

Response of the invader *Cortaderia selloana* and two coexisting natives to competition and water stress

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Abstract Alien species' resistance and adjustment to water stress and plant competition might largely determine the success of invasions in Mediterranean ecosystems because water availability is often limiting biomass production. Two outdoor pot experiments were conducted to test the hypotheses that at the recruitment stage the invader perennial tussock grass *Cortaderia selloana* is a superior competitor, and that it is more resistant to water stress than the two coexisting native species of the same functional group, *Festuca arundinacea* and *Brachypodium phoenicoides*. *C. selloana* reduced aboveground biomass of target native species, but not more than target native species on each other. Moreover, *C. selloana* did not resist interspecific competition more than target native species. Under control conditions, *C. selloana* did not have larger specific leaf area (SLA) and root–shoot ratio (R/S) ratio than target native species, contradicting the general statement that these traits are associated to invasiveness.

F. arundinacea was the species which performed best but also the one most affected by water stress. Both *C. selloana* and *B. phoenicoides* performed in a similar way under water stress conditions. However, the alien species' capacity to adjust to water stress, indicated by the increase in the root–shoot ratio under moderate and severe water stress, was slightly better than that of *B. phoenicoides*. Overall, at early recruitment stages, *C. selloana* is not a better competitor than the coexisting native species. However, it seems to be more resistant to water stress because as water becomes scarce *C. selloana* maximizes water uptake and minimizes water losses more than the native species.

Keywords Alien plant · *Brachypodium phoenicoides* · *Festuca arundinacea* · Intra- and interspecific competition · Perennial grasses · Relative interaction index · SLA · Root–shoot ratio

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Introduction

The intentional or accidental introductions of alien species are the causes of biological invasions that pose a major threat to biodiversity worldwide (Vitousek 1994; Keane and Crawley 2002; Davis 2003), yet only a few introduced species succeed in establishing in the recipient community (Holdgate 1986;

Parker and Reichard 1998). Thus, invasive success of alien species depends on the biotic and environmental characteristics of the recipient community as well as on biological attributes related to its potential to colonize and expand (i.e., invasiveness) (Lonsdale 1999).

Some alien plant species have characteristics that seem to make them successful invaders such as a large production of viable seeds which disperse widely, the ability to germinate and grow in a broad range of environmental conditions, and being a good competitor (Baker 1965; Noble 1989; Roy 1990; Gordon 1998). When an alien plant is introduced, competition for limited resources is one of the first interactions the species has with the recipient community (Vilà and Weiner 2004). Field observations and experiments have proved that the threat alien species pose to the persistence of native species is usually driven by the competition effect of the alien species on natives (Parker and Reichard 1998; Levine et al. 2003). However, most studies are biased because they have focused on highly aggressive invaders competing with less vigorous species of dissimilar lifeform or life-history stage (Vilà et al. 2004). Furthermore, when analyzing competitive abilities of alien species, the competitive effect that the native species has on the alien should be simultaneously compared (Vilà and Weiner 2004).

It has also been argued that resource pulses (e.g., soil nutrients and water) provide the triggering conditions for invasions (Davis et al. 2000). In the case of both invaders and native species being limited by the same resources, invasion would take place if the invader has a higher resource acquisition rate or a lower maintenance requirement than that of the native species (Shea and Chesson 2002). It has been postulated that alien species might have a superior response to particular resources, to resources found in certain places or times, or to certain abundances of resources compared to native plants (Shea and Chesson 2002). Superior responses to resource acquisition require plant traits related to physiological processes. In particular specific leaf area (SLA) has been shown to be related to invasiveness (Grotkopp et al. 2002; Grotkopp and Rejmánek 2007) in phylogenetically related species. Plants with large SLA have thinner or lighter leaves that can intercept more light and contribute to plant fast growth especially in shaded environments.

In Mediterranean ecosystems where the climate is characterized by hot, dry summers, water availability is often limiting biomass production. Competition for water is very common in Mediterranean ecosystems (Vilà and Sardans 1999). Moreover, Mediterranean ecosystems are predicted to be very susceptible to water availability fluctuations caused by climate change (Lavorel et al. 1998), which will possibly modify species distribution and plant–plant interactions. In this scenario, alien species' resistance to plant competition and adjustment to water stress are important for invasion. In order to determine the importance of competition on plant invasions in Mediterranean ecosystems it is necessary to quantify the importance of the competitive abilities of alien species simultaneously with that of native species; in addition, knowledge of the resistance and adjustment to water stress of both alien and native is required.

Cortaderia selloana (Schultes et Schultes fil.) Asch. et Graebner is a perennial tussock grass native to South America now invading Mediterranean old fields and grasslands of Catalonia (NE Spain) dominated by perennial native grasses such as *Festuca arundinacea* (Schreber, *F. elatior* L.) and *Brachipodium phoenicoides* (Roem. et Schultes) (Masalles et al. 1982). We suspect that *C. selloana* is a better competitor than coexisting native species of the same functional group and that it possesses traits that allow it to take advantage of low water resources. We conducted two outdoor pot experiments to test the following hypotheses related to plant recruitment stage: (1) *C. selloana* is a superior competitor than *F. arundinacea* and *B. phoenicoides*; consequently, we expect *C. selloana*'s effect on native species to be stronger than vice versa, and (2) *C. selloana* seedling traits related to resource acquisition (e.g., SLA and R/S ratio) are larger than in *F. arundinacea* and *B. phoenicoides*.

Material and methods

Study species

C. selloana (Pampas grass) is a South American long-living perennial grass which is considered invasive worldwide. It was first introduced to Europe between 1775 and 1862 (Bossard et al. 2000). This species is planted for many purposes such as a windbreak or to prevent erosion but due to the

attractiveness of its plumes it has mainly been used as an ornamental. It has escaped from cultivation and is invading abandoned agricultural lands, ruderal areas, shrublands, grasslands, and wetland communities. *C. selloana* threatens native vegetation and poses a fire hazard due to the accumulation of dry leaves and flowering stalks on the plant (Bossard et al. 2000). It flowers from mid to late summer; the inflorescences consist of showy plume-like heads at the end of a stiff stem. Plumes produce copious amounts of small, wind-dispersed seeds (as many as 10^6 seeds per mature plant for females and 10^5 for hermaphrodites) (Connor and Edgar 1974; Lambrinos 2002).

F. arundinacea is a perennial grass native to Europe frequently found in humid grasslands. Its maximum growth takes place during spring and autumn. Its deep and extensive root system helps it to withstand drought conditions. *F. arundinacea* flowers in spring and seeds mature in early summer. It is adapted to a wide range of soil and climatic conditions (Tutin et al. 1980; Bolòs and Vigo 2001).

Brachipodium phoenicoides is a perennial grass native to the Mediterranean Basin. It forms dense communities in open habitats such as field margins, pastures, grasslands, and abandoned agricultural fields. *Brachipodium phoenicoides* is considered an essential species for ecological succession in pastures since it establishes during the initial stages and allows establishment of other species (Tutin et al. 1980; Bolòs and Vigo 2001).

The three species coexist in many habitats and can be considered as belonging to the same functional group (i.e., tussock perennial grass) but they differ in size and biomass when mature. *C. selloana* is considerably larger than the other species. It can reach from 2 to 4 m in height including inflorescences (Bossard et al. 2000) and its maximum diameter can reach 3.5 m whereas *F. arundinacea* and *B. phoenicoides* can reach only from 40 to 60 cm in height and the diameter of the tussock is five to ten times smaller than that of *C. selloana* (Domènech 2005).

Plant material

In summer 2003, fresh plumes of *C. selloana* were collected from old fields in Aiguamolls de l'Empordà (NE Spain). Seeds were removed from inflorescences and mixed. Seeds of *F. arundinacea* and *B. phoenicoides* were bought from Semillas Silvestres S.L.

(<http://www.semillasilvestres.com>). In January 2004 seeds of the alien and the two native grasses were sown in flat trays and left outdoors at the Universitat Autònoma de Barcelona (UAB) campus to germinate before transplanting.

Competition experiment

In April 2004, 3 months after sowing, seedlings of *C. selloana*, *B. phoenicoides* and *F. arundinacea* were transplanted outdoors at the UAB campus into 2–l pots filled with Plantaflor gardening soil which contained 200 mg/l of N, 180 mg/l of P_2O_5 , and 230 mg/l of K_2O . The climate in Barcelona is Mediterranean with mild wet winters and hot dry summers. Mean annual temperature and annual precipitation are 15.0°C and 673.1 mm, respectively (<http://www.meteocat.com>).

In order to determine the mean initial aboveground biomass of the three target species we weighed the leaves from 20 seedlings of each species after air-drying at 70°C to constant weight. Mean aboveground biomass was 0.0014 ± 0.0001 g for *B. phoenicoides*, 0.0016 ± 0.0001 g for *C. selloana*, and 0.0039 ± 0.0003 g for *F. arundinacea*. Aboveground biomass was significantly different (ANOVA, $F_{2,55} = 38.00$, $P < 0.0001$), being the largest in *F. arundinacea* (Fisher's least significant test (LSD) $P < 0.0001$).

Nine competition treatments which included all possible pair-wise combinations of intraspecific and interspecific competition and no competition were replicated 12 times, as follows: (1) two seedlings of *C. selloana* per pot (C:C), (2) one seedling of *C. selloana* and one of *B. phoenicoides* per pot (C:B), (3) one seedling of *C. selloana* and one of *F. arundinacea* per pot (C:F), (4) one seedling of *C. selloana* per pot (C), (5) two seedlings of *F. arundinacea* per pot (F:F), (6) one seedling of *F. arundinacea* and one of *B. phoenicoides* per pot (F:B), (7) one seedling of *F. arundinacea* per pot (F), (8) two seedlings of *B. phoenicoides* per pot (B:B), and (9) one seedling of *B. phoenicoides* per pot (B).

Pots were watered every 2 days to avoid water stress and were randomly moved every 15 days to ensure that all the plants were growing under the same environmental conditions. In July 2004, when plants started to produce panicles, plants were collected and weighed after air-drying at 70°C to

constant weight. At this stage, plants had overtopped the pots and roots were filling all pot soil volume. Some of the plants had totally or partially been eaten by snails, and were excluded from analysis. In order to correct for the initial differences in the seedling's aboveground biomass we calculated the relative increase in aboveground biomass for the experimental period (AB) of each species as: $(B_{t1} - B_{t0})/B_{t0}$, where B_{t1} is the biomass at harvesting time and B_{t0} is the estimated biomass before treatment.

Differences in the AB of each species growing alone, under intraspecific competition, and under interspecific competition were compared with a four-level one-factor analysis of variance (ANOVA). Data was log transformed to meet the assumptions of parametric analysis. Only one plant per pot was randomly selected to evaluate the effect of intraspecific competition. Fisher's LSD test was used to establish pairwise comparisons. According to our hypothesis of *C. selloana* being a superior competitor than the native species, we expected *C. selloana* to be less affected by interspecific or intraspecific competition than the other native species.

Furthermore, a second data analysis was conducted to test if *C. selloana* had a superior competitive ability than the two native species. We considered both the impact and the resistance components of invasion by using two different approaches proposed by Vilà and Weiner (2004). First, with regard to the alien species impact we tested whether the effect of *C. selloana* on each of the two target native species was larger than the effect of one native species on the other native species. Secondly, focusing on the native species' resistance presented to the alien we tested if the effect of a native species on *C. selloana* was lower than its effects on the other native species. The relative interaction index (RII) proposed by Armas et al. (2004) was used to estimate the intensity of the size effect of competition in each pot. This index has revealed several advantages compared to other competition intensity indices such as the relative competition intensity or the log response ratio (Grace 1995; Goldberg et al. 1999). RII has values ranging from -1 to +1 and it is symmetrical around zero. A negative value indicates competition (i.e., growth of the target species is reduced) and a positive value indicates facilitation (i.e., growth of the target species is promoted). RII is expressed as:

$$\text{RII} = \frac{B_w - B_o}{B_w + B_o}$$

where B_w is the observed mass of the target plant when growing with another plant and B_o is the mean mass achieved by the target plant growing in the absence of inter- or intraspecific interactions.

If *C. selloana* has a higher competitive ability than the two native species we would expect the following results. First, with regard to the alien's impact, RII F:C and RII B:C would be more negative than RII B:F and RII F:B, indicating that the negative effect of *C. selloana* on the growth of native species is larger than the effect of a native on the other native. Second, with regard to the native's resistance, RII C:F and RII C:B would be less negative than RII B:F and RII F:B, indicating that the negative effect of a native species on the other native is larger than the effect on the alien. These contrasts were tested by unpaired *t*-tests.

Water stress experiment

In April 2004, 3 months after sowing, seedlings of *C. selloana*, *B. phoenicoides* and *F. arundinacea* were transplanted outdoors at the UAB campus into 2–l pots with gardening soil placed on benches under a shelter which consisted of a 6-m-tall plastic cover sustained by a metallic structure. Therefore the shelter excluded rainfall, allowing for the control of watering during the experiment. This shelter reduced incident light by 20%.

Before starting the experiment, all pots were watered to excess and allowed to drain during one night. Species were randomly assigned to one of the following watering treatments following the same protocol as in a previous study conducted with *C. selloana* and *C. jubata* seedlings (Stanton and DiTomaso 2004): (1) a fully watered treatment (hereafter called control) which was used as an indicator of unstressed growth; (2) an intermediate drought stress treatment (hereafter called moderately stressed), in which at the beginning of the experiment water was withheld from the plants for 6 days, which were then watered every day for the following 8 days, and not watered during for the successive 31 days; (3) a sustained drought treatment (hereafter called severely stressed), in which plants did not receive water during the course of the experiment.

Each treatment was replicated 12 times. The final number of pots was 108 (3 water stress treatments \times 3 species \times 12 replicates). Pots were randomly moved once a week in order to guarantee that all the plants were growing under the same conditions.

At the end of the experiment, 45 days after planting, in order to detect if the watering treatments had been homogeneous among species, we measured soil moisture with a time-domain reflectometer (TDR) in a subsample of seven pots per treatment and per species. At the end of the experiment three leaves of three plants of each species per treatment were randomly chosen to determine mean leaf area (LA). Leaves were immediately taken to the laboratory and their area was measured with a desk area meter (Li-COR, Lincoln, NE, USA). Leaves were weighed after air-drying at 70°C to constant weight, and the mean SLA was calculated for each plant as the ratio between mean leaf area and mean foliar weight.

All the plants were cut, air-dried at 70°C to constant weight, and weighed to measure final above- and below-ground biomass. Roots were washed very carefully in order to separate them from the soil without losing material. As for the competition experiment, in order to correct for the initial differences in above- and below-ground biomass we calculated the relative increase in aboveground biomass (AB) and below-ground biomass (BB) of each species as: $(B_{t1} - B_{t0})/B_{t0}$, where B_{t1} is the biomass at harvesting time and B_{t0} is the estimated biomass before treatment. We also calculated the root–shoot ratio (R/S ratio) for each plant as the ratio between below- and aboveground biomass.

Differences between water stress treatments and species on SLA, AB, BB, and R/S ratio were analyzed with a two-way ANOVA with species and water stress treatment as fixed factors. If *C. selloana* is less affected by water stress than the native species as predicted, we would expect *B. phoenicoides* and *F. arundinacia* to respond more drastically to moderate and severe water stress in all the measured plant parameters than *C. selloana*. Pairwise differences between stress treatments and between species were analyzed with a Fisher's LSD test. AB, BB, and R/S ratio was log transformed and SLA 1/log transformed to meet the assumptions of homogeneity of variances and to fit a normal distribution of data.

Results

Competition experiment

The relative increase in aboveground biomass (AB) of *C. selloana* and *F. arundinacea* seedlings was not significantly affected by any of the four competition treatments: ($F_{3,40} = 1.81$, $P = 0.16$, $\beta = 0.43$ and $F_{3,31} = 0.41$, $P = 0.75$, $\beta = 0.75$; respectively) (Fig. 1). However, significant differences were found for *B. phoenicoides* ($F_{3,42} = 5.04$, $P = 0.005$, $\beta = 0.9$). AB of *B. phoenicoides* seedlings in competition with *C. selloana* (Fisher's LSD test, $P = 0.006$) and with *F. arundinacea* (Fisher's LSD test, $P = 0.01$) was significantly lower than under intraspecific competition (Fig. 1).

Because our sample size was small, to reduce type II error we also analyzed data for each species by pooling the two interspecific competition treatments. We found interspecific competition not to reduce AB in *C. selloana* (Fisher's LSD test, $P = 0.20$) and *F. arundinacea* (Fisher's LSD test, $P = 0.105$) but only in *B. phoenicoides* (Fisher's LSD test, $P = 0.005$).

Regarding the alien species impact, on average we found negative values of RII either when *C. selloana* was growing with *B. phoenicoides* or with *F. arundinacea*, indicating that the alien species competed with the two native species (Fig. 2). However, the effect of *C. selloana* on *B. phoenicoides* was not significantly larger than the effect of *F. arundinacia* on *B. phoenicoides* ($t_{20} = 1.07$, $P = 0.30$). Similarly, the effect of the alien species on *F. arundinacia* was not significantly larger than the effect of *B. phoenicoides* on *F. arundinacea* ($t_{16} = 0.81$, $P = 0.43$). When focusing on the alien species resistance to the natives, a significant difference appeared: the effect of *B. phoenicoides* on *C. selloana* was negative while the effect of *B. phoenicoides* on *F. arundinacia* was positive ($t_{20} = -5.06$, $P = 0.001$). However, no significant differences were found between the effect of *F. arundinacea* on *C. selloana* and the effect of *F. arundinacea* on *B. phoenicoides* ($t_{16} = 0.86$, $P = 0.40$).

Water stress experiment

Drought treatments significantly reduced soil moisture with respect to the fully watered control treatment ($F_{2,54} = 321.12$, $P < 0.0001$). However,

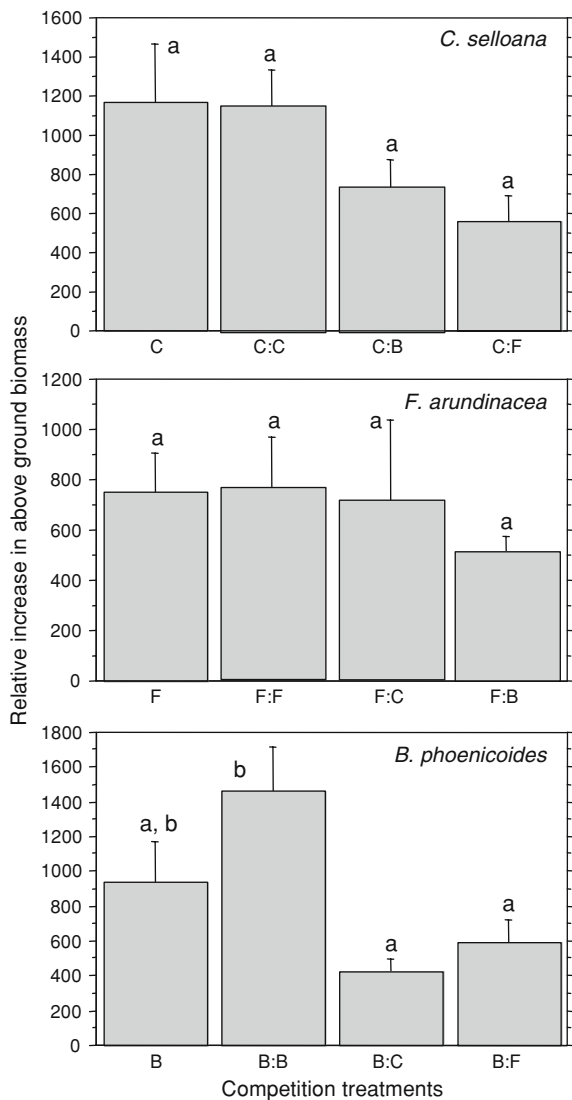


Fig. 1 Relative increase in aboveground biomass (mean + SE) of *C. selloana* (C), *F. arundinacea* (F), and *B. phoenicoides* (B) in four treatments: growing alone, under intraspecific competition, and under interspecific competition. Different letters above columns indicate significant differences between competition treatments according to Fisher's test

there were no significant differences in soil moisture between the three target species ($F_{2,54} = 2.75$, $P = 0.07$). As expected, the highest soil moisture was measured in control/nonstressed pots ($36.30 \pm 1.43\%$), followed by moderately stressed pots ($9.72 \pm 0.81\%$), and severely stressed pots ($5.98 \pm 0.51\%$). Consequently, moderate and severe water stress caused 73.22% and 83.5% reduction in soil moisture with respect to the control treatment.

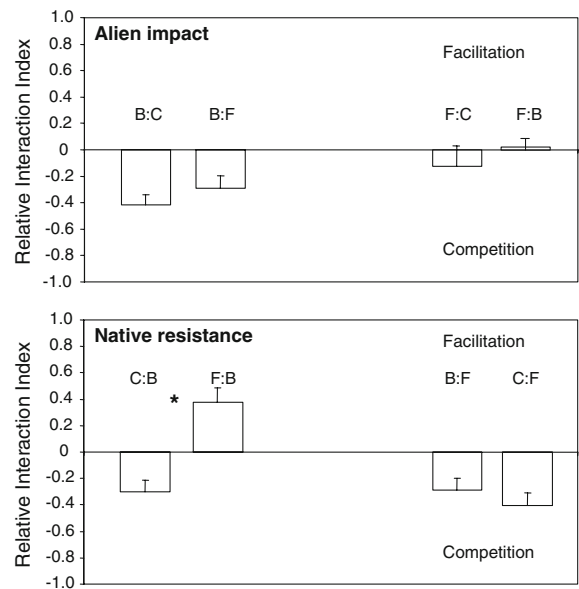


Fig. 2 Relative interaction indices (RII) (mean + SE) comparison using the alien's species impact and native's species resistance approaches. Positive RII indicate a facilitative effect between species and negative RII indicate competition between species. The asterisk indicate significant differences ($P < 0.05$). C: *C. selloana*, B: *B. phoenicoides*, F: *F. arundinacea*

The interaction between the soil moisture stress treatment and species was not significant ($F_{4,54} = 2.54$, $P = 0.05$), indicating that the water stress treatment was homogeneous across species.

The SLA was significantly different between the three target species ($F_{2,18} = 25.31$, $P < 0.0001$) and between water stress treatments ($F_{2,18} = 20.44$, $P < 0.0001$) (Fig. 3a). The SLA for *F. arundinacea* was significantly higher than in the other two species (Fisher's LSD test, $P < 0.0001$) and there were no significant differences between *B. phoenicoides* and *C. selloana* (Fisher's LSD test, $P = 0.15$). The highest SLA was measured in control plants (Fisher's LSD test, $P \leq 0.0001$). There was a significant interaction between species and water stress treatments ($F_{4,18} = 6.94$, $P = 0.001$), indicating that water stress affected in a different way the target species: the SLA of *F. arundinacea* was only reduced by severe water stress. In contrast, the SLA of *C. selloana* and *B. phoenicoides* started to be reduced under moderate water stress. Under severe water stress there were no significant differences in the SLA between the three species.

The AB was also significantly different between species ($F_{2,98} = 17.57$, $P < 0.0001$) and treatments

($F_{2,98} = 427.87$, $P < 0.0001$) (Fig. 3b). *F. arundinacea* produced significantly more AB than *B. phoenicoides* (Fisher's LSD test, $P = 0.02$) and *C. selloana* (Fisher's LSD test, $P = 0.0006$). AB of *C. selloana* was significantly lower than that of *B. phoenicoides* (Fisher's LSD test, $P < 0.0001$). AB was the highest in the control water stress treatments and the lowest in the severe water stress treatments (Fisher's LSD test, $P < 0.0001$). The interaction between species and water stress treatments was also significant ($F_{4,98} = 8.90$, $P < 0.0001$): AB of all species was reduced by moderate and severe water stress, yet *F. arundinacea* plants were the most negatively affected because the reduction caused by moderate and severe stress on AB was considerably larger than that experienced by *C. selloana* and *B. phoenicoides*.

The same pattern was observed for BB: there were significant differences between species

($F_{2,98} = 122.75$, $P < 0.0001$) and treatments ($F_{2,98} = 277.35$, $P < 0.0001$) and the interaction was also significant ($F_{4,98} = 17.19$, $P < 0.0001$). Severe water stress significantly reduced more the BB with respect to the control treatment than the moderate treatment (Fisher's LSD test, $P < 0.0001$). *F. arundinacea* produced the highest BB, especially in the control water stress treatment, but this species was again the most affected by moderate and severe water stress treatments (Fig. 3c).

Finally, the R/S ratio was significantly different between species ($F_{2,98} = 256.29$, $P < 0.0001$). *F. arundinacea* had the highest R/S ratio (Fisher's LSD test, $P < 0.0001$) and it was significantly lower in *B. phoenicoides* than in *C. selloana* (Fisher's LSD test, $P < 0.0001$). Water stress treatments also had a significant effect ($F_{2,98} = 5.22$, $P = 0.0007$). Furthermore, there was a significant interaction between species and water stress treatments ($F_{4,98} = 10.47$,

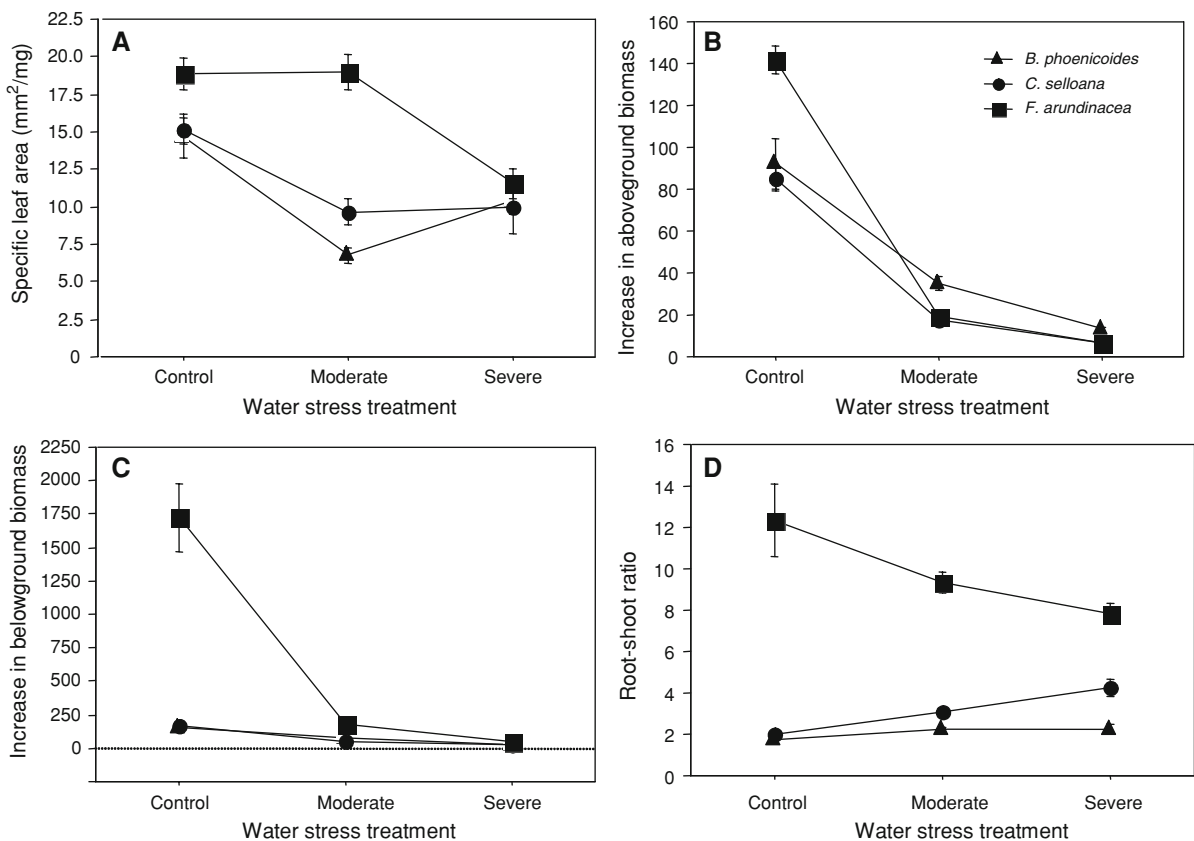


Fig. 3 Effect of water stress on (A) specific leaf area, (B) relative increase in aboveground biomass, (C) relative increase in below-ground biomass, and (D) root–shoot ratio

(mean + SE) in the alien *C. selloana* and in the natives *B. phoenicoides* and *F. arundinacea*

$P < 0.0001$). Both *C. selloana* and *B. phoenicoides* increased their R/S ratio under moderate or severe drought conditions, and the increase experienced by *C. selloana* was higher than that of *B. phoenicoides*. However, *F. arundinacea* behaved in an opposite manner (Fig. 3d).

Discussion

Our competition experiment between seedlings of the alien *C. selloana* and the two native grasses *F. arundinacea* and *B. phoenicoides* rejected the hypothesis that at early recruitment stages *C. selloana* is a superior competitor than the two coexisting native species. Interspecific competition has been reported to play an important role in determining the likelihood of plant invasions (Crawley 1990). In particular, alien species are hypothesized to be superior competitors than native species as a result of different evolutionary histories (Baker 1965; Holdgate 1986; Roy 1990; Keane and Crawley 2002). However, this statement should be carefully considered since the native species chosen to perform competitive experiments with alien species usually tend to belong to different functional groups (Huenneke and Thompson 1994). For instance, alien annual grasses in California grasslands have been reported to negatively affect the perennial bunchgrass *Nassella pulchra*, especially when competing for water (Hamilton et al. 1999). Similarly, a strong suppressive effect of the alien *Lythrum salicaria* has been found on the rare native congener, *L. alatum* (Hager 2004).

Furthermore, when testing the hypothesis that an alien species is a better competitor than a native species, simultaneous consideration of both the invader's relative impact and the native species' relative resistance to the invader has rarely been attempted (Vilà and Weiner 2004). Considering the invader's relative impact, we expected *C. selloana* to reduce the growth of the target natives *F. arundinacea* and *B. phoenicoides* more than it could be reduced by growing with the coexisting native. Conversely, we found that the effect of *C. selloana* on both native species was not significantly different than the effect that *F. arundinacea* and *B. phoenicoides* had on *B. phoenicoides* and *F. arundinacea*, respectively.

With regard to native species' resistance, we expected that the negative effect of a native species

on the other would be greater than the effect on the alien *C. selloana*. However, our results confirmed the opposite outcome: *B. phoenicoides* reduced the growth of *C. selloana* whereas it facilitated *F. arundinacea* growth. Therefore, at the individual level and at an early stage of recruitment, *C. selloana* seems not to have the potential to displace any of the two native species and at the same time to resist competition posed by the native species.

With regards to response to water availability, our results do not suggest a better performance of *C. selloana* under water stress than the two coexisting native grasses. *C. selloana*'s invasive potential in Mediterranean ecosystems has been related to high water-use efficiency and to a high water capture when water is not limiting. Moreover, a broad tolerance to water stress has been reported (Lambrinos 2002). Another study which compared the growth response of *C. selloana* and *C. jubata* seedlings to different water availabilities in greenhouse experiments found that *C. selloana* tolerated water stress better than its congener (Stanton and DiTomaso 2004). Our water stress experiment only partially supports these results. *C. selloana* was not as affected by moderate and severe water stress treatments as *F. arundinacea*. However, the reduction in above- and below-ground biomass experienced by *C. selloana* due to moderate and severe water stress was similar to that of *B. phoenicoides*.

Invasiveness has often been related to traits associated with the ability to opportunistically capture available resources. SLA and root–shoot ratio are two parameters indicating plant ability to intercept solar energy and soil resources, respectively. The capacity to achieve a large R/S ratio as water becomes a limiting factor can determine plant survival especially in Mediterranean climates with a long summer drought (Specht et al. 1983; Broncano et al. 1998; Sardans et al. 2004). We found that under stress conditions the R/S ratio of *C. selloana* increased more than that of *B. phoenicoides*, indicating that *C. selloana* seems to maximize water uptake by increasing below-ground biomass and to minimize water losses by decreasing aboveground biomass (Matsuda et al. 1989; Poorter and Remkes 1990). In contrast, the opposite response was found for *F. arundinacea*, indicating that it is more affected by water stress than the other two species.

Similarly, we expected that if an invasive species has a better resistance to water stress than a native

species it should have high SLA and experience a lower reduction in its SLA when water is limiting as found in other studies comparing pairs of invasive and noninvasive species (Baruch and Goldstein 1999; Grottkopp et al. 2002; Lake and Leishman 2004; Grottkopp and Rejmánek 2007). However, our results proved that *C. selloana* was not the species with the highest SLA and in fact SLA was reduced at moderate water reduction. Garcia-Serrano et al. (2005) also found SLA not to be a good predictor of invasiveness for invasive and noninvasive *Senecio* species growing in Mediterranean conditions.

Most invaders do not always perform better than co-occurring native species (Daehler 2003). We found the invader *C. selloana* to display little competitive advantage or resistance to competition when growing with the two native grasses *B. phoenicoides* and *F. arundinacea*. In addition, *C. selloana* does not always perform better under moderate or severe water stress; yet, the greatest capacity to increase the R/S ratio when water is scarce can be an advantage during the driest Mediterranean season and seems to offer plasticity in the ability to capture soil resources. Although our study was conducted at a very early *C. selloana* growth stage, the results are in accordance with field observations, seedling transplant experiments in the field, and modeling simulations, which have found that *C. selloana* populations perform best in ruderal habitats and benefit from disturbances (Domènech and Vilà 2006; Domènech and Vilà 2008; Pausas et al. 2006).

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