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Synergistic effects of high temperature and sulfide on tropical seagrass

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Abstract

To examine the synergism of high temperature and sulfide on two dominant tropical seagrass species, a large-scale mesocosm experiment was conducted in which sulfide accumulation rates (SAR) were increased by adding labile carbon (glucose) to intact seagrass sediment cores across a range of temperatures. During the initial 10 d of the 38 d experiment, porewater SAR in cores increased 2- to 3-fold from 44 and 136 μmol L^{-1} d^{-1} at 28–29 °C to 80 and 308 μmol L^{-1} d^{-1} at 34–35 °C in *Halodule wrightii* and *Thalassia testudinum* cores, respectively. Labile C additions to the sediment resulted in SAR of 443 and 601 μmol L^{-1} d^{-1} at 28–29 °C and 758 to 1,557 μmol L^{-1} d^{-1} at 34–35 °C in *H. wrightii* and *T. testudinum* cores, respectively. Both *T. testudinum* and *H. wrightii* were highly thermal tolerant, demonstrating their tropical affinities and potential to adapt to high temperatures. While plants survived the 38 d temperature treatments, there was a clear thermal threshold above 33 °C where *T. testudinum* growth declined and leaf quantum efficiencies (Fv/Fm) fell below 0.7. At this threshold temperature, *H. wrightii* maintained shoot densities and leaf quantum efficiencies. Although *H. wrightii* showed a greater tolerance to high temperature, *T. testudinum* had a greater capacity to sustain biomass and short shoots under thermal stress with labile C enrichment, regardless of the fact that sulfide levels in the *T. testudinum* cores were 2 times higher than in the *H. wrightii* cores. Tropical seagrass tolerance to elevated temperatures, predicted in the future with global warming, should be considered in the context of the sediment-plant complex which incorporates the synergism of plant physiological responses and shifts in sulfur biogeochemistry leading to increased plant exposure to sulfides, a known toxin.

Keywords: Dissolved organic carbon; Florida Bay; Glucose; *Halodule wrightii*; *Thalassia testudinum*

1. Introduction

Sediments in seagrass and other shallow marine soft-bottom communities are characterized as highly organic (Hemminga and Duarte, 2000). The decomposition of organic matter in these coastal marine sediments is microbially mediated through the dissimilatory reduction of sulfate to sulfide (H_2S, HS^-) (Sørensen et al., 1979; Howarth and Hobbie, 1981; Jørgensen, 1982; Canfield, 1993; Holmer and Kristensen, 1996; Holmer et al., 2003). Consequently, without reoxidation, porewater sulfides build up in coastal marine sediments and can lead to a chronic exposure of seagrass belowground

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tissues to high concentrations of sulfide, a known phytotoxin (Linthurst, 1979; Havill et al., 1985; Koch et al., 1990; Goodman et al., 1995; Raven and Scrimgeour, 1997; Holmer and Bondagarrd, 2001; Barber and Carlson, 1993; Carlson et al., 1994). The degree to which seagrass below ground tissues are exposed to sulfides is determined by multiple factors: microbial respiration rates, the ability of plants to oxidize their internal lacunae tissue (aerenchyma), the extent of the oxidized microzone of sediment surrounding the roots (rhizosphere), and local sediment biogeochemistry (Eldridge et al., 2004).

Temperature and the availability of labile organic substrates are primary factors controlling microbial sulfate reduction rates (SRR) (Holmer and Kristensen, 1996; Blaabjerb et al., 1998; Cotner et al., 2004; Pallud and Van Cappellen, 2006; Marbà et al., 2006). Labile carbon produced by high rates of seagrass photosynthesis provides low molecular weight carbon substrates to fuel the sulfate reducing microbial community (Blaabjerb et al., 1998; Hines et al., 1999; Cotner et al., 2004). Thus high photosynthetic rates of tropical seagrasses, such as *Thalassia testudinum* Banks ex Köing (Fourqurean et al., 2001), and warm sub-tropical temperatures (>30 °C) probably account for the high millimolar porewater sulfide levels found in the sediments of Florida Bay (Barber and Carlson, 1993; Carlson et al., 1994), a large semi-enclosed subtropical lagoon at the terminus of the Florida peninsula. The dominant seagrass species in the Bay, *T. testudinum*, appears to be well adapted to reduced sediment conditions. It has extensive aerenchyma (Tomlinson, 1969) and a high capacity to oxidize its rhizosphere (Lee and Dunton, 2000; Borum et al., 2005), characteristics well established in the wetland plant literature as adaptations to sediment hypoxia (Iizumi et al., 1980; Sand-Jensen et al., 1982, Smith et al., 1984, Caffrey and Kemp, 1991; Lee and Dunton, 2000).

While *T. testudinum* and other seagrass species have a high capacity to oxidize their rhizophere, microbial SRR in the tropics may overwhelm the ability of plants to completely reoxidize reduced sulfur compounds in porewaters. Confounding this problem is the fact that tropical carbonate sediments low in iron are inefficient at binding sulfides into solid-phase forms, contrasting temperate marine sediments dominated by pyrite and iron sulfide compounds (Berner, 1984; Chambers et al., 2001). Seagrass systems in carbonate sediments and with high organic loads, either from high internal organic production and/or undergoing anthropogenic eutrophication, tend to be exposed to high levels of porewater sulfides (Azzoni et al., 2001; Holmer et al., 2003).

Sulfides have been shown to be phytotoxic to a range of aquatic plant species, including seagrasses (Ingold and Havill, 1984; Havill et al., 1985; Koch and Mendelssohn, 1989; Koch et al., 1990; Goodman et al., 1995). In fact, sulfide toxicity has been proposed as an important factor in promoting "die-off" events of *T. testudinum* in Florida Bay (Robblee et al., 1991) and other seagrass species worldwide (Seddon et al., 2000; Azzoni et al., 2001; Holmer and Bondagarrd, 2001; Plus et al., 2003; Holmer et al., 2005). Although these studies implicate sediment reducing conditions, and specifically porewater sulfide, as an agent causing mortality in seagrass, there is conflicting evidence on the direct role of sediment sulfide in causing seagrass mortality (Terrados et al., 1999), and few experimental studies have been conducted to determine the upper threshold levels of sulfide or compare different species tolerances. Further, sulfide accumulation is highest during warm summer months when plants may also experience high thermal stress, particularly in tropical climes, therefore this potential interaction requires evaluation.

Herein we present results of a large-scale mesocosm experiment where sulfide accumulation was stimulated by adding labile carbon (glucose) to intact sediment cores and the seagrass response determined. We also examined the effects of increased temperature on sulfide accumulation rates (SAR) and the synergism of these two stressors (high temperature and sulfide) on plant growth and physiological response in two dominant tropical seagrass species *T. testudinum* and *Halodule wrightii* Aschers. We hypothesized that high temperature may increase sulfide accumulation causing a cumulative impact on tropical seagrasses.

2. Materials and methods

2.1. Plant collection and experimental setup

Intact plant cores were collected from Florida Bay, at the southern terminus of the Florida (U.S.A.) peninsula May 21–29th, 2004. Intact cores of *H. wrightii* (15 cm diameter × 20 cm depth) were collected from Porjoe Key (25°13′41″N/80°47′37″W) and cores of *T. testudinum* were collected from Green Mangrove Key (24°55′20″N/80°47′33″W) and transported to the Florida Atlantic University Marine Lab (Boca Raton, FL) in coolers. Upon arrival, intact cores were immediately placed into mesocosm tanks with ambient coastal Atlantic seawater (36 psu), put on a 12:12 hr light–dark cycle and allowed to equilibrate for 4 weeks. The mesocosm setup included sixteen 500 L (3 m diameter × 3 m height)