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REGULAR PAPER

Biomass and clonal architecture of the cordgrass *Spartina patens* (Poaceae) as an invasive species in two contrasted coastal habitats on the Atlantic coast of the Iberian Peninsula

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Background and aims – The spread of invasive exotic species is one of the most important threats for salt marshes and cordgrasses (genus *Spartina*) are among the most invasive halophytes. Recent analyses have revealed low levels of genetic diversity within the European cordgrass *Spartina patens*, clarifying that it was introduced from a narrow genetic pool of plants from North America. As biomass and intratussock structure are key functional traits in the ecological behaviour of cordgrasses, our aim was to document this here for the first time in *Spartina patens* in Europe.

Methods – This work analyses above- and below-ground biomass and intratussock structure for two *Spartina patens* populations in Southern Spain in the two main invaded habitats in Europe, coastal dunes and brackish marshes.

Key results – *Spartina patens* showed higher above-ground biomass and higher above: below-ground biomass ratio in the brackish marsh than on the coastal dunes due to higher live shoot densities with similar shoot heights. Sexual reproduction of *Spartina patens* was very limited in both studied populations since only a few inflorescences were recorded in just one tussock in the marsh.

Conclusions – Our results for introduced *Spartina patens* in Spain are compared with those recorded for cohabiting cordgrasses, the native European *Spartina maritima* and the invasive *Spartina densiflora*, as well as with *Spartina patens* in North American marshes. *Spartina patens* appears as a species with moderate invasive potential in European coastal marshes and dunes since it shows very low sexual reproduction but a high phenotypic plasticity, which would support its invasive capacity. Eradication efforts are most cost effective in the early stage of infestation, when population sizes are still relatively small, and should thus be a focus of the control efforts of *S. patens* in the Southwest Iberian Peninsula as well as in other European areas, where this cordgrass is still not very abundant.

Key words – Asperillo sea-cliff, exotic species, Guadiana river, invasive species, intratussock shoot density, *Spartina versicolor*.

INTRODUCTION

Salt marshes fulfil many ecosystem services, such as promoting biodiversity, water quality improvement, flood control, or carbon capture (e.g. Zedler & Kercher 2005, Laegdsaard 2006). However, they have been affected by anthropogenic degradation worldwide, with 50 % of the original wetlands that existed before human intervention now lost (Mitsch 2010). In addition, the spread of invasive exotic species is one of the most important threats for coastal wetlands (Bromberg Gedan et al. 2009) and European salt marshes are not an exception (Leppäkoski et al. 2002). Invasive species in estuaries change the physical structure of the marshes, reduce their biological diversity and affect their ecological functions (Bromberg Gedan et al. 2009).

Cordgrasses (Genus *Spartina*, Poaceae) are among the most widespread halophytes in salt marshes around the world. They are powerful ecological engineers that are highly valued where they are native since they facilitate ecological succession development, give spatial structure to marshes through sediment accretion, carry out different regulating ecosystem services such as water decontamination, and promote biodiversity of flora and fauna (Curado et al. 2013a, 2013b, 2013c). But cordgrasses are also among the most invasive halophytes, colonising salt marshes all around the world after recurrent intercontinental introduction events

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(e.g. Daehler & Strong 1996, Baumel et al. 2001, Chen et al. 2004, An et al. 2007, Castillo et al. 2008a, Strong & Ayres 2013). When *Spartina* species are invasive they overgrow native salt marshes and open intertidal mudflats, diminish biota, hybridize with native *Spartina* species, increase costs of managing wildlife, and interfere with human uses of estuaries (Strong & Ayres 2013).

Spartina maritima (Curtis) Fernald is the only cordgrass species native to European salt marshes. Nowadays there are, however, several additional invading species such as *Spartina densiflora* Brongn., native to South America, that has spread to eight estuaries in the Gulf of Cádiz (Southwest Iberian Peninsula) (Bortolus 2006, Nieva et al. 2001), where it has hybridized with *S. maritima* (Castillo et al. 2010a). In addition, *Spartina alterniflora* Loisel., native to the Atlantic and Gulf coasts of North America, is invading the North Atlantic Coast of Europe (France and England, mainly) (Baumel et al. 2003) and has been introduced to the Tunisian coast (Hessini et al. 2009). Further, *S. alterniflora* occurs in Southern England and in Southwest France where it hybridized with *S. maritima* (Day et al. 1998), leading to the formation of two sterile F1 hybrids: *Spartina* × *townsendii* Groves and *Spartina* × *neyrautii* Fouc., respectively. Moreover, there is the vigorous and fertile allododecaploid *Spartina anglica* Hubb. (Guénégou et al. 1988), which originated from *S.* × *townsendii* and is rapidly spreading in western Europe (Ayres & Strong 2001).

Furthermore, *Spartina patens* (Aiton) Muhl., native to the Atlantic and Gulf coasts of North America where it is characteristic of high and brackish salt marshes and coastal dunes (Bertness 1991), occurs now also in Europe, in particular all along the western Mediterranean coasts as well as on the Atlantic coasts of the Iberian Peninsula (Sanz-Elorza et al. 2001, Baumel et al. 2016). It was first detected in Europe in Southern France near Agde in 1849 (Fabre 1849). *Spartina patens* grows in European brackish marshes and humid coastal dunes in the western Mediterranean (Fabre 1849, Jeanmonod & Burdet 1989, Menéndez & Sanmartí 2007). On the Iberian Peninsula, it colonised the Portuguese coast (Daveau 1897) and, in Spain, the North Atlantic and Cantabrian coasts (SanLeón et al. 1999, Campos et al. 2004, Page et al. 2010), the South Atlantic coast (Vicioso 1946, Sánchez-Gullón 2001) and the Mediterranean coast (de Bolós 1947).

In some studies of the European flora *S. patens* is still considered native to the Mediterranean (e.g. Tison et al. 2014) and in a few publications the European individuals of *S. patens* have been renamed as *Spartina versicolor* (Menéndez & Sanmartí 2007). However, based on morphological traits, Mobberley (1953) considered *S. versicolor* as synonymous to *S. patens*, and recent genetic analyses have revealed very low levels of genetic diversity within plants from Europe (Baumel et al. 2016). Here a single haplotype was identified that is identical to one haplotype of American *S. patens* from along the Atlantic North American coast from Mexico to Delaware. This result clarified that the introduction of *S. patens* into Europe occurred from a narrow genetic pool from North America (Baumel et al. 2016). We will thus in this article keep the name *S. patens* but always specify whether we refer to the American or European individuals of *S. patens*.

Invasiveness in cordgrasses is partially determined by their clonal growth strategy and their biomass accumulation (Castillo et al. 2016). Thus, below- and above-ground biomass (BGB and AGB, respectively) and intratussock structure are key functional traits in the ecological behaviour of clonal plants such as cordgrasses (Castellanos et al. 1994, Neumeier & Ciavola 2004, Castillo et al. 2010b). The clonal growth strategy has been described as a significant factor contributing to invasiveness (Martina & von Ende 2013), so increasing our understanding of the clonal growth strategy would allow us to better identify environmental conditions that promote invasiveness, predict future invasions, and manage existing invasions (Drenovsky et al. 2012). Cordgrasses propagate through both sexual and clonal reproduction, involving the formation of sexual and asexual propagules (seeds and rhizomes, respectively) that differ in size, resource status, genetic identity and invasive potential. The balance between sexual and clonal reproduction varies markedly between species and environments and depends partially on the pattern of biomass allocation (Eckert et al. 2016). Thus, some clonal plants may reduce severely their sexual reproduction due to unfavourable conditions for sexual reproduction together with trade-offs between sexual reproduction and clonal propagation (Ren et al. 2005). The growth pattern of invasive plants determines their biomass and litter dynamics that in turn may affect their nutrient accumulation and start cascading effects on ecosystem processes beyond short-term nutrient inputs in the soil resulting in the displacement of native species (te Beest et al. 2015).

Within invasive populations, phenotypic plasticity in response to different environments and genetic differentiation are two potential mechanisms that may confer fitness advantages and allow invasive plants to cope with environmental variation (Drenovsky et al. 2012). Phenotypic plasticity may increase the niche breadth of invaders, and plasticity of important functional traits such as those related to clonal architecture is expected to benefit invasive plants during the invasion process (Castillo et al. 2016). In spite of this, there is no study that reports on *S. patens* biomass and its phenotypic plasticity, and very little is known about its growth pattern in the invaded habitats in Europe (Menéndez & Sanmartí 2007).

Our main objective was to quantify the pattern of accumulation of BGB and AGB by *S. patens* in the two main habitats that this invasive species is colonizing in Europe. Thus, this work describes AGB and BGB and intratussock structure (clonal architecture characterised by density and height of vegetative live, spiked (producing inflorescence) and dead shoots within clumps) for *S. patens* on a coastal dune system and in a brackish marsh. The phenotypic responses of this species with low genetic diversity (Baumel et al. 2016) colonizing dunes and marshes were compared between the invaded habitats to explore the species' phenotypic plasticity. Our study was carried out in the Gulf of Cádiz, and our results were compared with data from the literature on *S. patens* in its native environment in North American marshes as well as cordgrasses cohabiting in Europe, the native European *S. maritima* and the invasive *S. densiflora* from South America.

MATERIALS AND METHODS

Study sites

Work was carried out in two *Spartina patens* populations growing in very contrasted coastal environments on the Atlantic coast of southwest Iberian Peninsula (Huelva, Spain): a coastal sand dune system at the base of a sea cliff known locally as ‘Asperillo’ (37°06′N 6°44′W – 37°05′N 6°44′W) and a brackish marsh at the estuary of the Guadiana river (37°17′N 7°25′W – 37°17′N 7°24′W) (fig. 1). The two locations have a Mediterranean climate with Atlantic influence and the semidiurnal 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. Both *Spartina* populations were genetically analysed by Baumel et al. (2016). The most abundant plant species accompanying *S. patens* on the coastal dunes were *Ammophila arenaria* (L.) Link, *Carex hispida* Willd. Ex Schkuhr, *Cyperus capitatus* Vand., *Ditrichia viscosa* L. (Greuter), *Echium gaditanum* Boiss., *Equisetum ramosissimum* Desf., *Elymus farctus* (Viv.) Runemark ex Melderis, *Helichrysum picardii* Boiss. & Reut., *Juniperus phoenicea* L. subsp. *turbinata* (Guss.) Nyman, *Plantago coronopus* L., *Pteridium aquilinum* (L.) Kuhn, *Phragmites australis* (Cav.) Trin. ex Steud., *Rubus ulmifolius* Schott, and the invasive species *Arundo donax* L. and *Carpobrotus edulis* (L.) L.Bolus. *S. patens* in the brackish marsh was growing on a tidal channel bank occupied also by *Fraxinus* sp. and *Tamarix* sp. and surrounded by agricultural fields.

Above-ground structures

Plant material was determined following Mobberley (1953). AGB of *S. patens* was harvested along one radial transect per tussock (electronic appendix) in five representative randomly chosen tussocks. Collection was conducted in December 2005 as cordgrasses on the Iberian Peninsula reach their maximum biomass during winter time (Figueroa et al. 1988, Nieva et al. 2001) and *S. patens* reaches its maximum shoot height at the end of summer (Menéndez & Sanmartí 2007). Each transect consisted of contiguous quadrats (10 cm radially × 15 cm wide) established from the outer edge of the tussock to its centre (electronic appendix). This allowed to record zones of different density within the clones of *Spartina* (Nieva et al. 2001). To analyse the intratussock structure, the quadrats of each radial transect were equally grouped into two parts: the centre and the periphery; in case of an odd number of quadrats along one transect, the periphery included one quadrat more than the centre (electronic appendix). A shoot was considered dead when no green leaves remained. The number of vegetative live, dead and spiked (producing inflorescence) shoots and the height of every live shoot were recorded in the laboratory for each sampling plot. AGB was classified in dead and live leaves of live shoots and live and dead shoots (including their dead leaves). Dry mass was determined after drying at 80 °C for 48 h to constant dry weight (DW). AGB per tussock was calculated as a weighted arithmetic mean according to the area of every concentric ring in relation to the total tussock area. Live AGB was calculated as the sum of the biomasses of live shoots and their live leaves, and total AGB was calculated as the sum of live AGB and the biomass of dead shoots, including their leaves.

Below-ground structures

Vertical distribution of BGB was determined by taking sediment cores (10.5 cm diameter × 20.0 cm deep) under the canopy area of *S. patens* in the central area (one per tussock) and within a 15 cm wide margin along the tussock’s edge (one per tussock) of the same sampled tussocks used for AGB. Once in the laboratory, cores were divided into four portions of 5 cm in depth. Roots and rhizomes were washed carefully before being dried and weighted (Figueroa et al. 2003); this method may underestimate the amount of BGB by 20–50 % (Johnen & Sauerbeck 1977). The BGB at the periphery and the centre of each tussock was obtained as the sum of its four BGB portions recorded at different depths. The mean BGB for each population at the periphery and the centre of its tussocks was calculated as the arithmetic mean of the recorded values for the five sampled tussocks per population. AGB:BGB ratio was calculated as the fraction between live AGB and total BGB.

Statistical analysis

Analyses were carried out using SPSS release ver. 12.0 (SPSS Inc.). Deviations were calculated as Standard Error (SE). The a level of significance was $p < 0.05$ for all tests. Homogeneity of variance and normality of raw data se-

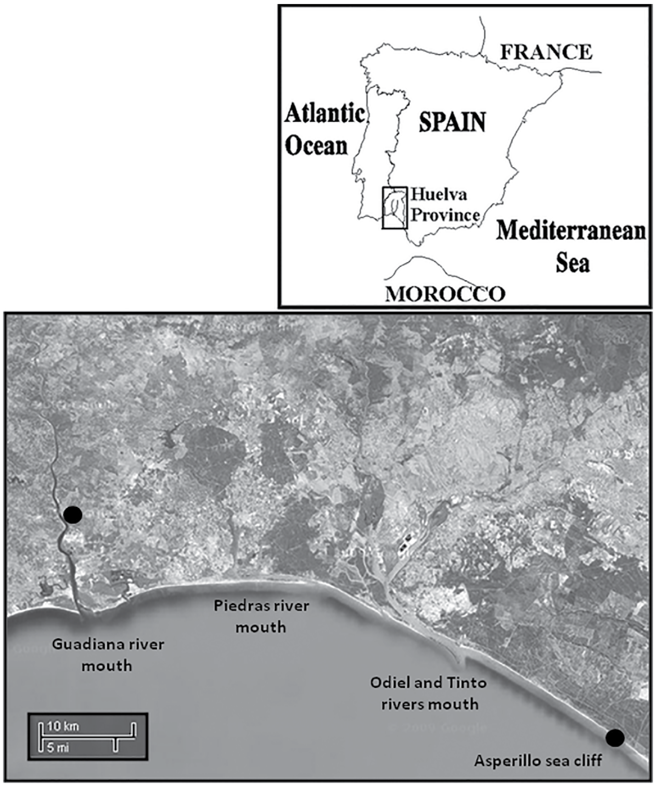

Figure 1 – Map showing the location of the Guadiana Marshes and Asperillo coastal dunes on the southwest coast of the Iberian Peninsula and aerial photography showing sampling points for *Spartina patens* (●).

ries were tested with the Levene test and the Kolmogorov-Smirnov test, respectively. When homogeneity of variance was violated, data series were transformed using the function √x. Plant traits were compared between the two studied populations by Student's *t*-test for independent samples and between the centre and the periphery within tussocks by Student's *t*-test for paired samples. To test if the periphery and the centre of the tussocks showed common biomass accumulation responses in the two *S. patens* populations, two-way analysis of variance (ANOVA) was performed using population (marsh vs. dune) and tussock area (centre vs. periphery) as grouping factors. The Pearson correlation coefficient was used to analyse linear relationships between plant traits separately for each of the populations (marsh vs. dune). The relationship between the live shoot density (dependent variable) and the radius of the tussock (independent variable) was analysed applying the best-fitting regression function to explore the form of the relationship between both variables.

RESULTS

Above-ground structures

Spartina patens tussocks growing in the brackish marsh showed a much higher total AGB (4 946 ± 1 816 g DW m^{-2}) than on the dunes (768 ± 262 g DW m^{-2}) (*t*-test = −4.865, $p < 0.005$). Total AGB increased with live and dead shoot mass on the dunes, being independent of dead shoot mass in the marsh (table 1). Thus, the percentage of AGB corresponding to dead shoots was much lower in the marsh (12 ± 4 %) than on the dunes (36 ± 9 %) (*t*-test = 2.507, $p < 0.05$) (fig. 2). Nevertheless, total AGB increased with live and dead shoot densities for both populations (table 1). The percentages of dead and live leaves of live shoots were similar for both populations (between 22 and 34 % for live leaves and between 16 and 19 % for dead leaves; *t*-test, $p > 0.05$). AGB of live shoots tended to be higher at the periphery than at the centre of the tussocks for both populations, without showing significant differences (table 2). The biomass of live and dead shoots (including their leaves) and total AGB were higher at the periphery than at the centre of the tussocks of both populations (two-ways ANOVA, $p < 0.05$; data transformed using √x).

Live shoot height was similar for both populations (marsh: 58.3 ± 2.0 cm; dune: 59.8 ± 5.3 cm; *t*-test $p > 0.05$) and independent of all other measured tussock traits (table 1). Live shoots were taller at the periphery than at the centre of the tussocks in the brackish marsh, without showing significant differences between tussock zones on the dunes (table 2).

Live shoots were much more packed in the brackish marsh (3 104 ± 976 live shoots m^{-2}) than on the dunes (477 ± 165 live shoots m^{-2}) (*t*-test = −2.653, $p < 0.05$). Dead shoot density tended to be also higher in the marsh (marsh: 729 ± 165 dead shoots m^{-2}; dune: 351 ± 101 dead shoots m^{-2}) but this interpopulation difference was not significant (*t*-test, $p > 0.05$) (fig. 2). Dead shoot density was independent of live shoot density on the dunes, showing a negative correlation in the marsh (table 1). Live shoot density was lower at the centre than at the periphery of the tussocks, especially in larger individuals, for both populations (*t*-test, $p < 0.05$). In contrast, dead shoot density was higher at the centre than at the periphery (*t*-test, $p < 0.05$) (table 2). In addition, live shoot density decreased exponentially with increasing tussock size ($p < 0.0001$). Tussocks growing on the dunes were larger than those colonising the brackish marsh (tussock radius: dunes, 111 ± 15 cm, marsh, 66 ± 10 cm; *t*-test = 2.433, $p < 0.05$) (fig. 3). No spiked shoots (either alive or dead) were recorded in tussocks on the coastal dunes and they appeared only at very low density at the periphery of just one tussock in the brackish marsh (67 spiked shoots m^{-2}) (table 2).

Below-ground structures

BGB at the centre and the periphery of *S. patens* tussocks was similar for both populations (c. 3 500 g DW m^{-2}) (*t*-test, $p > 0.05$) (table 2, fig. 4), but it was much more variable on the dunes than in the marsh. No rhizomes or roots were found below 20 cm. Most of the BGB was concentrated in the upper 10 cm, especially in the marsh population (marshes: 87 ± 5 %; dunes: 72 ± 7 %). Tussocks growing on coastal dunes

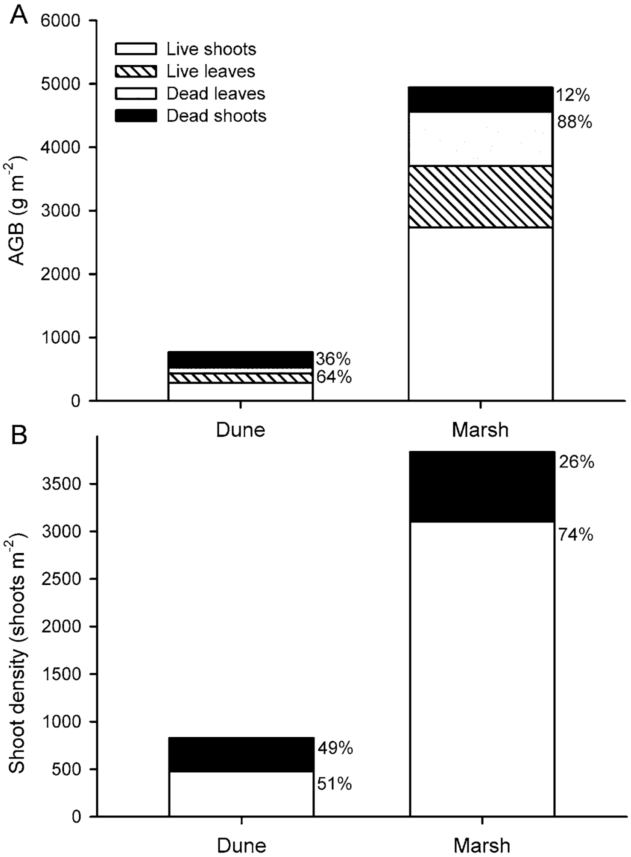

Figure 2 – Intratussock above-ground biomass (AGB, g m^{-2}) (live shoots, live and dead leaves of live shoots, and dead shoots with their leaves) (A) and density of live and dead shoots (shoots m^{-2}) (B) for two populations of *Spartina patens* in brackish marshes and on coastal dunes on the southwest coast of the Iberian Peninsula (n = 5 tussocks). Percentages correspond to dead shoots and to live shoots (together with their dead and live leaves in the case of AGB).

Table 1 – **Linear correlation analyses between tussocks traits for *Spartina patens* populations.**
Pearson correlation coefficient (r) and its probability level (p) between aerial traits (total above-ground biomass (AGB), AGB of live shoots and dead shoots (g m^{-2}; including leaves), live shoot height (cm) and live and dead shoot density (shoots m^{-2}) of *Spartina patens* tussocks colonising a brackish marsh and a coastal dune system on the southwest coast of the Iberian Peninsula (n = 5 tussocks). ***: $p < 0.0001$, **: $p > 0.001$; *: $p < 0.05$; n.s.: non-significant result.

Populations	Tussock traits	Total AGB	AGB (live shoots)	AGB (dead shoots)	Live shoot height	Live shoot density	Dead shoot density
Brackish marsh	Total AGB	–	–	–	–	–	–
	AGB (live shoots)	0.99***	–	–	–	–	–
	AGB (dead shoots)	n.s.	n.s.	–	–	–	–
	Live shoot height	n.s.	n.s.	n.s.	–	–	–
	Live shoot density	0.99**	0.99***	n.s.	n.s.	–	–
	Dead shoot density	0.91*	0.91*	n.s.	n.s.	−0.89*	–
Coastal dunes	Total AGB	–	–	–	–	–	–
	AGB (live shoots)	0.98*	–	–	–	–	–
	AGB (dead shoots)	0.90*	n.s.	–	–	–	–
	Live shoot height	n.s.	n.s.	n.s.	–	–	–
	Live shoot density	0.99*	0.98*	n.s.	n.s.	–	–
	Dead shoot density	0.90*	n.s.	0.99*	n.s.	n.s.	–

Table 2 – **Tussocks traits for *Spartina patens* populations.**
Above-ground biomass (AGB) of live shoots and dead shoots (g m^{-2}; including leaves), live shoot height (cm), live, dead and spiked shoot density (shoots m^{-2}), and below-ground biomass (BGB, g m^{-2}) at the centre and the periphery of *Spartina patens* tussocks colonising a brackish marsh and a coastal dune system on the southwest coast of the Iberian Peninsula. Values are means + SE (n = 5 tussocks). Different letters indicate significant differences between tussocks' zones: centre vs. periphery (paired sample *t*-test, $p < 0.05$). The centre and the periphery of a tussock included the same number of sampling quadrats (10 cm radially × 15 cm wide) distributed across its radius; in case of an odd number of quadrats, the periphery included one quadrat more than the centre.

Populations	Tussock traits	Centre	Periphery
Brackish marsh	AGB (live shoots)	752 ± 189 a	3 813 ± 1751 a
	AGB (dead shoots)	382 ± 129 a	325 ± 119 a
	Live shoot height	54.3 ± 2.2 a	63.0 ± 1.9 b
	Live shoot density	467 ± 107 a	2 636 ± 921 b
	Dead shoot density	173 ± 64 a	556 ± 116 b
	Spiked shoot density	0	67 (*n* = 1)
	BGB	3 278 ± 931 a	3 844 ± 668 a
Coastal dunes	AGB (live shoots)	118 ± 51 a	399 ± 176 a
	AGB (dead shoots)	43 ± 19 a	202 ± 96 a
	Live shoot height	59.1 ± 6.4 a	60.7 ± 10.9 a
	Live shoot density	82 ± 32 a	395 ± 161 b
	Dead shoot density	83 ± 38 a	268 ± 117 b
	Spiked shoot density	0	0
	BGB	6 445 ± 1 932 a	3 658 ± 1 189 a

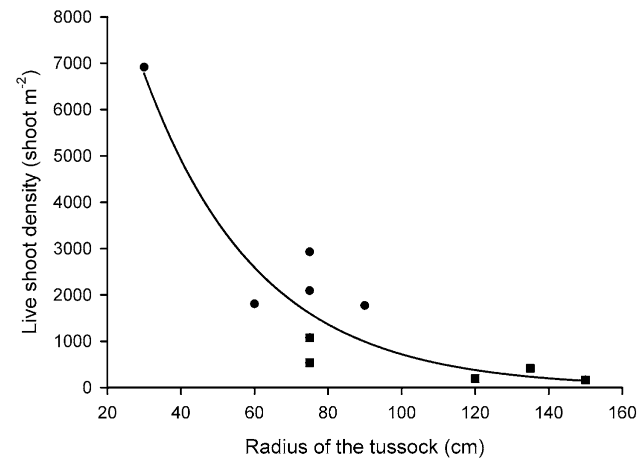

Figure 3 – Relationship between live shoot density and tussock radius for *Spartina patens* colonising a brackish marsh (●) and a coastal dune system (■) on the southwest coast of the Iberian Peninsula. Regression equation (n = 10): $y = 17732.426 \times \exp(-0.032\,x)$ ($p < 0.0001$).

tended to show more roots in relation to rhizomes at their periphery at 5–10 cm depth and higher BGB between 10 and 20 cm depth at their centres than those tussocks colonising the marsh (*t*-test, $p < 0.05$) (fig. 4).

AGB:BGB ratio was much higher for the marsh (1.13 ± 0.35) than for the dunes (0.17 ± 0.07) (*t*-test = −2.664, $p < 0.05$) and it was higher at the periphery than at the centre of the tussock for both populations (two-way ANOVA, F = 11.583, $p < 0.005$; data transformed using $\sqrt{x}$).

DISCUSSION

Our study shows that *Spartina patens* develops contrasted biomass accumulation patterns and clonal architectures when invading brackish marshes vs. coastal dunes in the Gulf of Cádiz (Southwest Iberian Peninsula). In comparison with the other cordgrasses colonizing the Gulf of Cadiz, the AGB of *S. patens* in the brackish marsh (c. 5 000 g DW m^{-2}) was three times higher than that recorded for the native *S. maritima* in low salt marshes (c. 1 000 g DW m^{-2} in Castellanos et al. 1994, Figueroa et al. 2003 and Castillo et al. 2008a, 2008b) but almost eight times lower than that of the invasive *S. densiflora* in brackish marshes (c. 38 000 g DW m^{-2}). Here *S. densiflora* showed c. 4 400 shoots m^{-2} more than *S. patens* (Nieva et al. 2001). Adult live shoots of *S. patens* were c. 58 cm tall for both populations, a similar height to those recorded for *S. maritima* and *S. densiflora* (Castillo et al. 2003, 2005, 2008a, Nieva et al. 2005). Menéndez & Sanmartí (2007) recorded maximum live shoot heights between 75 and 95 cm for *S. patens* in a Mediterranean brackish marsh at the end of the summer. AGB of *S. patens* in its native range in North America (c. 100–1 000 g m^{-2}) (Valiela et al. 1975, Hopkinson et al. 1978, Hester et al. 1996, Bertness 1991, Buchsbaum et al. 2009, Charles & Dukes 2009) was lower than the AGB recorded in our study for the brackish marsh (c. 5 000 g DW m^{-2}), but similar to our data for the

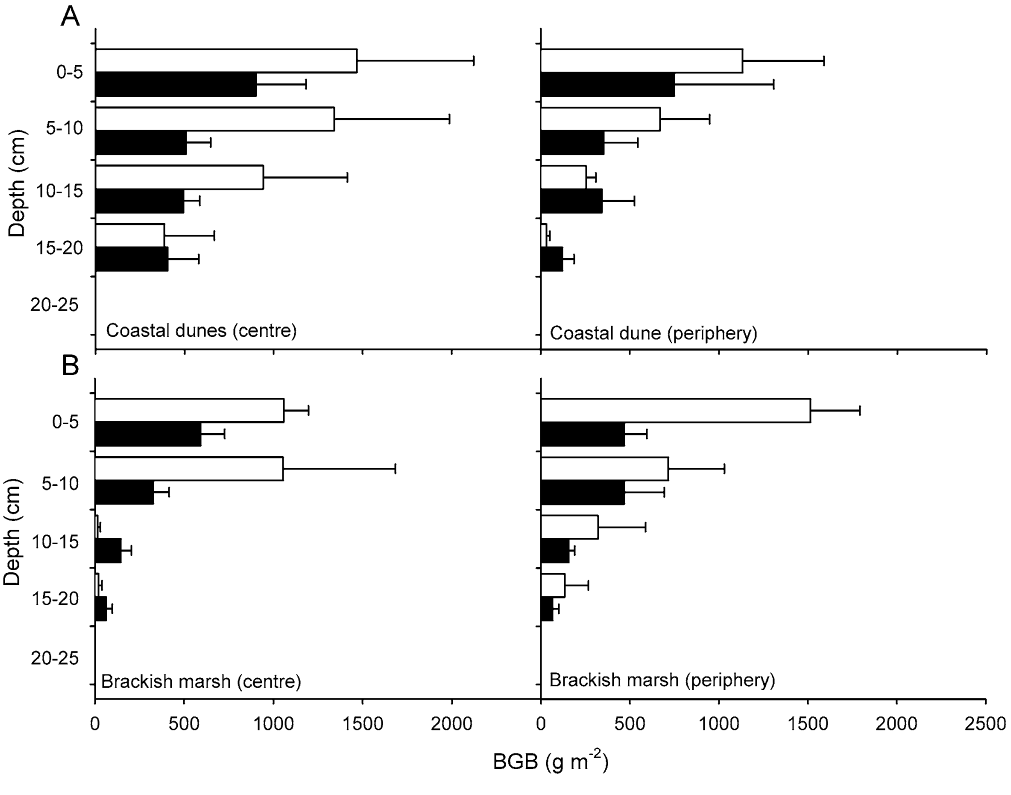

Figure 4 – Depth profiles of below-ground mass (BGB) (roots – black bars, rhizomes – white bars) at the centre and the periphery of tussocks of *Spartina patens* colonising a coastal dunes system (A) and a brackish marsh (B) (n = 5 tussocks) (mean and SE).

dunes. Considering biomass, similar patterns were found in populations of *S. patens* in Europe and North America with higher biomass in marshes than on dunes (Silander 1979). In our case, this interpopulation variation was due to higher live shoot densities in the marsh than on the dunes with similar shoot heights. Additionally, *S. patens* in the marsh presented lower proportions of dead shoots than on the dunes with similar dead shoot densities, which seemed to be related with the removal of dead biomass by tides and currents (Schubauer & Hopkinson 1984, Nieva et al. 2001). This hypothesis was supported by the fact that live and dead shoot masses and densities did not show any direct relationship for the dunes, pointing to an accumulation of dead ramets during clone development. The accumulation of dead shoots was concentrated at the centre of the tussocks, their oldest areas where live shoot density was lower. This accumulation of dead shoots at the tussocks' centre did not prevent them from being colonized by other species such as *Ammophila arenaria* (L.) Link, *Carex hispida* Willd. ex Schkuhr, *Equisetum ramosissimum* Desf., *Phragmites australis* (Cav.) Trin. ex Steud., *Plantago coronopus* L. and *Pteridium aquilinum* (L.) Kuhn. on the dunes and mainly *Polygonum equisetiforme* Sibth. & Sm. in the brackish marsh. This colonisation of the interior of the tussocks of *Spartina patens* by other plant species would be favoured by the recorded decrease in live shoot density during their expansion. This finding is similar to observations made on the native *S. maritima* which favours ecological succession by allowing *Sarcocornia perennis* (Mill.) Scott to colonise the central areas of its clones (Castellanos et al. 1994, Figueroa et al. 2003). In contrast, the invasive *S. densiflora* avoids the establishment of other species inside its tussocks by producing a high density of tall shoots across the whole tussock in the salt marshes of Southwest Iberian Peninsula (Nieva et al. 2001). In the native high marsh habitat of *S. patens* in North American, *S. patens* acts as a competitive dominant, forming monocultures (Bertness 1991), however, plant debris accumulation may cause significant mortality of *S. patens* favouring the colonization of its tussocks by *Distichlis spicata* (L.) Greene (Brewer et al. 1998).

Similar BGB but higher AGB in *S. patens* yielded a higher AGB:BGB ratio in tussocks from the marsh than from the dunes, however, both within the range reported for other cordgrasses (Hester et al. 1996, Nieva et al. 2001, Windham et al. 2003, Castillo et al. 2008b). The subterranean system of *S. patens* was as shallow as described for other *Spartina* species in salt marshes (Castellanos et al. 1994, Nieva et al. 2001) but it showed marked differences among populations on dunes and in marshes. *S. patens* tussocks tended to produce more roots in relation to rhizomes and its BGB was higher at depths of 10 to 20 cm on the dunes than in the marsh, which may be related to the need to use more soil volume in a nutrient-poor and well-aerated environment such as the sandy soils of dunes compare with the fine-textured soils of marshes (Gregory et al. 1987, Saunders et al. 2006). Mean BGB for both *S. patens* populations (c. 3 500 g DW m^{-2}) was within the wide range recorded for *S. maritima* (400–8 000 g DW m^{-2}) (Castellanos et al. 1994, Figueroa et al. 2003, Castillo et al. 2008b) and for American *S. patens* populations (c. 4 000 g DW m^{-2}) (Saunders et al. 2006), but it was much lower than that of *S. densiflora* in brackish marshes (c. 31 000 g DW m^{-2}) (Nieva et al. 2001).

Previous studies have shown a high intraspecific variation in biomass accumulation, clonal architecture and shoot morphology for cordgrasses such as *S. alterniflora* (Lessmann et al. 1997, Proffitt et al. 2005), *S. densiflora* (Nieva et al. 2001, Castillo et al. 2008a, 2014, 2016), *S. maritima* (Castellanos et al. 1998, Otero et al. 2000, Castillo et al. 2005, 2008a, 2008b) and *S. patens* from American populations (Silander & Antonovics 1979). These intraspecific differences can correspond to both phenotypic plasticity in contrasted environments and/or genotypic differentiation. While European *S. patens* showed contrasted clonal architectures based on shoot densities and BGB among marsh and dune populations, it showed a fixed configuration for its adult shoots, keeping a constant shoot height and a stable leaf representation (recorded as percentage of AGB) in both environments. These results together with the low genetic diversity recorded for European *S. patens* studied populations (Baumel et al. 2016) pointed to a genetic fixation of some plant traits in all populations irrespective of the environmental conditions, and also, in other plant traits, to phenotypical plasticity as response to different environments. *S. patens* at the Atlantic coast of North America also colonises marshes and dunes as it does in Europe, but showing high genetic variation, together with phenotypic plasticity among habitats (Silander & Antonovics 1979, Silander 1985). Our results showed that the low genetic diversity recorded for *S. patens* in Europe related to its introduction from a narrow genetic pool from North America (Baumel et al. 2016) was not an impediment to developing different phenotypes responding to contrasted environmental conditions. Common garden studies or reciprocal transplant experiments would be required to ultimately distinguish phenotypic plasticity from genetic differentiation.

Sexual reproduction of *S. patens* was very limited in both studied populations since only a few inflorescences were recorded in just one tussock in the marsh. This lack of sexual reproduction has been shown previously for Mediterranean *S. patens* populations (Fabre 1849, de Bolós 1947, Pignatti 1982). In contrast, *S. patens* in America quickly spread by seeds to Cox Island at the Pacific coast of North America (Frenkel & Boss 1988) and it has been recorded producing more seeds in marshes than on dunes in its native distribution range (Silander & Antonovics 1979). The recorded low level of seed production in Europe may be slowing down and limiting the invasion of *S. patens* along the Atlantic coast of the Iberian Peninsula as well as at other European coasts.

In comparison with the other cordgrasses colonizing the Gulf of Cadiz, the AGB of *S. patens* in the brackish marsh (c. 5 000 g DW m^{-2}) was three times higher than that recorded for the native *S. maritima* in low salt marshes (c. 1 000 g DW m^{-2} in Castellanos et al. 1994, Figueroa et al. 2003 and Castillo et al. 2008a, 2008b) but almost eight times lower than that of the invasive *S. densiflora* in brackish marshes (c. 38 000 g DW m^{-2}). Here *S. densiflora* showed c. 4 400 shoots m^{-2} more than *S. patens* (Nieva et al. 2001). Adult live shoots of *S. patens* were c. 58 cm tall for both populations, a similar height to those recorded for *S. maritima* and *S. densiflora* (Castillo et al. 2003, 2005, 2008a, Nieva et al. 2005). Menéndez & Sanmartí (2007) recorded maximum live shoot heights between 75 and 95 cm for *S. patens* in a Mediterranean brackish marsh at the end of the summer. AGB of *S. patens* in its native range in North America (c. 100–1 000 g m^{-2}) (Valiela et al. 1975, Hopkinson et al. 1978, Hester et al. 1996, Bertness 1991, Buchsbaum et al. 2009, Charles & Dukes 2009) was lower than the AGB recorded in our study for the brackish marsh (c. 5 000 g DW m^{-2}), but similar to our records for the dunes. Considering biomass, similar patterns were found in populations of *S. patens* in Europe and North America with higher biomass in marshes than on dunes (Silander 1979).

In view of our results, *S. patens* appears as a species with moderate invasive potential in European coastal marshes and dunes. On the one hand, it showed a high phenotypic plasticity, which would support its invasive capacity (Martina & von Ende 2013). But on the other hand, it showed low levels of sexual reproduction, which seems to limit its dispersion. Further, it allowed other species to colonise the interior areas of its clumps due to medium levels of biomass accumulation and intratussock shoot densities in contrast to the very aggressive exotic species *S. densiflora*.

A study on the introduction, establishment and spread of *S. patens* in Oregon shed light on the invasion process of this species. It shows that it is in the early stage of infestation, when population sizes are relatively small, that control efforts can be most cost effective (Frenkel & Boss 1988). In southwest Iberian Peninsula as well as in other European areas eradication efforts should start as soon as possible on the isolated populations of *S. patens* to prevent the spread of this invasive species.

SUPPLEMENTARY DATA

Supplementary data is available in pdf at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data) and consists of a diagram showing the location of one radial transect with contiguous quadrats along a *Spartina patens* tussock from the outer edge of the tussock to its centre.

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