Understanding and fighting the invasion of *Spartina densiflora*

Humboldt Bay (California, USA) & the Gulf of Cádiz (Andalusia, Spain)

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The main threat to the conservation of salt marshes in the Gulf of Cadiz is the invasion of the South American neophyte *Spartina densiflora*, which was introduced to this coast around the 16-17th centuries.
This conservation problem is shared by salt marshes in Northern California, including Humboldt Bay and Mad River wetlands, and Corte Madera Marsh at San Francisco Bay, where \textit{S. densiflora} was introduced during 19th century.

The austral cordgrass \textit{Spartina densiflora} Brong.: its taxonomy, biogeography and natural history

\textbf{ABSTRACT}

Recently, the austral cordgrass \textit{Spartina densiflora} has been observed aggressively invading estuarine environments in the USA, Spain, and Morocco. Whereas this species is one of the three most widely distributed worldwide, it is among the least studied within the genus. The objective of this work is to summarize baseline information about the taxonomy, biogeography, natural history, and general ecology of \textit{S. densiflora} in native and invaded marsh worldwide, in order to help strengthen management efforts currently directed at controlling or eradicating it before it becomes established.

\textbf{Location} Worldwide.

\textbf{Methods} A review, update, and discuss relevant scientific literature about \textit{S. densiflora} published in peer-reviewed papers, including those in journal with limited international distribution. Data were reviewed and updated from recent published literature containing critical up-to-date information.

\textbf{Results} While some information about \textit{S. densiflora} remains in need of thorough scientific attention, key information on its taxonomy, distribution, and invasive biology has been overlooked because it was published in languages other than English, and/or in journals with limited international distribution.

\textbf{Main conclusions} \textit{Spartina densiflora} seems to have originated along the east coast of North America, but, however, many other regions worldwide serve as donor for this invasive species, including China, the USA, Spain and Morocco. While invasive species is a transgressive species, tolerant of a broad spectrum of environmental conditions and able to re-shape the structure of invaded communities not just in matrices, but also in sand dunes, mudflats and sand dunes as well as in coastal beaches. Only by integrating local and regional knowledge with different geographical regions will we be able to understand the invasive species of its biogeographical spread, which will be the focus of the design of more effective conservation strategies.

\textbf{Keywords} Cordgrass, interactions, intertidal, invasion, plant ecology, salt marshes, North America, \textit{Spartina densiflora}.
The final outcome of the *S. densiflora* invasion is almost monospecific communities where the alien species colonise most of the available space.
S. *densiflora* has already occupied close to 100% of the space at some marshes in both geographic regions. However, it is still spreading out in many other marshes, and many others have not been yet been colonised by the alien species.
Then, we are still in time to control the invasion and to eradicate *S. densiflora* in many locations…

… but we must act as soon as possible so our objectives will be easier to achieve, since *S. densiflora* shows a very high capacity to disperse by seeds.

If we do not do anything we will lose the biodiversity, the landscapes and other environmental resources and functions of our salt marshes.
S. densiflora starting its invasion of a salt marsh at Humboldt Bay
The most impacted taxa by the invasion of *S. densiflora* are rare taxa growing at middle (at SW Iberian Peninsula) and high marshes (at Humboldt Bay, California).

Ej.

**SW Iberian Peninsula**

*Artemisia caerulescens* subsp. *caerulescens* L.
*Aster tripolium* subsp. *panonicus* (Jacq.) Soó
*Triglochin barrelieri* Loisel.
*Limonium algarvense* Erben
Etc.

**Northern California**

*Carex lyngbyei*
*Cirsium loncholepis*
*Cordylanthus maritimus* ssp. *Palustris*
*Puccinellia pumila*
*Limonium sp.*
Etc.

Middle marsh at Piedras River Estuary (Andalusia)
S. *densiflora* is able to colonise many different habitats because:

It tolerates very wide ranges of many abiotic environmental conditions such as salinity and flooding;

and it is a very competitive species due to its ‘phalanx’ growth form.

Image from Terrestrial Vegetation of California. 3rd edition. Chapter 5.
Spartina densiflora colonising a high marsh with high salinities during summer

Short-term responses to salinity of an invasive cordgrass

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Keywords: chlorophyll fluorescence, gas exchange, Gulf of Cádiz, leaf expansion, salt marsh, South American neophyte, Spartina densiflora, water potential

Abstract

Salinity is one of the main chemical factors in salt marshes. Studies focused on the analysis of salinity tolerance of salt marsh plants are very important, since they may help to relate their physiological tolerance with distribution limits in the field. Spartina densiflora is a South American cordgrass, which has invaded the European coastline from the south-western Iberian Peninsula. In this work, short-term responses in adult tussocks of S. densiflora from south-western Spain are studied over a wide range of salinity in a greenhouse experiment. Our results point out that S. densiflora has a high tolerance to salinity, showing high growth and net photosynthesis rates from 0.5 to 20 ppt. S. densiflora showed at the lowest salinity (0.5ppt) high levels of photoinhibition, compensated by higher levels of energy transduction between photosystems. Adaptive mechanisms, as those described previously, would allow it to live in fresh water environments. At the highest salinity (40ppt), S. densiflora showed a high stress level, reflected in significant decreases in growth, net photosynthesis rate and photochemical efficiency of Photosystem II. These responses support S. densiflora invasion patterns in European estuaries, with low expansion rates along the coastline and faster colonization of brackish marshes and river banks.

Abbreviations: A – net photosynthesis rate; Chi – chlorophyll; F0 – basal fluorescence; Fm – peak of fluorescence; Fv/Fm – variable fluorescence; F0/Fm – potential photochemical efficiency of PSII; Gs – stomatal conductance rate; PPFD – photosynthetic photon flux density; PS II – Photosystem 2; T1/2 – half-life for transition from F0 to Fm; Ψwet – leaf water potential

Introduction

Coastal ecosystems, such as salt marshes, are one of the areas most affected by the introduction of alien species. The genus Spartina counts different species that behave as salt marsh invaders all around the world. Their invasion patterns seem to depend on complex relationships between biological interactions with autochthonous species and habitat physical conditions such as salinity (Kettlewell and Boyd 1997; Hacker et al. 2001). Thus, salinity is one of the main chemical factors in salt marshes, determining vegetation distribution with respect to elevation (Banse 1993) and distance to the sea (Wilson et al. 1996), through species tolerance to ion concentration and modulation of the outcomes of interspecific interactions (Broome et al. 1995; Gough and
Field Variability of Invading Populations of Spartina densiflora Brong. in Different Habitats of the Odiel Marshes (SW Spain)


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Spartina densiflora is a species of South American origin that has invaded the marshes of the Gulf of Cádiz, in many of which it has become the most abundant plant. This work studies the populations of S. densiflora representative of the phytogeographic positions most commonly occupied by the species. The aspects considered are redox potential, conductivity and pH of the sediment, below- and above-ground biomass, stem density, rate of flowering and production of vegetative propagules. Eh and conductivity values vary greatly, responding to differences in tidal effect. The below-ground biomass (in particular, live biomass) is accumulated mainly in the first centimeters of the soil, mean values of total below-ground biomass are between 6961 and 30,691 g DW m⁻². Above-ground biomass levels for the populations range between 419 and 15,251 g DW m⁻². The stem density within the mosaics is high, between 3963 and 10,213 stems m⁻², with higher percentages of live stems on low and brachial marshes compared with those on higher topographic levels. The accumulation of dead and live intramosaic biomass is important for the ability to exclude competitors. The flowering rates vary depending on topographic position, with maximum values being recorded in the low marsh (77-69%) and minima is the high marsh (0% to 5%). Besides the production of internodes from below-ground rhizomes (common to all species of the genus), S. densiflora presents another mode of asexual reproduction, in which submerged aerials are originated from the nodes of vegetative stems. Populations on the higher levels of the marshes present higher densities of these propagules, with a negative correlation between rate of flowering and rate of propagule production. Nevertheless, the contribution of these propagules to the total stem population is very small. Our results show a high tolerance of S. densiflora to different environmental factors, an intense occupation of the available below-ground and above-ground space, and the capacity of sexual reproduction and of producing stems that grow directly from the upper part of the canopy of S. densiflora, aspects that help to explain the ecological success of this species in the marshes of the Gulf of Cádiz.

Keywords: invasive Spartina; marshes; biomass; reproduction; Gulf of Cádiz; SW Spain

Introduction

The introduction of exotic plants is an increasing problem in many ecosystems. In tidal marshes, the high plant cover and the stressful environment are a curb on such invasions, but species of the genus Spartina, considered among the most aggressive invaders in the world, have managed to install themselves successfully outside their original geographic range of distribution and, in some cases, are more successful in new continents than in the equivalent habitats of their original home (Adam, 1990). The entry of exotic species into marshes can mean a series of negative impacts that include competition with the native flora (Kittel and Boyd, 1997), alteration in the amount and nature of the detritus (Adam, 1990), alteration of the habitat of the native fauna (Partridge, 1987), and alterations in estuarine sedimentary dynamics (Long and Mason, 1985). Spartina densiflora is a species native to South America (Meehan, 1996) that has invaded the marshes of the Gulf of Cádiz (SW Iberian Peninsula), probably introduced by the humber trade between South America and Spain. It has become very abundant, and in wide areas displaces the original saltmarsh tussilago vegetation, particularly on the middle topographic levels of marsh, where it predominates almost mono-specifically. This species is found from the lower topographic levels of tidal marshes to the highest ones, including ecotones with adjacent terrestrial ecosystems (Costa, 1997). It tolerates a broad range of edaphic and hydrological conditions, competing with almost all of the autochthonous species of the Mediterranean marshes. Recently, Kittel and
S. *densiflora* at river mouths

Mad River (California)

Guadalquivir River (Andalusia)
S. densiflora at tidal channel banks

Humboldt Bay
(California)

Piedras River
(Andalusia)
S. densiflora at brackish marshes

Humboldt Bay (California)

Nicoba River (Andalusia)
S. *densiflora* at intertidal plains

Humboldt Bay
(California)

Odiel marshes
(Andalusia)
S. *densiflora* at sandy deposits

Humboldt Bay
(California)

Odiel marshes
(Andalusia)
The phenotypical plasticity of *S. densiflora* is reflected even in the duration of its life cycle. In the Odiel marshes (SW Iberian Península), it behaves as a biennial at its lower distribution limit in the tidal frame and as a perennial at higher elevations.
But *S. densiflora* is not able to colonise lower elevations in the tidal frame and areas with very high salinities or exposed to temporal drought (salt ponds and high marshes at SW Iberian Peninsula).

*Arthrocnemum machrostachyum* growing on a salt-pan during summer at the Odiel marshes.
Lower limits of Spartina densiflora and S. maritima in a Mediterranean salt marsh determined by different ecophysiological tolerances

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Summary

1. Salt marshes in south-west Spain are being invaded by Spartina densiflora, a South American species, although the native S. maritima still dominates many lower marshes. A transplant experiment was used to investigate the limits by which physical and chemical factors may determine lower vegetation limits in the total form. Both species were transplanted from a mid- to lower-march to lower, unvegetated salt flats.

2. The survival and growth of transplanted clones and their constituent tillers were monitored in an environmental gradient. The photophysiological parameters of transplants were assessed by measurements of leaf gas exchange and the leaf anatomy of chlorophyll fluorescence. Subsequent growth, intensity, mid-power and total photosynthesis in the plants were also measured in the transplantation trial.

3. Neither species survived for a year at the lowest transplant point (1.00 m elevation) in Santi petal Hydroporphic Salt). At c. 0.40 m elevation, S. maritima survived well but all clones of S. densiflora died. At higher elevations (c. 0.45 m), changes of both species had high survival rate. Tillers growth rates in surviving clones of both species increased with elevation, but those of S. densiflora was more sensitive to low elevation.

4. S. maritima showed no improvement of photosynthetic performance, even at the lowest elevation. In the rate of gas exchange were independent of elevation, as was its chlorophyll fluorescence parameters. In contrast, S. densiflora showed a significant rise in CO₂ uptake and chlorophyll fluorescence in the photostationary state. At the lowest elevation, both of these photosynthetic measurements were lower than those at mid-power potential. Nonetheless, both species did not reach any irreversibility.

5. S. maritima is a potentially well-adapted species and can tolerate lower limits substantially below that of S. densiflora. The progressive cellular growth and survival of S. densiflora at lower levels appear to result primarily from improvement of photosynthesis when next conditions are appear. This effect is mediated through effects on the photosynthetic apparatus rather than on stomatal resistance or CO₂ uptake.

6. These studies define lower limits to the fundamental niches of the two species in Mediterranean-type salt marshes and provide a basis for future investigations of interactions between them. The conclusion that chlorophyll fluorescence and high-temperature survival of S. densiflora may be a valid tool.
On the other hand, *S. densiflora* may form hybrids with native cordgrasses as described in San Francisco Bay between *S. densiflora* and *S. foliosa* and in the Odiel marshes with *S. maritima*.
S. *densiflora* slows down its production during winter when it finds dormant perennials in Northern California and non-dormant perennials in Andalusia.
A few salt marsh restoration projects based on fighting *S. densiflora* invasion are being developed at Andalusia and California…

Salt marsh at Humboldt Bay recovering after mowing of *S. densiflora*
Removing *S. densiflora* at San Francisco Bay (California)
Removing *S. densiflora* at the Odiel marshes (SW Spain)