



## Early growth interactions between a mangrove and an herbaceous salt marsh species are not affected by elevated CO<sub>2</sub> or drought



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### ABSTRACT

Increasing atmospheric carbon dioxide (CO<sub>2</sub>) concentrations are likely to influence future distributions of plants and plant community structure in many regions of the world through effects on photosynthetic rates. In recent decades the encroachment of woody mangrove species into herbaceous marshes has been documented along the U.S. northern Gulf of Mexico coast. These species shifts have been attributed primarily to rising sea levels and warming winter temperatures, but the role of elevated CO<sub>2</sub> and water availability may become more prominent drivers of species interactions under future climate conditions. Drought has been implicated as a major factor contributing to salt marsh vegetation dieback in this region. In this greenhouse study we examined the effects of CO<sub>2</sub> concentration (~380 ppm, ~700 ppm) and water regime (drought, saturated, flooded) on early growth of *Avicennia germinans*, a C<sub>3</sub> mangrove species, and *Spartina alterniflora*, a C<sub>4</sub> grass. Plants were grown in monocultures and in a mixed-species assemblage. We found that neither species responded to elevated CO<sub>2</sub> over the 10-month duration of the experiment, and there were few interactions between experimental factors. Two effects of water regime were documented: lower *A. germinans* pneumatophore biomass under drought conditions, and lower belowground biomass under flooded conditions regardless of planting assemblage. Evidence of interspecific interactions was noted. Competition for aboveground resources (e.g., light) was indicated by lower *S. alterniflora* stem biomass in mixed-species assemblage compared to biomass in *S. alterniflora* monocultures. Pneumatophore biomass of *A. germinans* was reduced when grown in monoculture compared to the mixed-species assemblage, indicating competition for belowground resources. These interactions provide insight into how these species may respond following major disturbance events that lead to vegetation dieback. Site variation in propagule availability and physico-chemical conditions will determine plant community composition and structure following such disturbances when these two species co-occur.

### 1. Introduction

Plant responses to increasing atmospheric carbon dioxide concentration ([CO<sub>2</sub>]) have been the focus of thousands of scientific studies (Körner, 2006). In general, rising [CO<sub>2</sub>] acts to reduce stomatal conductance and transpiration in plants, improving water-use efficiency, and stimulates photosynthetic rates and increases light-use efficiency (Drake et al., 1997). Elevated [CO<sub>2</sub>] can alter plant productivity and community composition across a variety of habitats (Bazzaz, 1990; Woodward et al., 1991). Much work has focused on the effect of [CO<sub>2</sub>] on photosynthesis, and the different response of plants that utilize the C<sub>3</sub> photosynthetic pathway compared to those that utilize the C<sub>4</sub> pathway. Atmospheric [CO<sub>2</sub>] below about 350 ppm limits photosynthesis in C<sub>3</sub> plants (Arp et al., 1993). Concentration above this level can stimulate growth in both groups of plants, but productivity

enhancement is often higher in C<sub>3</sub> than in C<sub>4</sub> plants (reviewed in Poorter, 1993; Wand et al., 1999). Functional group differences based on data for isolated plants, however, are poor predictors for the response of species grown in competition (Poorter and Navas, 2003). In addition, the influence of other factors such as soil nutrient levels and water availability in moderating the effects of enhanced [CO<sub>2</sub>] has been emphasized (Körner, 2006; Leakey et al., 2009; Reich et al., 2014).

Research focusing on how wetland plants respond to elevated [CO<sub>2</sub>] in concert with changes in other environmental resources has identified interesting trends. Surface elevation in coastal marshes was stimulated by elevated [CO<sub>2</sub>] through increased belowground productivity (Langely et al., 2009; Reef et al., 2017), and this increased productivity was found to offset stress associated with increased salinity (Cherry et al., 2009). Elevated [CO<sub>2</sub>] increased total biomass production in a C<sub>3</sub>-dominated marsh community while having no effect on a C<sub>4</sub>-dominated

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community, leading to a shift in dominance to favor  $C_3$  plants in mixed communities (Erikson et al., 2007). In another study a  $C_3$  wetland sedge displayed increased aboveground productivity under high nitrogen availability and elevated  $[CO_2]$ , whereas increased productivity in a  $C_4$  wetland grass under high nitrogen availability was diminished under elevated  $[CO_2]$  (White et al., 2012).

Interest exists in describing interactions between the  $C_3$  woody species *Avicennia germinans* (L.) L. (black mangrove) and the  $C_4$  wetland grass *Spartina alterniflora* Loisel. (smooth cordgrass). Both are common species along the subtropical coast of the northern Gulf of Mexico, where studies have documented mangrove forest encroachment into grass-dominated marshes over the past few decades at many sites (Ross et al., 2000; Krauss et al., 2011; Raabe et al., 2012; Armitage et al., 2015). Shifts in the distributions of mangrove and herbaceous marsh species can have considerable impact on the provision of ecosystem services in coastal wetlands, including carbon storage and habitat availability for fauna (Kelleway et al., 2017). Factors that influence this distribution shift include sea-level rise (Record et al., 2013; Krauss et al., 2014), reduced freshwater inflow (Ross et al., 2000), and climate-change effects on winter temperatures (e.g., increased intervals between freeze events); this latter factor reduces stress on freeze-intolerant mangrove species (Cavanaugh et al., 2014). Interactions between the two species may be influenced by other factors, such as life stage, soil conditions, and  $[CO_2]$ . It has been demonstrated that elevated  $[CO_2]$  up to 485 ppm significantly decreased stomatal conductance and transpiration and increased instantaneous transpiration efficiency of *A. germinans* leaves (Snedaker and Araújo, 1998). McKee and Rooth (2008) studied the effects of competition, elevated  $[CO_2]$ , and increased nitrogen on *A. germinans* establishment, growth, and maturity in salt marshes; they found that mangrove seedling growth was enhanced under elevated  $[CO_2]$  and nitrogen in the absence of competition, but was suppressed when *S. alterniflora* was present. Suppression of *A. germinans* early growth by herbaceous marsh communities was also documented by Howard et al. (2015). The McKee and Rooth (2008) and Howard et al. (2015) studies were conducted in greenhouses and used sections of marsh (i.e., mesocosms) that included native plant assemblages, and *A. germinans* propagules were introduced into established marsh communities. It is possible that interactions between mangrove and herbaceous marsh species will vary depending on the life stages examined.

We found little information in the literature on the effects of increasing  $[CO_2]$  on regeneration or early growth of wetland plant species. A study that examined mangrove seedling response to elevated  $[CO_2]$  identified a 12–47% increase in growth relative to that under ambient concentrations (Lovell et al., 2016). A seed bank study concluded that  $[CO_2]$ , salinity, and flooding interacted to affect germination density and early seedling growth of floating freshwater marsh species (Middleton and McKee, 2012). Interactions between *A. germinans* and *S. alterniflora* during establishment and early growth are likely when unvegetated sediment exists. Large expanses of bare sediment may be present after wetland restoration using dredged sediment or following an acute salt marsh dieback (SMD) event, a phenomenon that has occurred along the Atlantic and Gulf of Mexico coasts of the US (Silliman et al., 2005; Alber et al., 2008; Hughes et al., 2012). It was noted that an extensive SMD event affecting *S. alterniflora* in Louisiana in 2000 did not affect survival or growth of *A. germinans* (McKee et al., 2004).

In this study we examined early growth of *A. germinans* and *S. alterniflora* under different  $[CO_2]$  and water regimes when growing on a substrate lacking aboveground and belowground plant tissues. Plants were grown in a greenhouse setting in monocultures and in mixed-species assemblages. For monoculture assemblages we hypothesized (1) *A. germinans* will respond to elevated  $[CO_2]$  by increasing seedling growth, (2) *S. alterniflora* will either not respond to  $[CO_2]$ , or if it does, the magnitude of the response will be lower than that of *A. germinans*, and (3) growth of both species in monoculture will be reduced when

water availability is restricted, and that increased  $[CO_2]$  will ameliorate that reduction in *A. germinans*. We further hypothesized that in the mixed species assemblage early growth of *S. alterniflora* will be reduced by the presence of *A. germinans* under elevated  $[CO_2]$ , and the reduction in growth will be greater when water availability is restricted.

## 2. Materials and methods

### 2.1. Experimental material collection and design

#### 2.1.1. Plant and soil collection

We collected *Avicennia germinans* propagules in December 2014 along a canal (29°10' N, 90°14' W) near Bayou Lafourche in Leeville, Louisiana. The canal was surrounded by salt marshes dominated by *Spartina alterniflora*, and *A. germinans* was present along the canal banks only. Propagules were collected by hand from the sediment surface (i.e., after they had fallen from the trees); only bright green, healthy-appearing propagules that had not yet developed a radicle were selected. The propagules were kept moist during transport to the greenhouse facility at the U.S. Geological Survey, Wetland and Aquatic Research Center in Lafayette, Louisiana, where they were placed in reservoirs (plastic coolers) containing fresh well water with salinity adjusted to 30 practical salinity scale using Instant Ocean® Marine Salt (Spectrum Brands, Blacksburg, Virginia). The propagules were stored floating in the reservoirs until we initiated the experiment 6 weeks later.

Our original design included examining treatment effects on growth of plants emerging from the marsh seed bank. However, no seeds germinated from marsh soil samples obtained when the *A. germinans* propagules were collected. Therefore, *S. alterniflora* seeds were provided by the Louisiana State University Agricultural Center, Rice Research Station, in Crowley, Louisiana. The seeds were harvested in December 2011 from a plot at the Rice Research Station containing an experimental variety of *S. alterniflora* adapted for high seed production. The seeds were threshed, cleaned, and stored dry in an airtight container held at 1–3 °C until they were introduced to the experiment.

#### 2.1.2. Treatment application and experimental design

The experiment was initiated in January 2015 in the Elevated  $CO_2$  Experimental Facility (Facility) at the U.S. Geological Survey Wetland and Aquatic Research Center. The Facility (described in McKee and Rooth, 2008) consisted of four individual greenhouses, each with an area of 12 m<sup>2</sup>. We applied three main treatment factors: atmospheric  $[CO_2]$  (two levels), plant assemblage type (three levels), and water regime (three levels). Water salinity was held at equal values in all treatment combinations. To avoid stressing seeds and young seedlings, salinity during the experiment was initially set at 4 and was gradually raised to a final level of 20; all salinity adjustments during the experiment were made using Instant Ocean® Marine Salt. The  $[CO_2]$  treatment was applied at the greenhouse level, with two greenhouses held at ambient  $[CO_2]$  (~380 ppm) and two at elevated concentrations (~700 ppm). Plant assemblage types (hereafter referred to as assemblages) were designated as (1) *A. germinans* monoculture, (2) *S. alterniflora* monoculture, and (3) *S. alterniflora* and *A. germinans* mixture. The water regime treatments consisted of flooded (water depth 10 cm above the sediment surface), saturated (water within 1 cm of the sediment surface), and drought (water at 10 cm below the sediment surface). We believed it was reasonable to expect that the simulated drought treatment would impose stress on *S. alterniflora* based on the greenhouse study of Brown et al. (2006), who found that shoot growth in this species was decreased when water levels at high tide did not exceed 10 cm below the sediment surface. In addition, a field study indicated that, in salt marshes restored with sediment slurry additions, soil elevations of 11 cm above local mean sea level led to reduced marsh resilience and stability because of insufficient and infrequent flooding (Stagg and Mendelsohn, 2011).

We prepared pots (24-cm diameter by 28-cm tall) for the

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