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Geochemical factors promoting die-back gap formation in colonizing patches of *Spartina densiflora* in an irregularly flooded marsh

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ABSTRACT

Circular (RP) and ring-shape (RP) patches of vegetation in intertidal flats have been associated with the radial expansion of tussock growth forms and die-back gap in older central stands, respectively. RP formation has not yet been sufficiently explained. We accomplished a comparative geochemical study of CP and RP structures of *Spartina densiflora* within a single saltmarsh in a microtidal estuary (<0.5 m). The pore water under these structures demonstrated distinctive physical-chemical properties by marked seasonal changing in water level and salinity. During high-water period dissolved H_2S was frequently low in pore waters of *S. densiflora* structures due to reactive-Fe, which scavenge the sulfide from solution and form solid sulfides. During less flooded-brackish water period, pore water pH goes down below 4 inside the vegetated bordering areas of RP. In these locations the concentration of soluble sulfides dramatically increases up to 140 μM L^{-1}. The high concentration of protons in pore water is the result of solid sulfides atmospheric oxidation to sulfuric acid. High dissolution of H_2S, along with the low pH, creates a toxic environment for *S. densiflora* and die-back central gap formation in RP. CP structure was 5 cm higher in the intertidal than RP but shows frequent presence of a water layer, less severe oxidation of sulfides and limited building-up of toxic condition to plants. Development of *S. densiflora* RP probably indicates the uplift of sediment by this bioengineer grass and/or periodic lowering of the water surface below a certain critical level.

1. Introduction

The development of vegetation in saltmarshes is a complex process involving a number of biotic and abiotic factors. The spatial expansion of plant stands could have irregular shape as well as symmetrical shape in form of circles and rings. The circular patch corresponds to the normal radial expansion of plant species, especially vegetative propagation by rhizomes with tussock formation, on a homogeneous substrate in the absence of a strong competitive species (Feist and Simenstad, 2000; Lewis et al., 2001; Perillo and Iribarne, 2003; Dennis et al., 2011; Marangoni and Costa, 2012). Widely separated circular patches at the leading edge of the mud flat invasions grow until coming in contact with another patch, however very frequently after years and even decades of growth, the central part of the patches show signs of die-back, leaving a depleted plant cover or empty central gap and finally a ring-shape patch (Lewis et al., 1990, 2001; Castillo et al., 2003; Perillo and Iribarne, 2003; Minkoff et al., 2006; Escapa et al., 2015). Meanwhile these central gaps may be colonized by other successional plant species (Lewis et al., 1990; Castellanos et al., 1994; Alberti et al., 2008). The formation of vegetation ring patches in estuarine and coastal areas has not been sufficiently explained yet, in fact, it has been almost overlooked in scientific literature.

Fonseca and Kenworthy (1987) explained the appearance of round patches of the sea grass *Zostera marina* L. by the action of waves and currents, contributing to alluvium deposits and raising the bottom in the outermost parts of meadows. With increasing current velocities, the shape of sea grass meadow becomes more ellipsoid, and tends to develop perpendicular to the water flow (Fonseca et al., 1983). The sea grass die-off in the center of the patches is probably caused by excessive sand accumulating inside the patches during storm events.

The ring structure of *Z. marina*, the so-called 'fairy rings', appearing on the chalk plates in shallow water outside the calcium carbonate cliffs of the island of Møn, Denmark were well described by Borum et al. (2014). The authors found that neither the clonal growth pattern of this sea grass, sediment burial of shoots,

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hydrodynamic forcing nor nutrient limitation could explain the ring-shaped pattern. They conclude that the most likely explanation must be the accumulation of toxic sulfide in the sediment due to low iron availability in the carbonate-rich environment invaded by *Z. marina* shoots.

Circular and ring-shaped patches were described to several species of the genus *Spartina*. For example, *Spartina maritima* colonization can alter intertidal physiography. Over time, sediment accretion, accelerated by colonizing *S. maritima* and this biogenic process, can rapidly transform unvegetated littoral flats into monotypic circular patches. Castellanos et al. (1994) described the process of ring patch formation in SW Spain saltmarshes as successional replacement between *S. maritima* and *Arthrocnemum perenne*, i.e. the central area of *Spartina* tussocks are invaded by *A. perenne* leaving, over time, only a fringe of *Spartina* around the edge of the tussocks. Areas invaded by *A. perenne* were characterized by oxidizing sediment, while the *Spartina*-dominated areas remained highly reducing, even in the surface layers. However, the authors did not identify specific inhibitory agents which caused plant die-off in the centers of *Spartina* patches. According to Lewis et al. (1990) *Spartina argentinensis* (sin. *Spartina spartinae*) is a dominant species of saline soils in the Great Chaco region, at Santa Fé Province (northern Argentina), and their dense tussocks with round shapes prevent other plants settlement in saltmarshes by light interference. According to these authors, as the tussocks age, gaps like a "monk's tonsure" develop at their center and they are later colonized by *Solidago chilensis* and *Neptunia pubescens*. Lewis et al. (2001) found that the soil of *S. argentinensis* gap is richer in organic matter and phosphate and it has lower pH than that of the soil outside the gap. Alberti et al. (2008) pointed out that the colonization of central part of *Sarcocornia perennis* colonizing patches in NE Argentina saltmarshes by *Spartina densiflora* resulted in out-competition of this forb and probably not due to differences in desiccation or salt stress between evaluated health circular patches and depleted ring patches of *S. perennis*. Contrariwise, salt pan formation inside ring patches of *S. perennis* has been related to physical processes (water-logging, ice-scouring, sub-surface drainage, surface erosion and tidal wrack deposition) and bioturbation by activity of the burrow crab *Neohelice granulata* (Perillo and Iribarne, 2003; Minkoff et al., 2006; Escapa et al., 2015). *N. granulata* is widespread between southern Brazil and northeast Argentinean coast, being saltmarsh productivity and physical-chemical conditions influenced by its borrowing activities (Fanjul et al., 2007; Martinetto et al., 2016). Finally, Castillo et al. (2003) found a distinct central die-back phenomenon in *S. densiflora* tussocks with radius larger than 20 cm at SW Spain marshes and that areas remained occupied by high amount of plant debris.

At southern Brazil, the estuary of Patos Lagoon is characterized by the development of saltmarshes largely occupied by two *Spartina* species (*S. alterniflora* and *S. densiflora*). The colonization patches of *Spartina* species on intertidal flats have a distinctive circular shape, but specially tussocks of *S. densiflora*. This circular patches are very common and the long-term monitoring (56 years) pointed to a steady lateral spread over mud flats for either species but at different spread rates (Costa and Marangoni, 2010; Marangoni and Costa, 2012). Organic matter and sediments accumulate inside the *S. densiflora* tussocks'crowns lifting the soils several centimeters above general ground level (Castillo et al., 2003; Costa and Marangoni, 2010). The central part of old ring structures is free of vegetation, or may have signs of incipient re-colonization of *S. densiflora* and other types of vegetation. The hydrological regime of this microtidal estuary is controlled by the dominance of the river flow but particularly during rainy winter/spring; sea water enters the estuary as a result of wind surge in a weakened river flow (Costa et al., 1988; Marangoni and Costa, 2012). The changing fresh and brackish water periods have a long-term character and specifically impacts on the development of vegetation and geochemical processes in sediments of Patos Lagoon estuary (Costa, 1997; Costa et al., 2003; Marangoni and Costa, 2012).

The simultaneous presence of ring and circular patches of *S. densiflora* indicates the existence of non-biological specific factors causing the death of plants in the centers of the ring structures. Furthermore, similar occurrence of *S. densiflora* tussocks with and without central gaps was observed in the Argentinean Chaco region (Lewis et al., 2001) and SW Spain marshes (Castillo et al., 2003). We conducted the present study based on the assumption that these factors may be geochemical processes accompanying diagenetic changes in sediments of saltmarshes. The aim of the study was to compare the geochemical parameters of sediments in the rhizome horizon along transects across the ring and circular patches of *S. densiflora* in contrasting hydrological periods of the estuary, and to disclose possible factors of suppression or death of shoots inside its tussocks while they expand over the intertidal flat and alter the bathymetry.

2. Material and methods

2.1. Study area

The study was carried out on an intertidal mudflat 15–25 cm below the mean water level of the Patos Lagoon estuary, which is located in Pólvora Island (Rio Grande, Brazil, 32 ° 01′S, 52 ° 06′W). The island is situated in the center of the estuary, and at a distance of about 25 km from its mouth (Fig. 1). This site is characterized by a warm temperate climate and by a microtidal regime (<0.5 m) with an irregular flooding pattern driven primarily by winds and freshwater runoff from a 200 000 km^2 watershed (Costa et al., 1988, 2003; Marangoni and Costa, 2012). The hydrologic pattern shows marked seasonal variation from high water levels and low salinities (0–5) during a rainy winter/spring to low water levels and high salinities (20–30) during summer/fall (Costa et al., 2003; Vaz et al., 2006; Möller et al., 2009). This hydrologic pattern can be disrupted by inter-annual variability associated with the quasiperiodic El Niño Southern Oscillation phenomenon. El Niño (warm phase) events in the tropical Pacific promote excessive rainfall and a high discharge of rivers in southern Brazil during the austral spring of the event year and summer–fall of the year following the start of El Niño (Vaz et al., 2006; Möller et al., 2009; Marangoni and Costa, 2012).

2.2. Sampling

The sampling was carried out in two periods: i) April 2015 - corresponding to the maximum water salinity in the estuary and ii) in November of the same year with high standing of fresh water under a El Nino event. Circular and ring patches of *Spartina* species on Pólvora Island have been extensively identified and mapped in aerial photos through GIS imaging processing tools (Lélis et al., 2001; Costa and Marangoni, 2010; Marangoni and Costa, 2012). We studied two *S. densiflora* patches: circular (D~7 m; hereinafter called "CP") and ring (D~20 m; "RP") located approximately 70 meters from each other (Fig. 1). RP and CP were located 45 m and 95 m respectively from the east margin of the island. The RP central gap showed an incipient re-colonization by *Scirpus maritimus* (<5 tillers m^{-2}). In the last 12 years CP diameter increased 75% over the mud flat, whereas RP diameter keep practically constant surrounded by *S. alterniflora* patches and its central gap developed after 2008. These two patches were chosen as representative of the observed vegetative propagation pattern of *S. densiflora* at local