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Relationships between spatio-temporal changes in the sedimentary environment and halophytes zonation in salt marshes

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ABSTRACT

This study reports the soil-plant relationships along the intertidal gradient from unvegetated mudflats to the ecotone between high marshes and coastal dunes. The main objective was to establish the integrated role of spatial and seasonal changes in the sedimentary abiotic environment in relation to the establishment of the halophytes zonation pattern. The sedimentary environment and the halophytes coverage were sampled bi-monthly during a year in nine intertidal habitats characterized by different plant communities. The highest values of sediment water content (40–60%) and electrical conductivity (20–30 mS cm^{-1}) were registered in low-middle marshes, the highest organic matter content (ca. 23%) was found in middle marshes, and the highest pH (8.5–9.0) was recorded in high marshes. The conductivity and the pH of the marsh sediments changed seasonally. The sediment conductivity reached its highest values during spring and summer. The spatial variations in the sedimentary environment were closely associated with the distribution of most of the recorded halophytes, especially in low and high marshes where the abiotic environment was more stressful. At the same time, cyclical seasonal changes in conductivity seemed to determine the distribution of the halophytes in high marshes, where the seasonality was very marked under Mediterranean climate. The combination and integration over time of these spatio-temporal changes in the sedimentary environment defined habitats with contrasted abiotic conditions parallel to the tidal line and complex abiotic mosaics inside some of these habitats, allowing the cohabitation of > 30 plant species along the intertidal gradient.

1. Introduction

The spatial ecological zonation is determined by differences in the tolerances to the abiotic environment among the interacting species (Chapman, 1974; Vince and Snow, 1984; Bertness, 1991). In general, zonation patterns are shaped mostly by interspecific competition in less-stressful environments (Gill and Marks, 1991; Grime, 1979), and by other biotic interactions such as herbivory (Alberti et al., 2015) and mostly by the tolerance to abiotic factors in the most stressful environments (Pennings and Callaway, 1992).

The environmental factors responsible of the abiotic stresses that limit the distribution of species can change in space and seasonally. In this context, the seasonal changes in the abiotic factors can determine temporal distribution patterns (Mourglia et al., 2015) and they can also influence on the establishment of spatial distribution patterns (Álvarez-Rogel et al., 2000, 2001; Tug et al., 2012). Nevertheless, diachronic studies analysing the integrated influence of seasonal changes in the abiotic environment on the spatial ecological zonation are scarce.

Tidal salt marshes are excellent ecosystems to study the effect of edaphic factors on the ecological zonation since these ecosystems are generally dominated by a few numbers of species and the sedimentary conditions vary strongly in short distances and throughout the year. The sedimentary environment in the salt marshes is mainly conditioned by the tidal flooding, which is responsible for marked zonation patterns (e.g. Apaydin et al., 2009; Callaway et al., 1990; Davis et al., 1996; Tug et al., 2012). In addition, Mediterranean salt marshes are especially suitable to explore the effects of seasonal changes in the sedimentary environment on the distribution of species due to their marked seasonal

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drought during summertime (Callaway et al., 1990; Rubio-Casal et al., 2001).

The tides fluctuate with the moon cycle and the seasons and, together with the marsh elevation, determine marked abiotic gradients between the lowest and the highest tidal levels, particularly in the sedimentary environment (Adam, 1990). In this sense, spatial changes in the soil water content, oxygenation and salinity are considered to be among the main abiotic factors affecting the plant zonation pattern in salt marshes (e.g. Cantero et al., 1998; Cott et al., 2013a). Sediment organic matter content and pH may also be important abiotic factors (Álvarez-Rogel et al., 1997a, 1997b; Onaindia and Amezaga, 1999). Thus, the observed spatial distribution of the vegetation (in bands parallel to the tidal line) is the result of the combined and integrated effect of multiple abiotic factors (Silvestri et al., 2005). In addition, the zonation pattern along the intertidal gradient is not universal, but changes with the specific abiotic characteristics as well as with the flora and fauna of every location and biogeographic region (Farina et al., 2009; Pennings et al., 2003; Valiela and Teal, 1974).

The integrated effects of seasonal changes of the sedimentary environment on halophytes' spatial distribution are poorly understood. The study of seasonal changes in the abiotic environment is useful in determining extremes and means of every abiotic factor that each plant species is subject to and the cumulative effect of the abiotic environment on every plant species.

The aim of the present study was to analyse the spatio-temporal changes in the sedimentary environment (water and organic matter contents, conductivity and pH) during a year along the intertidal gradient of salt marshes under Mediterranean climate on the Atlantic coast of Southwest Iberian Peninsula, and to relate these abiotic changes with the spatial abundance of halophytes species. Thus, we looked at how each plant species integrated all the abiotic conditions and the spatial and seasonal changes it experienced to occupy a specific habitat in the marsh, but we did not look at vegetation changes in time. We hypothesised that the combination of spatial and seasonal changes on different sedimentary factors would play a key role on determining the spatial abundance of halophytes along the intertidal gradient and within each vegetation band parallel to the tidal line. Seasonal variations on salinity would be especially relevant on determining the plant zonation pattern in Mediterranean high marshes.

2. Material and methods

2.1. Study area

The present study was carried out in the tidal salt marshes of the island of Tavira (37° 05′ N 7° 40′ O) located in the Ria Formosa Natural Park (Algarve, Portugal, Gulf of Cádiz, Southwest Iberian Peninsula; Fig. 1) (permit issued by Instituto da Conservaçao da Natureza e das Florestas, Portugal) that is included in the Ramsar List of Wetland of International Importance and in the network Natura 2000 due to its environmental features and its geographical emplacement. The area is under Mediterranean climate with Atlantic influence with mild and wet winters and hot and dry summers. The Ria Formosa mesotidal lagoon is a system of salt marshes and tidal flats, separated from the Atlantic by a belt of sand dunes that extends for 55 km along the coast (Fig. 1). The entire lagoon includes a large intertidal zone, two peninsular sand spits, five sandy barrier islands and six inlets, occupying an area of ca. 100 km^2, of which 48 km^2 are covered by salt marshes (Teixeira and Alvim, 1978). Only 14% of the lagoon surface is permanently flooded and about 80% of the lagoonal bottom emerges during spring low-water tides. The main morphosedimentary features are sandy to muddy tidal flats, salt marshes and channels, the intertidal forms representing 90% of the surface (Andrade et al., 2004). The low and middle salt marshes in the Ria Formosa are established on fined-grained alluvial sediments, usually with a considerable proportion of sand (> 25%) (Fitzsimons et al., 2005; Aníbal et al., 2007; Redondo-Gomez et al., 2009), between 1.80 m and 3.40 m above hydrographic chart *datum* and with sediment accretion rates ca. 8–9 mm a^{-1} between 1941 CE and 2000 CE (Arnaud-Fassetta et al., 2006). Cohesive sediments, fine sand and silt delivered from the terrestrial margin as suspended load, are partly retained in intertidal flats and marshes. The high-energy current regime of the lagoon explains its textural unbalance, biased towards the coarser fractions when compared with the signature expected due to the efficient energy sheltering offered by the barrier chain (Andrade et al., 2004). The soils in the studied low and middle marshes were Fluvisols developed on intertidal sediments, and the soils at the highest elevations of high marshes close to the coastal dunes were Aquic Quartzipsamments (poorly to moderately well drained) and Typic Quartzipsamments (moderately well to excessively drained).

The semidiurnal tides in the Gulf of Cádiz have a mean range of 2.10 m and a mean spring tidal range of 2.97 m (Castellanos et al., 1994). Tidal amplitude inside the Ria Formosa lagoon varies from 0.5 m (neap tide) to 3.5 m (spring tide) (Águas, 1986). A rather intensive exchange of 50–75% of the water mass per tidal cycle makes its entire water mass residence time fluctuates between 12 and 48 h (Neves et al., 1996).

The study area was selected for presenting a gentle slope along a wide intertidal gradient in such a way that small changes in marsh elevation corresponded to large marsh areas. Therefore, the distance between the lower and the higher limit of salt marshes reached 800 linear meters in some areas, showing a very clear plant zonation pattern. Three different zones are distinguished in these salt marshes based on the tidal influence and their elevation (Packham and Willis, 1997). Low marshes are defined between Mean High Water Neap (MHWN) and Mean High Water (MHW), middle marshes go from Mean High Water (MHW) to Mean High Water Spring (MHWS), and high marshes from Mean High Water Spring (MHWS) to Highest Astronomical Tide (HAT) (Long and Mason, 1983). Sampled habitats (H1–9) corresponded to the main vegetation bands parallel to the tidal line (Fig. 2) and they were defined based on previous studies on vegetation of Ria Formosa (Arnaud-Fassetta et al., 2006) and on the observed vegetation zonation pattern prior to the first survey. The characterization of these habitats in the three above-mentioned marsh zones is presented in Table 1.

2.2. Sedimentary environment

Sediment samples were collected bimonthly in March, May, July, October and December 2012 with the aim to obtain a representation of the different seasons of the year. Samples were collected starting always from the low marsh upland during low tide. For each of the above-described habitats, 9 samples of sediment were collected randomly always at the same marsh areas using stainless steel cores of 50 mm diameter and 50 mm height. Samples were placed in polyethylene bags that were hermetically closed and stored at − 20 °C until the analysis in the laboratory. We sampled 9 sediment cores in 9 habitats at 5 times during the year (n = 9 samples per habitat and date), resulting in a total of 405 soil samples.

Soil water content was gravimetrically determined using samples of 50 g of sediment that were dried to constant weight in a forced air oven at 80 °C for 48 h. The sediment was weighed again and the water content was calculated as the proportion of weight loss compared to the original weight (Castillo et al., 2010).

Organic matter content was determined by the loss-on-ignition method from samples of 5 g of dehydrated soil (as previously described) that were placed in a muffle oven at 500 °C for 5 h and then transferred to a desiccator to cool down. Organic matter content was calculated as the proportion of weight that was lost compared to the weight of the dry sample before incineration (Gavlak et al., 2005).

Electrical conductivity was used as a measure of soil salinity (Richards, 1974). From each sample, a mix of 5 ml of wet sediments and the same volume of distilled water (1:1, v:v) was placed in a tube, homogenised and the conductivity was measured in the unfiltered