



ORIGINAL
ARTICLE

The austral cordgrass *Spartina densiflora* Brong.: its taxonomy, biogeography and natural history

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ABSTRACT

Aim During the last 20 years, the austral cordgrass *Spartina densiflora* has been recorded 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 integrate baseline information about the taxonomy, global distribution, centre of origin, and general ecology of *S. densiflora* in native and invaded marshes worldwide in order to help to strengthen management efforts currently directed at controlling or eradicating it from locations where it has been introduced.

Location World-wide.

Methods I review, update and discuss relevant information about *S. densiflora* published in peer-reviewed papers, including those in journals with limited international distribution. I also review theses and major technical reports containing critical up-to-date information.

Results This work indicates that, although *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 restricted distribution.

Main conclusions *Spartina densiflora* seems to have originated along the east coast of South America; today, however, many other regions worldwide serve as donors for this invasive species, including Chile, the USA, Spain and Morocco. *Spartina densiflora* is a bioengineer organism, tolerant of a broad spectrum of environmental conditions and able to re-shape the structure of invaded communities not just in mudflats, but also on sandy, muddy, and rocky shores as well as on cobble beaches. Only by integrating local-scale research conducted in different geographical regions will we be able to understand the between-site variations of its biological cycle, which in turn will aid in the design of more effective conservation strategies.

Keywords

Cordgrass, interactions, intertidal, invasion, plant ecology, salt marsh, South America, *Spartina*, *Spartina densiflora*.

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INTRODUCTION

Spartina Schreber (Schreber, 1789) is one of the most studied genera of salt-marsh plants worldwide, mainly because of its abundance in space and time and because it offers a wide range of ecosystem services (Adam, 1990; Chung, 1993; Li & Gallagher, 1996). Although the cordgrass *S. densiflora* is

presently one of the three most widely distributed species of the genus, along with *S. alterniflora* and *S. anglica*, it has not received the attention of ecologists until recently (Bortolus, 2001). Given that this species has been reported to be aggressively invading a variety of environments in North America, Europe and Africa, more studies are urgently needed to understand its biology, ecology and natural history in order

to control or eradicate it. The objective of this work is to supply an integrated review of the taxonomy, global distribution, centre of origin, and ecology of *S. densiflora* in both native and invaded marshes worldwide, in order to facilitate the design of more effective management strategies. I do this by analysing peer-reviewed papers from international sources, including South American journals with restricted international distribution, and by reviewing doctoral theses and major technical reports containing critical information.

TAXONOMY

The first known samples of *S. densiflora* were collected between 1822 and 1825 in Concepcion, Chile, and named by Brongniart in 1829 (Brongniart, 1829). Other halophyte species described during the following decades in Chile (*Chauvinia chilensis*; Steudel, 1855), Uruguay (*S. montevidensis*; Arechavaleta, 1894) and Argentina (*S. patagonica*; Spegazzini, 1897) are now recognized as phenotypic variations of *S. densiflora* (Parodi, 1919, 1967; Moberley, 1956). In spite of this, some of these names are still used erroneously in ecological articles, *S. montevidensis* being the most common. For decades, cytological and molecular studies have been conducted in order to understand the past and recent history of the *Spartina* genus (e.g. Marchant, 1968; Baumel *et al.*, 2002; Ainouche *et al.*, 2004). However, none of these studies is directed at clarifying the obscure taxonomy of *S. densiflora* through

comparison of the different populations from which the various taxonomic synonyms originated. Such a study would greatly complement alpha-taxonomy works by clarifying whether more than one species – and/or hybrids – are involved in the phenotypic variability observed in the field. The significance of such work becomes even clearer if we consider that the conclusions of all phylogenetic studies involving *S. densiflora* may be severely compromised by the origin of the chosen samples (Baumel *et al.*, 2002).

GEOGRAPHIC DISTRIBUTION AND CENTRE OF ORIGIN

South America

Spartina densiflora appears to be distributed from Sao Paulo State, Brazil (c. 23°20' S) to Rio Gallegos city, Argentina (c. 51°33' S), showing its highest abundance in the temperate marshes of southern Brazil and Buenos Aires province (Saint-Yves, 1932; Moberley, 1956; Bortolus, 2001; Fig. 1). No sources make reference to well-developed *Spartina* salt marshes in southern Argentina, suggesting that in this region this species is probably restricted to isolated inlets and coastal islands (Parodi, 1919; Hauman, 1926; author's personal observations). In contrast, vast extents are covered by productive *S. densiflora* salt marshes in Samborombon Bay (36° S), Mar Chiquita Coastal Lagoon (37°40' S), and Bahia Blanca (38° S).

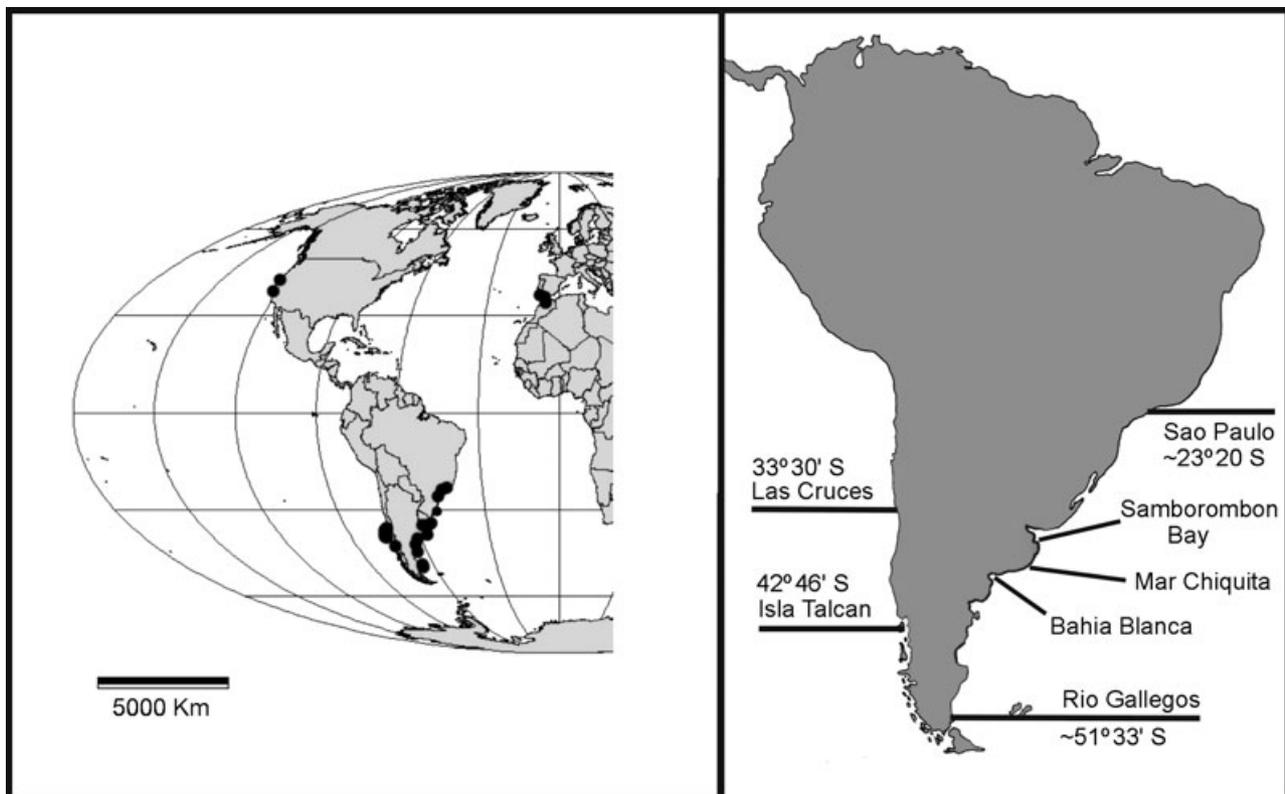


Figure 1 Maps showing the currently known global (Mollweide projection) distribution of *S. densiflora* (left) and its limits of distribution, and sites with the highest abundance within South America (right).

(38° S; Vervoost, 1967; Bortolus, 2001; Iribarne, 2001; Vicari *et al.*, 2002). In Chile this species is reported between 36°50' and 41°28' S, with a patchy distribution along the coast (Saint-Yves, 1932; Mobberley, 1956; Schlatter *et al.*, 1998). However, the Herbario CONC (Universidad de Concepcion, Chile) holds samples collected in 1982 from Talcan Island (42°46' S; CONC no. 26390), and in May 2005 I found well-established populations in various protected areas around Las Cruces, San Antonio (33°30' S), suggesting that *S. densiflora* may be extending its distribution in this country (Fig. 1).

Europe

The first report locating *S. densiflora* outside the Americas was from Spain (Tutin *et al.*, 1980; Nieva, 1996). Its introduction to the European continent is considered accidental, and probably resulted from the lumber trade between South America and Spain (Nieva *et al.*, 2001). More specifically, it seems to have been introduced in the Odiel and Tinto rivers (Huelva province, southeast Spain), where it currently shows the highest regional productivity and most uniform distribution, populating intertidal and terrestrial habitats (Nieva, 1996; Nieva *et al.*, 2002). In recent decades, *S. densiflora* has aggressively spread over the Gulf of Cadiz (south-west Iberian Peninsula) from Cape San Vicente to Gibraltar, and it has probably already been introduced into Galicia (north-west Spain) (Nieva, 1996; Nieva *et al.*, 2002). Although found at 51°33' S in Argentina, it has been suggested that this species may have physiological constraints limiting its winter production and therefore the extent of its distribution and abundance at higher latitudes in Europe (see Nieva *et al.*, 2003).

Africa

Spartina densiflora was transported from Spain to Morocco (Africa: Fennane & Mathez, 1988; Nieva, 1996), but the process by which this may have happened remains uncertain. A specimen of *S. densiflora* that was thought to be *S. versicolor* Fabre (now *S. patens*; see Fennane & Mathez, 1988; Le Floc'h *et al.*, 1990) could have been brought unintentionally to the botanical garden of the Scientific Institute of the Merja Zerga (Morocco). Another hypothesis, based on the process by which *S. alterniflora* was introduced into Europe, proposes that *S. densiflora* may have been introduced into Africa via solid ballast (Marchant, 1967; Briggs & Walters, 1997; Nieva *et al.*, 2001). Presently, its distribution within Africa seems to be restricted to the Merja Zerga lagoon (Nieva, 1996; Benhoussa, 2000), where the first sample of *S. densiflora* was collected in 1978 (Fennane & Mathez, 1988).

North America

Costa & Davy (1992) listed *S. densiflora* on the Atlantic coast of North America, but no subsequent records exist. During the late 1970s, a team of managers and landscapers transplanted propagules of *S. foliosa* from Humboldt Bay to Creekside Park

in San Francisco (California, USA) as part of a restoration project that happened to involve the only *Spartina* species native to the West Coast (further detail in Faber, 2000). Unfortunately, they failed to realize that the plants they were transplanting belonged to a cryptic introduced population of *S. densiflora*, and that they were in fact spreading an exotic species (Grossinger *et al.*, 1998; Faber, 2000; Clifford, 2002). Spicher & Josselyn (1985) confirmed the existence of a well-established population of *S. densiflora* in San Francisco Bay, and hypothesized that the plants were introduced via solid ballast during the late eighteenth century. Almost a century later, Chilean scientists confirmed the samples as *S. densiflora* (Kittelson & Boyd, 1997). Presently, this species dominates the landscape within Humboldt Bay and is spreading dramatically at several other invaded sites (Clifford, 2002). New reports suggest that the progress of *S. densiflora* invasions in the north-east Pacific has accelerated during the last few years in comparison with previous decades (e.g. Grossinger *et al.*, 1998; Pickart, 2001; Smith *et al.*, 2001). In addition, *S. densiflora* has reappeared in areas where it was believed eradicated in San Francisco Bay (Smith *et al.*, 2001; Ayres *et al.*, 2004), and has colonized a number of new sites along the Pacific Coast of the USA. The latest invasion was recorded in 2001 at Grays Harbor (Washington; Pfauth *et al.*, 2003), c. 10 latitudinal degrees north of the nearest established *S. densiflora* population. Considering its wide distribution within South America, Western Europe and North Africa, the invasion of Grays Harbor suggests that this species is able to invade most estuarine environments along the West Coast of the USA and Canada.

Centre of origin

The centre of origin of an invasive species is the region in which it originated and from which it spread to other regions. For more than a century, all records placed *S. densiflora* in austral South America (Chile: Brongniart, 1829; Steudel, 1855; Saint-Yves, 1932; Argentina: Spegazzini, 1897; Parodi, 1919; Hauman, 1926; Brazil: Saint-Yves, 1932; Uruguay: Arechavaleta, 1894). Concordantly, it was absent from all botanic lists referring to other continents (e.g. Merrill, 1902; Saint-Yves, 1932; Mobberley, 1956). Only recently was this species reported in Western Europe (Spain: Tutin *et al.*, 1980), North America (USA: Spicher & Josselyn, 1985), and North Africa (Morocco: Fennane & Mathez, 1988; Fig. 1).

Although it is usually considered a temperate-clime species, *S. densiflora* is historically recorded as the most austral of the *Spartina* species, under the name of *S. patagonica* Spegazzini (Parodi, 1919; Hauman, 1926). This species is found on the east (Atlantic) and west (Pacific) coasts of South America, with a distributional discontinuity in the southern end of the continent (Chapman, 1977). Its distribution on the east coast covers c. 28 latitudinal degrees, while on the west coast it only covers c. 6 degrees and seems to be concentrated in small isolated inlets along the central part of Chile (Mobberley, 1956; Schlatter *et al.*, 1998). On the east coast *S. densiflora*

commonly forms extensive marshes in which it may occur as the only *Spartina* species. Most marshes at Mar Chiquita Coastal Lagoon (Buenos Aires province) are characterized by large mono-specific grasslands of *S. densiflora*. Some of these marshes are almost terrestrial systems, rarely affected by tides. Similarly, in northern Buenos Aires and southern Cordoba and Santa Fe (Argentina) this species populates strictly terrestrial systems (Mobberley, 1956; Cantero *et al.*, 1998; Vicari *et al.*, 2002). In Chile, on the other hand, it is only reported to populate estuarine environments. The fact that *S. densiflora* exhibits a greater abundance, broader phenotypic spectrum (including the Chilean phenotypes), and broader spectrum of habitats along the South American east coastline than anywhere else (Parodi, 1919; Mobberley, 1956; Bortolus, 2001) strongly suggests that this species originated on this coast, from where it eventually spread to the west coast of South America first and to the Northern Hemisphere later. Molecular research might help to evaluate this hypothesis.

ECOLOGY OF SPARTINA DENSIFLORA

Whereas between 1829 and 1998 several morphological (e.g. Perazzolo & Pineiro, 1991) and taxonomic descriptions and distributional records of *S. densiflora* were made (as mentioned above), little is currently known about the ecological interactions in which this species participates. There is, however, significant evidence suggesting that, compared with other invasive *Spartina* species, such as *S. alterniflora* and *S. anglica*, *S. densiflora* is able to colonize sites exhibiting an unusually large spectrum of environmental conditions.

Habitat

The areas populated by *S. densiflora* vary from brackish to hypersaline (Nieva, 1996; Kittelson & Boyd, 1997; Vicari *et al.*, 2002), from intertidal to strictly terrestrial (Mobberley, 1956; Clifford, 2002; Nieva *et al.*, 2002), and from subtropical to austral (Fig. 1). This species is found well established in

substrates that vary from muddy and anoxic (Cabrera & Zardini, 1978; Nicora & Rugolo de Agrasar, 1987) to well drained and oxygenated (Vicari *et al.*, 2002), and in protected estuaries and bays as well as on exposed coastlines (Bortolus, 2005). In addition, *S. densiflora* is found on cobble beaches as well as on hard (volcanic stones) and soft (sand, clay and limestone) rocky shores, thus maximizing the spectrum of coastal environments where it can be introduced (Bortolus, 2005). *Spartina alterniflora* beds are commonly found on New England cobble beaches, where they lie on top of a thick layer of marsh soil from which the plants seem to obtain support and nutrients (Bertness, 1999). In contrast, *S. densiflora* successfully populates cobble beaches and rocky shores of Argentinean Patagonia without a developed marsh soil substrate by recruiting in the crevices on the top and sides of the rocks in areas exposed to wave action (Bortolus, 2005). This may be possible because the small size that *S. densiflora* usually reaches when living in such conditions increases its mechanical resistance to waves and wind, and lowers its nutrient requirements to a minimum. Although these *S. densiflora* populations are much smaller than those located in protected salt marshes, their ecological importance is greater, because they are likely to be important seed-suppliers for other marshes within the region (Bortolus, 2001). Presently, it is only in Argentina that this species is found occupying the entire spectrum of habitats mentioned above.

Reproduction and production

The tiller density, biomass production, flowering period and phenotype of *S. densiflora* are highly variable among regions (Table 1). This salt-tolerant species has a C₄ metabolism and it is able to develop different growing strategies to enable it to cope better with local environmental variables and micro-habitat conditions (Kittelson & Boyd, 1997; Nieva *et al.*, 1999, 2005). As reported for other *Spartina* species (Thompson *et al.*, 1993; Bertness, 1999), *S. densiflora* shows a faster ramet turnover in exposed low marsh areas than in the high marsh,

Table 1 Average production (dry weight) and flowering period of *S. densiflora* in native and invaded areas. Standard deviations are given in brackets; NAPP: net annual primary production; nd: no data are available

	Above-ground biomass (g m ⁻²)	Below-ground biomass (g m ⁻²)	Tiller density (ind. m ⁻²)	NAPP (g m ⁻² y ⁻¹)	Flowering period	References
Southern Brazil	1123–3575	nd	nd	nd	November–May	Smith <i>et al.</i> (1981), Giacobbo & Boechat (1988), Nieva <i>et al.</i> (2001)
Argentina/Uruguay	771–1336	7729–7994	2445	1450	November–May	Arechavaleta (1894), Bortolus & Iribarne (1999), Bortolus (2001), Vicari <i>et al.</i> (2002)
USA	774–2500	nd	nd	nd	April–July	Spicher & Josselyn (1985), Clifford (2002)
Spain	419–15,251	6961 (1074)–30,969 (4633)	3985 (487)–30,000	nd	June–December	Valdés <i>et al.</i> (1987), Nieva (1996), Nieva <i>et al.</i> (2001), Castillo <i>et al.</i> (2003)

Table 2 Description of dispersive structures of the three most common and invasive *Spartina* species worldwide (based on Parodi, 1919; Moberley, 1956; Gray & Benham, 1990; Bertness, 1999; Bortolus, 2001)

	<i>Spartina densiflora</i>	<i>Spartina alterniflora</i>	<i>Spartina anglica</i>
Rhizomes	Compact, strong, dark brownish	Elongated, thick-fleshy, whitish	Fleshy, whitish
Rhizome growing pattern	Guerrilla, phalanx-like	Guerrilla, phalanx	Phalanx
Spike size (cm)	2–8	5–15	2–12
Spikes per inflorescence	2–15	10–25	3–30
Spikelets per spike	2–15	10–30	5–35
Spikelets per inflorescence	4–225	100–750	15–1050

resulting in increased mechanical resistance to wave action, which favours its success in this zone (Nieva *et al.*, 2005). In Spain and Argentina, this species seems to enhance sexual and asexual reproduction through clonal integration (Bortolus *et al.*, 2004; Nieva *et al.*, 2005). It is, however, in freshwater and brackish marshes that it shows its fastest colonization and expansion rates, presumably as a result of the predominant salinity stress condition in marine coastal areas (Castillo *et al.*, 2005).

Even though 'densiflora' is the Latin for 'densely flowered', researchers have noted that this species has a much smaller and lower number of florets per spike and of spikes per inflorescence than other aggressive invasive *Spartinas* (e.g. *S. alterniflora* and *S. anglica*; Table 2). Moreover, the number of *S. densiflora* inflorescences per square metre varies from none to some thousands (Nieva, 1996; Bortolus, 2001; Vicari *et al.*, 2002; Bortolus *et al.*, 2004; Nieva *et al.*, 2005), with great variation possible even between plants growing within a few metres of each other (Bortolus *et al.*, 2004). In Humboldt Bay (USA), the seeds of *S. densiflora* showed a higher germination rate in freshwater and brackish conditions (with salinities < 11‰), and the survival and growth of seedlings were also greater in fresh water (Kittelson & Boyd, 1997). In marshes in southern Spain, the percentage of seeds germinating under laboratory conditions was as high as 65% of the developed seeds (Nieva, 1996). However, if the percentage of undeveloped seeds (90–95%) is considered in the estimation, the value falls to 3–7% of the complete pool of seeds produced in the field (Bortolus, 2001).

In Humboldt Bay (USA), the presence of competitive neighbours may trigger the highest seed production (a less clear pattern was found in Brazilian marshes; see Costa *et al.*, 2003): c. 79% of seeds from this site were found to be viable (Kittelson & Boyd, 1997). Although the specific mechanism driving this plastic response remains unclear, it may be induced by a number of direct and indirect ecological interactions. In New England (USA) salt marshes, for example, the experimental removal of the burrowing fiddler crab *Uca pugnax* generated a decrease of c. 50% in the number of flowering stems of *S. alterniflora* (Bertness, 1999). In a similar vein, in Mar Chiquita coastal lagoon (Argentina), the edaphic changes generated by the burrowing activity of the crab *Chasmagnathus granulata* were positively related through experimental manipulation with the production of viable

seeds of *S. densiflora* (Bortolus, 2001; Bortolus *et al.*, 2004). These works suggest that a variety of ecological interactions may modulate habitat characteristics that enhance the sexual reproductive success of *S. densiflora*. The resulting effect in all cases is that a larger quantity of viable seeds is exported from out-welling marshes. Thus, by mediating the expression of *Spartina* phenotypes, resulting in increased sexual reproductive success and longer-distance dispersion, burrowing/herbivore organisms and competitive neighbours may increase the rate of biological invasions (Bortolus *et al.*, 2004). As regards ecological interactions with a negative impact on the sexual reproductive success of *S. densiflora*, the only case recorded has been the aggressive spike infestation by *Claviceps* fungi in Argentina and Chile (Ringuelet, 1935; Fischer *et al.*, 2005; author's personal observations). At present, there are no studies evaluating the effects of this fungus on the production and reproduction of *S. densiflora*. Birds, insects, crustaceans and mammals have been observed consuming *S. densiflora* seeds in Spain and Argentina, but this has not been rigorously studied (Bortolus, 2001).

Plant–plant associations

As in the USA (Kittelson & Boyd, 1997) and Spain (Castillo *et al.*, 2000), in the northern marshes of Argentina *S. densiflora* seems to be restricted to the middle and high levels if other marsh plant species are present (Gulf of Cadiz, Spain: Nieva *et al.*, 2002; Humboldt Bay, USA: Clifford, 2002; Sanborombom and Blanca Bays, Argentina: Bortolus, 2005). Although this pattern may be attributable to salinity factors, more studies on the isolated and combined effects of interspecific competition, tidal flooding and air/water temperature are needed to gain a better understanding of what factors control *S. densiflora* zonation patterns. The high marsh of Buenos Aires marshes is patchily populated by *S. densiflora* along with *Salicornia ambigua* (= *Sarcocornia perennis*), *Distichlis spicata*, *Limonium* sp., *Cressa* sp. and *Juncus acutus* (Vervoost, 1967; Cabrera, 1970; Iribarne, 2001). In this region, *S. densiflora* is also found sharing the intertidal zone with *S. longispica* (a hypothetical hybrid of *S. densiflora* and *S. alterniflora*, based on phenotypic analyses; see Cabrera, 1970 and Giacobbo & Boechat, 1988) and *S. alterniflora*, which occupy the high, middle and low intertidal zones respectively. This may be interpreted as a competitive exclusion effect exerted by

S. densiflora over *S. alterniflora* and *S. longispica*, similar to that which occurs in New England marshes between *S. patens* and *S. alterniflora* (Bertness, 1991). However, recent studies conducted in Brazil suggest that competition between *S. alterniflora* and *S. densiflora* alone may not explain this pattern (Costa *et al.*, 2003). Moreover, the fact that *S. densiflora* is rarely found in the low intertidal zone, even when it is the only species present (Bortolus, 2001), suggests that the pattern is probably driven by the physiological constraints that this species shows under anoxic and hypersaline conditions in flooded areas (Kittelson & Boyd, 1997; Castillo *et al.*, 2000, 2005; Clifford, 2002; Nieva *et al.*, 2003). In fact, *S. densiflora* populations located on the lower part of the intertidal zone are expected to have the lowest net photosynthesis rate owing to high salinity, anoxic sediment and the reduction of the photosynthetic period by consecutive tides (Nieva *et al.*, 2003). The competitive exclusion of other species attributed to *S. densiflora* (in, for example, the USA: Kittelson & Boyd, 1997; and Spain: Nieva *et al.*, 2005), although possible (Costa *et al.*, 2003), needs further solid experimental evaluation within native and invaded marshes worldwide.

As with the invasive *S. alterniflora* and *S. anglica*, a successful *S. densiflora* invasion starts with the optimization of the microhabitat use through the colonization of bare unvegetated areas by seeds or plant fragments. Competitive interactions with native neighbours, where they occur, seem to be ineffective in preventing the exotic population from reaching a critical size, after which, favoured by its lack of a dormant period, it can rapidly overgrow native species (Nieva *et al.*, 2005). In old *S. densiflora* grasslands, the rhizomes of different ramets living together are usually packed tightly in a complex pattern that makes them look like a single ramet spreading with a compact multidirectional phalanx-growing pattern. Phalanx-growing salt-marsh plants are often considered more successful competitors than guerrilla-growing plants because, albeit slowly, they colonize available above- and below-ground space with closely packed modules. Guerrilla-growing plants, on the other hand, are capable of rapid lateral expansion but with loosely packed modules. *Spartina densiflora* seems able to combine the best of both growing strategies by overlapping guerrilla clones growing in different directions, generating multi-clone phalanx-growing modules. Since *S. densiflora* can rapidly colonize nearby bare areas by expanding laterally, in some cases it may even facilitate its own expansion by generating the wrack that creates the open areas, as in Humboldt Bay (Kittelson & Boyd, 1997). Its wrack production is usually not, however, as abundant as that described for *S. alterniflora* (Bertness, 1999).

The aggressive spreading of *S. densiflora* worldwide is only paralleled by that of its relatives *S. alterniflora* and *S. anglica*. Thus, we may find the best strategy to control it by carefully studying, for example, why *S. alterniflora* became virtually extinct in England after a century of apparently successful establishment (Adam, 1990). A similar process may have taken place in Argentina, where the aggressive *S. anglica* was recorded decades ago but now seems to be extinct (Orensanz

et al., 2002). These three species may be able to combine their physiological adaptations to cope successfully with the entire intertidal range of an invaded area. Whereas *S. densiflora* usually colonizes the middle and high marshes, *S. alterniflora* and *S. anglica* can successfully withstand frequent tidal submergence in the lower marsh. Such a triple introduction was recorded in the Pacific coastal marshes of the USA, and is probably occurring in other regions of Europe. In such cases, native botanical biodiversity is likely to decrease rapidly where management strategies fail. The fact that *S. densiflora* is one of the species with which *S. alterniflora* may produce hybrids (Parodi, 1919; Cabrera, 1970; Bortolus, 2001) makes it an even more dangerous threat to native plant community assemblages, as exemplified by the cross between *S. alterniflora* and *S. maritima* that originated the invasive *S. towsendii* and *S. anglica* (Gray & Benham, 1990).

Plant–animal associations

The *S. densiflora* marshes of the south-west Atlantic offer shelter and food for several species of animals, many of which are seriously threatened native species (e.g. the wild cat, *Oncifelis geoffroyi*, and the crake, *Porzana spiloptera*), and some of which are exotic and invasive ones (e.g. the European hare, *Lepus europaeus*, and starlings, *Acridoteres* sp.) (Iribarne, 2001). In spite of this, little attention has been directed to the study of vertebrates in these marshes, and at present, reptiles, fish and amphibians remain virtually ignored (Iribarne, 2001).

Birds are probably the most abundant and diverse group of vertebrates whose interactions with *S. densiflora* have been studied. *Spartina densiflora* marshes are among the few coastal environments receiving intra- and inter-continental migratory birds in southern South America (e.g. sandpipers, *Callidris canutus*, *C. fuscicollis*, the plover, *Pluvialis squatarola*, and the godwit, *Limosa haemastica*; Yorio, 1998; Isacch *et al.*, 2001). In Argentina, nearly 35 species of birds can be found in the *S. densiflora* marshes (Isacch *et al.*, 2001), including two rare endemic species (the wren-spinetail, *Spartonoica maluroides*, and the crake, *Porzana spiloptera*; Martinez *et al.*, 1997). *Spartina densiflora* offers a variety of resources for birds. Some of them (e.g. the long-winged harrier, *Circus buffoni*) use it as nest-building material. Most of them find protection from predators (e.g. the Argentinean common rail, *Pardirralus sanguinolentus*, and the wren-spinetail, *Spartonoica maluroides*), or a place to find prey (e.g. *C. buffoni*), and at least one of them (*Rhea americana*; Herrera, 2000; Isacch *et al.*, 2001) eats *Spartina*. The edges of the *Spartina* marsh are particularly important for many birds as shelter against strong cold winds (e.g. for ducks, swans and shorebirds; Bortolus *et al.*, 1998; Martinez & Ferrero, 2001).

Several mammals find in *S. densiflora* marshes a last refuge in regions dominated by urban landscapes. Top predators such as the wild cat, *Oncifelis geoffroyi* and the pampean fox, *Pseudalopex gymnocercus* can be found feeding and breeding in these marshes along with the wild pig, *Sus scrofa*, country mice (e.g. *Calomys* sp., *Akodon* sp., *Cavia* sp.), the armadillo,

Dasyus hybridus, the opossum, *Didelphis albiventris*, the invasive European hare, *Lepus europaeus*, the coipus, *Myocastor coypus*, and the giant rodent, *Hydrochaeris hydrochaeris* (Bo *et al.*, 2001; Farias & Canepuccia, 2001; Malizia *et al.*, 2001). Marshes are patchily distributed along the coast, but they serve as corridors for many mammals, providing hunting/feeding and breeding areas (e.g. Farias & Canepuccia, 2001). Introduced cattle are able to modulate the presence of marsh areas where native animals feed and rest by heavily grazing on and trampling the aboveground plant structures (Bortolus & Iribarne, 1999; Isacch *et al.*, 2001). In Mar Chiquita marshes, disturbances such as fire and cattle grazing frequently generate dramatic and long-lasting changes in plant–animal composition, since the recovery of old *S. densiflora* stands may take several years (Bortolus *et al.*, 2004; Isacch *et al.*, 2004).

Spartina–invertebrate associations have been studied in the temperate and subtropical marshes of Brazil (e.g. Lana & Guiss, 1991; Lana *et al.*, 1991; Costa *et al.*, 2003), but they have been little studied in the southern marshes of Uruguay and Argentina (Bortolus *et al.*, 2002) and completely ignored in the Patagonian marshes (Idaszkin, 2005). Studies have shown that *S. densiflora* marshes in the south-west Atlantic are commonly dominated by burrowing crabs (e.g. *Chasmagnathus granulata* and *Uca uruguayensis*; Olivier *et al.*, 1972). The species richness and abundance of most epifaunal and infaunal invertebrates (polychaetes, mites, spiders, and larval and adult insects) were positively related to the presence of *S. densiflora* (Bortolus & Iribarne, 1999). Such a pattern is common for most *Spartina* species (e.g. *S. alterniflora*: Lana & Guiss, 1991; *S. anglica*: Hedge & Kriwoken, 2000). *S. densiflora* is an ecosystem-engineer (*sensu* Jones *et al.*, 1994), expected to mediate and modulate community structure changes in both native and invaded

marshes (Bortolus *et al.*, 2002). For example, in Mar Chiquita lagoon, *S. densiflora* and *Sarcocornia perennis* enable crabs to expand into the high marsh by increasing crab survival under critically stressful thermal conditions (Bortolus, 2001; Bortolus *et al.*, 2002), while in the middle and low marsh the roots and rhizomes of *Spartina* offer refuge and food to a number of epifaunal and infaunal organisms (Bortolus & Iribarne, 1999).

Within the last decade, the few experimental studies conducted on *S. densiflora* have provided important baseline information on plant–animal interactions in Argentinean salt marshes (Bortolus & Iribarne, 1999; Bortolus *et al.*, 2002, 2004) (see Fig. 2). These works challenge the current understanding of the relative importance of bottom-up and top-down processes in controlling plant productivity of salt-marsh communities worldwide (Bortolus & Iribarne, 1999; Silliman & Bortolus, 2003). They have basically shown that the crab *Chasmagnathus granulata* – also a bioengineer species – is able to simultaneously (1) affect the edaphic characteristics of the substrate, which can in turn modulate *Spartina* production, (2) change the composition of the associated soil community, (3) directly decrease *Spartina*'s primary production, (4) alter the phenotype and physiology of the plant, and (5) induce changes in the structure of communities in other regions by amplifying *S. densiflora* invasiveness (Bortolus *et al.*, 2004). The crab *C. granulata* was also found heavily grazing on *S. alterniflora* and *S. densiflora* in Brazilian marshes (Costa *et al.*, 2003). However, more research is needed to understand the effects generated by the burrowing activity and herbivory separately. These works suggest that *S. densiflora* may be unexpectedly susceptible to the attack of invertebrates in invaded marshes, but also that its invasiveness may be enhanced by native organisms.

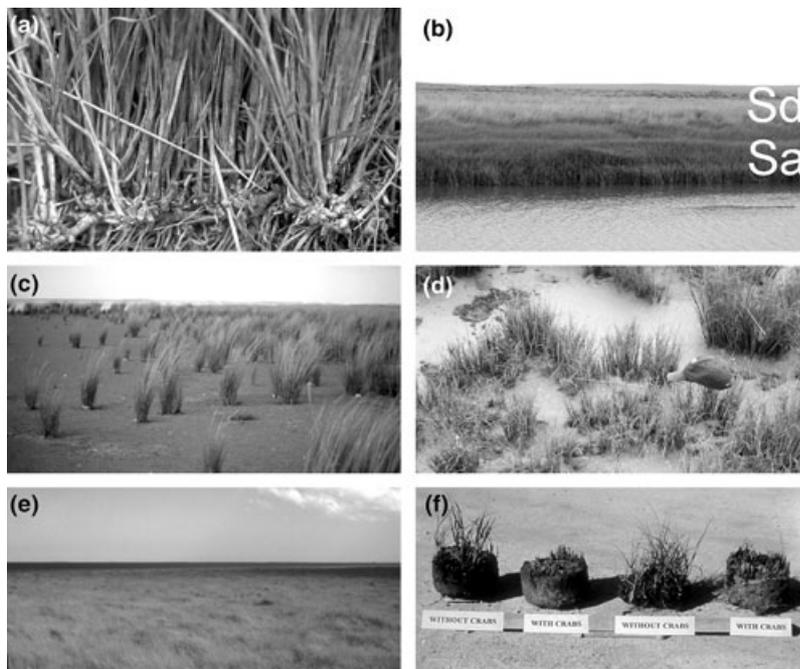


Figure 2 (a) Close up showing the compact appearance of stems, rhizomes and roots in an old *S. densiflora* stand. (b) View of a North Patagonian marsh showing a clear *S. densiflora* (Sd) zone above the *S. alterniflora* (Sa). (c) Colonization of a bare mudflat by *S. densiflora* in Mar Chiquita coastal lagoon. (d) Photo showing the characteristic spatial association between *Spartina* cover and crab burrows in the high marshes of Buenos Aires, Argentina. (e) View of a *S. densiflora*-dominated salt marsh. (f) First evidence – recorded in 1995 – showing the effect of the crab *C. granulata* on young *S. densiflora* plants. Photo credits: A. Bortolus.

CONCLUDING REMARKS

Although *S. densiflora* seems to have originated on the south-west Atlantic coast, there are currently many regions worldwide acting as donors for this species. *S. densiflora* is a major factor in shaping the pattern of distribution of organisms both above- and below-ground in native and invaded salt marshes. Its aggressive and successful invasiveness is comparable only to that of *S. alterniflora* and *S. anglica*, with which it can coexist if a multi-specific introduction occurred. Devastating effects on local ecosystems are predicted to occur whenever such triple introduction occurs. *Spartina densiflora* colonizes not only mudflats, as usually supposed, but also sandy, muddy, and rocky shores, and cobble beaches as well. Therefore, caution should be exercised when planning monitoring programmes within regions where it has been introduced and where management efforts are typically concentrated on low-energy mudflat and marsh areas. Whereas edaphic and ecological microhabitat conditions are known to be critical for the establishment and further success of this species, little is known about the ecological interspecific interactions in which *S. densiflora* participates during an invasion. In addition, more regional-scale research is urgently needed to identify and eliminate routes of international introduction and control accidental regional translocations.

Many important questions still need further attention and research in order to facilitate the design of more effective management strategies for this species worldwide. Does *S. densiflora* always reproduce and spread successfully after being introduced under different environmental conditions? What limits its reproduction and spread within the native range of distribution? Is it always negative in its effect on invaded communities? Does this species increase the availability of shelter and/or food to the native species in invaded marshes? How often do native plant and animal species favour the success of *S. densiflora* through positive interactions? How does the invasion of *S. densiflora* affect local ecosystem services? These and other questions focused on the ecology of *S. densiflora* within native and invaded areas must be addressed in detail through comparative experimental research. Only by integrating local-scale research, conducted in a variety of geographical regions, will we be able to understand the between-site variations of its biological cycle, and thereby be able to create more effective local/global conservation strategies.

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BIOSKETCH

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