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Original article

Cortaderia selloana seed germination under different ecological conditions

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ABSTRACT

Biological invasions are causing the extinction of native species and modifying ecosystem functions. Invasion success depends, among other factors, on the biological attributes of the invaders and the abiotic characteristics of the recipient community. *Cortaderia selloana* is a gynodioecious perennial grass native to South America which is considered invasive worldwide. It is known that seedlings of this species tolerate a wide range of environmental conditions. However, the abiotic factors that may favour its seed germination have not been studied in much detail. For this reason, we conducted an array of germination tests with different degrees of shading, soil textures and water availability. Although *C. selloana* usually grows in disturbed sites where light is highly available, we found that seed germination was higher under shaded conditions than under 100% light. Seed germination was higher in sandy soil textures and decreased in soils which contained increased levels of clay. Mature *C. selloana* plants have been reported to tolerate water stress, yet we found that the shortage of water availability constrained seed germination to approximately 60%. Overall, *C. selloana* seeds seem to germinate under a wide range of environmental conditions, yet germination rate can be improved under shading, high levels of sand and with high water availability.

1. Introduction

The success of introduced plant species depends largely on the biological attributes of the species (i.e. invasiveness), and on appropriate environment conditions (Lonsdale, 1999). Large seed production is a trait of many successful invaders (Baker, 1965). However, even for species that produce a great amount of viable seeds, the response of early life-history stages to the new ecological factors are crucial for the invader to succeed (Holdgate, 1986; Parker and Reichard, 1998; Shea and Chesson, 2002). Alien species are supposed to perform best in disturbed areas, right from the germination stage (Hobbs and Huenneke, 1992). Moreover, for an alien species to invade it is essential to tolerate a wide range of environmental conditions such as different degrees of shading and different soil conditions. In addition, it has been reported that invader species might have a superior response to resource pulses compared to native plants (Shea and Chesson,

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2002). For example, a short period of high water availability may increase the invasibility of ecosystems through an increase of seed germination and seedling establishment (Milchunas and Laurenroth, 1995).

Cortaderia selloana (Shultes et Shultes fil.) Asch. et Graebner, is a gynodioecious perennial grass native to South America and introduced to Europe as an ornamental that is invading a wide variety of environments (e.g. roadsides, grasslands, wetlands, old fields and ruderal habitats) in Catalonia (NE Spain). This species has been reported to tolerate a wide range of environmental conditions once seedlings are established such as different soil textures, moderate drought and shading (Bossard et al., 2000; Lambrinos, 2002) but it performs best in sandy, open, disturbed soils (Domènech, 2005; Domènech and Vilà, 2006). However, little is known about the specific ecological factors that favour seed germination, a stage in plant reproduction essential for invasion to succeed, and very important to set up the attributes necessary to predict its response to disturbance regimes (Pausas et al., 2006).

As part of the explanation for the ecological factors influencing *C. selloana* establishment ability we conducted an array of germination tests to determine the environmental conditions under which *C. selloana* seeds germinate. We tested different degrees of shading, different soil textures and whether germination continues for extended periods of water availability. Based on field distribution patterns (Domènech, 2005), we expected that seed germination would be higher under full light than under shade, in sandy soils, and would not be very dependent on water availability.

2. Material and methods

2.1. *Seed collection*

By the end of September 2003, seeds were collected from a large population on *Parc Natural dels Aiguamolls de l'Empordà* (NE Spain). Ten panicles were collected from each of 25 female plants for a total of 250 panicles. We used seed from female plants for this experiment because of their high rates of germination (Domènech, 2005). All seeds were removed from panicles, mixed and stored at room temperature in paper bags. As in other experiments with the genus *Cortaderia*, seeds were not stored longer than 1 year (Stanton and DiTomaso, 2004; Drewitz and DiTomaso, 2004).

2.2. *Effect of shading on* C. selloana *germination*

To test the effect of shading on seed germination we constructed three cubes of $50 \times 50 \times 50$ cm and covered them with three different woven materials that filtered light allowing sunlight penetration of 50%, 30% and 5%. Each cube contained 15 5-cm diameter Petri dishes with 10 *C. selloana* seeds from female plants placed on one layer of autoclaved filter paper. We also studied seed germination in 15 uncovered 5-cm diameter Petri dishes with 10 *C. selloana* seeds from female plants under 100% light. The filter paper was continuously maintained saturated with distilled water and Petri dishes were randomly moved twice a week to avoid position effects and to guarantee that they were all under homogeneous conditions. Cubes were placed 1 m apart to avoid shading effects. Germination was recorded every day and germinated seeds were removed from the Petri dishes. Seeds were considered as germinated when the radicle or coleoptile was visible. Differences between the four shading treatments were analysed after 26 days by ANOVA and a subsequent Scheffé multiple-comparisons test. Percentage germination was transformed as arcsine $(1 - X)$ to meet the assumptions of homogeneity of variances.

2.3. *Effect of soil texture on* C. selloana *germination*

Seed germination was tested in a gradient of four different substrate textures that differed in their increasing percentage of sand and decreasing percentage of clay. The texture gradient was obtained by adding four progressively higher fixed quantities of sand to a soil base whose texture was coarse clay. Base soil contained 31.2% sand, 29.7% silt and 38.6% clay. The first texture was coarse clay and was obtained by mixing 2.42 kg of base soil and 0.58 kg of sand. To obtain a sandy-clay-loam texture we mixed 1.76 kg of base soil and 1.24 kg of sand. The third texture was sandy loam and it was made with 1.10 kg of base soil and 1.90 kg of sand. Finally, the fourth texture was sandy and it was made with a mixture of 0.44 kg of base soil and 2.56 kg of sand (Table 1).

Each experimentally made soil was placed in 2-litre pots that were progressively watered for 2 weeks and homogenized once they were dry. Twenty-five seeds from a pooled seed lot from 25 female plants were placed on 12 cm diameter Petri dishes ($n = 10$) and filled with substrate from each texture. Dishes were sprayed with distilled water every day and were randomly moved every two days in order to avoid position effects and to guarantee that all dishes received the same amount of light. Germination was recorded every day and seedlings were removed. Seeds were considered as germinated when the cotyledon emerged from the soil. The effect of soil texture on the percentage of germination after 42 days was analysed using ANOVA and a subsequent Scheffé multiple-comparisons test.

2.4. *Effect of water availability on* C. selloana *germination*

To test the effect of the duration of water availability on *C. selloana* germination we applied three watering treatments:

Table 1 – – Percentage of soil fractions (ISSS criteria) for the four experimentally made textures used for *C. selloana* germination tests

Soil fractions (%)	Soil texture			
	Coarse clay	Sandy-clay-loam	Sandy loam	Sandy
Sand ($2000 < \varnothing < 20\ \mu m$)	45.0	60.0	75.0	90
Silt ($2 < \varnothing < 20\ \mu m$)	31.1	22.6	14.1	5.7
Clay ($\varnothing < 2\ \mu m$)	23.9	17.4	10.9	4.3

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(i) a long-duration water availability treatment in which Petri dishes were sprayed with distilled water every day in order to maintain them constantly moist, (ii) an intermediate-duration water availability treatment in which Petri dishes were sprayed with water every day during the first five weeks, (iii) a short-duration water availability treatment in which Petri dishes were only sprayed with water during the first three weeks. Each Petri dish was 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, and contained 25 seeds from female plants. We used gardening soil to avoid effects of local soil chemistry. There were 10 Petri dishes for each water availability combination. Petri dishes were randomly moved every two days to avoid position effects and to guarantee that they received the same amount of light. Germination was recorded every day and germinated seeds were removed. Seeds were considered as germinated when the cotyledon emerged from the soil. The effect of the duration of water availability was analysed after 2 months, when no additional seed germination under intermediate and short-duration water availability was observed, with a one-way ANOVA. Differences between water duration availabilities were calculated with a one-way ANOVA. A Scheffé test was used for pair-wise comparisons between watering treatments.

3. Results

Shade significantly increased percentage germination ($F_{3,56} = 7.57$, $P = 0.0002$), with about 20% fewer seeds germinating under 100% light (Scheffé test, $0.001 \leq P \geq 0.003$) than under the other light treatments, which did not differ (Fig. 1).

Percentage germination of *C. selloana* seeds varied with soil texture ($F_{3,36} = 8.52$, $P = 0.0002$), increasing with increasing sand content (Fig. 2), being significantly higher in sand than in coarse clay, sandy-clay-loam and sandy-loam textures (Scheffé test, $0.0003 \leq P \geq 0.02$).

Shortage in water availability had a significant negative effect on final seed germination ($F_{2,27} = 25.35$, $P < 0.0001$).

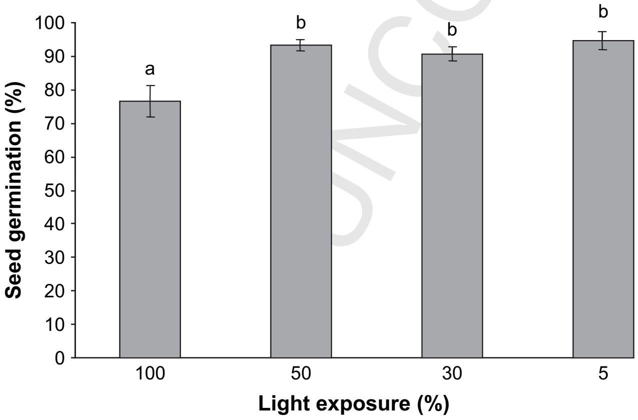

Fig. 1 – Mean percentage germination (±s.e.) of *C. selloana* seeds on a light exposure gradient. Different letters above columns indicate significant differences between light exposure treatments ($P < 0.05$).

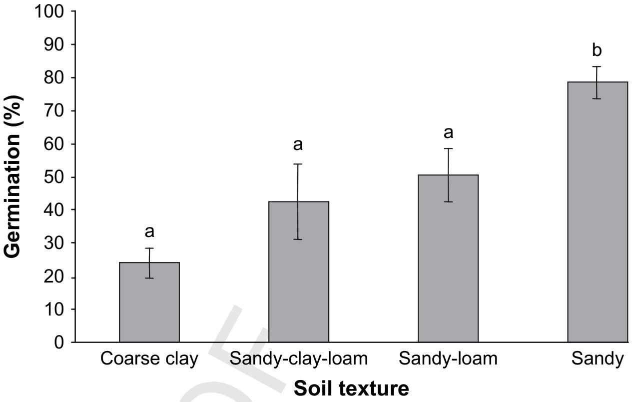

Fig. 2 – Mean percentage germination (±s.e.) of *C. selloana* seeds on four experimentally made textures. Different letters above columns indicate significant differences between soil textures ($P < 0.05$).

Seed germination of *C. selloana* was not completely synchronous, continuing at the short-duration water availability treatment even when seeds were not watered but Petri dishes remained moist (Fig. 3).

4. Discussion

C. selloana usually invades areas where there is a high percentage of bare ground as a result of frequent disturbances (Harradine, 1991), therefore we expected high *C. selloana* seed

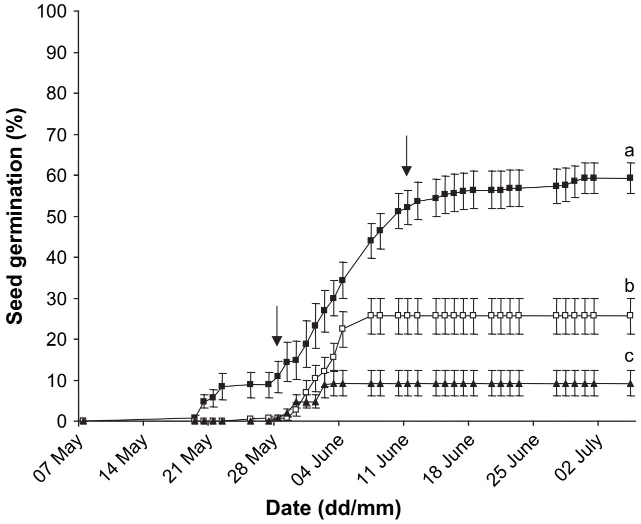

Fig. 3 – Cumulative curves of *C. selloana* seed germination (mean±s.e.) under long (filled squares), intermediate (empty squares) and short-duration (filled triangles) water availability. Black arrows show the date when watering was stopped in the intermediate and short-duration water availability treatments. Different letters above the last day in which germination was recorded show significant differences between water availability treatments ($P < 0.05$).

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germination under high light. On the contrary, we found that shading significantly improved seed germination by 16.2%, a result which contrasts with seed germination of the congener *C. jubata* which is 3.3 times higher in high light than under dark conditions (Drewitz and DiTomaso, 2004). However, despite higher seed germination under dark conditions, seed germination under 100% light exposure was also very high, so this species can still benefit from disturbances, shown to be essential both by simulations (Pausas et al., 2006) and field experiments (Domènech and Vilà, 2006) for the persistence and expansion of this species.

Previous germination tests proved that *C. selloana* seeds can germinate in a wide variety of soil types such as dune scrub, maritime chaparral, grassland and wetland soil (Lambrinos, 2002) though seedling establishment is said to require sandy soils (Bossard et al., 2000). This is consistent with our findings that sandy soil texture significantly enhanced *C. selloana* seed germination. Furthermore, a field survey conducted in ruderal and non-ruderal habitats across a Mediterranean coastal strip revealed that *C. selloana* was invading habitats whose soil had more than 60% sand (Domènech, 2005). Conversely, we found that this species also germinated in soils which contained lower percentages of sand, showing that germination in *C. selloana* can proceed in wide range of soil textures.

We also suspected that *C. selloana* seed germination would not be severely affected by water availability, as it had been previously found that *C. selloana* mature plants can resist moderate and severe water stress (Bossard et al., 2000). In addition, greenhouse experiments conducted with seedlings have revealed that *C. selloana* seedlings are more drought tolerant than those of *Festuca arundinacea* and *Brachypodium phoenicoides*, two co-existing native species of the same functional group (Domènech, 2005). We found that seed germination of *C. selloana* did not cease completely after stopping watering, and that some seeds remained viable in the Petri dish for several weeks before germinating, suggesting that this species has a staggered germination strategy.

Overall, *C. selloana* seed germination was increased under shaded conditions, in sandy soils and when water was highly available for a long time. However, the germination requirements of this species were not very stringent, so the invasive success of *C. selloana* may be partially attributable to a great capacity to germinate under a wide range of ecological conditions. Moreover, it must be considered that *C. selloana* mature plants produce a high quantity of viable seeds (Domènech, 2005) which the wind disperses widely and have the potential to invade a wide variety of new environments if they find suitable germination conditions.

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