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The role of successional stage, vegetation type and soil disturbance in the invasion of the alien grass *Cortaderia selloana*

Domènech, Roser[1*] & Vilà, Montserrat[1,2]

[1]*CREAF (Center for Ecological Research and Forestry Applications) and Unit of Ecology, Department of Animal and Plant Biology and Ecology, Autonomous University of Barcelona, 08193 Bellaterra, Spain; [2]E-mail montse.vila@uab.es;*
[*]Corresponding author: Fax: +34 935814151, E-mail r.domenech@creaf.uab.es

Abstract
Question: This paper studies the establishment and performance of *Cortaderia selloana* (Pampas grass), an alien South American ornamental species that is invading many parts of the world. We asked whether (1) early successional stages were the most susceptible to *C. selloana* invasion; (2) soil microdisturbances increased invasion at any point of succession, and (3) *C. selloana* invasion of later successional stages was modulated by vegetation type
Location: Delta del Llobregat (Catalonia, NE Spain).
Methods: We monitored survival and growth of transplanted *C. selloana* seedlings in disturbed and non-disturbed plots throughout a successional gradient with an age range of < 1 to > 10 years in different vegetation types and within the area of influence of coexisting species with similar growth form.
Results: Although seedling survival was extremely low in all treatments, our results revealed that early successional stages were not the most easily invaded since we found no significant differences in the percentage survival of *C. selloana* along the successional gradient. However, survival and seedling biomass were enhanced by soil disturbance at any seral stage. This result suggested that inhibition ruled *C. selloana* invasion. Invasibility neither depended on the invaded vegetation type nor on the co-existing species with similar growth form. Finally, *C. selloana* invasion was not enhanced by decreasing competition with *Phragmites australis*, a native coexisting species because survival rates after a year were not significantly different. However, *Phragmites* increased *C. selloana* leaf length probably due to shading.
Conclusions: *C. selloana* recruitment appears to be positively affected by soil disturbance but it is independent of successional stage or vegetation type.

Keywords: Additive experiment; Facilitation; Invasibility; Microdisturbance; Pampas grass; Removal experiment; Successional mechanism.

Introduction

Biological invasions caused by the intentional or accidental introduction of alien plant species are threatening the conservation of biodiversity through the local displacement of native species and the modification of ecosystem functions (Vitousek 1994; Enserink 1999). It is widely known that ecosystems vary in their invasibility (i.e. susceptibility to invasion). Invasibility depends on several biotic factors such as the competitive abilities of the native species, the presence of effective herbivores, pathogens and mutualisms in the recipient community, and environmental factors such as the region's climate and disturbance regimes (Tilman 1999; Davis et al. 2000). Since ecosystems are dynamic, invasibility also might change within an ecosystem through time as has been suggested by analysing chronosequences of invasion patterns after disturbance (Witkowski & Wilson 2001).

It has been found that disturbances *per se* or alterations of disturbance regimes can increase community invasibility since they can provide safe sites for alien species to establish and spread either by reducing herbaceous cover and levels of competition or by increasing the availability of specific resources (Davis et al. 2000; D'Antonio & Corbin 2003). Invasibility also depends on vegetation types since each herbaceous community has particular micro-environmental conditions that may, or may not, favour the establishment of alien species (Huenneke et al. 1990). It has also been predicted that invasibility declines during the course of succession (Rejmánek 1989; Hobbs & Huenneke 1992). Moreover, most alien species are by their nature ruderals, *r*-strategists (Heywood 1989). Therefore, 'pioneer communities' will exhibit a larger number and proportion of invaders than successionally more advanced stages. Theoretical models support this idea (Rejmánek 1989) but field data evidence is contradictory. On the one hand, it has been observed that vegetation types occurring at late seral stages are rarely invaded (Lepart & Debussche 1991), but on the other hand, mid-successional stages have been proved to be the most favourable for the establishment of alien species (Bastl et al. 1997).

Differences in invasibility between successional stages could be related to models of species replacement along seral stages: facilitation, tolerance and inhibition (Connell & Slatyer 1977). The facilitation model of succession can partly explain the results found by Bastl et al. (1997) since alien species recruitment is enhanced by early occupants, once they have changed the abiotic environment in a way that is less suitable for them and more suitable for other alien species to invade. According to the tolerance model, alien species invasion can occur at any time in succession since the sequence of species is determined by life-history characteristics (Ward & Jennings 1990; Booth et al. 2003) and provided that alien species are more resistant to reduced resource levels under intense competition, they will be able to dominate in the later stages (Mac Dougall & Turkington 2004).

Finally, the inhibition model states that early species inhibit the establishment of subsequent species. Therefore, alien species will only be able to colonize once local disturbances have progressively killed early species (Ward & Jennings 1990; Booth et al. 2003). However, there are few studies linking ecosystem invasibility with the mechanisms of species colonization along succession (Davis et al. 2001) since most of these studies focus on the effects (i.e. reduction of species richness, changes in species composition, changes in the shading conditions) that alien species have on succession (Wearne & Morgan 2004; Bellingham et al. 2005; Clarke et al. 2005). Therefore, it is necessary to use an approach that integrates succession and invasion ecology by studying the several ways that resident species can facilitate, inhibit or tolerate the establishment and spread of new species (Davis et al. 2005).

We conducted several transplanting experiments to study how the early establishment stages of the invader *Cortaderia selloana* depend on disturbance, successional stage, vegetation type and species neighbour identity. *C. selloana* is a perennial tussock grass native to South America now invading many temperate and Mediterranean areas of the world. The grass tolerates a wide range of environmental conditions such as winter frost, intense sunlight, warm summer temperatures and moderate drought (Bossard et al. 2000). However, *C. selloana* has been reported to have a low germination rate and percentage survival in non-disturbed habitats independently of vegetation type (Lambrinos 2002). Moreover, land-use changes, resulting in soil disturbances, can promote the invasion of this species (Domènech et al. 2005) and a simulation analysis of *C. selloana* invasion supports the hypothesis that disturbances are essential for the persistence and expansion of this species (Pausas et al. 2006). Therefore, our main hypothesis is that *C. selloana* invasion will be enhanced by soil disturbances at any point of succession. Consequently, *C. selloana* invasion will be ruled by the successional mechanism of inhibition. We also want to know whether *C. selloana* invasion of later successional stages is related to the type of vegetation type it has been found that some vegetation types, such as grasslands, are less easily invaded than other vegetation types (Huenneke et al. 1990). We expect that *C. selloana* invasion will not depend on vegetation types provided that local soil microdisturbances take place.

Material and Methods

Study species

Cortaderia selloana (Pampas grass) is a South American gynodioecious long living perennial grass which is considered invasive worldwide (Weber 2003). It was first introduced to Europe between 1775 and 1862 (Bossard et al. 2000). This species is planted for many purposes, for example 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 it is now invading abandoned farmlands, roadsides, old-fields, shrublands, wetlands and riparian communities. *C. selloana* is threatening native vegetation and it is posing a fire hazard due to the accumulation of dry leaves and flowering stalks on the plant (Bossard et al. 2000). This species forms a tussock that can reach 2 - 4 m in height with long (1 - 2 m) sharply serrated leaves. It flowers from mid-August to early September, the inflorescences consisting of showy panicles at the end of a stiff stem. Panicles produce copious amounts of small, wind-dispersed seeds (as much as 10^6 seeds per mature plant for females and 10^5 for hermaphrodites) (Lambrinos 2002; Saura-Mas & Lloret 2005).

Study site

The study site (41° 15' - 41° 17' N; 1° 55' - 1° 59' E) was located in the Delta del Llobregat (Catalonia, NE Spain), a protected 297-ha area bordered by Barcelona airport to the south and by a commercial harbour to the north (see App. 1). Transplanting experiments were conducted in three areas within the Delta: (1) in an agricultural old-field matrix in the west of the Delta; (2) in a shore of a lagoon in Prat del Llobregat and (3) in an old-field in the area of Remolar-Filipines close to Barcelona airport). The climate is Mediterranean with mild, wet winters and hot, dry summers. For soil, micro-environmental and vegetation characteristics, see App. 2.

Experiment along a successional gradient

In May 2003, 44 fields from an agricultural-old field matrix were selected and grouped into a successional series according to information given by local peasants and from aerial photograph analysis, as follows: (1) fields with some annual grasses and herbs that had been abandoned 2 to 3 years ago, 'F2'; (2) fields with perennial grasses and shrubs that had been abandoned 5 to 10 years ago, 'F5' and (3) fields that were abandoned at least 10 years ago, consisting of more mature communities dominated by either *Phragmites australis*, F10P', or *Juncus acutus*, 'F10J'. In addition, we included one field that had been abandoned just before the experiment started, hereafter referred to as F1). We could not find more replicates for this stage because we did not obtain permission from landowners to conduct more experiments. Data obtained from this field were only used in the seedling survival analysis. All successional stages, except F1, were replicated ten times, but at the beginning of the experiment we lost two F2 fields because they were cultivated, and one 10P field and four F10J fields due to a wildfire.

In each field, four 50 cm × 50 cm experimental plots separated by at least 1 m were randomly established. In two randomly chosen plots we applied a soil disturbance treatment by manually raking the first 25 cm of a 90 cm × 90 cm area (the experimental 50 cm × 50 cm plot was centred inside the disturbed area in order to avoid side effects). We planted 16 3-month old seedlings of *C. selloana* in each plot with a distance of 10 cm from each other. Seedlings had emerged and were grown outdoors in trays filled with gardening soil at the Universitat Autònoma de Barcelona (UAB) Campus. In disturbed plots seedlings were planted within the 50 cm × 50 cm area, and the remaining 40 cm frame area was a buffer zone. Seedlings had on average 2.5 ± 0.03 leaves and total leaf length was 11.7 ± 0.3 cm. Total leaf length (X) proved to be a good estimator of plant biomass (Y) through the allometric regression $Y = 0.0003X - 0.00009$, $n = 67$, $r^2 = 0.76$.

These seedling measures were repeated at the end of the experiment in January 2004. We did not measure their final biomass because plots were destroyed before we could cut the seedlings.

Seedling survival was monitored from May to September 2003 at 15-day intervals and from October 2003 to January 2004 once a month. Within each field, we calculated the mean percentage survival of each pair of disturbed and non disturbed plots. At the end of the experiment no seedlings planted in non-disturbed plots had survived, except in F5. Therefore, differences in final leaf length and the number of leaves in the other non-disturbed plots could not be calculated.

Vegetation type experiment

In order to determine if there were differences in vegetation invasibility to *C. selloana* invasion within late successional stages we selected 30 F10 old-fields from the same agricultural old-field matrix. Old-fields were grouped into three categories according to the dominance of their herbaceous cover: (1) *Phragmites* cover, F10P; (2) *Juncus* cover, F10J, and (3) herb cover, F10H. All the dominant plant species belonged to the same life form, monocotyledonous perennials. We had 10 replicates for each vegetation type (see App. 2).

Seedling transplanting and monitoring followed the same protocol as in the previous experiment, except that at the end of the experiment plants were cut and weighed after drying at 70 ºC to constant weight.

Additionally, we established two 15 cm × 15 cm plots in each field centred in an area of 30 cm × 30 cm that had been disturbed as described before; the remaining 15-cm frame was left as a buffer area, hereafter referred to as Seed addition experiment. Several pieces of panicles from female plants containing an average of 4243 ± 170 seeds were sown at the centre of each plot. The number of seeds sown (Y) in each plot was estimated with panicle dry weight (X) by the regression: $Y = 3571.1X - 80.3$; $r^2 = 0.87$, $n = 25$.

Plots were sampled at 15-day intervals for two months and each time emerged *C. selloana* seedlings were removed. Mean percentage of germination was calculated for each pair of plots. We did not study *C. selloana* seedling emergence on non-disturbed plots because a previous study conducted in California reported that *C. selloana* germination was very low in non-disturbed soils (Lambrinos 2002).

Clipping experiment with Phragmites

Many late successional stages invaded by *C. selloana* are dominated by *Phragmites*. Therefore, in order to determine the neighbouring effect of this species on *C. selloana* invasion, we established, in May 2002, 36 50 cm × 50 cm experimental plots in a part of the Prat del Llobregat study site which was dominated by *Phragmites*. Half of the plots were randomly chosen and the stems of *Phragmites* were clipped, an area of 30 cm around each plot was also clipped and left as a buffer zone. We periodically clipped sprouting stems in order to minimize aerial interaction. Inside each plot, with a 10-cm distance between seedlings, we planted 3-month old seedlings of *C. selloana* that had germinated and were grown outdoors in trays filled with gardening soil at the campus. Seedlings had on average 3.7 ± 0.1 leaves and total leaf length was 28.4 ± 0.8 cm. Measurements were repeated at the end of the experiment in October

2002. Seedling survival was monitored twice in June, September and October 2002.

Transplantation experiment

In order to determine the influence of similar life forms on *C. selloana* establishment at late successional stages another experiment was carried out in May 2003 in a highly diverse old-field in Remolar-Filipines invaded by *C. selloana* (see App. 2).

We established 60 50 × 50 cm experimental plots down the area of influence of *C. selloana* (15 plots), *Juncus* (15 plots) and *Phragmites* (30 plots). Additionally, in 15 randomly chosen *Phragmites* plots we clipped above-ground biomass as in the previous experiment; 16 3-month old seedlings of *C. selloana* were planted in each plot. Seedlings had on average 2.6 ± 0.03 leaves and a total leaf length of 14.2 ± 0.2 cm.

Seedling survival was monitored every two weeks from May to October, once a month from October to January and once in April and in June. Seedlings were harvested and weighed after drying at 70 ºC to constant weight to obtain their final biomass.

Statistical analyses

A survival analysis was used to compute the product-limit (Kaplan-Meyer) estimations of mean survival time of *C. selloana* seedlings in each experiment. Differences were analysed with a Gehan-Wilcoxon test and pair-wise comparisons were established with a Scheffé-test. Differences in percentage survival at the end of the experiments were analysed with Kruskal-Wallis and Mann-Whitney tests since data did not follow a normal distribution.

Differences in the final leaf length and the number of new leaves were analysed with ANOVA or unpaired *t*-tests. Both variables were transformed when necessary to meet the assumptions of parametric statistical analysis. No significant differences in leaf number and in total leaf length were found among the planted seedlings before the experiments. Dry weight was analysed with ANOVA or Kruskal-Wallis when data did not follow a normal distribution. Finally, an ANOVA was used to analyse differences between vegetation types in percentage seed germination.

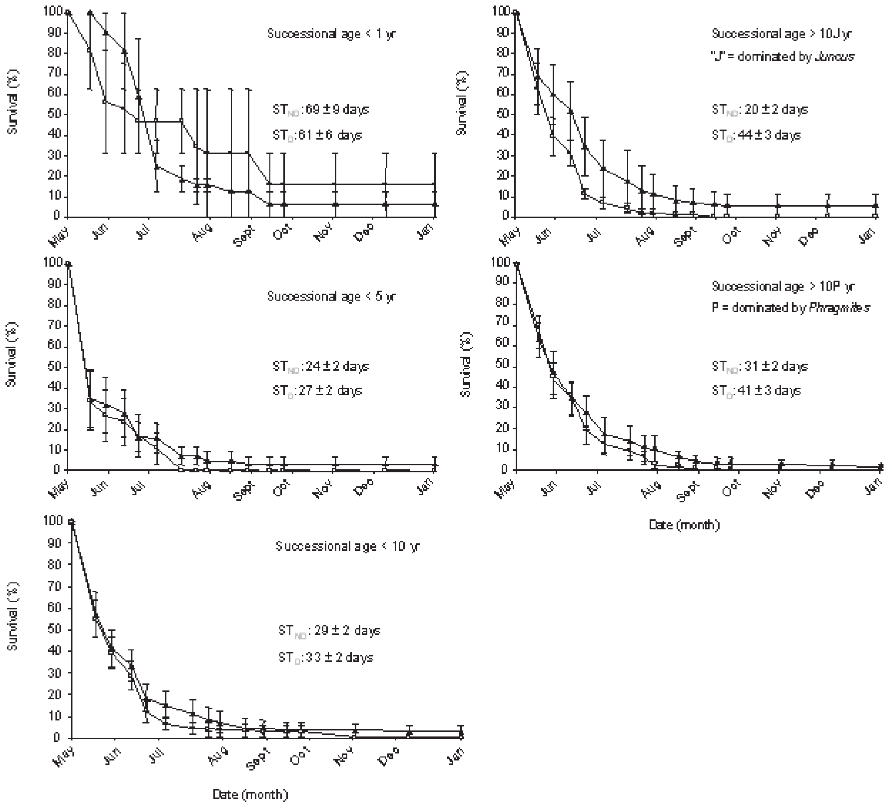

Fig. 1. *Cortaderia* seedling survival and product-limit (Kaplan-Meyer) estimations of survival time (means ± SE) in fields of different successional stages in disturbed (filled triangles) and non-disturbed plots (empty squares) along the sampling period in the succesional gradient experiment. ST_{ND} = Survival time in non-disturbed plots; ST_D = Survival time in disturbed plots.

Results

Successional gradient experiment

Of the 1838 seedlings of *C. selloana* we planted, only 2.0 % remained alive by the end of the experiment. Survival of *C. selloana* seedlings rapidly decreased during the summer of 2003 (Fig. 1). No significant effect of successional stage was found on percentage survival ($H = 0.27$, $df = 3$, $P = 0.97$), but significant differences were found between disturbed (3 ± 1 %) and non-disturbed (0.1 ± 0.1 %) plots ($Z = 2.21$, $P = 0.03$). However, significant differences were found in the mean survival time between successional stages ($\chi^2 = 109.12$, $df = 4$, $P < 0.0001$) and also between disturbed and non-disturbed plots ($\chi^2 = 13.12$, $df = 1$, $P < 0.0003$). Mean survival time of the F1 field was the highest (Scheffé-test, $P < 0.0001$). For disturbed plots, mean survival time on field F1 was higher than that on the F2, F5 and F10P fields (Scheffé-test, $P < 0.001$, $P = 0.005$ and $P = 0.004$, respectively). Mean survival time on the P5 fields was higher than on F10J (Scheffé-test, $P = 0.003$). Furthermore, F2 fields had a higher mean survival time than F10J and F10P (Scheffé-test, $P = 0.0004$ and $P = 0.03$, respectively) (Fig. 1).

Total leaf length of *C. selloana* seedlings in disturbed plots was significantly different along the successional gradient ($F_{3,\ 25} = 9.23$, $P = 0.0003$). The highest value was measured in F10J fields (Scheffé-test, $0.001 < P \leq 0.03$) (Fig. 2). The same pattern was found for the production of new leaves ($F_{3,25} = 3.58$, $P = 0.03$): seedlings of successional stage > 10J were the ones that produced more leaves (Scheffé-test, $0.007 < P \leq 0.03$) (Fig. 2). This comparison could not be established with non-disturbed plots because at the end of the experiment non-disturbed plots of F5 fields were the only successional stage with live seedlings.

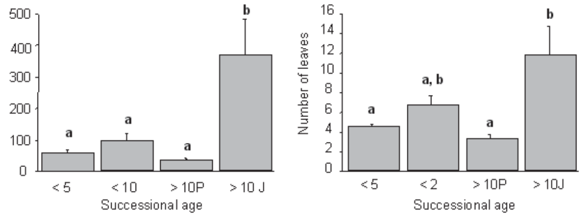

Fig. 2. Total leaf length and production of leaves (means ± SE) of disturbed plots along a successional gradient in the succesional gradient experiment. A Scheffé-test was used to establish pair-wise comparisons. J = Stands dominated by *Juncus*; P = Stands dominated by *Phragmites*.

Vegetation type experiment

Of the 1903 seedlings we planted only 3.9 % remained alive at the end of the experiment (Fig. 3). Percentage survival of *C. selloana* seedlings was not significantly different between vegetation types ($H = 0.73$, $df = 2$, $P = 0.69$) but soil disturbance had a significant effect on survival ($Z = 2.74$, $P = 0.002$). Percentage survival of disturbed plots was higher (7 ± 2 %) than in non-disturbed plots, which was very low (0.7 ± 0.3 %).

Significant differences were found in mean survival time between vegetation types ($\chi^2 = 6.30$, $df = 2$, $P = 0.04$) and also considering soil disturbance ($\chi^2 = 45.80$, $df = 1$, $P < 0.0001$). Regarding non-disturbed plots, *C. selloana* seedlings beneath *Juncus* had a longer survival time than beneath herbs (Scheffé-test, $P = 0.0007$) or beneath *Phragmites* (Scheffé-test, $P = 0.001$). However, when establishing pair-wise comparisons between vegetation types in disturbed plots no significant differences appeared (Fig. 3).

Seedling dry weight did not significantly vary between vegetation types ($H = 1.27$, $df = 2$, $P = 0.53$). However, significant differences appeared when considering soil disturbance ($Z = 3.30$, $P = 0.001$). Dry weight of seedlings from non-disturbed plots was lower (0.009 ± 0.003 g) than in disturbed plots (0.2 ± 0.3 g).

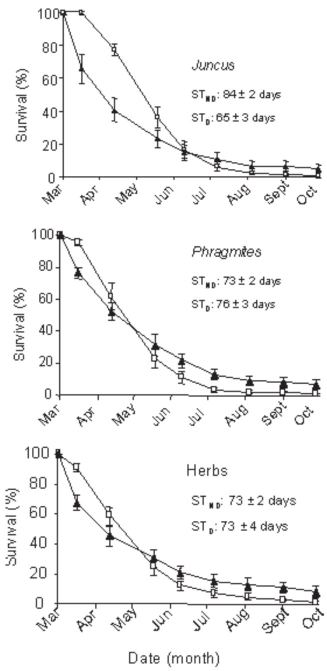

Fig. 3. Survival and product-limit (Kaplan-Meyer) estimations of survival time (means ± SE) of *Cortaderia selloana* transplanted seedlings in disturbed (filled triangles) and non-disturbed (empty squares) *Juncus*, *Phragmites* and herb vegetation types and effect of soil disturbance in the vegetation type experiment. ST_{ND} = Survival time in non-disturbed plots; ST_D = Survival time in disturbed plots.

In the Seed addition experiment, the percentage of germination of *C. selloana* seeds was 13.5 ± 9.6 % in the *Juncus* type, 12.6 ± 3.9 % in the herb type and 10.7 ± 3.8 % in the *Phragmites* type. However, differences were not significant ($F_{2,27} = 0.12$, $P = 0.88$).

Clipping experiment with Phragmites

Of the 432 seedlings we planted only 13.9% remained alive until the end of the experiment. *C. selloana* percentage seedling survival in *Phragmites* clipped plots (13 ± 4%) was not significantly different ($Z = 0.11$, $P = 0.91$) from in plots with *Phragmites* (18 ± 7 %). Survival time also did not differ between treatments (79 ± 3 days and 83 ± 3 days, respectively) ($\chi^2 = 2.42$, d.f. = 1, $P = 0.12$).

Seedlings of plots with *Phragmites* produced 0.2 ± 0.2 leaves during the course of the experiment and seedlings of plots without *Phragmites* produced 0.4 ± 0.3 leaves. These differences were not significant ($Z = 0.80$, $P = 0.43$). However, significant differences appeared in total leaf length ($t_{64} = 2.85$, $P = 0.006$). Leaves of seedlings of plots with *Phragmites* were longer (67 ± 7 cm) than seedlings of *Phragmites* clipped plots (36 ± 8 cm).

Transplantation experiment

Of the 960 *C. selloana* seedlings we planted, only 2.5 % remained alive by the end of the experiment. All seedlings where *Phragmites* was clipped died before the end of the experiment (Fig. 4). However, there were no significant differences in percentage survival of *C. selloana* seedlings between the three remaining treatments ($H = 2.28$, $df = 2$, $P = 0.32$): percentage survival beneath *C. selloana* was 4 ± 2%, 3 ± 2% beneath *Juncus* and 3 ± 2 % beneath *Phragmites*. Mean seedling survival time varied significantly between treatments ($\chi^2 = 384.20$, $df = 3$, $P < 0.001$). Seedlings beneath *C. selloana* had the longest survival time and seedlings in *Phragmites* clipped plots had the lowest value (Scheffé-test, $P < 0.0001$). Final biomass of plants varied significantly between treatments ($F_{2,21} = 6.76$, $P = 0.005$): seedlings beneath *Phragmites* produced the highest biomass and seedlings beneath *Juncus* and *C. selloana* produced the lowest (Fig. 4). Final biomass of plants varied significantly between treatments ($F_{2,21} = 6.76$, $P = 0.005$): seedlings beneath *Phragmites* (0.170 ± 0.066) produced the highest biomass and seedlings beneath *Juncus* (0.008 ± 0.004) and *C. selloana* (0.032 ± 0.016) produced the lowest.

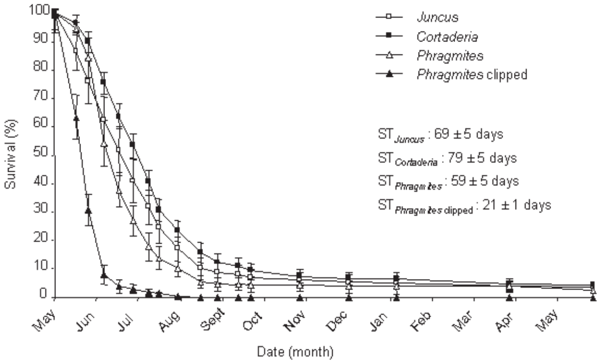

Fig. 4. Survival (means ± SE) of *Cortaderia selloana* seedlings transplanted beneath *Juncus*, *Cortaderia*, *Phragmites* and *Phragmites* clipped. ST = Survival time.

Discussion

It has generally been assumed that invasibility declines during succession (Rejmánek 1989; Lepart & Debussche 1991). Specifically, young successional stages should be more susceptible to invasions since they are less complex communities (Crawley 1989). This prediction follows from the successional mechanism of facilitation which may provide a window of time in which invasions can occur: local species may not establish during early succession due to a lack of required resources and they can neither establish at later stages since natural enemies may be too abundant (Crawley 1989). However, higher invasibility during early succession could also be due to the availability of unused resources caused by the initial disturbance. The Successional gradient experiment showed that early successional stages are not more invaded than later stages since there are no differences in *C. selloana* seedling survival. In addition, *C. selloana* invasion is not promoted in advanced successional stages, when the availability of unused resources is low and competition is severe. Consequently, neither the facilitation model nor the tolerance model, but rather the inhibition model of succession (Connell & Slatyer 1977; Ward & Jennings 1990) can account for our results because resident species inhibit *C. selloana*, but soil disturbances promote *C. selloana* invasion at any point of succession.

It has also been suggested that ecosystem invasibility not only depends on vegetation succession but also on the type of vegetation. For instance, grasslands have been reported to be less invaded than other vegetation types (Huenneke et al. 1990; Burke & Grime 1996). However, the Vegetation types experiment showed that at later successional stages invasibility did not depend on vegetation type since communities dominated by *Phragmites*, *Juncus* or herbs did not differ in resistance to invasion measured as seedling survival and growth. This result is consistent with the lack of significant differences found in the Seed addition experiment, showing that invasibility was the same for the three vegetation types. This can also be used to infer that the different micro-environmental conditions of each successional stage or vegetation type did not affect *C. selloana* invasion. In addition, considering the triggering attribute approach (Gurvich et al. 2005), *C. selloana* may not have a 'special' attribute, absent in the local species, that allows it to spread and invade non-disturbed sites.

The continued existence of species or communities often requires some type of disturbance. There is overwhelming evidence that different types of disturbance promote biological invasions either through a reduction of herbaceous cover or levels of competition or through an increase in the availability of specific resources (Hobbs & Humphries 1995; Davis et al. 2000). Our results confirm this, both in the Successional gradient experiment and in the Vegetation type experiment. Soil micro-disturbances increased seedling survival and growth regardless of the successional stage and vegetation type. This is also translated at a larger scale because in the Successional gradient experiment, the mean survival time of *C. selloana* seedlings in the F1 field was higher than in any later seral stage, indicating that the absence of any plant cover enhanced *C. selloana* invasion.

Consequently, although some alien species, e.g. *C. selloana*, may be unsuccessful invaders due to their low capability of invading different successional stages or different vegetation types, disturbances can increase their potential to invade because safe sites favourable to seedling establishment are provided (Crawley 1989). Other invasive species, e.g. *Reynoutria* spec., follow a similar pattern since this species easily invades habitat types in the Czech Republic that are frequently flooded. Therefore, *Reynoutria* invasion depends on floods because they provide safe sites to get established through the destruction of the resident vegetation and the spread of its rhizome (Bimova et al. 2004). In addition, emergence time can strongly influence future seedling fecundity and survival among perennials (Verdú & Traveset 2005). Our results also highlight the importance of time in *C. selloana* invasion. Seedlings in disturbed plots survive longer, increasing the probability that they benefit from a mid or late precipitation event which may enhance invasion.

Local soil disturbances are not the only factor that can promote plant invasions but also decreased competition with natives promoted by management. *Phragmites* has been traditionally clipped in the studied areas to promote its regeneration and we suspected that this management could enhance *C. selloana* invasion through a reduction of competition because *Phragmites* is known to inhibit the germination or establishment of other species through the modification of biotic and abiotic factors (Keller 2000; Meyerson et al. 2000). However, we did not find a negative effect of *Phragmites* on *C. selloana* establishment. Nevertheless, *Phragmites* clipping decreased mean survival time of *C. selloana* seedlings and without clipping it increased leaf length probably due to shading (App. 2), survival rates after a year were not significantly different.

Our study contributes to linking ecosystem invasibility and succession ecology, which is essential to assess the vulnerability of ecosystems and to study the mechanisms that rule invasions (Davis et al. 2005). In summary, we found that although *C. selloana* seedling survival was very low due to summer water stress, it can be increased by disturbance. Therefore, our study suggests that the inhibition model rules *C. selloana* invasion because soil disturbance enhances this invasion at any point of succession. However, this does not necessarily mean that all native neighbour species compete with the invader. The low survival of *C. selloana* seedlings is counterbalanced with a high production of small seeds. *C. selloana* produces large amounts of small wind-dispersed seeds (106 seeds per mature plant for females and 105 for hermaphrodites; Lambrinos 2002; Saura & Lloret 2004) and consequently, the propagule pressure is very high. Therefore, even if *C. selloana* seedling percentage survival is very low, a mature *C. selloana* plant will produce on average from 2800 to 5400 new seedlings every year provided safe sites are available.

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For App. 1, see JVS/AVS Electronic Archives; www.opuluspress.se/

App. 1. Description of the study site.

The study site with mainly wetlands in the Delta del Llobregat was changed to pine forest and agricultural land, and in recent times into industrial and urban areas. However, wetlands still remain scattered along the sea. The ecological importance of the Delta is due to the concentration of a wide variety of natural environments in a relatively small area within a cultural landscape mosaic. The existence of a gradient from the sea shore to the inland which includes humid, dry or salty environments ranging from sandy soils to textures richer in silt or clay, creates special microhabitats that determine its vegetation (Orta et al. 1992).

The soil is mainly sandy and the water table level is at ca. 50 cm from the soil surface (Anon. 1995). The climate is Mediterranean with mild, wet winters and hot, dry summers. Mean monthly temperatures for the coldest (January) and the hottest (July) months are 9.0 ºC and 23.3 ºC, respectively. The annual precipitation is 739 mm (data available in http://www.meteocat.com).

App. 2. Environmental and soil characteristics of the study sites.

Successional gradient experiment

Vegetation characteristics of each field were estimated by the point-intercept method conducted in one 25-m line transect in each field (Henderson 2003). Differences between successional stages and vegetation types were analysed with ANOVA and subsequent pair-wise comparisons with a Scheffé-test.

Diversity ($F_{3,22} = 14.60$, $P < 0.0001$), species richness ($F_{3,22} = 6.94$, $P = 0.002$) and total cover ($F_{3,22} = 15.50$, $P < 0.0001$) were significantly different between stages. The F2 fields were the less diverse and had the lowest total cover (Scheffé-test, $0.0001 < P < 0.05$ and $0.0001 < P \leq 0.03$, respectively). Species richness at this stage was only significantly lower than species richness of F5 fields (Scheffé-test, $P = 0.003$) (Table A1). Diversity was also significantly different among vegetation types ($F_{2,18} = 5.59$, $P = 0.01$): F10H fields had the highest diversity. However, species richness ($F_{2,18} = 2.98$, $P = 0.08$) and total cover ($F_{2,1}8 = 2.32$, $P = 1.23$) did not significantly differ among the three vegetation types (Table A1).

Vegetation type experiment

In order to characterize the micro-environmental conditions of the vegetation where *Cortaderia* seedlings were planted, four random measures of soil moisture by a Time Domain Reflectometry (TDR) and four perpendicular Photosynthetic Active Radiation (PAR) measures below the vegetation were taken in each field on 16.06 and 13.07. Mean soil moisture and mean PAR in each field were calculated with these values, without considering disturbed and non-disturbed plots.

PAR measures were significantly higher at the second sampling which took place in July ($F_{1,27} = 116.59$, $P < 0.0001$). However, vegetation types did not receive different PAR ($F_{2,27} = 1.17$, $P = 0.33$) and there was no significant interaction between vegetation types and sampling date ($F_{2,27} = 3.23$, $P = 0.05$) (Table A2). Neither did mean soil moisture differ between vegetation types ($F_{2,27} = 2.01$, $P = 0.15$) and it significantly decreased during the summer sampling ($F_{1,27} = 10.34$, $P = 0.003$). There was no significant interaction between vegetation types and sampling date ($F_{2,27} = 1.98$, $P = 0.45$) for soil moisture (Table A2).

Table A1. Vegetation characteristics (mean ± SE) within each successional stage in the Successional gradient experiment.

Stage	Species richness	Diversity *H'*	Total cover (%)	Dominant species (% cover)
F2	2.6 ± 0.4	0.98 ± 0.11	74 ± 6.	*Plantago coronopus* (13.8) *Aster squamatus* (8.5)
F5	5.6 ± 0.7	2.08 ± 0.13	149 ± 14	*Torilis nodosa* (29.1) *Agrostis stolonifera* (24.3)
F10P	4.0 ± 0.3	1.60 ± 0.11	165 ± 12	*Phragmites australis* (43.9) *Plantago coronopus* (17.46)
F10J	5.0 ± 0.3	1.95 ± 0.09	201 ± 5	*Agrostis stolonifera* (34.39) *Juncus acutus* (16.9)
F10H	5.8 ± 0.7	2.20 ± 0.15	169 ± 15	*Torilis nodosa* (31.2) *Agrostis stolonifera* (27.5)

App. 1 & 2. Internet supplement to: Domènech, R. & Vilà, M. 2006.
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Table A2. PAR and soil moisture (mean ± s.e.) in *Phragmites*, *Juncus* and herbs vegetation types in the Vegetation types experiment.

	16th June		13th July	
Vegetation types:	PAR	Soil moisture (%)	PAR	Soil moisture (%)
Phragmites	1503 ± 81	19.7 ± 2.5	903 ± 48	18.2 ± 2.4
Juncus	1514 ± 72	23.3 ± 3.2	750 ± 63	21.6 ± 2.8
Herbs	1295 ± 70	15.5 ± 2.4	873 ± 95	14.9 ± 2.0

Clipping experiment with Phragmites

To characterize the environmental conditions where *Cortaderia selloana* seedlings were growing, four measures of PAR and four random measures of temperature at 2 cm from the soil surface were taken with a digital thermometer in each plot. Mean PAR and mean soil temperature per plot were calculated for each sampling date.

Phragmites clipped plots received a significantly higher PAR (1004 ± 143) than *Phragmites* plots (509 ± 93) (t_{34} = 2.90, $P = 0.006$). However, mean soil temperature in *Phragmites* clipped plots was not higher (25.3 ± 0.6 ºC) than in plots with *Phragmites* (24.9 ± 0.5 ºC) ($t_{34} = 0.43$, $P = 0.67$).

Transplantation experiment

In order to characterise soil properties in each plot at the beginning of the experiment, one sample of the first 20 cm mineral soil was obtained from each plot beneath *Juncus*, *Cortaderia* and *Phragmites* with a 6 cm diameter drill. Soil samples were labelled and air-dried on flat trays in the laboratory. From each soil sample we analysed soil total C, total N, pH and $CaCO_3$. Total C and N content were determined with an elemental analyser of Carlo Erba Instruments (EA1108 model). Organic carbon was calculated by subtracting the C of the $CaCO_3$ from the total C. pH was measured with a glass pH-meter in a soil suspension with water 1:2.5 (w:v); calcium carbonate was analysed following the pressure calcimeter method. Four random soil moisture measures were taken two times in each plot during summer 2003. PAR was also measured. Mean soil moisture and mean PAR were calculated for each plot.

Differences in PAR and soil moisture were tested with a Repeated Measures ANOVA and unpaired *t*-tests. Soil temperature was analysed with an unpaired *t*-test. The other soil properties were analysed with a Kruskal-Wallis test. We considered the invaded old-field of Remolar-Filipines highly diverse since in four 25-m transects we found 22 plant species. Total plant cover in this area was 229.44%, the most abundant species being *Agrostis stolonifera* (56.21%), *Phragmites* (53.60%), *Juncus maritima* (19.61%) and *J. acutus* (9.15%). *C. selloana* was less abundant (3.27%). *Juncus* was chosen instead of the more abundant *J. maritimus* because it had a larger plant biomass and was more similar to *C. selloana* size and shape.

Soil under *C. selloana* was not significantly different from soil under *Juncus* and *Phragmites* for all the soil properties studied (Table A3). Treatments received significantly different PAR ($F_{3,55} = 47.13$, $P < 0.0001$): PAR values were the highest in plots where *Phragmites* had been clipped (Scheffé-test, $0.0001 < P \leq 0.02$) (Table A4). Measures of PAR did not change between 19th to 30th June ($F_{1,55} = 0.003$, $P = 0.95$) and there was no significant interaction between treatments and the date of PAR sampling ($F_{3,55} = 2.55$, $P = 0.06$).

Soil moisture also varied significantly between treatments ($F_{3,55} = 3.67$, $P = 0.02$). In general, plots with *Phragmites* and plots where *Phragmites* had been clipped had the highest soil moisture. In addition soil moisture decreased with time ($F_{1,55} = 3111.40$, $P < 0.0001$). There was a significant interaction between treatments and the date of sampling ($F_{3,55} = 5.28$, P = 0.003). While no significant differences were found between treatments at the first sampling date (Table A4) (Scheffé-test, $0.20 \leq P \leq 1.00$), significant differences appeared at the second sampling date. Soil moisture beneath *Cortaderia* and *Juncus* was the lowest. Moreover, soil moisture of *Phragmites* plots was higher than soil moisture of *Juncus* plots (Scheffé-test, $P = 0.02$) (Table A4).

Table A3. Soil properties (mean ± SE) beneath *Cortaderia*, *Juncus* and *Phragmites* in the Vegetation type experiment.

Plots beneath:	$CaCO_3$ (%)	Total N (%)	Organic C (%)	pH
Cortaderia	19.53 ± 0.26	0.16 ± 0.02	4.16 ± 0.26	8.00 ± 0.06
Juncus	20.06 ± 0.41	0.24 ± 0.03	5.13 ± 0.15	8.06 ± 0.05
Phragmites	19.70 ± 0.21	0.18 ± 0.01	4.40 ± 0.15	8.13 ± 0.07
(H, *df* = 2, *P*)	(4.07, 2, 0.13)	(5.17, 2, 0.07)	(1.63, 2, 0.44)	(2.05, 2, 0.36)

Table A4. PAR and soil moisture measures (mean ± s.e) beneath *Juncus*, *Phragmites* and *Cortaderia* in the Transplanting experiment. Values within a column followed by different lower-case letters are significantly different between treatments at a sampling date.

	PAR		Soil moisture (%)	
Treatment:	19/06/2003	30/06/2003	8/06/2003	19/06/2003
Juncus	514 ± 73 a	652 ± 98 a	13.64 ± 1.29 a	8.60 ± 0.88 a
Cortaderia	622 ± 132 a	653 ± 152 a	15.49 ± 1.39 a	11.64 ± 1.33 a, b
Phragmites	1316 ± 122 b	1166 ± 139 a	21.28 ± 2.20 a	17.69 ± 2.20 b
Phragmites clipped	2153 ± 70 c	2142 ± 69 b	20.52 ± 2.10 a	12.13 ± 2.14 a, b