly 250 $/H_2/2$M (ca. 130% air saturation) after mid-day. Meristem oxygen in the model declined to a lower concentration than measured in the early evening, but minimum oxygen concentration at night was consistent with those measured. The model predicted negligible nighttime sulfide intrusion in this healthy seagrass population, with sulfide concentrations in the meristem < 0.02 $/H_2/2$M (Fig. 4C).

In an aquarium experiment, Borum et al. (2005) observed that water column oxygen and light controlled internal oxygen and hydrogen sulfide content in $T. testudinum$. We formulated a model simulation to accommodate the seawater oxygen manipulations and light/dark transitions in Borum et al. (2005) experiment. An effort was made to initiate the model using sediment conditions representative of the study, where $T. testudinum$ plants were placed in homogenized sediment for 3 days before measurements. We interpreted homogenized sediment as low in sulfide content, and the model was spun-up using a plant DOC release rate (5% gPP) that resulted in sediment profiles that ranged 0–180 $/H_2/2$M sulfide. High meristem oxygen concentrations in the light were allowed to decrease to near steady-state in 2 h darkness, and then a water column oxygen time course was simulated as in the experiment. Borum et al. (2005) measured oxygen and sulfide with micro-electrodes inserted into $T. testudinum$ rhizomes. As the model below-ground component is a significant simplification of a complex, 3D organ network, we chose the region of the model plant at the water/sediment interface as the best model analog to the rhizome in Borum et al. (2005). This region is 2 cm below the model leaf meristem. At water column concentrations near saturation, the model plant maintainedoxic conditions and reproduced the internal oxygen decrease as water column oxygen was lowered to 15% air saturation (Fig. 5). When hypoxic seawater conditions were simulated, sulfide intruded at a rate and magnitude similar to those measured, though redox conditions in the model meristem were not completely anoxic as in the experiment. With the onset of light and
photosynthesis, internal sulfide quickly declined with values measured, but model oxygen increased much more rapidly than observed. In darkness and oxygen depleted seawater, measured and modeled oxygen diminished until sulfide again intruded with a close correspondence between model and measurement.

Though the model is based on anatomy and morphology of *T. testudinum*, it can be generalized to other seagrass species of similar architecture. To compare our model with measurements, we tailored a simulation to the setup and experimental time course in the Pedersen et al. (2004) study with *Z. marina*. The model was first modified to include *Z. marina* metabolic rates (Marsh et al., 1986), and then the model was spun-up using a 45% DOC release rate to achieve sediment sulfide conditions similar to the experiments (1–2 mM H$_2$S). Next, the rhizosphere was developed with an 8 h saturating light treatment followed by 2 h of darkness in oxygen-saturated water such that model meristem oxygen concentration reached a quasi-steady state. Water column oxygen content was then stepped down in intervals as in Pedersen et al. (2004). The model closely tracked experimentally measured oxygen in the meristem (Fig. 6), and both model and experiment demonstrate that in the absence of photosynthesis, meristem oxygen concentration is directly dependent on water column oxygen concentration.

Pedersen et al. (2004) further demonstrated that the hydrogen sulfide intrusion rate in *Z. marina* meristems correlates with oxygen conditions in the meristem. The authors inserted oxygen and sulfide microelectrodes (~1 mm apart) in plant meristems, and seagrasses were exposed to different experimental manipulations of water column oxygen while plants were kept in darkness. Using the same sediment conditions, pre-time course light treatment, and seagrass parameterization as in the Z. marina comparison above (Fig. 6), we simulated the three illustrated sulfide experiments in Pedersen et al. (2004) by varying water column oxygen time courses accordingly. The temporal response and magnitude of oxygen and sulfide variations were similar between the model and measurements when water column oxygen was decreased from saturation to 35% saturation (Fig. 7 A). Model results and measurements agreed that oxygen and sulfide coexist in the meristem under these experimental conditions. If water column oxygen was lowered from 70 to 14% saturation (Fig. 7B), the meristem became anoxic and sulfide entered the meristem at a greater rate than in the Fig. 7 A treatment. The initial sulfide accumulation rate was greater in the model (ca. 4 μM H$_2$S min$^{-1}$), and the model did not achieve the maximum sulfide concentration measured. However, sulfide concentration after 2 h (146 μM H$_2$S) was near the mean value reported for 14 replicate experiments (150 ± 49 μM H$_2$S). Model sulfide accumulation in the meristem was also within the reported experimental range (0.5–9.0 μM H$_2$S min$^{-1}$). The simulation in Fig. 7 B produced slower oxygen recovery and sulfide depletion rates than measured after seawater oxygen was returned to 70% saturation. In the final experiment, water column oxygen was completely removed (Fig. 7C). Measured oxygen responded more slowly than the model to the initial drop in seawater oxygen. Sulfide entered the plant more gradually in the experiment, but the simulation resulted in a sulfide increase near 6 μM H$_2$S min$^{-1}$ with a 225 μM internal sulfide concentration after 2 h, both within ranges specified in Pedersen et al. (2004). Sulfide depletion rates were nearly identical when oxic conditions were returned in the water column.

4.2. Sensitivity analysis

Three indicators (maximum daily meristem oxygen concentration, minimum daily meristem oxygen concentration, and
maximum daily meristem sulfide concentration) were chosen for parameter sensitivity analysis, and the Rabbit Key diel simulation served as the baseline model (Fig. 4). The three indicators are representative of conditions in the meristem during the day and night in a healthy seagrass plant. A variety of environmental (e.g., water column oxygen concentration, PAR irradiance, turbulent mixing coefficient, etc.), plant (e.g., maximum photosynthesis rate, leaf height, ramet density, etc.), and estimated, model-specific (e.g., leaf diffusivity, percent DOC release, plant sulfide oxidation rate) parameters, $p$, were varied by ±1% of their values in the baseline model. Each sensitivity simulation was run for 5 days to ensure repeated cycles after perturbation. Sensitivity, $S$, of the indicator concentration, $C$, was calculated as:

$$ S = \frac{p_b \Delta C}{C_b \Delta p} $$

where $p_b$ and $C_b$ are the values from the baseline simulation, and $\Delta C/\Delta p$ is linearly approximated using the results from the perturbation runs. A 1% change in $p$ corresponds to a 5% change in the indicator concentration.

During daylight hours, processes in the water column and plant leaf largely control the oxygen concentration in the seagrass meristem (Fig. 8). Maximum oxygen concentration was most sensitive to photosynthetic rate, i.e., the primary oxygen source in the light. Transport path length (i.e., leaf length), water column oxygen, DOC release and leaf diffusivity were also important parameters determining the variation in daytime oxygen. Less significant were small variations in irradiance, plant respiration rate and fluid flow around the plant. Maximum meristem oxygen was insensitive to all other parameters that were varied.

In contrast, the water column oxygen concentration was the predominant process that determined oxygen concentration in the plant at night (Fig. 9). All other parameters were less significant.

Fig. 7 – Meristem oxygen and hydrogen sulfide dynamics in response to water column oxygen. Model simulations followed Z. marina experiments in Pedersen et al. (2004). Other than the water oxygen time courses, simulations were parameterized exactly as in Fig. 6. (A) Water oxygen concentration decreased from 255 to 90 μM for 2 h, (B) water oxygen concentration decreased from 140 to 35 μM for 4 h, and (C) water oxygen concentration decreased from 255 to 0 μM for 6 h.

Fig. 8 – Sensitivity factors of maximum daily oxygen in the leaf meristem to select model parameters. Parameters were varied ±1%.

Fig. 9 – Sensitivity factors of minimum daily oxygen in the leaf meristem to select model parameters. Parameters were varied ±1%.
Maximum hydrogen sulfide intrusion at night depended primarily on water column oxygen content and plant DOC release into sediments (Fig. 10). In general, sulfide sensitivity responses were an order of magnitude greater than either maximum or minimum daily oxygen responses elicited in the analysis. In all sensitivity analyses, the model oxygen and sulfide concentrations were insensitive to our parameterization of the below-ground plant (e.g., below-ground diffusivity).

4.3. Importance of advective flow

The governing equation (Eq. (1)) includes both advective and diffusive mass transport through the air-phase lacunae. The relative magnitude of advective and diffusive flow was evaluated in the meristem region of the model using a 24-h Rabbit Key simulation (Fig. 11). Advective velocities ranged from 0.7 to 2.4 mm s\(^{-1}\) in the downward direction from the leaf to the below-ground structure (Fig. 11A), and peak velocities coincided with high irradiance and maximum photosynthesis rates. Increasing the leaf diffusive boundary layer from \(X_{dbl} = 100\) to 300 and 500 \(\mu\)m increased advective velocities in the light. As irradiance increased after sunrise, advection accounted for one-fifth to a quarter of total oxygen transport through the meristem (Fig. 11B), but the significance of mass flow declined in darkness with transport <10% advection before dawn. In the late morning hours, relative mass flow increased with greater diffusive boundary layer thickness around the leaf. On the whole, diffusion was the dominant transport process throughout the day. Total lacunae pressure in the above-ground portion of the plant ranged from ca. 90 kPa at night to ca. 125 kPa mid-day (Fig. 12A). Mass flow is maximum during the day and greatest between the transition of the photosynthetic leaf, leaf sheath, and connection to the short shoot at the meristem (Fig. 12).

5. Discussion

5.1. Model performance

Oxygen and hydrogen sulfide dynamics in the seagrass model reproduce well those observed in the field and in laboratory studies with \(T.\ testudinum\) and \(Z.\ marina\). In particular, the simulation in Fig. 4 results in diel patterns of oxygen concentration in the seagrass meristem that are comparable to microelectrode measurements made \(in situ\) in Florida bay. The model also simulates changes in internal oxygen and sulfide concentrations produced by laboratory manipulation of light and water column oxygen concentration (Figs. 5–7).

Although the model reproduces the main features observed in the laboratory experiments, modeled oxygen concentrations in the meristem respond faster to sudden changes in light than those measured (Fig. 5). Following the dark to light transition, modeled internal plant oxygen increases by about 70 \(\mu\)M \(O_2\) in the first hour when the rate decreases to give a maximum concentration of 90 \(\mu\)M \(O_2\) after 3 h illumination. Measured oxygen in the \(T.\ testudinum\) rhizome increases at a fairly constant, and slower, rate of 25 \(\mu\)M \(O_2\) h\(^{-1}\). A number of factors may contribute to this discrepancy. First, laboratory measurements were made in the rhizome, a 3D structure
Data are from the baseline simulation (Terrados et al., 1999) rhizomes and roots of *Cymodocea nodosa* to light (Fig. 5) differs from the oxygen dynamics observed in and between morphologically similar species. The more moderate rate of oxygen increase seen in the laboratory response to light (Fig. 5) differs from the oxygen dynamics observed in *Cymodocea nodosa* (Terrados et al., 1999) rhizomes and roots and at the root surface of *C. rotundata* (Pedersen et al., 1998) under similar light–dark manipulations. When lights were initially turned on in the *Cymodocea* studies, oxygen concentration increased linearly, but the accumulation rate decreased until oxygen approached a steady concentration after about 2 h. This pattern is more similar to the model result in Fig. 5.

Sulfide intrusion is dependent on the sediment microclimate around individual roots, particularly surfaces near the root tips where solute exchanges with the sediment occurs (Connell et al., 1999; Jensen et al., 2005; Frederiksen and Glud, 2006). Model accumulation rates and sulfide concentrations fall within the ranges given in the Pedersen et al. (2004) study, and results shown graphically in the study represent the lower limit (Fig. 7 B and C). Considering that plant and sediment parameters were kept exactly the same in all *Z. marina* simulations (Figs. 6 and 7 A–C), plant–sediment heterogeneity between experimental replicates is one possible explanation for differences in the simulations and the representative examples given in the study.

When oxic water conditions are re-established, model oxygen concentrations in the meristem lag those observed (Fig. 7 A–C). One possible explanation for this difference is the potential for incomplete sulfide oxidation to thiosulfate, sulfite or elemental sulfur in the experimental plants (Somero et al., 1989); the oxidation reaction is complete to sulfate in the model. The rate of sulfide decrease after the return of oxic waters in Fig. 7 C is nearly identical to that measured in the laboratory. Without detailed knowledge of the experimental plant, sediment conditions, and experimental details such as diffusive boundary layer thickness as affected by water flow velocity (Binzer and Middelboe, 2005), strict correspondence between the model simulation and the experiment remains difficult to evaluate. In spite of this, model results compare favorably with the experimental observations.

### 5.2. A multidimensional approach

Eldridge and Morse (2000) and Eldridge et al. (2004) demonstrate that 1D reactive-transport models of seagrass systems are instructive in understanding how seagrasses interactively modify the redox conditions in the sediment and how the system responds to environmental stresses. Our approach was to reduce the number of chemical species included in these models in favor of increasing the spatial dimension. A 2D approach is expected to better capture the dynamics of biogeochemical processes in a spatially complex system (Vrugt et al., 2001; Meile et al., 2005; Meysman et al., 2006). The approach also allows for the representation of a gas-phase lacunae distinct from plant tissues and sediments. The seagrass leaf is essentially a 2D structure, but the below-ground seagrass plant forms an entwined, 3D network of roots and rhizomes. Each below-ground organ interfaces with its own redox microenvironment that varies spatially in the sediment and changes over time. The central assumption in the dimension reduction is that surface areas of exchange across the plant–sediment interface reflect rhizome and root biomass distributions with depth. This assumption is implemented as a modification of the diffusion coefficient across the below-ground plant boundary (Eq. (4)) and implies that the concentration gradient across the plant–sediment boundary is uniform at a given depth.

---

**Fig. 12** – (A) Simulated daily total gas pressure (kPa) and (B) advective mass flow (nmol h⁻¹) in *T. testudinum* lacunae. Data are from the baseline simulation (X_db = 100), and the domain plotted includes the lacunae from the short shoot at the water–sediment interface up through the leaf sheath to the leaf. The meristem location in Fig. 11 is defined as the transition between the short shoot and leaf sheath and is indicated by the bottom-most dashed line.
in the sediment. Another compromise in this approach is that the lacunal path length in the below-ground structure is likely less than the total path length from the tip of a root connected to the most distal portion of the rhizome. Nevertheless, changing the value of the below-ground effective diffusion coefficient had little effect on the result of all three indicators chosen for the sensitivity analysis (Figs. 8–10). This suggests that our approach to modeling exchange between the below-ground plant and the sediment is less important than some of the central chemical and biological processes, such as seawater oxygen uptake, photosynthesis, and sediment remineralization, in driving oxygen and sulfide concentrations in the plant. Indeed, the greater sensitivity of sulfide dynamics compared to oxygen dynamics underscores the significance of below-ground processes in seagrass systems.

5.3. Model insight into system processes

The model captures the temporal processes that underpin the water–plant–sediment system, and the model can be used to give additional insight into mechanisms that affect internal oxygen concentrations and sulfide intrusion. For instance, oxygen availability in the water controls both the minimum oxygen concentration and maximum hydrogen sulfide concentration expected in the meristem at night (Figs. 4–7). Model sensitivity analysis further supports this conclusion as night-time redox conditions inside the plant are most responsive to variations in water column oxygen content (Figs. 9 and 10). This indicates that nighttime is the most likely time for sulfide intrusion and that water column processes are integral to the phenomenon. As plant respiration consumes seawater oxygen at night, less oxygen is released into the surrounding sediments. Bacterial organic matter metabolism in the rhizosphere reverts from aerobic to sulfate reduction pathways, and sediment sulfide is no longer effectively reoxidized. Sulfide concentration builds in close proximity to the root surfaces, and sulfide intrusion can occur. Accordingly, given a set of environmental parameters, the model can be used to predict conditions conducive to sulfide intrusion in seagrasses.

The maximum amount of sulfide in the simulated T. testudinum plant is also sensitive to the parameterization of sulfur cycling within the rhizosphere (Fig. 10). The trophic connection between sediment microbial activity and seagrass detrital and organic carbon exudation is increasingly evident, particularly in sub-tropical systems (Moriarty et al., 1986; Holmer et al., 2001) including T. testudinum seagrass communities (Kaldy et al., 2006; Jones et al., 2003). A DOC release rate of 20% gPP results in meristem oxygen dynamics similar to those observed in Florida Bay (Fig. 4). The fact that the model is sensitive to the value of DOC release underscores the fundamental nature of the process in determining the magnitude of sulfide invasion into the plant. Seagrass DOC release (Ziegler and Benner, 1999), bacterial productivity (Moriarty et al., 1986), and sulfate reduction (Blabberget al., 1998) vary with diel cycles of photosynthesis, though little is known how seagrass carbon exudation changes over longer time scales and during periods of environmental stress. Another important component of the model is the incorporation of a biologically mediated sulfide oxidation reaction inside the seagrass plant. In order to decrease internal sulfide, sulfide oxidation must meet and exceed the net sulfide flux into the plant. In the model, the sulfide oxidation reaction is necessary to account for three observed features of the system: (1) oxic conditions throughout the plant with no internal sulfide during daylight hours, (2) expected patterns of oxygen and sulfide dynamics in the meristem at night, and (3) rapid displacement of internal sulfide with the onset of photosynthesis or re-establishment of oxic waters. In the Rabbit Key simulation, only about 1% of the DOC exudate is metabolized through aerobic respiration such that seagrass DOC predominantly drives microbial sulfate reduction and sulfide production in the sediment. Nevertheless, sulfide does not accumulate in the sediment as efficient sulfide oxidation reactions in the plant and sediment balance daily sulfide production, a result consistent with measurements in Florida Bay (Ku et al., 1999). Notably, seagrasses strongly impact sulfur cycling in the sediments. Daily integrated sulfide production and oxidation rates are 20× greater in the vegetated Rabbit Key simulation than in simulations run without the seagrass, i.e., bare sediment conditions. Sulfur isotope signatures in leaf and below-ground plant tissues are evidence that marshgrasses and seagrasses, including T. testudinum, incorporate sulfide oxidation products (Carlson and Forrest, 1982; Fry et al., 1982; Chambers et al., 2001; Frederiksen et al., 2006), but it is inconclusive whether the sulfide source is oxidized inside the plant or in the rhizosphere. These findings highlight the importance of experimental confirmation of biological sulfide oxidation inside T. testudinum. It is not known whether T. testudinum has the physiological capacity to remove sulfide once it has entered the plant. Pedersen et al. (2004) and Borum et al. (2005) argue that spontaneous chemical re-oxidation is sufficient to account for the internal sulfide dynamics in Z. marina and T. testudinum. They suggest that the time scale for internal sulfide depletion in their experiments (ca. 0.5 h half-lives for both seagrass species) is on the same order as the 1 h half-life expected from chemical re-oxidation alone (Cline and Richards, 1969; Chen and Morris, 1972; Almgren and Hagström, 1974). However, this estimate is based on the assumption that the reaction occurs in a closed system. If the meristem is considered an open region which includes physical transport to and from the region, then much higher sulfide oxidation rates are necessary to explain the measured dynamics. Model results are consistent with a hypothesized symbiotic relationship between seagrasses and sulfide oxidizing bacteria. Otherwise, seagrasses may detoxify sulfide enzymatically or in their mitochondria (Somero et al., 1989; Raven and Scrimgeour, 1997).

In part, our high biological rate constant may also reflect the absence of iron cycling in the model sediment and rhizosphere. This reflects computational limitations plus large uncertainty regarding the kinetics of (poorly characterized but presumably very reactive) iron oxide phases. While Fe cycling in the bulk sediment is likely to be minimal in the low-Fe carbonate sediments of Florida Bay (Ku et al., 1999; Chambers et al., 2001), localized iron cycling cannot be excluded.

Goodman et al. (1995) have shown that Z. marina exhibit sulfide inhibition on photosynthesis. However, T. testudinum plants collected in Florida Bay do not show a similar effect (Erskine and Koch, 2000), even when plants were maintained in 10 mM sulfide conditions for 14 days (Koch and Erskine, 2001). T. testudinum simulations run in our study have had
relatively low (~600 μM) sulfide concentrations, and Z. marina simulations were of experiments under dark conditions. Consequently, sulfide inhibition of photosynthesis has not yet been implemented in the model.

5.4. **Mass flow in the lacunae**

Advective gas transport has not been conclusively demonstrated in seagrasses. Smith et al. (1984) assert that diffusion alone cannot account for oxygen transport rates measured in Z. marina, yet Larkum et al. (1989) contend that diffusion is sufficient to supply seagrass roots with oxygen. Sorrell and Dromgoole (1988) directly measured the evolution of pressure gradients in the freshwater macrophyte, *Egeria densa*, during light/dark transitions, and they concluded that oxygen transport is primarily diffusive but can be assisted by mass flow under changing environmental conditions. The model suggests diffusion is the dominant gas transport mechanism in *Thalassia testudinum* lacunae, but advection can account for up to 25% of total gas transport as photosynthesis pressurizes the leaf lacunae (Fig. 11). Advective velocities in the meristem region range approximately from 0.5 to 2.5 mm s⁻¹, depending on the time of day, and are about one-tenth to one-third of the transport rates measured in *E. densa* (Sorrell and Dromgoole, 1988). Anatomical differences aside, direct comparison with *E. densa* is difficult because velocities were measured following rapid light–dark transitions. In comparison, the model responds to a slowly, continuously varying light regime, and consequently, we would expect to see slower advective velocities in the model. In both macrophytes, changes in total gas pressure result from changes in oxygen partial pressure, and the daily pressure range in the model is similar to internal pressures measured in *E. densa*. The model predicts that internal gas pressure decreases below atmospheric pressure as respiration consumes oxygen at night (Fig. 12, Sorrell and Dromgoole, 1988).

Mass flow is a function of the pressure gradient established within the lacunae and is greatest just below the photosynthetic leaf. In addition, as the pressure gradient between the leaf and the below-ground tissues steepens, the relative contribution of mass flow to total gas transport increases. Pressure differentials increase during periods of increasing photosynthesis or high subterranean oxygen demand (i.e., increased plant biomass and respiration). indoorspoxidation and sediment metabolism (Smith et al., 1984), sulfide oxidation and sediment metabolism. Lacunal pressures in the leaf also increase in stagnant waters when the diffusion boundary layer thickens around the leaves. In this situation, diffusive resistance is greater between the leaf and the water, and more photosynthetic oxygen enters the lacunae. The situation is reversed at night when high water stagnancy results in a relative decrease in lacunal pressure.

5.5. **Conclusions**

Overall, the model reproduces temporal changes in meristem oxygen and sulfide content in response to experimental oxygen manipulations and natural irradiance patterns. The model demonstrates that oxygen and sulfide dynamics depend largely on seawater oxygen available to support nighttime plant respiration and sediment microbial metabolism. Sediment metabolism and benthic respiration in dense seagrass communities consume water column oxygen at night, and these processes can exhaust seawater oxygen under physical conditions that decrease solubility (high temperature and high salinity) and/or increase stagnancy (less atmospheric exchange, less current advection, increased diffusive boundary layers). Ultimately, internal aeration and sulfide intrusion in seagrasses depends on evolving feedbacks between water column chemistry, plant physiology (Goodman et al., 1995; Greve et al., 2003), and sediment biogeochemistry.

**Acknowledgments**

We gratefully acknowledge the fruitful discussions and support of Chris Madden and Amanda McDonald from the South Florida Water Management District. This research was funded in part by the USGS (grant 02ERAG0060). CM acknowledges support and hospitality at the Hanse Institute for Advanced Study (Delmenhorst, Germany) and the Section of Biogeosciences at the Alfred Wegener Institute Bremerhaven. His contribution was supported by Georgia Sea Grant of the National Sea Grant College Program of the U.S. Department of Commerce’s National Oceanic and Atmospheric Administration, grant #NA04OAR4170033. The views expressed herein do not necessarily reflect the views of any of those organizations.

**REFERENCES**


