



Morphological responses to competition modulated by abiotic factors in two monoculture-forming wetland plants



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ABSTRACT

We investigated the relative roles of competition and environmental stressors in two wetland plants important for coastal restoration in the northern Gulf of Mexico. *Phragmites australis* and *Schoenoplectus deltarum* are ubiquitous in tidal freshwater marshes along the northern Gulf of Mexico coast. *Schoenoplectus deltarum* and *Phragmites australis* were grown in both monoculture and competition, and subjected to two levels each of nitrogen, salinity, and soil organic matter in a factorial greenhouse experiment. Productivity in both species was consistently suppressed under competition; the extent of this depended on the abiotic treatments. In monoculture, *Schoenoplectus* productivity responded negatively to low organic matter and reproduction responded negatively to brackish water; *Phragmites* productivity responded negatively to increased nitrogen. *Schoenoplectus* root-to-shoot ratio responded positively to brackish water when grown in soil with high organic matter, and *Phragmites* root-to-shoot ratio responded negatively to increased nitrogen. The sediment diversion operation strategy that has been recommended by experts familiar with Louisiana coastal wetland restoration may result in marshes characterized by increased nitrogen, periodic brackish water conditions, and increased soil organic matter. Such a strategy may therefore promote species coexistence and increased root production, which are respectively associated with increased ecosystem services and soil stability. The differential responses of the two species to the same conditions illustrates the importance of considering individual species to a restoration project.

1. Introduction

Understanding habitat requirements and competitive interactions associated with wetland plant species is important to the planning of successful and sustainable wetland restoration. The Mississippi River Delta (MRD) in southern Louisiana is an example of a dynamic system whose community composition is governed by the local hydrology and geomorphology (White, 1993; Cahoon et al., 2011). The MRD has occupied six distinct lobes over the past 7500 years, each characterized by a predictable cycle of rapid elevation and aerial gain due to sediment deposition, geomorphic stability during the period when sediment supply and subsidence balance, and deterioration due to wave erosion and subsidence in the later years (Roberts, 1997). While the lifespans of these major delta lobes are approximately 1000–2000 years, smaller sub-deltas within the major lobes exhibit the same pattern within 150–200 years (Roberts, 1997). Coastal Louisiana sub-deltas currently experiencing the depositional phase can gain between 1.5 and

5.6 cm yr⁻¹ in elevation from sediment accumulation, although the net increase in elevation is often reduced due to natural subsidence (Kolker et al., 2012; Esposito et al., 2013; Rosen and Xu, 2015). As a result, even if the river stages were identical in two consecutive years, vegetation at the same location on a sub-delta would experience less cumulative inundation in the second year if the elevation gain from sediment deposition is greater than the elevation loss from subsidence. Plant species in freshwater marshes are often restricted to characteristic elevations as a response to differing degrees of inundation tolerance (Mitsch and Gosselink, 1993). Under such conditions, the role of flood regime as a limiting factor on vegetation would slowly but consistently diminish as the marsh develops. Restoration-based studies of wetland plant habitat requirements often test flood regime as a primary or sole controlling factor (e.g. Frazer and Karnezis, 2005; Alleman and Hester, 2011; Sloey et al., 2016). However, in primary successional environments on the Mississippi River Delta, the highest species diversity was found at the lowest elevations in the first two growing seasons (White, 1993). It is

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therefore possible that in the earliest phases of wetland building, the niches of wetland plant species are defined by axes other than elevation.

Diversion of the Mississippi River through gate-controlled structures has recently become the focus of restoration efforts in the lower MRD region (Louisiana Coastal Protection and Restoration Authority [LACPR] 2017). A consequence of these diversions will be to restart the sub-delta cycle within the floodplain, which has been starved of sediment throughout the 20th century as a result of flood control levees (Louisiana Coastal Protection and Restoration Authority, 2017). Wetlands formed in the new sub-deltas are expected to experience annual elevation gain, and vegetation dynamics may be affected as flooding stress is abated over time.

Here we examine three abiotic factors that could influence wetland plant community composition in the MRD in the absence of flooding stress. First, one of the most widely cited concerns regarding sediment diversions is their potential to introduce high levels of nitrogen, largely derived from agricultural operations throughout the Mississippi River's watershed, into the surrounding wetlands. This can result in reduced belowground productivity by wetland vegetation leading to higher susceptibility to erosion (Darby and Turner, 2008; Deegan et al., 2012). Excess nitrogen loading has been found to promote different patterns in biomass allocation between C3 and C4 species (White et al., 2012) and favor C4 species in competition (Langley and Megonigal, 2010) due to higher nitrogen use efficiency and increased productivity associated with the C4 pathway (Brown, 1977). Second, the receiving basins of many of the planned diversions are currently brackish, intermediate, or salt marshes, but will likely become tidal freshwater marshes due to the input of Mississippi River water. Tidal freshwater marshes may experience episodes of saltwater intrusion if the influence of wind- or tidal-driven seawater is greater than that of the river's freshwater input (Anderson and Lockaby, 2012). Salt tolerance differs among plant species, and community composition can shift over a salinity gradient (La Peyre et al., 2001). Third, the sediment to be introduced by diversions to build the initial marsh platforms will be sand from the riverbed, which is highly mineral and low in organic content. The organic matter content of marsh soils can vary based on sediment input, the amount of plant litter entering the soil, the rate of decomposition, and the age of the marsh (Nyman et al., 1990). The amount of organic material in soil can affect plant growth in non-flooded environments by changing the physical density or porosity of the soil, modifying the water retention of the system as well as the ability of plants to produce belowground biomass (Mitsch and Gosselink, 1993).

We hypothesized that dynamic changes in nitrogen, salinity, and type of deposited sediment will be important in determining freshwater wetland plant community structure. We tested these predictions under greenhouse conditions using the disturbance-adapted (Zedler and Kercher, 2010), salt-tolerant (Meyerson et al., 2000), C4-capable (Srivastava et al., 2014) grass *Phragmites australis* (common reed) and the less opportunistic (White, 1993), less salt-tolerant (Howard and Mendelssohn, 1999), C3 (Bruhl and Wilson, 2007) sedge *Schoenoplectus deltaicum* (delta bulrush). Both species are ubiquitous in the MRD, form dense monospecific stands, and propagate vegetatively (White, 1993; Hauber et al., 2011). First, we predicted that the C4 grass *Phragmites australis* will be a superior competitor compared to the C3 sedge *Schoenoplectus deltaicum* such that under elevated nitrogen conditions, root-to-shoot ratios of the latter will decrease. Second, we predicted that the salt-tolerant *Phragmites australis* will be a superior competitor compared to the freshwater *Schoenoplectus deltaicum* such that under brackish conditions, the latter will exhibit greater senescence. Third, we predicted that disturbance-adapted *Phragmites australis* will be a superior competitor to the less opportunistic *Schoenoplectus deltaicum* such that under low-organic conditions, the former will have more biomass. This study tests the roles of nitrogen, salinity, and soil organic matter in limiting and modulating competitive interactions between these important freshwater marsh species, and discusses the implications of our

findings for restoration in the MRD.

2. Methods

We designed a blocked additive pairwise competition experiment to test the effects of environmental factors on *Phragmites australis* (hereafter *Phragmites*) and *Schoenoplectus deltaicum* (hereafter *Schoenoplectus*). We replicated the experiment across three blocks, each of which contained a randomly assigned factorial array of community (3 levels), salinity (2 levels), nitrogen (2 levels), and soil organic matter content (2 levels). Blocking was motivated by the spatial variation in sunlight throughout the greenhouse due to shadows cast by adjacent buildings.

2.1. Collection and propagation

Plants were collected in August 2014 in a sub-delta complex that began forming in 2011 in the West Bay Sediment Diversion receiving basin. The sub-delta is located approximately 8 km upstream from the mouth of the Mississippi River and continues to expand in area (Yuill et al., 2016). Sods of approximately 1500 cm³ containing young (1 m or shorter) clones of *Phragmites* and *Schoenoplectus* were harvested on August 23, 2014 from one monospecific stand of each species on the West Bay sub-delta (*Schoenoplectus*: 29.21206N, 89.30127W. *Phragmites*: 29.21207N, 89.30280W), and transported to the Tulane University greenhouse in New Orleans, LA. Upon arrival, the sods were rinsed of sediment and transplanted across 36 pots for each species, at a density of 5 stems per pot. The plants were allowed to grow in the greenhouse until July 2015. Pots were watered for one hour every six hours at a rate of 12.1 L h⁻¹ pot⁻¹ using a timed watering system, and weeded on a weekly basis.

2.2. Treatment applications

72 experimental units were planted between July 20 and July 31, 2015, each receiving one of three species mixtures, one of two water sources (fresh or brackish), and one of four soil mixtures (factorial combinations of low and high nitrogen and soil organic matter). Experimental units were grown in plastic nursery pots with volume of 15,137 cm³ and an open surface area of 769 cm². All stems were cut to 100 cm at time of transplanting to account for initial size bias (Gibson et al., 1999). During planting, excessive plant stress due to temperature and evapotranspiration were noted in the first 18 experimental units. This issue was corrected by applying cypress mulch to all pots. Automated watering began on the fifth day of planting, and all treatments were implemented by the 11th day.

Additive pairwise competition experiments include experimental units containing the two species in mixture, as well as each species in monoculture (Gibson et al., 1999). Densities were determined by averaging stem counts taken within 1 m² quadrats throughout West Bay in June 2014 (Ameen et al., 2017). Initial planting densities were either 8 stems per pot (*Phragmites* monoculture), 26 stems per pot (*Schoenoplectus* monoculture), or 4 *Phragmites* plus 13 *Schoenoplectus* stems (competition treatment).

The high-organic soil used was HapiGro Potting Soil (Hope Agri Products, Hope, AR), which contains sand, pine bark mulch, ash, and perlite. The organic content was estimated by calculating loss on ignition (LOI) (Flemming and Delafontaine, 2000). The high organic soil had an LOI of 29.6%, which is consistent with mature, high-organic marsh soils in south Louisiana (Day et al., 2011; Kolker et al., 2012). The low organic soil was achieved by mixing the same HapiGro soil with Quikrete Play Sand (Quikrete Companies, Atlanta, GA), which had a nearly-negligible LOI of 0.05%. Based on the densities of the two products, a mixture of 2 parts sand to one part potting soil was calculated to yield an LOI of approximately 5%, which is typical of young mudflat sediment within West Bay where the plants were collected (Ameen et al., 2017).

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