Can asexual reproduction by plant fragments help to understand the invasion of the NW Iberian coast by *Spartina patens*?

José M. Sánchez, Cora Sánchez, Luis Navarro*

Department of Plant Biology and Soil Science, Faculty of Biology, University of Vigo, E-36310 Vigo, Spain

ABSTRACT

A common characteristic of alien plant invasions is the founder effect, resulting in low genetic variability and thus limited sexual reproduction. In some circumstances, asexual reproduction helps to overcome this hindrance, especially in coastal areas exposed to extreme weather events that help produce plant fragments acting as propagules. *Spartina patens* (Aiton) Muhl (Poaceae) is an alien invader colonizing most saltmarshes in NW Iberia (Spain and Portugal). The extent of the invasion in the area is quite large, but it remained unnoticed until recently due to the absence of flowering shoots that would have allowed for quick detection and identification. Here we ask whether vegetative propagules can help to understand the extensive spread of the invader. Both propagule characteristics (number and diameter of nodes) and environmental conditions (season and sediment covering) influenced the sprouting rate. In winter, around 30% of the fragments sprouted and produced short shoots of on average 2.8 cm tall. In spring, 40% of the fragments sprouted and produced larger shoots of 13.3 cm tall. Thus, even when conditions are harsh, this species can sprout from plant fragments abundantly. These results may help explain the success of this species invading NW Iberia, and suggest that asexual reproduction plays a role in the invasion by *S. patens*. Also, eradication techniques which can release plant fragments should be avoided as a measure to control the invasion of this plant.

1. Introduction

Coastal wetland ecosystems are especially fragile and sensitive to biological invasions (Zedler and Kercher, 2010) in part because coastal vegetation comprises a limited number of species resulting in simpler interaction networks (see Levine et al., 2004). Also, sea currents act as long-distance dispersion vectors for a number of plant propagules (Thiel and Gutow, 2005; Morgan and Sytsma, 2013). On top of that, the shipping industry delivers the propagules of alien species to and from coasts all over the world (Barney, 2005). Also, human activity (both intensive and extensive) carried out all along the shoreline results in severe disturbances to coastal ecosystems, increasing their vulnerability to biological invasion (Minchinton and Bertness, 2003). As a result, a number of serious ecological and evolutionary consequences are affecting coastal ecosystems due to colonization by alien species (Grosholz, 2002). The European coast is no exception. Since 1975 the importance and extent of biological invasions affecting coastal vegetation in NW Iberia began to be acknowledged (Campos et al., 2004; Buján, 2007; Castro et al., 2007, 2013; Page et al., 2010; Roiloa et al., 2010, 2013; Caño et al., 2013; Ferrero et al., 2013; Novoa and González, 2014; Novoa et al., 2014).

Of the species invading the NW Iberian coasts, the cordgrass *Spartina patens* is among the most aggressive in terms of the expansion it has attained and its ability to outcompete and displace native species even in undisturbed areas (Duarte et al., 2018). It is also an example of cryptic invasion since it went undetected until most of the NW Iberian coast was already colonized (SanLeón et al., 1999). Although a precise quantification of the extent of the invasion is still lacking, *S. patens* is present in all Galician saltmarshes with large pure stands in many of them (unpublished observations). It is present even in most protected coastal areas of the region (Fagúndez and Barrada, 2007).

Many cordgrass species (*Spartina* spp.) have been counted among the most aggressive plant invaders affecting saltmarshes all over the world ever since the publication of the seminal work on *Spartina* X *townsendii* (Oliver, 1925). *Spartina patens* forms extensive monospecific meadows by outcompeting native saltmarsh plants in NW Iberia (SanLeón et al., 1999). Although little is known about the beginning of the invasion (Daveau, 1897; SanLeón et al., 1999), the plant in Europe is quite efficient at reproducing asexually (Baumel et al., 2016). Also, its capacity for sexual reproduction in this area remains to be proven since flower production is rare (Duarte et al., 2018). Therefore, all or most of the extensive populations in NW Iberia are thought to originate from

vegetative propagules (SanLeón et al., 1999). That view was supported by Baume et al. (2016) who found that the invasion in Europe is a genetically impoverished variation of *S. patens*. The very low genetic diversity in Europe could be the result of founder effect from e.g. very few individuals as the origin of the invasion. They even hypothesized that the current low level of genetic variation could be the result of somatic mutation, stressing the importance of clonal propagation (Baumel et al., 2016).

Many cordgrass species propagate through both sexual and clonal reproduction (Castillo et al., 2017). If *S. patens* is reproducing mainly asexually in NW Iberia, most propagules responsible for such an outstanding invasive success could be plant fragments brought by sea currents. There are a number of studies on this long-distance dispersal capacity (Oliver, 1925; Morgan and Sytsma, 2013), but far fewer deal with the characteristics of the plant fragments that become efficient propagules (e.g. Morgan and Sytsma, 2004 on *Spartina alterniflora*, and Bando et al., 2016 on *Urochloa arrecta*). To the best of our knowledge, none has been done on *S. patens* and from NW Iberia.

Propagule pressure is a measurement of the number of dispersal units (propagules) released into a region to which they are not native (Lockwood et al., 2005). It comprises both the absolute number of propagules in a certain event (i.e. propagule size) and the number of propagule-releasing events (i.e. propagule number; Lockwood et al., 2005, 2009). Propagule size is therefore highly dependent on the abundance and density of the invading populations that produce and export propagules. The invasion of cordgrasses by plant fragments and seeds as propagules is widely accepted, although the balance between sexual and clonal reproduction varies markedly between species and environments (Castillo et al., 2017). For asexual propagules, fragment sizes vary from whole detached specimens (Oliver, 1925) to 25 mm rhizome fragments (Morgan and Sytsma, 2004). Since there is a conspicuous lack of evidence of sexual reproduction of this species in NW Iberia (SanLeón et al., 1999; Baumel et al., 2016), supported by the low genetic variability in the European populations (Baumel et al., 2016), we hypothesize that most reproduction in the area is by clonal fragments dispersed by tidal currents. Here we attempted to evaluate the ability of *S. patens* to produce a significant number of clonal propagules, which could help shed light on the successful establishment of this invasive species on the NW Iberia coast. To that end we used small stem fragments. If small fragments sprout in new individuals at a significant rate, that would greatly increase propagule size and help explain the success of the invasion in the context of propagule pressure. Specifically, we addressed the following questions. (1) What is the proportion of small plant fragments that are able to sprout? (2) What are the main propagule characteristics influencing sprouting? (3) Do season and arrival conditions for the propagule (deposited on / buried under the soil) have any influence on its sprouting probability? (4) Once propagules have sprouted, is shoot size dependent on the initial propagule characteristics?

2. Materials and methods

2.1. The plant

Spartina patens (Aiton) Muhl (Poaceae) is a North American invader on the Atlantic Iberian coast mainly colonizing saltmarsh ecosystems (SanLeón et al., 1999; Duarte et al., 2018), especially the mid-to-upper part of saltmarshes (Daehler and Strong, 1996). It was not reported in the area until the very last year of the 20th century, and by then it was already colonizing vast extensions of the saltmarshes. The delay in detecting its presence was due to the absence of flowering stems, which prevented the identification of the species. It is precisely this lack of flowering, and therefore sexual reproduction, that leads to the assumption that asexual reproduction is the main – if not the only – way for the plant to spread (SanLeón et al., 1999 after Saint Yves, 1932 therein). Although seed dispersal could have been the origin of the NW
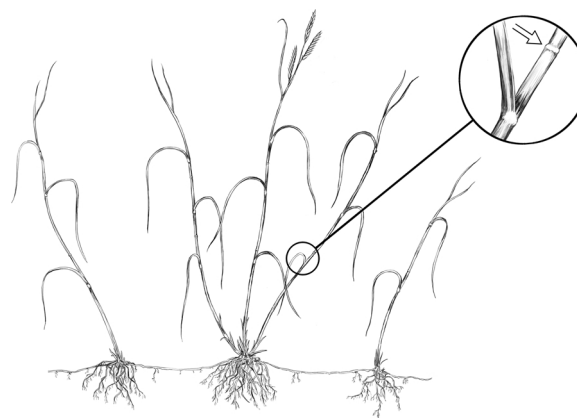

Fig. 1. Structure of *Spartina patens* clumps. Buds are at nodes at the base of sheaths. A node is pointed at in the inset.

Iberian populations, as has been suggested for *S. alterniflora* in several parts of the world (Strong and Ayres, 2013), the absence of current or historical records of flowering plants or seed production in the area makes that unlikely. Species nomenclature follows ITIS.

Plants grow in dense clumps. As for most grasses, leaves are produced from the stem nodes which contain a dormant growth bud. When touching the soil, the buds in the mid-basal part of the aerial stems can develop into new clonal shoots. Plagiotropic stems may become rhizomes when buried in sediment (Fig. 1).

Plant samples were collected from the saltmarsh of Vilaboa, in Ría de Vigo, NW Iberian Peninsula, Spain (42.351 ˚N, 8.633 ˚W). The climate in the area is Atlantic-temperate, with a hyper-oceanic bioclimate (Rodríguez-Guitián and Ramil-Rego, 2007). Aerial adult shoots were randomly gathered throughout the saltmarsh, taking one stem per clump. Since flowering is scarce and sexual reproduction in the invaded area remains to be detected (e.g. no flowering spikes or seeds were noticed at this population while sampling), the samples were assumed to have a high genetic homogeneity.

2.2. Experimental setting

The plant material collected was taken to an unheated glasshouse at Vigo University to be processed within 24 h of collection. In the glasshouse, mid-to-basal fragments of the shoots (*propagules* henceforth) were cut and potted. Six subgroups were formed considering the interaction of the following treatments: (1) propagules comprising one, two or three nodes; (2) propagules were placed in independent pots either on the soil or buried (approx. 1 cm deep) to simulate the conditions they would experience in nature after being transported by tides, either uncovered on top of the soil or covered by sediment after arrival.

Prior to potting, the propagules were measured for length, diameter and weight. To avoid any factor derived from the heterogeneity of natural saltmarsh soil, a standard *Siro-royal* ® universal substrate was used for the potting and fresh water was used for watering. Pots were randomly placed on glasshouse benches, and an automatic irrigation system was programmed to operate every 12 h to simulate watering by the semidiurnal tidal regime in the area. A 4-day drought period was forced at mid-term for each experiment, simulating the neap tide periods when tides do not reach the middle-upper parts of the saltmarsh where this species lives.

To find out whether (1) plant propagation is active during the harsher season, i.e. winter, and (2) if there are substantial differences among seasons, the experiment was conducted twice in 2018, for 71 days after February 2 during winter and for 65 days after March 21 in spring. Climatic values in the area for those periods were, respectively as follows: average temperature 7.7 and 11.6 ˚C, average minimum

temperature 5.3 and 8.5 °C, mean number of sunny hours per day 4.2 and 7.4 h, respectively (MeteoGalicia, 2018). The number of samples for each subgroup was 30 and 20 for winter and spring experiments, respectively, with 6 subgroups each. A larger number of samples were used for the winter experiment as we anticipate the possibility of lower propagation.

At the end of the experiment, the presence/absence of sprouts from any of the nodes of each sample was recorded. When sprouts were produced, aerial shoot and roots were measured. Root data were later discarded due to the variability arising from the difficulty encountered when trying to remove them entirely from the soil. For propagules with more than one node sprouting, only the largest shoot was considered.

2.3. Data analysis

To estimate the resources available for each bud (node) to grow, the relationships of number of nodes with propagule length and propagule weight were calculated to be included in the model. A Generalized Linear Model with a logit link function was used to analyze the influence of the experimental factors – diameter, length and weight per node, soil condition (on/under soil), and number of nodes (1, 2, or 3) – on the likelihood of a propagule producing shoots (presence/absence of sprouts from each propagule). Models including interactions were ruled out because the best predictive model was selected considering the lowest value of Akaike's information criterion. We also tested for the overall effect of number of nodes in the model with a Wald test.

A multiple regression analysis was performed to determine whether the size of the plants produced depends on the initial conditions. Shoot length was the dependent variable and diameter, length per node, number of nodes (1, 2, or 3), soil condition (on/under soil) and season (winter/spring) were used as independent variables. Normality was verified with Kolmogorov-Smirnov test ("nortest" R package). All statistical analyses were performed using R v.3.5.1 (R Core Team, 2018).

3. Results

The number of propagules that succeeded in producing sprouts was relatively high in both winter (28.1%) and spring (37.1%). Season was the most influential factor on the model's ability to predict vegetative reproductive success (Table 1). During the winter the small propagules (less than 3 nodes) placed on the soil surface had the lowest sprouting levels, with no sprouting at all in propagules with just one node (Fig. 2). The number of successful propagules in winter was therefore related to both the number of nodes per propagule and propagule placing (on/under the soil), while that relationship was not so clear in spring (Table 1). According to the result of the Wald test, the overall effect of number of nodes was statistically significant in the model ($\chi^2 = 10.4$, df = 2, $P = 0.006$), although the effect of the 3-node group seemed to be larger (Estimate 1.37, Table 1). The sprouting rate was significantly related to propagule diameter, but not to the length or weight of the propagule per node (Table 1).

Table 1
Result of the GLM analysis for the effects on sprouting ability of propagules.

	Estimate	SE	z	P
Intercept	−5.662	0.934	−6.06	< **0.001**
Diameter	1.807	0.347	5.20	< **0.001**
Weight per node	−3.492	4.843	−0.721	0.471
Length per node	−0.025	0.019	−1.315	0.188
Soil condition	0.795	0.293	2.71	**0.007**
Season	1.904	0.385	4.94	< **0.001**
Number of nodes (2)	0.821	0.383	2.14	**0.032**
Number of nodes (3)	1.370	0.426	3.21	< **0.001**

Likelihood ratio test, $\chi^2 = 73.11$, df = 7, $P < 0.001$.
Cragg and Uhler's pseudo-$R^2 = 0.31$.

As expected, the shoots produced by the propagules that succeeded in sprouting attained larger sizes in spring than in winter (mean shoot size 133.1 mm and 28.4 mm respectively). Season was therefore the main factor responsible for shoot size, and propagule diameter was the only other factor with a significant effect (Table 2, Fig. 3).

4. Discussion

The importance of propagule pressure has been recognized in invasion ecology and it has been related to the initial stages of the invasion and the relevant concept of minimum viable population size. As Lockwood et al. (2009) proposed, the more the propagules to arrive, the more likely the invader population to survive environmental or demographic stochasticity, overcome the Allee effect, or have sufficient genetic variation to adapt to local conditions. Nonetheless, propagule pressure is also important in helping to understand other aspects of the invasion process, such as the speed of spreading and the pattern of colonization (Morgan and Sytsma, 2013).

As expected, *S. patens* is quite efficient in reproducing asexually from plant fragments. As has been found in other cordgrass species, the probability of survival and establishment is higher for larger propagules than for smaller ones. For instance, small rhizome fragments (25 mm) of *S. alterniflora* could survive with a probability close to 40% when already sprouted, but small fragments were unable to produce new individuals when planted before sprouting (Morgan and Sytsma, 2004). An important finding is that even the very small propagules of *S. patens* carrying only one node are able to produce a new plant. In winter this happened only if the single-node fragments were buried in the sediment and the sprouting probability was ˜30%, while in spring the sprouting probability was higher (˜40%) and also did not depend on whether they were buried or not (Fig. 2). The probability is strikingly similar to the survival rate reported by Morgan and Sytsma (2004) for *S. alterniflora*.

Even though the plant fragment used had only 1 to 3 nodes, they produced shoots in a large proportion (30–40 %). Taking into account (1) the vast extension already occupied by the *S. patens* invasion in the NW Iberia saltmarshes (SanLeón et al., 1999), and that (2) most of the dispersed fragments in nature are probably larger and therefore even more prone to sprout, it is reasonable to assume that propagule pressure can be massive. If that is the case, it could be among the main causes of the success of *S. patens* as an invader. The total extent of the cordgrass invasion in NW Iberia remains to be ascertained. However, if the data reported by Peralta et al. (2008) and Castillo et al. (2010) are taken as a reference (cordgrass density 100–4000 shoots m^{-2}), we can presume that large invasion rates could be explained by clonal spreading alone. Even though a continuing rain of propagules may dilute the genetic bottleneck effect of invasions when propagules come from a variety of sources (Simberloff et al., 2009), it is likely that propagules reaching the NW Iberia saltmarshes are somewhat genetically homogeneous due to the conspicuous absence of flowering in the area (suggesting an asexual origin of propagules). This assumption is consistent with the low genetic variability reported for the species in the area (Fernández-Prieto et al., 2011; Baumel et al., 2016).

One propagule characteristic that significantly related to the probability of sprouting was propagule diameter, possibly because it more accurately reflects the resources available for the buds to sprout than length and weight per node (Table 1). This result is consistent with the stem architecture of cordgrasses being thicker at the base, which is the part of the plant with a higher probability of making contact with the soil, becoming buried by sediment and producing rhizomes (see Maun, 1998). For other coastal grasses such as *Elymus farctus*, the likelihood of a buried rhizome fragment to produce viable shoots was found to be even higher than that of seeds (Harris and Davy, 1986). This is likely because of the greater accumulation of resources available for the new shoots to sprout in the rhizomes as stated by Maun (1998) for coastal sand-dune species. Accordingly, our results seem to indicate that stems with larger diameters have more resources accumulated in their tissues,
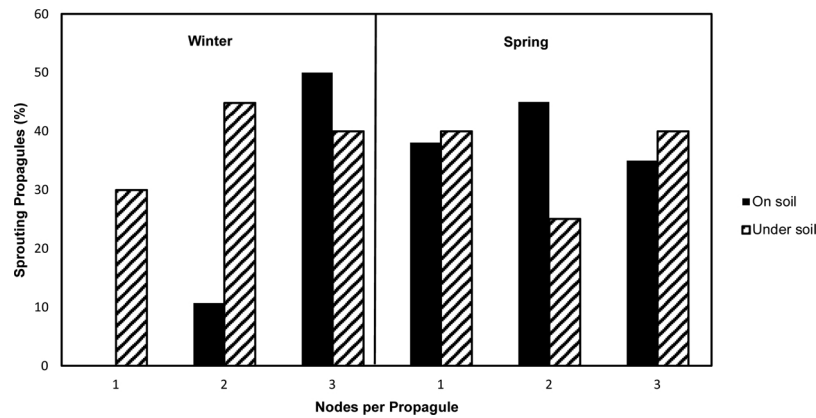
Fig. 2. Percentages of propagules producing shoots in winter and spring, on the soil and buried under soil surface, considering the number of nodes per propagule.

Table 2
Result of the multiple regression analysis for effects on shoot size.

	Estimate	SE	t	P
Intercept	−149.821	68.841	−2.18	**0.033**
Length per node	0.531	1.344	0.40	0.694
Diameter	53.344	20.134	2.65	**0.010**
Soil condition	13.066	26.902	0.49	0.629
Season	151.224	33.744	4.49	**< 0.001**
Number of nodes (2)	36.224	36.617	0.99	0.326
Number of nodes (3)	14.661	38.323	0.38	0.703

$F = 4.66$, df = 6, 79, $P < 0.001$, $R^2 = 0.21$.

which would make them more successful in producing new shoots.

Besides these propagule features, the seasonal timing of the dispersion and the soil conditions that propagules encounter on arrival are also related to the probability of producing new shoots (Table 1). Our results suggest that propagules buried by sediment after arrival are more prone to produce new shoots in most of the groups (Fig. 2), in accordance with results previously reported for other coastal plant species including cordgrasses (Sánchez et al., 2001; Thampanya et al., 2002; Deng et al., 2008). In fact, for some sand-dune grasses it has been proven that the shoots produced from vegetative propagules can emerge from greater burial depths than seedlings (Maun, 1998) thanks to the larger accumulation of resources. Burial seems to be an especially important factor during winter, possibly because the buds of unburied propagules are exposed to extremely low temperatures. In this study, the average minimum temperature values for the winter group was

more than 3 °C below than in spring, and the lowest temperature recorded in winter was 0 °C, a value never reached in spring.

It is important to note that, even though lower than in spring, propagule success in winter was also remarkable (28.1% in all). It is in winter when storms are more frequent (Oberle et al., 2014). Since living aerial shoots do not detach easily from tussocks, winter storms may play a role in breaking plants into fragments to be dispersed as wrack. This is especially likely in coastal habitats, exposed to extreme weather events (Nathan et al., 2008). Sediment mobilization in the area is also higher during winter (Oberle et al., 2014), increasing the probability for propagules to be buried after arrival and therefore also increasing their chance of sprouting, as our data seem to indicate.

For shoots that sprouted from propagules, the only factors related to shoot size were season and propagule diameter (Table 2). The relationship between the growing-rate of cordgrass and season must obviously be mediated by temperature, as was also reported for other cordgrasses (e.g. Callaway and Josselyn, 1992). The influence of propagule diameter on the growth rate is probably due to the greater amount of resources available for the shoots from thicker propagules (Maun, 1998), as discussed above.

5. Conclusions

Our results shed light on the successful invasion of *S. patens* in the saltmarshes of NW Iberia, even when sexual reproduction is low or non-existent. Therefore, this work corroborates previous reports on the importance of propagule pressure (Colautti et al., 2006; Simberloff, 2009). The results are also an important reminder of the need for
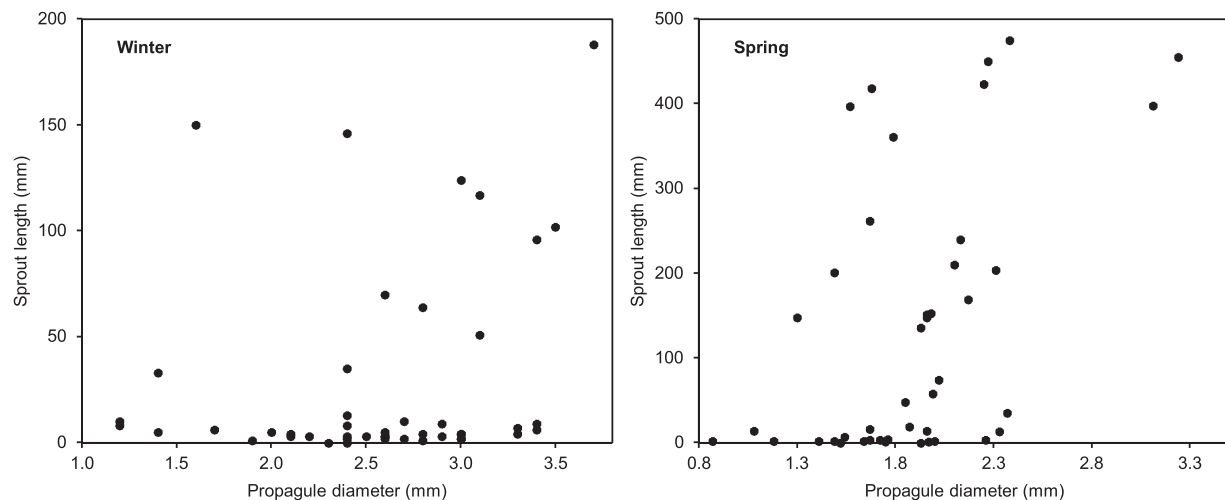

Fig. 3. Relationship between the length of the shoot produced and propagule diameter.

extreme caution when applying some aggressive management techniques intended to eradicate invasive plants. Some efforts are based on the destruction of plants by fragmentation, but that may only worsen things even further. An extreme example was the rototilling of some cordgrass marshes in an attempt to stop their spread, but instead caused the massive production of propagules (fragments) (Morgan and Sytsma, 2004). Future studies improving the knowledge of the invasion process of *S. patens* in NW Spain must include other aspects, such as the quantification of propagule production in natural conditions, the characteristics and survival of propagules in the wrack, the environmental conditions of the invaded system, and the biotic interactions taking place in that environment (e.g. Vilà and Weiner, 2004).

Declarations of interest

None.

Acknowledgements

References

Bando, F.M., Michelan, T.S., Thomaz, S.M., 2016. Propagule success of an invasive Poaceae depends on size of parental plants. Acta Limnol. Bras. 28, e23. https://doi.org/10.1590/s2179-975x2216.

Barney, J.N., 2005. North America history of two invasive plant species: phytogeographic distribution, dispersal vectors, and multiple introductions. Biol. Invasions 8, 703–717.

Baumel, A., Rousseau-Gueutin, M., Sapienza-Bianchi, C., Gareil, A., Duong, N., Rousseau, H., Coriton, O., Amirouche, R., Sciandrello, S., Duarte, B., Caçador, I., Castillo, J.M., Ainouche, M., 2016. *Spartina versicolor* Fabre: another case of *Spartina* trans-Atlantic introduction? Biol. Invasions 18, 2123–2135. https://doi.org/10.1007/s10530-016-1128-z.

Buján, M.I.R., 2007. Flora exótica de Galicia (noroeste ibérico). Bot. Complutensis 31, 113–125.

Callaway, J.C., Josselyn, M.N., 1992. The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in South San Francisco Bay. Estuaries 15, 218–226.

Campos, J.A., Herrera, M., Biurrun, I., Loidi, J., 2004. The role of alien plants in the natural coastal vegetation in central-northern Spain. Biodivers. Conserv. 13, 2275–2293.

Caño, L., Campos, J.A., García-Magro, D., 2013. Replacement of estuarine communities by an exotic shrub: distribution and invasion history of *Baccharis halimifolia* in Europe. Biol. Invasions 15, 183–186.

Castillo, J.M., Leira-Doce, P., Figueroa, E., 2017. 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. Plant Ecol. 150, 129–138.

Castillo, J.M., Rubio-Casal, A.E., Figueroa, E., 2010. Cordgrass biomass in coastal marshes. In: Momba, M., Bux, F. (Eds.), Biomass. Sciyo, Rijeka, pp. 1–26.

Castro, S., Ferrero, V., Costa, J., Sousa, A.J., Navarro, L., Loureiro, J., 2013. Reproductive strategy of the invasive *Oxalis pes-caprae*: distribution patterns of flower morphs, ploidy levels and sexual reproduction. Biol. Invasions 15, 1863–1875.

Castro, S., Loureiro, J., Santos, C., Ater, M., Ayensa, G., Navarro, L., 2007. Distribution of flower morphs, ploidy level and sexual reproduction of invasive weed *Oxalis pes-caprae* in the western area of the Mediterranean Region. Ann. Bot. 99, 507–517.

Colautti, R.I., Grigorovich, I.A., MacIsaac, H.J., 2006. Propagule pressure: a null model for biological invasions. Biol. Invasions 8, 1023–1037.

Daehler, C.C., Strong, D.R., 1996. Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. Biol. Conserv. 78, 51–58.

Daveau, J., 1897. La flore littorale du Portugal. Bol. Soc. Broteriana 14, 4–54.

Deng, Z., An, S., Zhao, C., Chen, L., Zhou, C., Zhi, Y., Li, H., 2008. Sediment burial stimulates the growth and propagule production of *Spartina alterniflora* Loisel. Estuar. Coast. Shelf Sci. 76, 818–826.

Duarte, B., Mateos-Naranjo, E., Goméz, S.R., Marques, J.C., Caçador, I., 2018. Cordgrass invasions in Mediterranean marshes: past, present and future. In: In: Queiroz, A., Pooley, S. (Eds.), Histories of Bioinvasions in the Mediterranean. Environmental History, vol. 8 Springer.

Fagúndez, J., Barrada, M., 2007. Plantas invasoras de Galicia. Bioloxía, distribución e

métodos de control. Santiago de Compostela: Xunta de Galicia, Dirección Xeral de Conservación da Natureza, Spain.

Fernández-Prieto, J.A., Cires, E., Corominas, T.S., Vázquez, V.M., 2011. Systematics and management of natural resources: the case of *Spartina* species on European shores. Biol. Sect. Bot. 66, 1011–1018.

Ferrero, V., Castro, S., Costa, J., Jorge, A., Acuña, P., Navarro, L., Loureiro, J., 2013. Effect of invader removal: pollinators stay but some native plants miss their new friend. Biol. Invasions 15, 2347–2358.

Grosholz, E., 2002. Ecological and evolutionary consequences of coastal invasions. Trends Ecol. Evol. 17, 22–27.

Harris, D., Davy, A.J., 1986. The regenerative potential of *Elymus farctus* from rhizome fragments and seed. J. Ecol. 74, 1057–1067.

ITIS (Integrated Taxonomic Information System). Available at: http://www.itis.gov [Accessed 27 December 2018].

Levine, J.M., Adler, P.B., Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecol. Lett. 7, 975–989.

Lockwood, J.L., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. Trends Ecol. Evol. 20, 223–228.

Lockwood, J.L., Cassey, P., Blackburn, T., 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Divers. Distrib. 15, 904–910.

Maun, M.A., 1998. Adaptations of plants to burial in coastal sand dunes. Can. J. Bot. 76, 713–738.

MeteoGalicia, 2018. Meteorological Network, Vigo-campus Station. [Accessed 8 January 2019]. http://www.meteogalicia.gal.

Minchinton, T.E., Bertness, M.D., 2003. Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marsh. Ecol. Appl. 13, 1400–1416.

Morgan, V.H., Sytsma, M., 2004. Fragment propagules of *Spartina alterniflora* and potential Eastern Pacific dispersal, San Francisco. Proc. 3rd Conf. Invasive *Spartina* 255–261.

Morgan, V.H., Sytsma, M.D., 2013. Potential ocean dispersal of cordgrass (*Spartina* spp.) from core infestations. Invasive Plant Sci. Manage. 6, 250–259.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A., 2008. Mechanisms of long-distance seed dispersal. Trends Ecol. Evol. 23, 638–647.

Novoa, A., González, L., 2014. Impacts of *Carpobrotus edulis* (L.) NE Br. on the germination, establishment and survival of native plants: a clue for assessing its competitive strength. PLoS One 9, e107557. https://doi.org/10.1371/journal.pone.0107557.

Novoa, A., Rodríguez, R., Richardson, D., González, L., 2014. Soil quality: a key factor in understanding plant invasion? The case of *Carpobrotus edulis* (L.) NE Br. Biol. Invasions 16, 429–443.

Oberle, F.K., Storlazzi, C.D., Hanebuth, T.J., 2014. Wave-driven sediment mobilization on a storm-controlled continental shelf (Northwest Iberia). J. Mar. Syst. 139, 362–372.

Oliver, F.W., 1925. *Spartina townsendii*: its mode of establishment, economic uses and taxonomic status. J. Ecol. 13, 74–91.

Page, H.M., Lastra, M., Rodil, I.F., Briones, M.J.I., Garrido, J., 2010. Effects of non-native *Spartina patens* on plant and sediment organic matter carbon incorporation into the local invertebrate community. Biol. Invasions 12, 3825–3838.

Peralta, G., Van Duren, L.A., Morris, E.P., Bouma, T.J., 2008. Consequences of shoot density and stiffness for ecosystem engineering by benthic macrophytes in flow dominated areas: a hydrodynamic flume study. Mar. Ecol. Prog. Ser. 368, 103–115.

R Core Team, 2018. R: a Language and Environment for Statistical Computing. R foundation for statistical computing, Vienna, Austria. http://www.Rproject.org.

Rodríguez-Guitián, M.A., Ramil-Rego, P., 2007. Clasificaciones climáticas aplicadas a Galicia: revisión desde una perspectiva biogeográfica. Recursos Rurais 3, 31–53.

Roiloa, S.R., Rodríguez-Echeverría, S., de la Pena, E., Freitas, H., 2010. Physiological integration increases the survival and growth of the clonal invader Carpobrotus edulis. Biol. Invasions 12, 1815–1823.

Roiloa, S.R., Rodríguez-Echeverría, S., Freitas, H., Retuerto, R., 2013. Developmentally-programmed division of labour in the clonal invader Carpobrotus edulis. Biol. Invasions 15, 1895–1905.

Sánchez, J.M., SanLeón, D.G., Izco, J., 2001. Primary colonisation of mudflat estuaries by *Spartina maritima* (Curtis) Fernald in Northwest Spain: vegetation structure and sediment accretion. Aquat. Bot. 69, 15–25.

SanLeón, D.G., Izco, J., Sánchez, J.M., 1999. *Spartina patens* as a weed in Galician salt-marshes (NW Iberian Peninsula). Hydrobiology 415, 213–222.

Simberloff, D., 2009. The role of propagule pressure in biological invasions. Annu. Rev. Ecol. Evol. Syst. 40, 81–102.

Strong, D.R., Ayres, D.R., 2013. Ecological and evolutionary misadventures of Spartina. Annu. Rev. Ecol. Evol. Syst. 44, 389–410.

Thampanya, U., Vermaat, J.E., Terrados, J., 2002. The effect of increasing sediment accretion on the seedlings of three common Thai mangrove species. Aquat. Bot. 74, 315–325.

Thiel, M., Gutow, L., 2005. The ecology of rafting in the marine environment. I. The floating substrata. Oceanogr. Mar. Biol. 42, 181–263.

Vilà, M., Weiner, J., 2004. Are invasive plant species better competitors than native plant species?- Evidence from pair-wise experiments. Oikos 105, 229–238.

Zedler, J.B., Kercher, S., 2010. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Crit. Rev. Plant Sci. 23, 431–452.