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Interactions between transplants of *Phragmites australis* and *Juncus acutus* in Mediterranean coastal marshes: The modulating role of environmental gradients

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ABSTRACT

Interactions between two coastal marsh plants (*Phragmites australis* and *Juncus acutus*) were investigated along three natural gradients of salinity, water table and soil texture, variously combined in a microtidal Mediterranean coastal marsh. Our aim was to clarify to what extent plant interactions explain the occurrence of stands of both species, since they are not solely due to their tolerance to environmental conditions. We used a replacement series design of field transplants. Mortality and relative yield index of aerial biomass were analyzed to assess the outcome of interactions using Generalized Linear Mixed Models. Results show that mortality was entirely driven by natural gradients. Specifically, higher salinity and soil clay contents increased mortality in both species, whereas high water table increased survival only in *P. australis*. Growth was controlled by plant interactions and by natural gradients. According to these results *P. australis* can suppress *J. acutus* in waterlogged and non-saline conditions. Where water table is deeper, *J. acutus* can suppress *P. australis* along a wide range of saline conditions. In the driest situations both species exhibited mutual interference and, in some cases, *P. australis* can again suppress *J. acutus*. Facilitation occurred along the salinity gradient in situations that correspond to low, medium or high stress for the beneficiary species, pointing that exceptions to the stress gradient hypothesis may occur in systems including multiple stress gradients. Our results suggest that competitive interactions and environmental gradients are not fully responsible for plant distribution in microtidal coastal marshes.

1. Introduction

Although interactions among plants are a dominant driver of the dynamics and structure of natural plant populations and communities (Malkinson and Tielbörger, 2010) there is a lack of knowledge about how they change with biotic or abiotic factors (Agrawal et al., 2007). Based on the classical Gause's competitive exclusion principle, ecological research has traditionally focused on negative interactions. However, since the stress gradient hypothesis (hereafter SGH) was formulated (Bertness and Callaway, 1994), there has been a growing acknowledgement of the importance of facilitative interactions. This hypothesis suggests that in communities growing under high abiotic stress or high herbivory pressure competition is less intense and plant–plant interaction becomes facilitative. Over the last two decades, several empirical studies carried out in stressful environments such as coastal marshes (Bertness and Ewanchuk, 2002), alpine areas (Callaway et al., 2002), dry calcareous grasslands (Liancourt et al., 2005) or arid steppes (Pugnaire and Luque, 2001) support the SGH (see He et al., 2013 for a detailed review). Some studies mainly carried out in arid environments suggest that facilitative interactions cease at the limits of the stress gradients. (e.g., Tielbörger and Kadmon, 2000; Maestre and Cortina, 2004; Maestre et al., 2005). Despite the fact that these studies involve some methodological problems and cannot be considered a robust demonstration of an exception to the SGH (see He et al., 2013 and He and Bertness, 2014 for detailed explanations) their conclusions have motivated different theoretical reformulations of the SGH (Maestre et al., 2009; Holmgren and Scheffer, 2010; Malkinson and Tielbörger, 2010). According to He and Bertness (2014), the SGH keeps being a general applicable rule of thumb to predict general trends in species interactions under stress conditions, and exceptions may appear where the stress gradient considered is outside

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of the realized niche of the species, or where multiple co-occurring stress gradients not spatially correlated are found.

Plant communities in coastal marshes are commonly species-poor and dominated by a single or a few species (Adam, 1993; Day et al., 1988; Weiher and Keddy, 1995). Distribution of coastal marsh species is mainly consequence of two interacting factors: physiological tolerance of species to environmental constraints imposed by salinity and waterlogging (Adam, 1993; Pennings et al., 2005; Erfanzadeh et al., 2010) and by nutrient shortage (Levine et al., 1998); and biotic interactions, mainly between plants (Bertness, 1991; Pennings and Callaway, 1992; He et al., 2011) but also involving plant consumers (Costa et al., 2003; Crain, 2008). Past community ecology studies in macrotidal coastal marshes focused on the role of competitive interactions. The emerging paradigm proposed a clear niche segregation along environmental gradients, where the most competitive plants would occupy the least stressful zone of the coastal marsh, displacing the least competitive plants to the most stressful zones (Pennings et al., 2005). This paradigm agrees with the Grime's hypothesis previewing an inverse relationship between competitive ability and stress tolerance (Pennings et al., 2005). Moreover, since coastal marshes are stressful habitats for plant life, positive interactions according to the SGH were early detected in these habitats (Bertness et al., 1994). Further specific research demonstrated that facilitation determines secondary succession (Castellanos et al., 1994), plant diversity (Bertness et al., 1994) and distribution of non dominant plants (Crain, 2008; He et al., 2011) in macrotidal coastal marshes. In contrast, as far as we know, only Costa et al. (2003) have paid attention on the effect of competitive exclusion and the SGH in the case of microtidal (tidal range <2 m) coastal marshes. In Mediterranean microtidal marshes waterlogging dynamics is primarily driven by variations in rainfall and wind direction, therefore salinity and water table level are not easily predictable (Curcó et al., 2002). Moreover, salinity and waterlogging gradients are not mutually dependent. In summer, upper marshes may be more saline than lower ones because the high evaportanspiration cause salt ascension to top soil (Álvarez-Rogel et al., 2001). This situation may reverse by autumn storms, which flood the upper marshes with fresh water while causing meteorological tides that flood low marshes with marine water (Curcó et al., 2002). This seasonal pattern may be extremely complex because marine and freshwater inputs are highly variable within and among years.

The present study is focused on *Juncus acutus* and *Phragmites australis,* two herbaceous perennial species that form vast, dense stands in coastal Mediterranean marshes. Reed (*P. australis* s.l.) is a cosmopolitan rhizomatous grass able to grow in a wide range of ecologic conditions (Romero et al., 1999) and usually forming almost mono specific stands due to its high competitiveness (Wang et al., 2006; Wang et al., 2006). Clonal growth is the main competitive mechanism of reed, which creates a dense canopy and a large, branched rhizome system that prevents establishment of other marsh plants. It also modifies its habitat by increasing the accumulation of plant litter and altering the soil physico-chemical conditions (Meyerson et al., 2000; Minchinton et al., 2006). *J. acutus* is a perennial tussock rush with a broad geographic distribution, found in a wide range of ecologic conditions within coastal marshes. In Australia it performs an invasive behavior, being able to exclude other native *Juncus* species (Greenwood and MacFarlane, 2009). *J. acutus* can thrive better under dry and saline conditions than *P. australis*, whereas the latter tolerates waterlogging better than the former.

The fundamental aim of this study is to clarify the role of reciprocal interactions on the distribution of *P. australis* and *J. acutus* in Mediterranean microtidal marshlands. This is in line with Batriu

Fig. 1. Experimental locations within the Llobregat delta marshes. White points mark the experimental locations. Top-left locations, which were set up in meso-haline marshes, where caged in order to prevent rabbit predation.