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Environmental limitations on recruitment from seed in invasive *Spartina densiflora* on a southern European salt marsh

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ABSTRACT

The South American cordgrass, *Spartina densiflora*, has invaded a range of different habitats that can support different native species assemblages on salt marshes in the Gulf of Cadiz, Spain. Little is known about the mechanisms of invasion. We examined the potential for seed germination and recruitment in a field transplant experiment, representing a wide range of environments, on elevational gradients across marshes with muddy and sandy sediments. The biotic resistance of native, perennial vegetation (where present) to recruitment of the alien was also investigated. *Spartina densiflora* seeds were able to germinate over a greater than 2-m range of elevation in the tidal frame. Germination success on unvegetated muddy sediments was related to sediment redox potential, with poor germination at strongly negative redox potentials on the lower sites. On sandy, well-drained sediments, germination was apparently constrained by water availability at the highest elevations. Comparison of vegetated and cleared plots on the upper marsh showed that there was a negative relationship between the presence of *Atriplex portulacoides* and germination on the muddy sediments. Recruitment (survival of seedlings for 12 weeks) was seen only on unvegetated muddy sediments at the highest elevation. Hence the invasive success and wide elevational tolerance of *S. densiflora* on the marshes of the Gulf of Cadiz are not reflected in its short-term ability to become established from its prolific seed production. Colonization of sub-optimal habitats may be largely by vegetative propagules and clonal growth.

1. Introduction

The austral cordgrass, *Spartina densiflora* Brongn. (Poaceae), is invading salt marshes in southern Europe (Tutin, 1980; Figueroa and Castellanos, 1988), North Africa (Fennane and Mathez, 1988) and North America (Kittelson and Boyd, 1997). In its native South America, *S. densiflora* is a salt marsh dominant over a wide latitudinal range and shows considerable morphological variation (Bortolus et al., 2004; Bortolus, 2006; Isacch et al., 2006). It was probably introduced accidentally to SW Spain from South America by the lumber trade. In Spain, *S. densiflora* has proved to be a vigorous invader and ecosystem engineer that spreads by prolific seed production and consolidates its stands by clonal growth (Nieva et al., 2001). It can be a formidable competitor, because it produces dense tussocks, with tall canopies and persistently high above- and below-ground biomasses (Figueroa and Castellanos, 1988; Nieva et al., 2001). Physiological and morphological versatility apparently allows *S. densiflora* to tolerate a wide range of salinity, tidal submergence and drainage (Nieva et al., 1999; Castillo et al., 2005). In the salt marshes of the Gulf of Cádiz, experimentally transplanted clonal tussocks survived in all but the lowest, most hypoxic parts of the salt marsh gradient (Castillo et al., 2000). This is consistent with *S. densiflora* having colonized high, middle and low marshes, with their different characteristic assemblages of native species (Nieva et al., 2001). It is widely accepted that interactions between salt marsh species may be as important as their individual tolerances to physical and chemical factors associated with submergence in determining both the distribution of the species and the zonation of their communities (Bertness, 1991; Pennings and Callaway, 1992; Huckle et al., 2000, 2002).

Invasion by *Spartina densiflora* is one of the most important conservation problems affecting the extensive Odiel salt marshes in SW Spain. It has become the dominant plant species on recent tidal marsh restorations in the Doñana National Park (Fernández and García Novo, 2007), and there is a threat of it spreading to other

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southern European marsh systems. Nevertheless, we know little about the mechanisms by which it invades. In particular, the environmental and biotic constraints on germination and seedling recruitment of *S. densiflora* in the field have not been investigated. This information is important both to understand its behavior as a neophyte and to be able to design effective management strategies for it. Consequently, the aims of this study were: (1) to investigate the germination of seeds and early survival of seedlings on contrasting types of sediment across the salt marsh elevational gradient, in a transplant experiment; (2) to relate the seed and seedling performance to environmental conditions; and (3) to examine effects of the presence of established native species on germination and early survival.

2. Materials and methods

2.1. Study site and seed source

The work was located at Odiel Marshes, which are situated in the joint estuary of the Odiel and Tinto rivers at Huelva, on the Atlantic coast of SW Spain (37° 15′ N, 6° 58′ W). Hence, the salt marsh is subject to a Mediterranean climate with oceanic influences. Winter is wet and mild (mean temperature c. 11 °C in January) and summer is long and dry (mean temperature c. 25 °C). Mean annual precipitation is 510 mm, with an interannual variation coefficient of 31%. The semi-diurnal tides have a mean range of 2.10 m and a mean spring tidal range of 2.97 m, representing 0.40–3.37 m above Spanish Hydrographic Zero (SHZ). Mean sea level is +1.85 m relative to SHZ (Castellanos et al., 1994).

Ripe spikes of *Spartina densiflora* were collected during December 2005 from 25 clumps chosen randomly from a gently sloping intertidal plain in the Odiel Marshes. Caryopses were stripped from the spikes and those with filled seeds were selected and stored at 4 °C (in the dark) for 3 months. Experimental transplants of the caryopses were made in a well-drained lagoon at Odiel Marshes (the 'Laguna de Don Claudio'; Castellanos et al., 1994).

2.2. Germination and recruitment of seedlings

In March 2006 two parallel transects, 30 m apart, were established perpendicular to the tidal line. One, on muddy sediments (49 ± 2% fine sand, 44 ± 2% silt and 7 ± 1% clay, by mass) was 70 m long, with a mean inclination of c. 3.0%, and a height difference of 207 cm; the other, on sandy sediments (97 ± 0% fine sand, 2 ± 0% silt and 1 ± 0% clay) was 55 m long, with a mean inclination of c. 4.6%, and a height difference of 256 cm. This local transition from muddy to sandy sediments provided comparable transects on the two substrates close together. Unfortunately it was not possible to replicate entire transects because there were no other instances of the two sediment types in close proximity and showing the full range of elevation. However, detailed examination of the environmental characteristic of the two transects provided strong support for differences between them being representative of their substrate textures. Elevation was surveyed to a resolution of 2 cm with a Leica NA 820 theodolite (Leica Instruments, Singapore).

Sites were selected for a germination experiment across the range of elevation at both transects. On the transect with muddy sediments, the lower five of seven sites were naturally unvegetated. Sites six and seven (the higher elevations) were dominated by *Sarcocornia perennis* and *Atriplex portulacoides* respectively; consequently two sets of germination plots were established at these sites, in experimentally cleared areas and under the natural canopies (Fig. 1a). On the transect with sandy sediments, the four lower sites of six selected were in naturally unvegetated areas. At the two higher sites, sets of germination plots were sited in both experimentally cleared areas and under clumps of the dominant

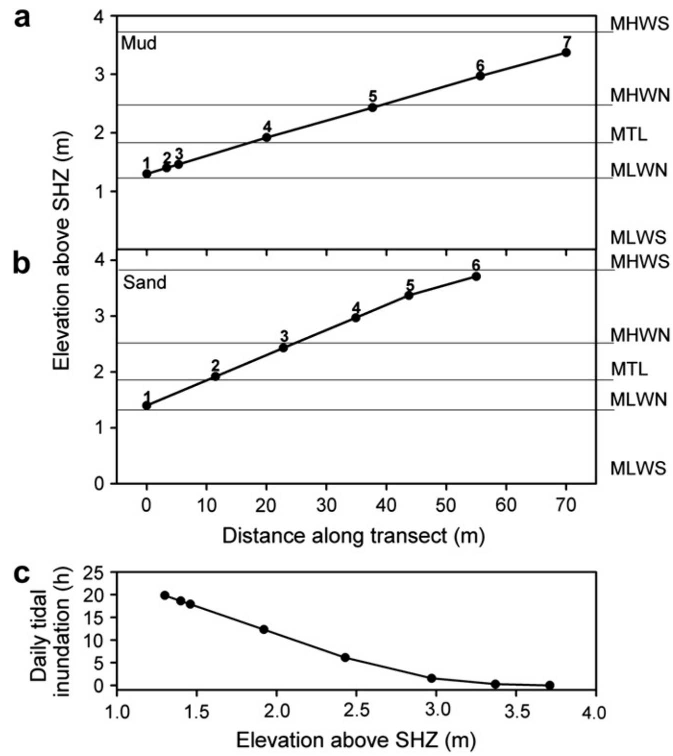

Fig. 1. Transects, perpendicular to the tidal line, across an intertidal gradient of elevation above Spanish Hydrographic Zero (SHZ) at Odiel Marshes, SW Spain with (**a**) muddy and (**b**) sandy sediments. Numbered points represent the seed transplant sites up the topographic gradient: MHWS, Mean high water spring tidal level; MHWN, Mean high water neap tidal level; MTL, Mean tidal level; MLWN, Mean low water neap tidal level; MLWS, Mean low water spring tidal level (means are long-term averages for this location). (**c**) Annual mean duration of daily tidal inundation in relation to marsh elevation above SHZ.

Limoniastrum monopetalum (Fig. 1b). Sites ranged in elevation from mean low water neap tidal level to close to that of mean high water spring tides on both transects. The annual mean of daily tidal inundation was c. 20 h at the lowest sites, declining to almost zero at the highest sites (Fig. 1c).

At each site (and in the cleared and vegetated areas of the upper marsh sites), four replicate 20 × 20 cm plots were located randomly and each was sown with 25 filled caryopses. For the purposes of comparing transects, these plots represent unavoidable pseudoreplication (see above). Caryopses were given protection from removal by the tide: a 1-cm plastic mesh was placed on the surface of each plot and caryopses were pressed gently into the surface of the sediment within the apertures of the mesh; then a 1-mm plastic mesh was placed over the top and the whole assembly was anchored at the corners by hooked steel pins (20 cm long) pushed into the sediment. Caryopses were inspected weekly for 90 days and seeds were considered to have germinated after coleoptile appearance. The fine plastic mesh was carefully removed after 8 weeks (when there was no more germination) to facilitate natural seedling growth.

Final germination percentage and mean time to germination (MTG) were determined. MTG was calculated as:

$$\mathrm{MTG} = \sum_i (n_i \times d_i)/N$$

where n is the number of seeds germinated at week i, d is the observation period in weeks and N is the total number of seeds germinating (Redondo-Gómez et al., 2007b). Hence shorter time indicates more rapid germination. The numbers of surviving