

Effects of Competition from the Invasive Cordgrass *Spartina densiflora* on Native *Atriplex portulacoides*

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Abstract— Invasion by the South American cordgrass *Spartina densiflora* Brongn. in European salt marshes is causing concern about potential impacts to native plant communities. *S. densiflora* colonization of mid-marsh habitats may be slowed by native *Atriplex portulacoides* L., but the mechanism behind this negative interaction is not known. The aim of this work was to study the establishment and growth response of *S. densiflora* seedlings growing in a competitive environment with mature *A. portulacoides* plants in controlled greenhouse conditions. With this aim we measured establishment, growth, foliar nutrients, and photosynthetic pigments of *S. densiflora* plants grown with and without *A. portulacoides*. Results showed that *S. densiflora* seedlings readily established in mature stands of *A. portulacoides*. Every *Spartina* clump growing with *Atriplex* survived, producing fewer tillers with similar heights than when growing without competition, which was reflected on lower above-ground biomass. These results indicated that *S. densiflora* was affected at the above-ground level by the interspecific competition with *Atriplex*, but the invasive cordgrass was able to keep similar below-ground biomass with and without competition, resulting in a decrease of below-ground biomass of *Atriplex* when competing with *Spartina*. Our results in greenhouse controlled conditions were in agreement with our field observations where *S. densiflora* plants have been observed growing within *A. portulacoides* monospecific communities.

Index Terms— Biomass accumulation, Brackish marshes, Competitive interactions, Greenhouse, Invasion, Salt marshes, Shoot production.

1 INTRODUCTION

Introduced invasive plants to natural areas sometimes threaten local communities and decrease native diversity [1], potentially through competitive mechanisms [2]. In this context, experimental studies to determine the outcome of interspecific competition between invasive and native species are necessary for conserving and restoring native communities in impacted habitats [3].

Plant distribution in salt marshes is determined by species tolerance to abiotic factors and by interspecific interactions such as predation, facilitation and competition [4]. Thus, interspecific competition is one of the most important processes determining plant distribution in salt marshes [5]. The introduction of alien halophytes may alter natural zonation patterns in salt marshes [6].

The South American cordgrass *Spartina densiflora* Brongn. (Poaceae) is invading estuaries in southwest Europe, northwest Africa and the West Coast of North America [7]. In The Gulf of Cádiz (southwest Iberian Peninsula), *S. densiflora* is colonising middle marsh communities dominated by *Atriplex portulacoides* L. *Atriplex portulacoides* L. is a halophyte that colonises low marshes, getting its maximum biomasses at middle marshes [8] and producing large quantities of seeds all around the coasts of Europe, North Africa and southwest Asia [9].

The aim of this work was to study the establishment of *S. densiflora* seedlings growing together with adult *A. portulacoides* plants in controlled greenhouse conditions. With this aim we recorded establishment, growth, foliar nutrients and photosynthetic pigments of *S. densiflora* plants coming from seeds in response to inter-specific competition with *A. portulacoides* and in the absence of competition. Experimental approaches working in controlled conditions have been used frequently to study competition between invasive and native species [10]. In view of our field observations, we hypothesized that *S. densiflora* would be able to establish and compete successfully with *A. portulacoides* adult plants.

2 MATERIALS AND METHODS

2.1 Plant Collection

Seeds of *S. densiflora* were collected in April 2008 from multiple mature individuals in a well-drained intertidal lagoon at the Odiel Marshes (southwest Iberian Peninsula; 37° 08' - 37° 20' N, 6° 45' - 7° 02' W) [11].

2.2 Experimental Design

The experiment was initiated in May 2008 and conducted over two years in the greenhouse facility of the University of Seville, Spain. *S. densiflora* seeds were planted one cm deep in peat soil in plastic pots (7.5 cm diameter and 12 cm height; volume of 1.85 l) and exposed to two competition treatments ($n = 6$ pots per treatment): (1) one seed of *Spartina* per pot (control treatment), and; (2) one seed of *S. densiflora* germinating in a pot colonised previously by one adult plant of *A. portulacoides* (1 year old), seeds planted in the middle of each pot.

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Six adult plants of *A. portulacoides* were also grown without competition. Plants were maintained at ambient light in the greenhouse and watered with salt water (20 mg l⁻¹), keeping the base of the pots permanently flooded to a height of 3 cm using pools. Mean monthly air temperature during the experiment in the greenhouse was 24 ± 0 °C, varying between 17 ± 0 °C and 33 ± 0 °C. Mean monthly air relative humidity was 60 ± 3%, varying between 45 ± 1% and 73 ± 0%.

2.3 Shoot Production, Height and Biomass

The number of *S. densiflora* live seedlings and their shoots were counted periodically from the beginning of the experiment for every clump in each pot (*n* = 6). *S. densiflora* shoot height was measured from the base of the shoot to the tip of the longest leaf (*n* = 6 shoots, one shoot per pot).

At the end of the experiment (June 2010), all plants were carefully excavated from the soil and roots were washed to remove soil particles. Roots and shoots were separated and above- and below-ground biomass (AGB and BGB, respectively) were recorded for all plants (*n* = 6 plants per treatment). Biomass was determined after drying plant material at 80 °C for 48 hours.

2.4 Leaf Nitrogen and Carbon Content

Total leaf carbon (C) and nitrogen (N) content were determined in May 2009 for the two plant species. Two leaves from each plant were chosen randomly and removed from stems by hand. The samples were dried to constant weight in an oven at 80 °C for 48 hours, pulverized using a grinder (Cyclotec, Foss Tecator AB, Höganäs, Sweden) and filtered using an 80-µm sieve. Total C and N content of filtered material was determined as percentage of total dry matter for undigested samples using an elemental analyzer (Leco CHNS-932, Spain). The value for each sample corresponded to the mean of three replicated measurements.

2.5 Photosynthetic Pigments

In October 2009, four leaves per treatment were chosen at random from different seedlings to determine leaf photosynthetic pigment content, chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*) and carotenoids (carotenes and xanthophylls, Cx + c). Pigments were using 0.1 g of fresh material in 5 ml of 80% aqueous acetone (*n* = 4). After filtering, 0.5 ml of the suspension was diluted with a further 2 ml of acetone and Chl *a*, Chl *b* and Cx + c concentrations were determined with a Hitachi U-2001 spectrophotometer (Hitachi Ltd., Tokyo, Japan) using three wavelengths (663.2, 646.8 and 470.0 nm). Concentrations of pigments (mg g⁻¹ DW) were obtained through calculation [12].

2.6 Statistical Analysis

Analyses were conducted using SPSS release 12.0 (SPSS Inc., Chicago, IL). Data were tested for normality with the Kolmogorov-Smirnov test and for homogeneity of variance with the Levene test (*P* > 0.05). A student's *t*-test for independent sam-

ples was applied to explore intraspecific differences in plant traits between the two competition treatments. Variances were calculated as the standard error of the mean. All tests were evaluated at a significance level of 0.05.

3 RESULTS

3.1 Seedling Survivorship, and Tiller Number and Height

Every *S. densiflora* clump survived with and without *A. portulacoides* competition. Competition with adult plants of *Atriplex* during 26 months decreased the number of live tillers of *S. densiflora* clumps. Thus, average tiller number for *S. densiflora* clumps growing alone was 33 ± 3 tillers clump⁻¹ at the end of the experiment and 23 ± 3 tillers clump⁻¹ for clumps growing with *A. portulacoides* (*t*-test, *t* = 2.37, *P* < 0.05) (Fig. 1a). *S. densiflora* tillers growing without interspecific competition were taller than those competing with *A. portulacoides* during the first year, but this difference disappeared since then showing similar maximum tiller height at the end of the experiment (110 ± 5 cm without competition and 98 ± 5 cm with competition; *t*-test, *t* = 1.80, *P* > 0.05) (Fig. 1b).

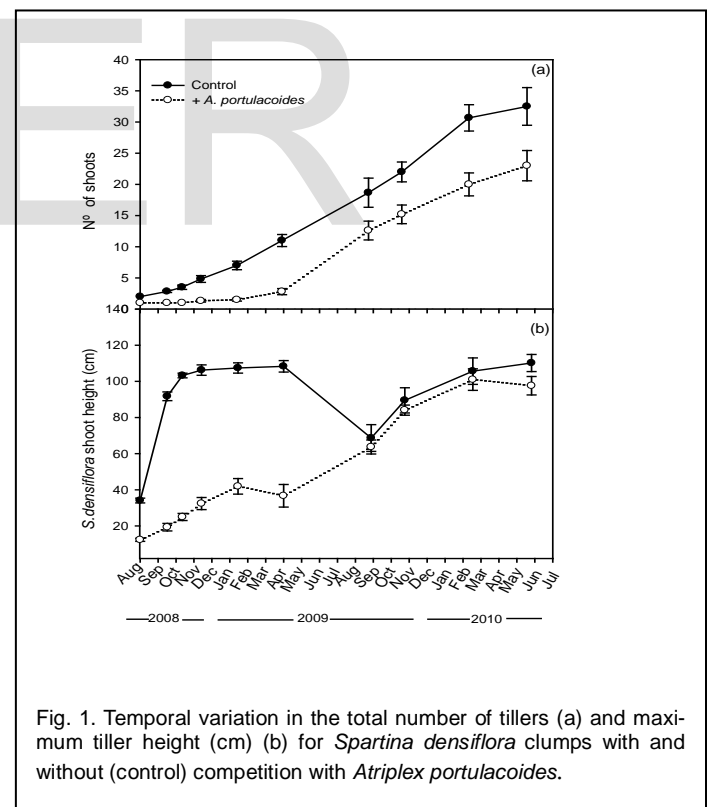


Fig. 1. Temporal variation in the total number of tillers (a) and maximum tiller height (cm) (b) for *Spartina densiflora* clumps with and without (control) competition with *Atriplex portulacoides*.

3.2 Leaf carbon and nitrogen and photosynthetic pigments content

Leaf C content was similar in both competition treatments for both species (*Spartina*: ~ 44 % C; *Atriplex*: ~ 38 % C; *t*-test, *P* >

TABLE 1

CARBON AND NITROGEN CONTENTS, C:N RATIO, LEAF PHOTOSYNTHETIC PIGMENTS CONCENTRATIONS (CHLOROPHYLL A, CHLOROPHYLL B, CAROTENOIDS (Cx+c) AND CHLOROPHYLLS : CAROTENOIDS RATIO), AND ABOVE- AND BELOW-GROUND BIOMASS (AGB AND BGB, RESPECTIVELY) FOR *SPARTINA DENSIFLORA* SEEDLINGS AND *ATRIPLEX PORTULACOIDES* ADULT PLANTS IN TWO DIFFERENT COMPETITION TREATMENTS (WITH AND WITHOUT INTERSPECIFIC COMPETITION). DIFFERENT LETTERS INDICATE SIGNIFICANT INTRASPECIFIC DIFFERENCE BETWEEN TREATMENTS FOR THE SAME SPECIES (T-TEST, P < 0.05).

	<i>Spartina densiflora</i>		<i>Atriplex portulacoides</i>	
	Without competition	Interspecific competition	Without competition	Interspecific competition
Nutrient content (%)				
% C	44.36 ± 0.18 ^a	44.71 ± 0.16 ^a	38.04 ± 0.25 ^a	38.00 ± 0.61 ^a
% N	0.75 ± 0.01 ^a	0.94 ± 0.03 ^a	1.38 ± 0.02 ^a	1.08 ± 0.08 ^a
C/N	59.03 ± 2.04 ^a	48.60 ± 2.80 ^b	27.18 ± 0.50 ^a	35.82 ± 2.57 ^b
Photosynthetic pigments (mg g⁻¹ DW)				
Chl a	6.2 ± 1.1 ^a	5.4 ± 0.3 ^a	3.0 ± 0.2 ^a	2.9 ± 0.4 ^a
Chl b	2.7 ± 0.4 ^a	2.2 ± 0.4 ^a	1.2 ± 0.1 ^a	1.1 ± 0.3 ^a
Cx+c	2.5 ± 0.2 ^a	2.6 ± 0.2 ^a	0.6 ± 0.0 ^a	0.5 ± 0.1 ^a
Chl a + b : Cx+c	3.4 ± 0.3 ^a	3.6 ± 0.3 ^a	7.4 ± 0.6 ^a	11.5 ± 3.3 ^a
Biomass (g m⁻²)				
AGB	1256 ± 97 ^a	987 ± 32 ^b	817 ± 62 ^a	758 ± 32 ^a
BGB	3085 ± 236 ^a	2867 ± 153 ^a	1869 ± 125 ^a	1522 ± 31 ^b

0.05). *Spartina* leaf N content was lower for clumps growing alone than for those growing together with *Atriplex* (*t*-test, *t* = 0.108, *P* > 0.05). *A. portulacoides* showed similar leaf N content with and without competition (*t*-test, *t* = 0.295, *P* > 0.05)

(Table 1). The highest C : N ratio was recorded for *S. densiflora* growing alone, which was higher than for the clumps growing with corresponded to *A. portulacoides* adult plants growing alone that was lower than with when exposed to competition (*t*-test, *t* = -3.222, *P* < 0.05) (Table 1).

S. densiflora and *A. portulacoides* showed similar Chl *a*, Chl *b* and Cx+c contents and similar Chl *a* + *b* : Cx+c ratio for both treatments (*t*-test, *P* > 0.05) (Table 1). *Atriplex* (*t*-test, *t* = 3.00, *P* < 0.05). The lowest C: N ratio ratio for both treatments (*t*-test, *P* > 0.05) (Table 1).

3.3 Biomass

At the end of the experiment, *Spartina* seedlings growing alone developed higher AGB than when competing with *Atriplex* (*t*-test, *t* = 2.64, *P* < 0.05), with similar BGB (*t*-test, *t* = 0.778, *P* > 0.05). AGB of *Atriplex* was not affected by interspecific competition (*t*-test, *t* = 0.841, *P* > 0.05), while its BGB was lower when growing together with *Spartina* (*t*-test, *t* = 2.67, *P* < 0.05). *Spartina* clumps accumulated more AGB and BGB than *Atriplex* in both treatments (*t*-test, *P* < 0.05) (Table 1).

4 DISCUSSION

Every *Spartina* clump growing with *Atriplex* survived, producing fewer tillers with similar heights than when growing without competition, which was reflected on lower AGB accumulation. The higher growth of *Spartina* without competition coincided with a lower leaf N content than when competing with *Atriplex* (without affecting photosynthetic pigments concentrations), which was probably related with the dilution effect related with faster growth rates [13]. These results indicated that *S. densiflora* was affected at the above-ground level by the interspecific competition with *Atriplex*, but the invasive cordgrass was able to keep similar BGB with and without competition, resulting in a decrease of BGB of *Atriplex* when competing with *Spartina*. Thus, the roots and rhizomes of *A. portulacoides* were not able to prevent the development of rhizomes and roots of *Spartina* seedlings. In contrast with our results, previous studies have recorded a limitation in *Spartina* development in the underground level when competing with other halophytes. [6] pointed out that the invasion of *S. densiflora* from seeds seemed to be limited by inter-specific subterranean competition with the native *Spartina maritima* (Curtis) Fernald. In this sense, it has been described that the invasion of *S. densiflora* at North American marshes is limited by competition with native species [14] and that *Typha domingensis*

Pers. and *Phragmites australis* (Cav.) Trin. ex Steud., limited the subterranean development of *S. densiflora*. However *A. portulacoides* has been described as well-adapted to competitive environments, being the distribution and frequency of species of its communities mainly conditioned by interspecific competition, [15]. [16], recorded that it was being displaced from some European marshes by the invasive grass *Elymus athericus*. Our results in greenhouse controlled conditions corroborated our hypothesis based on field observations since the presence of adult plants of *Atriplex* did not prevented the establishment and growth of *S. densiflora* that competed successfully with the native halophyte as observed in the field.

5 CONCLUSION

In this report, the invasive cordgrass *S. densiflora* is colonizing middle salt marshes in the southwest Iberian Peninsula where it gets into contact with plant communities dominated by the native halophyte *A. portulacoides*. Our experiment shows that *A. portulacoides* adult plants are not able to outcompete *S. densiflora* clumps coming from seeds in controlled greenhouse conditions. Our results in greenhouse controlled conditions corroborated our hypothesis based on field observations since the presence of adult plants of *Atriplex* did not prevented the establishment and growth of *S. densiflora* that competed successfully with the native halophyte as observed in the field.

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