

Original article

Neighbourhood association of Cortaderia selloana invasion, soil properties and plant community structure in Mediterranean coastal grasslands

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ABSTRACT

Invasion by alien species is threatening the conservation of native plant communities and the integrity of ecosystems. To gain a better understanding of such impacts, many studies have examined the traits that make alien species successful invaders as well as the factors involved in community invasibility. However, it is necessary to link invader effects on community structure and on ecosystem processes in order to unravel the mechanisms of impact. Cortaderia selloana is a perennial grass native to South America that is invading abandoned agricultural lands close to coastal human settlements in Catalonia (NE Spain). In invaded pastures, we examined the association between C. selloana invasion, soil properties and vegetation structure changes in pastures, comparing the neighbourhood area of influence of C. selloana with areas far from C. selloana. Areas under the influence of C. selloana had lower total soil nitrogen values and higher C/N values than in areas far from C. selloana. Furthermore, the areas affected by C. selloana had lower species, family and life form richness and diversity, and less plant cover. In addition, C. selloana also increased the vertical vegetation structure and changed species composition (only 44% similarity between invaded and non-invaded areas). Our results point out that C. selloana has an effect on its neighbourhood leading to an increase in small-scale variability within invaded fields.

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1. Introduction

Biological invasions constitute a global change component of major concern for the conservation of natural and managed areas. Many studies have examined the traits that make alien species successful invaders as well as the factors involved in community invasibility. But what really threats native communities are the impacts of the invaders (Parker et al., 1999; Levine et al., 2003). Alien species may affect the recipient community at all levels of ecological complexity, thus, having an impact on specific species, communities and ecosystems (Gordon, 1998; Parker et al., 1999). Most studies on the impact of alien plants focus either on their effects on plant community structure (e.g. species diversity and composition) or on some ecosystem processes (e.g. nitrogen cycling, hydrology, etc.) separately (but see Vivrette and Muller, 1977; Christian and Wilson, 1999). However, to gain a better understanding of the mechanisms underlying

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such impacts, it is necessary to link invader effects on community structure and on ecosystem processes simultaneously in the same system (Levine et al., 2003).

Mediterranean ecosystems of the world contain approximately 20% of the Earth flora despite representing less than 5% of its surface (Cowling et al., 1996). Nevertheless, Mediterranean ecosystems are predicted to be extremely susceptible to global change (Sala et al., 2000). In particular it is hypothesised that they will experience significant consequences as a result of their sensitivity to land-use changes and biological invasions (Sala et al., 2000). In the Mediterranean Basin, there have been many intentional or unintentional species introductions (Le Floc'h, 1991). For example, it has been estimated that in peninsular Spain there are more than 600 naturalised plant species (i.e. 13% of its total flora), mostly of American origin that can be grouped in more than 100 families (Vilà et al., 2001). The greatest diversity of alien plants is concentrated in agricultural, ruderal and coastal habitats (Vilà et al., 2001). The high invasibility of coastal habitats is favoured by the mild climate, the existence of greatly disturbed habitats and the significant human influence that increase alien propagule pressure via ornamental plant species (Sobrino et al., 2002).

We studied several ecological effects of the invasion of Cortaderia selloana (Schultes et Schultes fil.) Asch. et Graebner. This is a native South American species introduced to Europe as an ornamental that is now invading pastures in coastal areas of Catalonia (NE Spain). The study attempts to link the presence of C. selloana with its effect on vegetation structure and on soil properties at a local scale. It has been hypothesised that species with the largest impacts are those that are qualitatively different from species in the recipient community (Vitousek, 1990; Chapin et al., 1994). C. selloana is a large perennial grass with no similar counterparts in the community it invades. For this reason, we hypothesise that there is an association between C. selloana invasion, changes in plant community structure and changes in soil properties. Due to the recent invasion event at the study site, we expect these effects to be detected at the neighbourhood area of influence of C. selloana within invaded fields since it is known that the presence of a plant changes the environment of its neighbours and alter their growth rate and form (Harper, 1977; Vilà et al., 1994; Vilà and Terradas, 1995).

2. Methods

2.1. Study species

C. selloana is a long living perennial grass native to Argentina, Brazil and Uruguay. It can reach 2–4 m in height and forms a large fountain-like tussock. Leaves arise from the tussock and their margins are scabrous and sharp. Stems are equal to or slightly longer than the tussock. The inflorescences consist of attractive plumed-dense heads at the end of a stiff stem. C. selloana flowers from mid to late summer and it produces copious amounts of small, wind-dispersed seeds (as much as 10⁶ seeds per plant) (Connor and Edgar, 1974; Lambrinos, 2002). Lateral roots can spread to 4 m in diameter and 3.5 m in depth. Seedlings establish in spring. *C. selloana* tolerates winter frost, intense sunlight, warmer summer temperatures and moderate drought (Bossard et al., 2000).

C. selloana is considered a worldwide invasive alien species. It was first introduced to Europe by a Scottish horticulturist between 1775 and 1862, but its commercial production began in 1874 (Bossard et al., 2000). C. selloana is sometimes grown as a windbreak and to prevent erosion but due to the attractiveness of its plumes, it has mainly been used for ornamental purposes and has escaped cultivation. It is invading abandoned farmlands, roadsides, shrublands and wetland communities. It may compete with native vegetation in conservation areas, reducing its aesthetic and recreational value. This species also poses a fire hazard due to the accumulation of dry leaves, leaf bases and flowering stalks (Bossard et al., 2000).

2.2. Study site

The study area was located in the second most important wetland area in NE Spain, Parc Natural dels Aiguamolls de l'Empordà in the lowlands of Roses Bay. The climate is Mediterranean with mild, wet winters and hot, dry summers. Mean annual temperature and precipitation in the nearest meteorological station of Roses, are 15.5 °C and 739.4 mm/ year, respectively (Clavero et al., 1996; http://www.meteocat. com). Land-use of this zone has been subject to two different trends. During the period 1956–1975, land under permanently irrigated and non-irrigated cultivation increased throughout the area. At the same time, mass tourism on the coast flourished. The period 1975–1995 was marked by the creation of the natural park in the early 1980s and by the uncertain future of agriculture during the 1990s (Saurı́ et al., 2000).

The study site was located in La Rubina (UTM quadrat 31T EG17), an agricultural zone that is formed by small, uniform sized fields $(15 \times 160 \text{ m approximately } 2400 \text{ m}^2)$ surrounded by 2 m wide water channels bordered by Tamarix spp., Salix spp. and Phragmites australis as dominant species. This special structure is the result of Mendizabal's disentitlement in the XIX century. These agricultural patches were cultivated until the late 1960s, but during the following decades some were set aside. Nowadays, around 40% of the fields are still cultivated by forage herbs and grasses such as barley and lucerne (Domènech, personal observation); the remaining fields are abandoned or used as pastures for cattle. Pastures are mainly grasslands with Festuca arundinacea, Elymus pungens, Trifolium pratense and halophytic communities dominated by Juncus acutus. Land abandonment and the tourist development have contributed to the spread of C. selloana from residential areas and campsites. L. Rubina is a flat site that has sandy loam soils, with alkaline reaction, non-saline and high in soil organic matter. Soil moisture con be quite elevated due to unlined-irrigation channels around the fields.

We studied the association between *C. selloana* invasion with changes in plant diversity and soil properties at a local scale in *L. Rubina*. To this purpose we selected four invaded fields that had been pastures at least since 1956 and that

had had the same land use history according to information from peasants and the examination of aerial orthophotomaps from 1956, 1970, 1987, 1996 and 2002. We focussed on pastures because they are one of the most invaded land-uses in *L. Rubina: C. selloana* density has almost doubled during the last 5 years in this land-use (Domènech et al., 2005). We could not select more replicates because some fields had *C. selloana* only in their margins, and in some fields entry was not allowed. All the invaded fields selected were already invaded in 1998 and *C. selloana* had increased its density threefold by the 2002 sampling (Table 1). However, *C. selloana* density and cover was very heterogeneous among fields, varying from 90 to 1040 individuals per ha and from 4% to 20% cover. Therefore, our study was conducted in pastures that were not heavily invaded.

2.3. Soil sampling and analysis

Twelve samples of the first 20 cm of mineral soil were randomly obtained in autumn 2001 from each invaded field. We sampled the soil below six randomly selected *C. selloana* individuals (invaded areas, hereafter) in the South direction and six randomly selected soil samples in zones that were not under the influence of *C. selloana* individuals (non-invaded areas, hereafter). Considering that *C. selloana* roots can spread to 4 m in diameter, we took soil samples representing non-invaded areas at a random distance greater than 4 m away from any *C. selloana* individual.

For each soil sample we analysed soil total C, total N, pH, electrical conductivity, CaCO₃ and particle size fractions. Total C and N content was determined with an elemental analyser of CE Instruments (NA2100 model). Organic carbon was calculated by subtracting the C of the CaCO₃ 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; electrical conductivity was measured in an aqueous extract (1:5 w:v). For particle size analysis, we pooled samples from each invaded site and separately, pooled non-invaded site samples. Pooled samples were analysed following the pipet method proposed by Gee and Bauder (1986).

2.4. Plant community analysis

By the end of spring 2002, when a maximum number of species was expected to be present, we established three 142 m transects along each invaded field. Transects were equidistant from each other and from the fields margins. We identified all plant species found at every 25 cm interval by the

Table 1 – C. selloana density and cover in sampled invaded fields of L. Rubina			
		C. selloana density	C. selloana cover
		(individuals per ha)	in 2002 (%)
Field	1998	2002	
C236	13	88	4.00
C204	42	260	5.53
C232	110	380	12.99
C147	340	1040	19.64

point intercept method. Plant height at each interval was also measured. To establish the comparison between invaded and non-invaded areas we choose 20, 4 m subtransects in each invaded field. Ten transects were randomly located in areas of high density of *C. selloana* (> 15% *C. selloana* cover). The remaining 10 transects were randomly chosen to be far away from any *C. selloana* plant. We chose 4 m transects because within this distance more than half of the total number of species were detected.

Species, family and growth forms richness, total cover and the mean vegetation height were used to establish comparisons between invaded and non-invaded areas. Data of *C. selloana* were included in all calculations. On the other hand, we also classified all the species as common or rare in NE Spain according to Bolòs et al. (1993). To test for differences in species, family or growth form diversity between invaded and non-invaded areas the Shannon index (H) was estimated as:

 $H=-\textstyle\sum_{i}^{n}P_{i}log_{2}P_{i}$

Where " P_i " is the proportion of each species, family or growth form found in the transects.

The Sorensen index (S) was also determined to examine the species similarity between invaded and non-invaded areas.

 $\mathbf{S} = (\mathbf{2} \times \mathbf{C})/(\mathbf{A} + \mathbf{B})$

Where "C" is the number of common species between invaded and non-invaded areas, "A" is the overall total species number and "B" is the total species number in non-invaded areas.

2.5. Statistical analysis

Differences between invaded areas and non-invaded areas (N = 6) were studied with a two-factor ANOVA with field as a random factor and the influence of C. selloana as a fixed effect. When а significant interaction between field × C. selloana influence was found, a LSD test for each field was conducted. Differences in texture were assessed by a paired t-test (N = 4). Differences in community structure parameters (N = 10) were assessed with a two-factor ANOVA with field as a random factor and the influence of C. selloana as a fixed factor. For all analyses, data were log-transformed to meet the assumptions of homogeneity of variances if necessary. Mean ± S.E. values are given throughout the results.

3. Results

3.1. Soil properties

Texture was sandy loam, giving a good structure and suitable drainage properties. Particle size analysis of invaded areas was not significantly different from non-invaded areas (for coarse grain sand: $t_3 = 0.11$, P = 0.92; for fine grain sand: t_3

= 0.005, P = 0.99; for silt: t_3 = 0.48, P = 0.66; for clay: t_3 = 1.59, P = 0.21). No significant differences were found in organic carbon (F_{1, 40} = 3.43, P = 0.07), CaCO₃ (F_{1, 40} = 2.14, P = 0.15), pH $(F_{1, 40} = 0.23, P = 0.63)$ and electrical conductivity $(F_{1, 40} = 0.17, P = 0.17)$ P = 0.69). Soil contained on average $1.66 \pm 0.06\%$ of organic carbon. It was also carbonated (12.27 \pm 0.21%) and levels of CaCO₃ were quite similar between fields. In addition, electrical conductivity values were not too high $(0.37 \pm 0.02 \text{ dS/m})$. However, significant differences in total N content were found between areas (F_{1, 40} = 17.58, P < 0.0001). Soil N of invaded areas was lower than the soil taken from non-invaded areas $(0.135 \pm 0.006\%$ and $0.169 \pm 0.008\%$, respectively). The significant interaction between field × C. selloana influence indicated that this difference was only significant in fields C232 and C236 (Fig. 1A). The C/N ratio was also significantly different between areas ($F_{1, 40} = 16.53$, P = 0.0002), being higher in invaded areas (11.786 ± 0.293) than in non-invaded areas (10.303 ± 0.211).

3.2. Plant community structure

Mean species richness was significantly higher in non-invaded areas than in invaded areas ($F_{1, 72} = 24.36$, P < 0.0001). This trend could be easily appreciated in fields C232 and C147. A similar pattern was observed for family richness: non-invaded areas had a significantly higher number of families than invaded areas ($F_{1, 72} = 63.03$, P = <0.0001). Gramineae and Fabaceae families were the most abundant in both areas. Growth forms richness was also greater in non-invaded areas than in invaded areas ($F_{1, 72} = 25.58$, P = < 0.0001). Hemicriptophyte and therophyte were the most abundant both in invaded and in non-invaded areas.

Similarly, there were significant differences in species diversity ($F_{1, 72}$ = 56.15, P < 0.0001) as well as in family diversity

A %N

N(%)

($F_{1, 72} = 90.43$, P = 0.0001): Shannon's index for species diversity was significantly higher in non-invaded areas than in invaded areas in all fields except in C236 (Fig. 2A). Growth form diversity was greater in non-invaded areas than in invaded areas (F_{1. 72} = 18.20, P < 0.0001) (Fig. 2C).

Only 44.2% of the species found in invaded areas were the same as those in non-invaded areas. Species such as Carex distans, Trifolium fragiferum, Medicago lupulina and Dactylis glomerata and families such as Umbelliferae, Linaceae and Verbenaceae were only present in non-invaded areas. However, no significant differences were found for species rarity between invaded and non-invaded areas ($F_{1, 6} = 1.78$, P = 0.23).

Plant cover was significantly greater in non-invaded compared to in invaded areas ($F_{2, 72} = 18.17$, P < 0.0001) in all fields except in C236 (Fig. 2D). N-fixing species cover was significantly different within invaded fields, being higher in non-invaded areas $(22.7 \pm 4.1\%)$ than in invaded areas (6.9 $\pm 2.7\%$) (F_{1, 16} = 81.67, P < 0.0001). Mean maximum height was higher in invaded areas (46.72 ± 4.82 cm) than in non-invaded areas (23.49 \pm 1.72 cm) (F_{1, 72} = 38.32, P < 0.0001).

4. Discussion

Invasion by alien plant species can change community structure and ecosystem properties (Christian and Wilson, 1999; Mack et al., 2001; Wedin and Tilman, 1990; Scott et al., 2001; Levine et al., 2003) especially when they have very different characteristics from the species in the recipient community (Chapin et al., 1994; Vitousek, 1990). C. selloana size is very large compared to the other species in the community studied. Therefore, we expected this species to have a great impact either on soil properties and/or the invaded community structure. Plants usually change the environment of their





Fig. 1 - Total N and C/N ratio differences between C. selloana invaded (white) and non-invaded (black) areas. Values are mean + S.E. (N = 4). Asterisks indicate a significant (* P < 0.05 and ** P < 0.005) effect in the area influenced by C. selloana within each field.



Fig. 2 – Diversity and total vegetation cover differences between invaded *C*. selloana (white) and non-invaded (black) areas. Values are mean + S.E. (N = 4). Asterisks indicate a significant (* P < 0.05 and ** P < 0.005) effect in the area influenced by *C*. selloana within each field.

neighbours and consequently interact with close neighbours by altering their growth rate and form (Harper, 1977). Field experiments support this idea since the removal of surrounding vegetation usually increases target plant biomass and vigor (Vilà et al., 1994; Vilà and Terradas, 1995; Vilà and Terradas, 1998).

In this study the results do not show any association of *C. selloana* with soil texture, electrical conductivity or pH. The low variability of these parameters indicated that fields were quite homogeneous concerning water infiltration, drainage and salinity (all samples were unsalty). Therefore, we could not determine if *C. selloana* presented a special soil preference in these invaded fields for its establishment and growth. Many studies have found an effect of some alien species on soil pH, either reporting a decrease in pH with the presence of the invading species (Scott et al., 2001; Rhoades et al., 2001) or an increase (Ehrenfeld and Scott, 2001). However, we did not expect any pH change effect with

C. selloana because the soil was alkaline, pH 8.7, with a high calcium carbonate content which provides the soil with a strong buffering capacity. Furthermore, although some studies have reported higher organic carbon concentrations in the presence of alien invasive species due to high dry-matter production (Scott et al., 2001), our data provide no evidence of a significant effect on soil organic carbon.

Nevertheless, we found a negative association between *C. selloana* presence and total soil nitrogen concentration and a positive association with *C*/N ratio. We should mention that these fields are periodically grazed by cattle and that the moderately high N content of the soil far from *C. selloana* tuffs could be due, among other factors, to grazing and cattle manure, enhancing differences between soil under *C. selloana* where cattle are excluded, and soil far from *C. selloana* where cattle graze. In addition, the greater cover of N-fixing species in non-invaded areas might be partially responsible for the higher N content and a lower *C*/N ratio in these areas. An-

other factor could be the likely poor N content in C. selloana leaves and roots compared to other species. Moreover, dead leaves remain attached to the mother plant for a long time, allowing N translocation from senescent to young leaves, which further decreases the N concentration in dead material. Therefore, several factors: grazing exclusion, less N-fixing species and the influence of C. selloana nutrient composition may effect soil N pools under its cover. Further research is needed in order to distinguish between direct and indirect effects, and to increase knowledge about the changes that this species may cause in N dynamics at the local scale.

Species' effects on nitrogen cycling have long been studied (Scott et al., 2001; Mack et al., 2001; Asner and Beatty, 1996) but they mainly focus on N-fixing species that tend to increase nitrogen pools (Stock et al., 1995). However, the opposite pattern can occur when non-N-fixing species infiltrate as found with invasion by the grass *Agropyron cristatum* in the Northern Great Plains (Christian and Wilson, 1999) or in the case of the present study.

Alien invasive species not only can affect soil chemistry but also can displace native species and reduce plant diversity (Christian and Wilson, 1999). We found a lower number and diversity of species, families, and growth forms in invaded areas as compared to non-invaded areas. These differences may be explained, in part, by the fact that C. selloana forms a large dense tussock and a large root system, which may hinder the establishment of other species. Different responses between invaded areas could not be related to a different land-use history since all the selected fields had been pastures at least since 1956. Therefore, although C. selloana invasion is a relatively recent event in the study site, time since invasion can account for these differences. Non-native species also appear to alter stand structure by changing the vertical structure of vegetation, especially when they add a vertical structure that is rare in the communities they invade (Gordon, 1998; Versfeld and van Wilgen, 1986). C. selloana is adding height to the community that is being invaded. The reverse situation can be found when plants in the invaded community are taller than C. selloana as happened in the case of C. jubata invading maritime chaparral (Lambrinos, 2000).

Overall, our study system shows that the effect of the differences found between invaded and non-invaded areas, whether in soil properties or in vegetation structure are leading to an increase in small-scale variability, probably interacting with pasture. In particular, the areas under the influence of *C. selloana* have less nitrogen and less diversity than areas that are far from the invading species.

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