



Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Species and tissue type regulate long-term decomposition of brackish marsh plants grown under elevated CO₂ conditions



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ARTICLE INFO

Article history:

Received 15 June 2015

Received in revised form

16 November 2015

Accepted 30 November 2015

Available online 8 December 2015

Keywords:

Climate change

Belowground

Decay rate

Mississippi River Delta

Schoenoplectus americanus

Spartina patens

ABSTRACT

Organic matter accumulation, the net effect of plant production and decomposition, contributes to vertical soil accretion in coastal wetlands, thereby playing a key role in whether they keep pace with sea-level rise. Any factor that affects decomposition may affect wetland accretion, including atmospheric CO₂ concentrations. Higher CO₂ can influence decomposition rates by altering plant tissue chemistry or by causing shifts in plant species composition or biomass partitioning. A combined greenhouse-field experiment examined how elevated CO₂ affected plant tissue chemistry and subsequent decomposition of above- and belowground tissues of two common brackish marsh species, *Schoenoplectus americanus* (C₃) and *Spartina patens* (C₄). Both species were grown in monoculture and in mixture under ambient (350–385 μL L⁻¹) or elevated (ambient + 300 μL L⁻¹) atmospheric CO₂ conditions, with all other growth conditions held constant, for one growing season. Above- and belowground tissues produced under these treatments were decomposed under ambient field conditions in a brackish marsh in the Mississippi River Delta, USA. Elevated CO₂ significantly reduced nitrogen content of *S. americanus*, but not sufficiently to affect subsequent decomposition. Instead, long-term decomposition (percent mass remaining after 280 d) was controlled by species composition and tissue type. Shoots of *S. patens* had more mass remaining (41 ± 2%) than those of *S. americanus* (12 ± 2%). Belowground material decomposed more slowly than that placed aboveground (62 ± 1% vs. 23 ± 3% mass remaining), but rates belowground did not differ between species. Increases in atmospheric CO₂ concentration will likely have a greater effect on overall decomposition in this brackish marsh community through shifts in species dominance or biomass allocation than through effects on tissue chemistry. Consequent changes in organic matter accumulation may alter marsh capacity to accommodate sea-level rise through vertical accretion.

Published by Elsevier Ltd.

1. Introduction

Decomposition of plant matter can influence the capacity of coastal wetlands to keep pace with sea-level rise through organic matter contribution to vertical accretion and soil volume expansion (Day et al., 1999; Cahoon et al., 2006; Mudd et al., 2009; McKee, 2011), as well as other properties such as carbon storage (Chmura et al., 2003; Mcleod et al., 2011). Decomposition rates are relatively slow under the anaerobic conditions of saturated wetland soils (Webster and Benfield, 1986) and typically decline with depth

or as soil moisture content increases (Mendelssohn et al., 1999). In tidal wetlands, decomposition is also influenced by salinity (Craft, 2007), sea-level rise (Miller et al., 2001; Kirwan et al., 2013), nutrient availability (Morris and Bradley, 1999; Sundareshwar et al., 2003; Wigand et al., 2009; Anisfeld and Hill, 2012; Deegan et al., 2012), temperature (White et al., 1978; Montagna and Ruber, 1980; Christian, 1984; Lewis et al., 2014), and herbivore activity (Middleton and McKee, 2001; Treplin et al., 2013). Many of these factors are affected by global, regional, and local environmental changes.

One factor that has received less attention in wetland decomposition studies is atmospheric CO₂, a main driver of global climate change. Previous studies have shown that CO₂ enrichment increases C:N ratios of plant litter in forests (Kominoski et al., 2007),

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grasslands (Reich et al., 2001), and wetlands (Erickson et al., 2007). Because plant matter with higher C:N ratios (refractory, low quality) generally decomposes more slowly than material with lower C:N ratios (labile, high quality) (Webster and Benfield, 1986; Enríquez et al., 1993), increased CO₂ may slow decomposition by altering C:N of plant litter.

In addition to influencing litter quality, elevated CO₂ may affect decomposition by driving shifts in plant community composition and biomass allocation to tissues differing in decay resistance. Elevated CO₂ can enhance the competitive ability of C₃ species relative to co-occurring C₄ species and alter their relative abundances in the community (Arp et al., 1993; Polley et al., 2003; Cherry et al., 2009), which could affect decomposition rates if species differ in relative decomposability. Elevated CO₂ increased production and accumulation of refractory belowground material (roots, rhizomes) in brackish marshes (Langley et al., 2009a) where its decomposition may be additionally limited by the anaerobic conditions of saturated soils.

Limited information exists about effects of CO₂ on plant litter decomposition in wetlands. One study conducted in a temperate, brackish marsh in Chesapeake Bay found no direct effect of CO₂ treatment on soil respiration when field plots exposed to higher CO₂ were compared to ambient CO₂ plots (Ball and Drake, 1997). Instead, soil respiration decreased 17% over a six-week period when shoot litter from the C₃ species grown under elevated CO₂ and characterized by high C:N ratio was added to experimental mesocosms (Ball and Drake, 1997). These results suggested that CO₂-driven increases in C:N ratio might slow decomposition in some brackish marshes. To date, no study has measured longer-term decomposition of CO₂-treated litter in a wetland environment to test this prediction; nor has any work of this type been conducted in sub-tropical tidal marshes where patterns of decay may differ compared to those in temperate marshes.

Wetland soil formation and sediment accumulation contribute to vertical accretion of marsh surfaces, a process vital to systems stressed by sea-level rise. Recent work investigating the contribution, or lack thereof, of sediments to coastal wetlands along the Atlantic and Gulf Coasts of North America has revealed significant declines in suspended sediment delivery to many marsh ecosystems (Weston 2014). For example, the Mississippi River Delta (MRD) is one of the largest deltaic systems in the world, containing ~37% of the coastal marshes in the conterminous U.S. (Couvillion et al., 2011). Reduced sediment delivery from river to marshes combined with subsidence of deltaic sediments (Cahoon et al., 1995; Day et al., 2007) has contributed to the loss of nearly 25% of MRD coastal wetlands during the last century (Couvillion et al., 2011). Because of this reduced delivery of mineral sediment and subsidence, MRD wetlands are increasingly reliant on organic matter accumulation to build soil volume and vertically adjust to sea-level rise, therefore becoming particularly susceptible to changes in factors that affect rates of biomass production and decomposition. Both greenhouse and field experiments have shown that CO₂ treatment can enhance root production by brackish marsh plants and belowground accumulation of organic matter in plant communities found in the Gulf and Atlantic coasts of North America (Cherry et al., 2009; Langley et al., 2009a). However, those studies did not measure decomposition rates. We addressed this information gap by investigating the effect of CO₂ concentration on litter quality and decomposition in brackish marshes of the MRD, which contain co-occurring C₃ and C₄ plants.

The main objective of our study was to determine if increases in atmospheric CO₂ concentration can affect plant decomposition rates in brackish marshes through changes in tissue chemistry or alternatively, by driving changes in plant species composition (C₃ versus C₄) or biomass allocation (above-versus belowground). Two

dominant species found in brackish marshes in the MRD, as well as along the Atlantic coast of the U.S., *Schoenoplectus americanus* (C₃ sedge) and *Spartina patens* (C₄ grass), were grown in greenhouse mesocosms as either a monoculture or mixture and under ambient or elevated atmospheric CO₂ conditions. Above- and belowground plant tissues were harvested and decomposed for 280 d in litter bags under ambient field conditions. This approach allowed examination of CO₂-driven changes in tissue quality in isolation from other factors that might interact with CO₂ to affect litter decomposition. The findings of this study provide insight into the potential effects of higher concentrations of atmospheric CO₂ on decomposition rates in subtropical, coastal marshes.

2. Methods

2.1. Site description

The study was conducted at Big Branch Marsh National Wildlife Refuge, Louisiana, USA (30° 15' N, 89° 56' W) in an oligohaline marsh (mean porewater salinity: 6.6 ± 0.2, all salinities reported using the Practical Salinity Scale). The refuge marshes are part of a larger complex of estuarine wetlands in the Pontchartrain Basin, which includes Lakes Pontchartrain, Maurepas, and Borgne. Total wetland area in the basin is 195,000 ha, consisting of 15,500 ha of freshwater marsh, 11,500 ha of intermediate marsh, 47,304 ha of brackish marsh, 34,000 ha of saline marsh, and 87,000 ha of cypress swamp (<http://lacoast.gov>, accessed 09/11/2015).

The study marsh site, located along Bayou Lacombe, is dominated by two plant species, *S. americanus* (Pers.) Volk. Ex Schinz & R. Keller (American bulrush) and *S. patens* (Ait.) Muhl. (marshhay cordgrass). *S. americanus* and *S. patens* are common in brackish marshes along the Gulf and Atlantic coasts of the USA and account for 4222 km², or approximately 29%, of the estimated 14,653 km² of wetlands in coastal Louisiana (Sasser et al., 2008). The study marsh experiences astronomical tides of low amplitude (diurnal range = 0.2 m; The Rigolets, LA; tide gauge station ID: 8761402; NOAA Tides and Currents), but water levels in the lakes and bays of Louisiana are strongly influenced by meteorological events (Feng and Li, 2010). The modern marsh formed over organic Holocene sediments, ranging from 2.5 to 3.0 m thick, that overlie compacted fluvial silts and fine sands deposited during the Pleistocene (McKee and Cherry, 2009; J. Kindinger, public communication; <http://pubs.usgs.gov/of/2002/of02-206/geology/geologic-setting.html>; accessed 3/1/2013). The study marsh is located in a region with a humid, subtropical climate; during the study period, maximum/minimum temperature and precipitation were 36.7/−6.7 °C and 5.7/0 cm, respectively (NOAA National Climatic Data Center, Station ID: USC00168539, Slidell, LA).

2.2. Experimental design

Our approach was designed to determine how relative differences in tissue chemistry between species and generated by CO₂ treatment would influence decomposition rates under ambient conditions at the study site. Plant material was collected from the study site in March 1998 and prepared by growing transplants of *S. americanus* and *S. patens* for one growing season under two CO₂ treatments. Two hundred transplants, consisting of a 3-cm diameter plug with 3–4 culms, were excavated from a 500 m² area and established in individual containers (4 L pot with drainage spout) filled with commercial potting soil (Jiffy-Mix—a mixture of sphagnum peat moss and vermiculite; see Pittenger (1986) for detailed properties) and placed in growth chambers. A standardized soil mixture was used to minimize variation among pots and ensure common edaphic conditions across treatments. Thirty pots

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