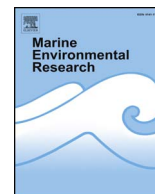




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Contrasting impacts of light reduction on sediment biogeochemistry in deep- and shallow-water tropical seagrass assemblages (Green Island, Great Barrier Reef)

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ABSTRACT

Seagrass meadows increasingly face reduced light availability as a consequence of coastal development, eutrophication, and climate-driven increases in rainfall leading to turbidity plumes. We examined the impact of reduced light on above-ground seagrass biomass and sediment biogeochemistry in tropical shallow- (~2 m) and deep-water (~17 m) seagrass meadows (Green Island, Australia). Artificial shading (transmitting ~10–25% of incident solar irradiance) was applied to the shallow- and deep-water sites for up to two weeks. While above-ground biomass was unchanged, higher diffusive O₂ uptake (DOU) rates, lower O₂ penetration depths, and higher volume-specific O₂ consumption (R) rates were found in seagrass-vegetated sediments as compared to adjacent bare sand (control) areas at the shallow-water sites. In contrast, deep-water sediment characteristics did not differ between bare sand and vegetated sites. At the vegetated shallow-water site, shading resulted in significantly lower hydrogen sulphide (H₂S) levels in the sediment. No shading effects were found on sediment biogeochemistry at the deep-water site. Overall, our results show that the sediment biogeochemistry of shallow-water (*Halodule uninervis*, *Syringodium isoetifolium*, *Cymodocea rotundata* and *C. serrulata*) and deep-water (*Halophila decipiens*) seagrass meadows with different species differ in response to reduced light. The light-driven dynamics of the sediment biogeochemistry at the shallow-water site could suggest the presence of a microbial consortium, which might be stimulated by photosynthetically produced exudates from the seagrass, which becomes limited due to lower seagrass photosynthesis under shaded conditions.

1. Introduction

Seagrasses are ubiquitous marine flowering plants inhabiting coastal zones from shallow to deep waters down to 90 m depth depending on the water clarity (Duarte, 1991a; Larkum et al., 2006). Seagrasses provide multiple important ecological services in marine environments such as facilitating nutrient cycling and sediment stabilization (Madsen et al., 2001), and delivering photosynthetically derived O₂ and organic carbon (C_{org}) (exudates) into below-ground environments (Moriarty et al., 1986; Pollard and Moriarty, 1991) thus representing an important site of substantial carbon sequestration (Fourqurean et al., 2012). Seagrass meadows cover a mere 0.1% of the ocean floor and yet are responsible for sequestering about 10% of the C_{org} bound in the oceanic sediment (Duarte et al., 2005; Fourqurean

et al., 2012). Australian seagrass ecosystems alone have been estimated to be capable of sequestering ~10.06 tons of C_{org} km⁻² yr⁻¹ equivalent to about 0.6% of Australia's annual CO₂ emission (Lavery et al., 2013). After frequent reports of large-scale seagrass diebacks, a major conservation effort has been made in the past decades (Orth et al., 2006; Robblee et al., 1991; Zieman et al., 1999). Decline of seagrass cover has been attributed to changes in abiotic parameters such as i) night-time O₂ conditions in the water column (Borum et al., 2005; Brodersen et al., 2015a; Koren et al., 2015; Pedersen et al., 2004), ii) thermal stress (Marba and Duarte, 2010; Fraser et al., 2014), iii) light availability and sediment toxicity (via H₂S intrusion) (Borum et al., 2006; Brodersen et al., 2015b; Chartrand et al., 2016), and iv) other shifts in the physico-chemical conditions of the anchoring sediment (Brodersen et al., 2015a; Jensen et al., 2007). However, research into

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changes in the above-mentioned environmental parameters and how they can alter the interaction between seagrasses and their surrounding microbial community and sediment biogeochemistry remains limited (Brodersen et al., 2014, 2015a; York et al., 2017).

Seagrasses are highly productive primary producers that reside mostly in reduced, anoxic sediments (Borum et al., 2006). The continuous leaching of photosynthetically-derived O_2 and C_{org} into their rhizosphere plays an integral role in shaping the physico-chemical microenvironment around the below-ground tissue of seagrasses (Blaabjerg et al., 1998; Brodersen et al., 2015a, 2016; Hansen et al., 2000; Jensen et al., 2007; Nielsen et al., 2001) and thereby the activity of the rhizospheric microbial community (Nielsen et al., 2001; Welsh, 2000). The O_2 produced by the leaves is transferred below-ground via specialised lacunae termed aerenchyma (Borum et al., 2006; Colmer, 2003). This transfer results in radial O_2 loss (ROL) into the immediate rhizosphere (Frederiksen and Glud, 2006; Jensen et al., 2005; Pedersen et al., 1998). The ROL occurs mostly at the root tips and the nodes of the rhizome, where the release of O_2 creates 'oxic microshields' that prevent phytotoxic compounds (e.g. H_2S) produced in the surrounding reduced sediments from diffusing into the plant (Brodersen et al., 2015b; Koren et al., 2015). At night-time when photosynthesis ceases, the diffusion of O_2 from the water column into the leaves maintains internal plant aeration and thus the belowground oxic microshield (Borum et al., 2006; Brodersen et al., 2015a; Pedersen et al., 2004). Photosynthetically derived C_{org} is also released from the rhizome and root tips into the surrounding sediment adding to the labile carbon pool in the sediment and stimulating the microbial activity in the seagrass rhizosphere (Moriarty et al., 1986; Pollard and Moriarty, 1991).

While a strong interaction of terrestrial plants with their microbiome is well documented (Bolan, 1991; Jeffries et al., 2003), the investigation of the seagrass microbiome is still relatively new (Cùcio et al., 2016) showing that microbes are closely associated with the below-ground tissue of seagrasses and are important for the benthic sulphur cycle. Tropical seagrass meadows often inhabit oligotrophic waters and sandy carbonate sediments that bind iron and essential nutrients such as phosphate, leading to low direct accessibility of nutrients (Duarte et al., 1995; Fourqurean et al., 1992; Nielsen et al., 2007; Short et al., 1990). *In situ* fertilization experiments have shown that tropical seagrasses are indeed nutrient limited (Agawin et al., 1996; Duarte et al., 1995), however, sulphate-reducing bacteria can fuel remineralisation and nutrient solubilisation in the surrounding sediment enhancing seagrass productivity (Holmer et al., 2006; Pagès et al., 2012). Such intricate dependency of seagrass on sediment microbial activity has been documented in both temperate and sub-tropical seagrass meadows (Holmer et al., 2001, Holmer and Laursen, 2002; Jones et al., 2003).

The photosynthetic activity of seagrasses is directly dependent on light availability, and light stress has been linked to decreased growth and initiation of seagrass dieback events (Ralph et al., 2007; York et al., 2015). Coastal development, land clearing, and dredging are major anthropogenic drivers of increased turbidity and reduced light availability causing negative effects on inshore seagrass meadows (Brodersen et al., 2017a; Erftemeijer and Lewis, 2006), whereas climate change related increases in sea surface temperatures can further enhance such negative effects (Marba and Duarte, 2010; York et al., 2013; Collier and Waycott, 2014). Decreasing photosynthetic activity in turbid waters leads to reduced O_2 transfer from leaves to below-ground tissue (Borum et al., 2006; Brodersen et al., 2017a; Greve et al., 2003; Pedersen et al., 1998), which can eventually cause tissue anoxia and intrusion of phytotoxic compounds such as ethanol, lactic acid, or H_2S from the surrounding anoxic sediment into the below-ground tissues (Brodersen et al., 2015a, 2017a; Pedersen et al., 2004). Increased levels of sulphate reduction can lead to an accumulation of high H_2S levels in the sediment, which can penetrate into the below-ground biomass of seagrasses and may induce increased seagrass mortality (Holmer et al., 2009; Pulido Pérez and Borum, 2010). However, reduced

photosynthesis also slows plant metabolism and reduces the amount of rhizome/root exudates available to fuel the adverse effects of the sulphate-reducing bacterial community (Moriarty et al., 1986).

In the tropics, seagrass meadows occur in both shallow and deep coastal waters (> 15 m) (Coles et al., 2015). The characteristics of these meadows differ considerably, where deeper areas are dominated by fast growing and low light adapted species from the genus *Halophila*, while species with more structural complexity, higher biomass and high light requirements occur in shallow water. Seagrass species in shallow water habitats comprise *Halodule uninervis*, *Syringodium isoetifolium*, *Cymodocea rotundata* and *C. serrulata* have a relatively deeper rhizosphere consisting of a dense, (~10 cm) thick mat of interwoven rhizomes and roots as compared to the much shallower (~2-3 cm) rhizosphere consisting of finer and sparser roots and rhizomes in the deep-water *Halophila decipiens* meadow (Duarte, 1991b; Duarte et al., 1998). These differences are expected to lead to different changes in sediment biogeochemistry between the two sites under shading conditions, where we expected a stronger effect of shading in the shallow-water seagrass assemblages. Recent studies in the Great Barrier Reef region have shown that these differences in species composition can result in quite different recovery outcomes in deep and shallow seagrass habitats exposed to natural (Rasheed et al., 2014) and anthropogenic (York et al., 2015) disturbances. It is likely that the differences in growth habits of these seagrass communities may also result in differing responses in sediment biogeochemistry when exposed to light stress impacts.

In this study, we examined the effect of shading on seagrass biomass, sediment O_2 demand, and H_2S levels within a densely-vegetated shallow-water seagrass meadow and a sparsely vegetated deep-water seagrass meadow in tropical North Queensland, Australia. We hypothesised that short-term (1-2 weeks) shading could affect seagrass biogeochemistry in two ways either by i) inducing tissue necrosis and shoot mortality that drives increased surface sediment microbial activity and a resultant surge in sediment H_2S production, or ii) reducing excretion of root/rhizome exudates lowering the microbial activity and thus the H_2S production in the sediment, and thereby reducing the threat of H_2S toxicity to the plant.

2. Material and methods

2.1. Study site

Green Island (16° 46' S, 145° 58' E) is a sandy cay within the Great Barrier Reef (GBR) Marine Park and World Heritage Area ~27 km northeast of Cairns in northern Queensland, Australia (Fig. 1). The lagoonal reef platform surrounding the island is ~12 km² in an area with carbonate sediments supporting dense multi-species seagrass meadows (Baxter, 1990). Shallow subtidal and intertidal meadows are dominated by *Halodule uninervis*, *Cymodocea serrulata*, *C. rotundata*, *Halophila ovalis*, *Thalassia hemprichii* and *Syringodium isoetifolium* (Rasheed, 2004), while deeper waters surrounding the reef platform support sparse, but extensive meadows of *Halophila decipiens* usually occurring seasonally between August and December (Coles et al., 2009). This study was conducted at two sites. Site A was a mixed species (*Halodule uninervis*, *Cymodocea serrulata*, *C. rotundata* and *Syringodium isoetifolium*) shallow subtidal seagrass meadow (~2 m below mean low tide levels) to the west of the island. Here the seagrass grows in carbonate sands (~80% calcium carbonate – McKenzie, 1994), organic matter content of ~0.28–1.33% C_{bulk} (Lavery et al., 2013) and porosity 0.56 ± 0.00 . Site B was a deep subtidal seagrass meadow (~17 m below mean low tide levels) with ephemeral *H. decipiens* growing on slightly finer sandy sediments with a porosity of 0.54 ± 0.01 and located ~2 km east, northeast of the island (Fig. 1). Both sites are exposed to moderate tidal currents with a tidal range in the area of ~3 m.

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