TESI DOCTORAL

CORTADERIA SELLOANA INVASION IN THE MEDITERRANEAN REGION: INVASIVENESS AND ECOSYSTEM INVASIBILITY

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Agraïments

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1

1. Introducció general

1.1 Les invasions biològiques

Les invasions biològiques representen el segon component més important del canvi global desprès dels canvis d'usos del sòl i de la destrucció d'hàbitats (Vitousek 1994). Des de temps immemorials, els éssers humans han contribuït fortament a la redistribució d'espècies tan animals com vegetals arreu del món mitjançant la introducció accidental o intencionada d'espècies natives d'un hàbitat concret cap a noves àrees on no hi eren presents. Aquest fenomen, però, s'ha vist agreujat durant els últims segles degut al desenvolupament del transport i del comerç a gran escala que ha trencat les barreres de la dispersió d'espècies a llarga distància (Vitousek 1994, Enserink 1999, Mack *et al.* 2000). En conseqüència, les invasions biològiques s'estan incrementant, fet que contribueix considerablement a la modificació de la biodiversitat (Dukes & Mooney 1999, Enserink 1999, Mack & Lonsdale 2001), perquè les invasions biològiques posen en perill la conservació de les espècies autòctones, modifiquen les propietats dels ecosistemes, contribueixen a l'homogenització del paisatge i generen grans pèrdues econòmiques (Vitousek 1994).

1.2 El procés d'invasió

El procés d'invasió es pot dividir en tres etapes. En primer lloc es dóna el transport i la introducció de noves espècies mitjançant la intervenció humana o els propis mecanismes de dispersió de l'espècie en qüestió. Durant la segona etapa, la naturalització, la nova espècie s'estableix i constitueix una població de dimensions reduïdes sense que calgui la intervenció humana. Finalment, la tercera etapa fa referència al procés d'invasió en el qual la nova espècie està naturalitzada i és capaç de reproduir-se amb èxit i escampar-se cap a nous territoris (Richardson *et al.* 2000, Shea & Chesson 2002). En aquesta última fase, l'èxit de la invasió de les espècies exòtiques depèn tant de característiques pròpies de l'espècie (*invasiveness*) com de la susceptibilitat de l'ecosistema receptor a la invasió, terme que es defineix sota el nom d'invasibilitat (*ecosystem invasibility*). També depèn de la pressió de propàguls i de la història d'introducció (ex: temps de residència) (Lonsdale 1999, Kolar & Lodge 2001).

Cal considerar, però, que la introducció d'una espècie exòtica no implica necessàriament que aquesta es naturalitzi i esdevingui invasora. Es calcula que només un 10 % de les espècies que són introduïdes es naturalitzen i d'aquestes un 10 % esdevindran espècies invasores (Di Castri 1990). Malgrat això, les xifres continuen essent alarmants ja que el nombre d'introduccions és molt elevat i per tant el nombre final d'espècies exòtiques que arriben a la fase d'invasió és considerable.

1.3 Èxit de les invasions biològiques

1.3.1 Característiques dels invasors

Algunes espècies exòtiques tenen unes característiques especials que els confereixen un caràcter invasor. En aquest sentit cal destacar el fet de tenir un creixement poblacional ràpid i una gran capacitat colonitzadora, que es sol traduir en una elevada taxa de fecunditat. Altrament, les espècies invasores sovint no tenen uns requeriments ecològics específics. En el cas de les plantes, les espècies exòtiques acostumen a reproduir-se vegetativament, a ser autocompatibles i a ser pol·linitzades pel vent. També, en relació a les espècies invasores en els Estat Units s'ha afirmat que és més probable que es tracti d'espècies herbàcies anuals o bianuals (Sutherland 2004). Tenen un creixement ràpid i produeixen una gran quantitat de llavors viables que solen ser dispersades àmpliament. També tenen la capacitat de tolerar un ampli ventall de condicions ambientals (Holdgate 1986, Noble 1989, Gordon 1998). En el cas dels animals, com que les taxes de creixement poblacional són més difícils de mesurar s'empren altres indicadors com per exemple, en el cas dels ocells, una massa corporal petita, un període de desenvolupament curt i produir vàries cries per estació (Duncan *et al.* 2003, Sol *et al. en publicació).* A més, es disposa d'evidències que indiquen que els que tenen un comportament més generalista podran establir més fàcilment poblacions viables després de l'alliberament. Per contra, els ocells classificats com a hàbitat especialistes tindran menys probabilitat d'establir-se (Duncan *et al.* 2003, Sol *et al. en publicació*).

Tanmateix, no tots els bons invasors posseeixen necessàriament aquestes característiques (Baker 1965). Per exemple, en un estudi on es comparen diversos trets d'espècies exòtiques amb els d'espècies natives s'ha vist que la reproducció vegetativa no és més freqüent en espècies exòtiques que en natives, el mateix passa amb el grau d'autocompatibilitat i la pol·linització pel vent. En canvi, sí que s'ha vist que tendeixen a ser plantes anuals i bianuals (Sutherland 2004). Altrament, els trets d'un bon invasor també poden variar en funció del sexe ja que s'ha demostrat que l'assignació de recursos destinats al creixement vegetatiu o a la reproducció difereix en funció del sexe de la planta (Putwain & Harper 1972, Lloyd 1975, Meagher & Antonovics 1982, Obeso 2002).

Altrament, diversos estudis han provat que l'amenaça de les espècies exòtiques sobre les espècies natives ve donada per una superioritat competitiva (Parker & Reichard 1998, Levine *et al.* 2003). Les relacions de competència són altament rellevants en les invasions biològiques perquè quan una espècie exòtica és introduïda, la primera interacció d'aquesta espècie amb la comunitat receptora es dóna mitjançant relacions de competència pels recursos limitants (Vilà & Weiner 2004). Malauradament, la majoria d'estudis dins d'aquesta temàtica relacionats amb les plantes estan esbiaixats ja que s'han basat principalment en espècies invasores extremadament agressives competint amb espècies natives menys vigoroses de diferent forma de vida i/o en diferent estadi de desenvolupament (Vilà *et al.* 2004). A més, les habilitats competitives d'una espècie exòtica rarament han estat comparades amb l'efecte competitiu que les espècies natives tenen en l'espècie exòtica (Vilà & Weiner 2004).

1.3.2 Pressió de propàguls

Un altre factor que està fortament relacionat amb l'èxit de les invasions és la pressió de propàguls, altrament anomenat esforç d'introducció, que es pot mesurar com el nombre d'individus o propàguls alliberats o la freqüència d'introducció (Williamson 1999). Diversos estudis on es compara introduccions que han tingut èxit i introduccions que han fracassat d'ocells i mamífers han conclòs que l'èxit de les invasions augmenta en la mesura en què el nombre d'individus alliberats creix (Forsyth & Duncan 2001, Cassey *et al.* 2004). En plantes terrestres s'ha observat que els ecosistemes propers a les àrees urbanes, tenen una elevada riquesa d'espècies exòtiques (Pysek *et al.* 2003, Pino *et al.* 2005). Així doncs, les zones urbanes actuen com a font de les invasions tot incrementant la pressió de propàguls cap als ecosistemes més propers.

La pressió de propàguls determina l'èxit en l'establiment de les espècies no només mitjançant el nombre d'individus alliberats sinó també mitjançant el nombre de vegades en què l'espècie en qüestió ha estat alliberada. Així, un gran nombre d'alliberaments pot incrementar la probabilitat que alguns individus trobin les condicions necessàries per establir-se i augmentar la mida de la població (Sol *et al. en publicació*).

1.3.3 Invasibilitat dels ecosistemes

La invasibilitat també varia en funció dels ecosistemes ja que depèn de diversos factors biòtics (habilitats competitives de les espècies natives, presència d'herbívors, patògens i mutualistes) i ambientals (clima i règim de pertorbacions) de l'ecosistema receptor (Maron & Connors 1996, Lonsdale 1999, Tilman 1999, Davis *et al.* 2000).

Algunes espècies exòtiques poden veure's limitades en les noves àrees on han estat introduïdes com a conseqüència de les interaccions amb les espècies residents. En aquest sentit, si les espècies natives són millor competidores podran prevenir o frenar la invasió. Concretament, un estudi on es realitzà un meta-anàlisi dels efectes competitius en l'establiment de les espècies invasores a partir de 65 experiments realitzats en 24 estudis diferents ha comprovat que la competència de les espècies natives pot reduir l'establiment i la invasió d'espècies exòtiques (Levine *et al.* 2004). La presència de predadors, herbívors i parasitoids també pot frenar la invasió de les espècies exòtiques (Bossdorf *et al.* 2004, Levine *et al.* 2004). Tot i així, s'ha observat que normalment les espècies exòtiques, com per exemple *Clidemia hirta*, una espècie nativa de Costa Rica que envaeix els boscos tropicals de Hawaii, es veuen afavorides pel fet que en les noves àrees on han estat introduïdes no hi ha presents els seus enemics naturals (DeWalt *et al.* 2004). Així doncs la selecció pot afavorir les espècies exòtiques amb menys defenses però més competitives (Maron & Vilà 2001, Bossdorf *et al.* 2004, Hastings *et al.* 2005), fet que ha estat confirmat per una revisió recent d'experiments de competència entre espècies exòtiques i natives (Vilà & Weiner 2004). Malauradament, altres estudis recents que testen la hipòtesi que les espècies exòtiques han evolucionat cap a habilitats competitives més elevades que les de les espècies natives han obtingut resultats ambigus (Bossdorf *et al.* 2004). Altrament, s'ha vist que els organismes mutualistes poden afectar la dispersió de les espècies exòtiques ja que per exemple una espècie no podrà esdevenir invasora fins que els seus pol·linitzadors o altres mutualistes arribin a la zona receptora (Hastings *et al.* 2005).

En relació als factors ambientals, diversos estudis empírics han mesurat i comparat les taxes de dispersió d'espècies exòtiques en diversos hàbitats i en general han trobat que la taxa depèn de les característiques ambientals i del tipus d'hàbitat (Hastings *et al.* 2005). Concretament, els hàbitats ruderals són molt més susceptibles a les invasions que no pas els no ruderals perquè són hàbitats àmpliament pertorbats per causes humanes i on la pressió de propàguls és elevada (Tyser & Worley 1992, Vilà *et al.* 2001, Pysek *et al.* 2003). Per exemple, a la República Txeca, el 62.8 % de les invasions té lloc en hàbitats que han estat modificats per l'home (Pysek *et al.* 2003), i a la Península Ibèrica, on es calcula que un 13 % de la flora total és exòtica, la majoria de plantes naturalitzades es concentra en hàbitats ruderals (Vilà *et* al. 2001).

Altrament, els canvis en els usos del sòl, entesos com a transformacions de l'estat d'un ecosistema vers un altre en termes d'estructura, composició i funcions, també contribueixen significativament a augmentar la invasibilitat dels ecosistemes ja que s'ha observat que els usos del sòl més envaïts són aquells que directament o indirecta han sofert més canvis ambientals o que són menys "naturals" (Hobbs 2000). Els usos del sòl que hi havia en el passat són de vital importància en l'estudi de les invasions perquè la història d'usos del sòl determina les característiques inicials dels ecosistemes, i per tant la colonització dels primers estadis successionals (Yurkonis & Meiners 2004). Malgrat les evidències observacionals, aquest és un camp relativament poc explorat (Thomson *et al.* 1993). Per tal d'estudiar la interacció entre els canvis d'usos del sòl i les invasions, i per tal d'esbrinar quins factors històrics impulsen les invasions és necessari estudiar els dos fenòmens (usos del sòl i invasió) en un mateix context espaciotemporal (Vilà *et al.* 2003).

Les pertorbacions també poden incrementar la invasibilitat dels ecosistemes independentment de l'ús que tinguin (Hobbs & Humphries 1995, Hobbs 2000, D'Antonio & Corbin 2003). Les pertorbacions redueixen la coberta vegetal i/o els nivells de competència entre espècies, i augmenten la disponibilitat de certs recursos, creant per tant les condicions idònies perquè les espècies exòtiques puguin establir-se (Hobbs & Huenneke 1992, Hobbs & Humphries 1995, Davis *et al.* 2000).

Els ecosistemes són entitats dinàmiques i per tant la invasibilitat pot canviar al llarg del temps tal i com s'ha suggerit a partir de l'anàlisi de patrons d'invasió després de pertorbacions mitjançant cronoseqüències (Witowski & Wilson 2001). La invasibilitat disminueix en la mesura en què la successió avança (Rejmanek 1998, Lepart & Debussche 1991, Hobbs & Huenneke 1992). Per tant, considerant que la majoria d'espècies exòtiques segueixen una estratègia ruderal (Heywood 1998), es preveu que les comunitats més joves tindran una proporció més gran d'espècies exòtiques que no pas els estadis successionals més avançats. Malgrat que aquesta hipòtesi està fonamentada en models teòrics (Rejmanek 1989), no tots els estudis realitzats han trobat el mateix resultat. Les diferències en invasibilitat dels estadis successionals pot ésser explicada pels mecanismes de colonització de les espècies (Connell & Slatyer 1977). Amb el model de facilitació, l'entrada d'espècies exòtiques es veu facilitada per les espècies pioneres, un cop han canviat les característiques abiòtiques de l'ambient, fent-lo més adequat per la invasió de les espècies exòtiques. El model de tolerància prediu que la invasió pot esdevenir en qualsevol moment de la successió sempre i quan les espècies exòtiques puguin resistir nivells baixos de recursos sota competència intensa, fet que els permetrà predominar en els estadis més avançats de la successió (Mac Dougall & Turkington 2004). Finalment, si es dóna el mecanisme d'inhibició, en el qual les espècies pioneres inhibeixen l'establiment d'altres espècies, l'entrada d'espècies exòtiques es veurà limitada a l'ocurrència de pertorbacions locals que progressivament eliminen les espècies pioneres (Ward & Jennings 1990, Both *et al.* 2003). Tot i l'evident relació que hi ha entre els mecanismes de colonització i la invasibilitat de diferents estadis successionals, ambdós termes han estat freqüentment estudiats de manera separada (Davis *et al.* 2001), fent necessari l'ús d'un marc que integri la successió i la invasió que permeti estudiar com les espècies residents poden facilitar, inhibir o tolerar l'establiment de noves espècies (Davis *et al.* 2005).

1.4 Àmbit d'estudi: la conca mediterrània

Els ecosistemes mediterranis són un bon marc per estudiar les invasions biològiques ja que contenen aproximadament un 20 % de la diversitat total del planeta malgrat representar menys d'un 5 % de la seva superfície (Cowling *et al.* 1996). A més, es creu que en un futur proper experimentaran una gran pèrdua de diversitat com a conseqüència de la seva extremada sensibilitat a tots els components del canvi global, entre els quals destaquen els canvis d'usos del sòl i la introducció d'espècies exòtiques (Sala *et al*. 2000).

D'una banda, el paisatge de la conca mediterrània ha estat intensament modificat per les activitats humanes al llarg de la història (Naveh & Vernet 1991). Durant els últims 10000 anys, les activitats que més han modificat el paisatge són les pràctiques forestals, les pastures i el foc (Thornes 1996). Enguany, aquestes pràctiques tradicionals han esdevingut econòmicament inviables, i han donat lloc a l'abandonament dels conreus i a un gran despoblament rural (Debussche *et al.* 1999). De l'altra, el gran nombre d'espècies exòtiques que s'ha introduït tant de manera accidental com intencionada constitueix una forta amenaça per la diversitat d'aquests ecosistemes (Le Floc'h 1991). Altrament, l'aparició del turisme de masses a partir de l'any 1960 ha suposat la creació de nombrosos complexos turístics a la costa (Saurí *et al.* 2000) que sovint han actuat com a font de propàguls d'espècies exòtiques. Concretament, les àrees costaneres són altament susceptibles a la invasió d'espècies exòtiques com a conseqüència del seu clima suau, l'existència d'hàbitats altament pertorbats i l'ús de plantes exòtiques ornamentals que augmenten la pressió de propàguls exòtics (Sobrino *et al*. 2002). Així doncs, la introducció d'espècies exòtiques i el turisme de masses han contribuït a l'expansió de les espècies exòtiques ja que l'aparició d'ecosistemes modificats per l'home com per exemple la desaparició dels antics camps de conreu ha facilitat la colonització d'aquestes espècies (Pino *et al*. 2005).

1.5 Espècie d'estudi: *Cortaderia selloana*

Cortaderia selloana, altrament anomenada herba de la Pampa, es una gramínia perenne de llarga vida nativa d'Argentina, Brasil i Uruguai, i considerada invasora arreu del món. Es creu que va ser introduïda per primer cop a Europa per un agricultor escocès entre el 1775 i el 1862, però no es començà a produir comercialment fins el 1874 (Costas Lippmann 1977, Bosssard *et al.* 2000). La primera referència de la seva presència escapada del cultiu a Espanya data de l'any 1969 (Sanz-Elorza *et al.* 2004). Sovint es planta per utilitzar-la com a paravent i per prevenir l'erosió, però com a conseqüència de la gran vistositat dels seus plomalls s'ha emprat fonamentalment com a planta ornamental en jardineria, fet que ha contribuït a la seva naturalització arreu del món. Actualment, *C. selloana* ha escapat de les zones on es va plantar i està envaint tant zones antropitzades i pertorbades, com per exemple, marges de carreteres i habitats ruderals, com zones que són més o menys naturals o seminaturals, com per exemple, antics camps de conreu, matollars, herbassars i zones d'aiguamolls. A la Península Ibèrica, *C. selloana* té una tendència poblacional invasora ja que es troba plenament naturalitzada a Catalunya, País Basc, Cantàbria i Astúries fet que ha motivat la preocupació d'entitats del món de la conservació, de governs autonòmics i autoritats locals (Sanz-Elorza *et al.* 2004). *C. selloana* genera un fort impacte visual ja que les seves grans dimensions fan que la seva presència sigui molt clara, tot alterant fortament el paisatge. A més, pot amenaçar la diversitat nativa (Harradine1991, Domènech *dades no publicades*) i pot contribuir a augmentar el risc d'incendis degut a la gran acumulació de fullaraca seca i plomalls (Harradine 1991, Bossard *et al.* 2000).

Aquesta espècie té una forma de vida en forma de tofa i pot assolir de 2 a 4 metres d'alçada. Les fulles són d'un color blau-verdós, glauques, llargues (1 – 2 m), planes, estretes, doblegades pel nervi central i arrissades a la punta. Les fulles neixen de la base de la planta i els seus marges són serrats i aspres al tacte. Les canyes d'on surten les inflorescències, altrament anomenats plomalls o panicles, són iguals o lleugerament més llargues que la planta (50 – 100 cm), són molt vistoses i surten del final de la canya (Bolòs & Vigo 2001).

Morfològicament, *C. selloana* és una espècie ginodioica (Connor 1971), per tant, hi ha plantes que únicament produeixen flors femelles i d'altres, les hermafrodites, produeixen al mateix temps flors femelles i masculines. Però funcionalment és una espècie bàsicament dioica, per tant per reproduir-se cal que ambdós sexes estiguin relativament propers l'un de l'altre (Connor 1973). L'emergència dels panicles en les plantes hermafrodites comença de 5 a 10 dies abans que la de les femelles. El color dels plomalls pot variar de violeta suau a blanc platejat, però en cap cas el color és indicador del sexe de la planta. La floració té lloc des de mitjan agost a principis de setembre (Connor & Edgar 1974). *C. selloana* produeix una gran quantitat de llavors, que són molt petites i es dispersen fàcilment amb el vent (10^6 llavors en el cas de les femelles i 10^5 en el dels hermafrodites; Lambrinos 2002, Saura & Lloret 2005, Domènech *capítol 2*). Les llavors de les plantes femella són transportades més fàcilment i més efectivament a grans distàncies pel vent. Per contra, les llavors de les plantes hermafrodites tendeixen a caure directament a terra com a conseqüència que el seu papus està menys desenvolupat (Connor & Edgar 1974).

La biomassa subterrània de *C. selloana* pot ser tant o més important que l'aèria, doncs les arrels laterals es poden estendre 4 metres en diàmetre i 3.2 metres en profunditat, ocupant un volum total de sòl de 100 m^2. Les plantes s'estableixen a la primavera i requereixen sòls sorrencs, humitat i llum, encara que també pot créixer en zones amb ombra. Tolera un ampli ventall de condicions ambientals com per exemple la congelació hivernal, grans intensitats de llum, les temperatures càlides de l'estiu i una sequera moderada (Bossard *et al*. 2000). A més, com a conseqüència dels marges serrats de les fulles, es suposa que no està sotmesa a l'herbivoria (Sanz-Elorza *et al*. 2004).

Un cop establerta, l'eradicació total de *C. selloana* és una tasca força difícil. No es coneix cap control biològic efectiu tot i que l'efecte de la pastura ha obtingut resultats positius com a control d'aquesta espècie en boscos comercials de Nova Zelanda (Harradine 1991). Si és ecològicament viable, també es poden emprar herbicides. Als Estats Units s'ha obtingut bons resultats amb diversos controls químics, entre els quals destaca la utilització de glifosfat. El control físic de *C. selloana* és complex i costós ja que consisteix en arrencar les plantes de manera manual, i quan el volum és massa gran emprant eines adequades, com per exemple serres mecàniques. És molt important arrencar completament les arrels ja que de no ser així la planta podria rebrotar, per això es sol cavar al seu voltant o s'utilitzen tractors per arrencar-la (Sanz-Elorza *et al*. 2004).

1.6 Objectius i estructura de la tesi

L'objectiu principal d'aquest treball és identificar aquells factors ambientals, biòtics i històrics que poden facilitar l'entrada i l'establiment de *C. selloana*. Aquest objectiu s'ha assolit mitjançant anàlisis observacionals (inventaris), experiments de camp, d'hivernacle i de laboratori.

El cos de la tesi s'estructura en 5 parts que han estat subdividides en resum, introducció, material i mètodes, resultats, discussió i agraïments. També s'inclou un capítol referent a les conclusions generals que s'han extret a partir del treball realitzat. Per evitar repeticions, la descripció de l'espècie d'estudi es pot trobar a la *Introducció general*. Altrament, les referències bibliogràfiques dels cinc capítols han estat agrupades al final de la tesi. En el primer capítol, s'examina la invasió de l'espècie d'estudi en hàbitats ruderals i no ruderals, tot relacionant-la amb els factors biòtics i abiòtics dels hàbitats en qüestió. El segon capítol explora el lligam entre la història dels usos del sòl i la invasió de *C. selloana.* El tercer, estudia l'efecte de l'edat successional, el tipus de vegetació i la pertorbació del sòl en la invasió de *C. selloana*. El quart analitza la resposta de l'espècie a la competència i a l'estrès hídric. Finalment, el cinquè capítol és breu i analitza la germinació de *C. selloana* en diferents condicions ecològiques de laboratori. A continuació es detallen els objectius, les hipòtesis de treball i el mètode emprat en cada una dels capítols.

1.6.1 Invasió de *Cortaderia selloana* al llarg de la franja litoral mediterrània

Objectius:

- Analitzar quines característiques poblacionals i individuals de *C. selloana* estan associades als factors biòtics i/o abiòtics característics d'hàbitats ruderals.

- Determinar si els individus femella o hermafrodita difereixen en l'assignació de recursos i en els trets reproductius.

Hipòtesis:

Esperem que l'èxit de la invasió de *C. selloana*, mesurat com una elevada densitat total de plantes i un reclutament gran de nous individus, sigui major en els hàbitats ruderals que no pas en els no ruderals. També esperem que l'èxit estigui determinat per un biaix cap al nombre d'hermafrodites.

Metodologia:

Es va realitzar un inventari de 27 poblacions de *C. selloana* repartides al llarg de la costa catalana i situades en hàbitats ruderals i no ruderals.

1.6.2 Llegat històric dels usos del sòl i invasió de *Cortaderia selloana* en la regió mediterrània

Objectius:

- Establir si hi ha un lligam entre els tipus i canvis d'usos del sòl i el grau d'invasió.

- Determinar quin component dels canvis d'usos del sòl (nombre, direcció i trajectòria) facilita la invasió.

- Esbrinar si l'edat d'abandonament d'un camp agrícola incrementa la invasió.

- Comprovar si hi ha una relació positiva entre la presència de zones urbanes i la invasió.

Hipòtesis:

S'espera que els antics camps de conreu siguin l'ús del sòl més envaït ja que l'abandonament del camp pot facilitar la invasió mitjançant la creació de llocs oberts. També s'espera que els camps que hagin sofert més canvis d'usos del sòl siguin els més envaïts com a conseqüència de les pertorbacions repetides que han experimentat. Altrament, es creu que els camps que hagin romàs abandonats durant més temps estiguin més envaïts que els que hagin estat abandonats recentment. A més, la invasió disminuirà en la mesura en què la distància als focus potencials d'invasió (àrees urbanes) augmenti.

Metodologia:

Es va realitzar un inventari de *C. selloana* a 332 camps de la Rubina, una zona agrícola protegida dins el parc natural dels Aiguamolls de l'Empordà durant dos períodes consecutius (1998 i 2003). Mitjançant l'observació de fotografies aèries (1:22000 i 1:18000) i ortofotomapes (1:5000) dels anys 1956, 1970, 1987, 1996 i 2002 s'identificaren els usos del sòl de cada un dels camps.

1.6.3 Paper de l'estadi successional, el tipus de vegetació i pertorbació del sòl en la invasió de *Cortaderia selloana*

Objectius:

- Determinar si els primers estadis successionals són més susceptibles a la invasió de *C. selloana* i veure quin mecanisme successional (facilitació, tolerància o inhibició) determina la invasió.

- Analitzar si la invasió de *C. selloana* en estadis successionals avançats depèn del tipus de vegetació resident.

- Esbrinar si la invasió es veu facilitada per la pertorbació del sòl.

Hipòtesis:

Creiem que els primers estadis successionals seran més vulnerables a la invasió de *C. selloana* i que per tant el mecanisme successional de facilitació determinarà la invasió. També s'espera que la invasió en estadis successionals avançats no depengui de la vegetació resident. Finalment, es creu que la pertorbació del sòl facilitarà la invasió independentment de l'estadi successional i del tipus de vegetació.

Metodologia:

Es dugueren a terme diversos experiments de trasplantament de plàntules de *C. selloana* al camp. Concretament, se'n monitoritzà la supervivència i el creixement en parcel·les pertorbades i no pertorbades al llarg d'un gradient successional, en diferents tipus de vegetació i dins l'àrea d'influència d'espècies d'igual forma de vida que coexisteixen amb *C. selloana*.

1.6.4 Resposta a la competència i a l'estrès hídric de l'invasor *Cortaderia selloana* i de dues espècies natives amb qui pot coexistir

Objectius:

- Determinar si *C. selloana* és millor competidor que les espècies natives d'igual forma de vida amb les que pot coexistir *Festuca arundinacea* i *Brachypodium phoenicoides*.

- Analitzar la resposta de *C. selloana*, *F. arundinacea* i *B. phoenicoides* a l'estrès hídric.

Hipòtesis:

Creiem que *C. selloana* és millor competidora que les espècies natives *F. arundinacea* i *B. Phoenicoides*. Concretament, esperem que l'efecte de *C. selloana* en les espècies natives sigui més gran que no pas l'efecte contrari. A més, també esperem que el creixement de *C. selloana* no es vegi tan negativament afectat per l'estrès hídric com el de les altres espècies natives.

Metodologia:

Es realitzà un experiment de competència i un de resposta a l'estrès hídric amb *C. selloana*, *F. arundinacia* i *B. Phoenicoides*, amb testos ubicats a l'exterior del campus de la Universitat Autònoma de Barcelona.

1.6.5 Germinació de *Cortaderia selloana* en diferents condicions ecològiques

Objectius:

- Analitzar la germinació de *C. selloana* en diversos graus d'ombra, diverses textures de sòl, diferents disponibilitats d'aigua.

- Esbrinar si la germinació de *C. selloana* està afectada negativament pels patògens del sòl.

Hipòtesis:

Creiem que *C. selloana* pot tolerar un ampli ventall d'ambients ecològics, per tant les llavors podran germinar en totes les condicions estudiades. Altrament, la germinació d'aquesta espècie no estarà gaire afectada pels patògens del sòl.

Metodologia:

Diversos tests de germinació es dugueren a terme al laboratori per tal d'estudiar la germinació de *C. selloana* en diversos graus d'ombra, al llarg d'un gradient textural progressivament enriquit amb sorra, en diferents disponibilitats d'aigua i en un tractament d'estirilització del sòl.

1.7 Objectives and structure of the thesis

The aim of this study is to identify the environmental, biotic and historic factors that may ease *C. selloana* establishment. This objective has been achieved through observational analyses (field surveys) and field, greenhouse and laboratory experiments.

This thesis is structured in 5 parts which have been divided into abstract, introduction, material and methods, results, discussion and acknowledgements. We have also added a chapter about the general conclusions of the thesis. To avoid repetitions, the description of the study species can be found in the *Introducció general*. Moreover, references have been assembled at the end of the thesis. In the first chapter, we study *C. selloana* invasion in ruderal and non-ruderal habitats by linking the invasion with the abiotic and biotic factors of these habitats. The second chapter, studies the relationship between land-use history and *C. selloana* invasion. In the third chapter, I study the role of successional age, vegetation-type and soil disturbances on *C. selloana* invasion. The fourth chapter analyses *C. selloana* response to competition and water stress. Finally, the fifth chapter is short and it analyses *C. selloana* seed germination under different ecological conditions in the laboratory. In the following paragraphs we explain the objectives, hypothesis and the methods of each chapter.

1.7.1 *Cortaderia selloana* invasion across a Mediterranean coastal strip

Objectives:

- Analyse which population and plant characteristics of *C. selloana* are associated to the biotic and abiotic factors of ruderal habitats.

- Determine if female and hermaphrodite plants have a different resource allocation or reproductive traits.

Hypotheses:

We expect that *C. selloana* invasive success (i.e. high total density and plant recruitment) will be higher in ruderal habitats than in non-ruderal habitats. We also expect that invasive success will be determined by a bias towards the number of hermaphrodites.

Methods:

We conducted a field survey of 27 *C. selloana* populations in ruderal and non-ruderal coastal habitats.

1.7.2 Historical land-use legacy and *Cortaderia selloana* invasion in the Mediterranean region

Objectives:

- Find out if there is an association between land-use types, land-use changes and *C. selloana* invasion.

- Determine which land-use component (number, direction and trajectory of land-use changes) enhances invasion.

- Study if successional age enhances *C. selloana* invasion.

- Check if there is a positive relationship between urban areas and invasion.

Hypotheses:

We expect old-fields to be the most invaded land-use because land abandonment provide open windows for the establishment of new species. We also expect that fields that have suffered more land-use changes will be the most invaded because of the multiple disturbances they have experienced. Moreover, we believe that the longer a field is abandoned, the more invaded it will be. Finally, we expect invasion to decrease as the distance to urban areas, which can be a potential focus of invasion, increases.

Methods:

We made a field survey of *C. selloana* in 332 fields from La Rubina, an agricultural protected land within the Parc Natural dels Aiguamolls de l'Empordà. We also used invasion data of a previous study which was conducted in the same study site. Moreover, we identified land-use types of all fields through the examination of aerial photographs (1:22000 and 1:18000) and ortho-photo maps (1:5000) from the years 1956, 1970, 1987, 1996 and 2002.

1.7.3 The role of successional stage, vegetation type and soil disturbance on *Cortaderia selloana* invasion

Objectives:

- Determine if early successional stages are more susceptible to *C. selloana* invasion than later successional stages and find out which successional mechanism (tolerance, facilitation and inhibition) rules invasion.

- Analyse if *C. selloana* invasion in the most advanced successional stage depends on the vegetation-type.

- Study if *C. selloana* invasion is enhanced by soil microdisturbances.

Hypotheses:

We believe that early successional stages will be more susceptible to *C. selloana* invasion than later stages. Therefore, invasion will be ruled by the successional mechanism of facilitation. We also expect that *C. selloana* invasion in later successional stages will not depend on vegetation-type. Finally, we expect that soil disturbances will enhance *C. selloana* invasion, independently of successional stage and vegetation-type.

Methods:

We conducted several transplant experiments in which we monitored survival and growth of transplanted *C. selloana* seedlings in disturbed and non-disturbed plots throughout a successional gradient, in different vegetation-types and within the area of influence of coexisting species with similar growth.

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

Objectives:

- Determine if *C. selloana* is a superior competitor than *Festuca arundinacea* and *Brachypodium phoenicoides*.

- Analyse *C. selloana F. arundinacea* and *B. phoenicoides* plant performance under water stress.

Hypotheses:

We believe that *C. selloana* is a superior competitor than the native species *F. arundinacea* and *B. phoenicoides*. Specifically, we expect that the effect of *C. selloana* on the 2 native species will be higher than viceversa. We also expect that *C. selloana* plant performance will not be as negatively affected by water stress than that of native species.

Methods:

A competition and a water stress pot-experiment with seedlings of *C. selloana* and two native species of the same functional group and life history stage, *F. arundinacea* and *B. phoenicoides*, were conducted outdoors at the Universitat Autònoma de Barcelona campus.

1.7.5 *Cortaderia selloana* seed germination under different ecological conditions

Objectives:

- Analyse *C. selloana* seed germination under different degrees of shading, soil textures and water availability.

- Determine if *C. selloana* seed germination is negatively affected by soil pathogens.

Hypotheses:

We expect *C. selloana* to tolerate a wide range of ecological conditions. Therefore, seeds will germinate under all the studied conditions. Moreover, *C. selloana* seed germination will not be negatively affected by soil pathogens.

Methods:

An array of germination tests were conducted in the laboratory in order to study *C. selloana* seed germination under several degrees of shading, under a textural gradient which had progressively been enriched with sand, under different water availabilities and under a soil sterilization treatment.

2. *Cortaderia selloana* invasion across a Mediterranean coastal strip

2.1 Abstract

Biological invasions are a major cause of biodiversity loss. Successful invasions depend on habitat characteristics and plant traits that may also differ between sex forms. For example, in gynodioecious species females need a compensatory mechanism to increase their reproductive success such as high seed production, in order to be maintained in natural populations. Given this scenario, the invasive success of these species may be limited by pollen availability if females become too abundant. Invasion success also depends on biotic and abiotic habitat factors such as soil nutrient pulses, species richness and disturbances. Ruderal habitats, where propagule pressure of alien species is very high and disturbances are frequent have a higher degree of invasion than non-ruderal habitats. However, the specific ecological factors (i.e. biotic and abiotic) driving successful invasions in ruderal habitats have not been analysed in detail.

We assessed the invasive success of *Cortaderia selloana*, an alien gynodioecious plant species native to South America, by comparing plant and population performance in ruderal and non-ruderal habitats across a Mediterranean coastal strip. We compared if population characteristics and plant performance were associated to biotic and abiotic habitat factors. Moreover, we explored if female and hermaphrodite plants differed in resource allocation. We expected a better performance of *C. selloana* in ruderal habitats than in non-ruderal habitats, not only due to a higher disturbance regime but also due to the absence of a high number of female plants, indicating that these ruderal populations are not limited by pollen availability.

The most frequently invaded habitats were ruderal which had less total soil N, organic C, total plant cover and higher percentages of bare ground and macro-elements. *C. selloana* recruitment in these habitats was very high (the proportion of juvenile plants was 0.54 ± 0.09). In consequence, *C. selloana* populations in ruderal habitats were smaller, produced less panicles, and demonstrated a low reproductive effort (i.e. number of panicles/plant volume), yet these characteristics did not differ between female and hermaphrodite plants. Nevertheless, females produced more seeds, which were also more viable than those of hermaphrodites. Some biotic and abiotic habitat factors were correlated with population characteristics. Total plant density was positively correlated with the percentage of bare ground, and negatively with pH and richness of plant functional groups. The proportion of juvenile individuals also increased with the percentage of bare ground. In contrast, the sex ratio (i.e. number of female plants/number of hermaphrodite plants) decreased with the percentage of bare ground. Overall, ruderal habitats provide the most suitable conditions for *C. selloana* invasion due to their characteristic abiotic and biotic habitat factors such as the existence of bare ground, low pH values, low richness of functional groups and to the absence of a bias towards the number of female plants.

Keywords: alien plant species, disturbances, gynodioecy, plant functional-group, ruderal habitat.

2.2 Introduction

The increasing number of intentional or accidental human introduction of species that is occurring around the world is promoting biological invasions, which are threatening the conservation of biodiversity through direct and indirect impacts on native species and the modification of ecosystem functions (Vitousek 1994, Enserink 1999, Mack & Lonsdale 2001, Cole & Landres 2004).

It is known that some alien plant species have special reproductive traits that seem to make them successful invaders (i.e. invasiveness) such as a large production of viable seeds and the ability to germinate in a wide range of environmental conditions (Noble 1989, Holdgate 1996, Gordon 1998). Invasiveness can also differ between sex forms because some plant characteristics and attributes such as plant morphology, ecology or growth can vary in relation to sex. For instance, it has been shown that male and female individuals in native dioecious plant species usually differ in their phenology, plant biomass and resource allocation. Vegetative growth of males is often greater than that of females, whereas females have a greater investment in sexual reproduction than males (Putwain & Harper 1972, Meagher & Antonovics 1982, Obeso 2002). Similarly, vegetative growth and reproductive success of males of androdioecious species may also differ from that of hermaphrodites because males only produce pollen while hermaphrodites produce both seed and pollen (Lloyd 1975). A similar pattern is found in gynodioecious species in which hermaphrodite individuals can contribute genes to the next generation through both the male (pollen) and female function (seeds), whereas female individuals are at disadvantage because they can only transmit their genes through seeds. Therefore, both sexual types can only be maintained in natural populations provided that females have compensatory mechanisms that increase their reproductive success, such as a high flower and seed production, a superior vegetative biomass or a lower reproductive effort (McCauley & Taylor 1997, Molina-Freaner & Jain 1992, Williams *et al*. 2000). Invasion success may also depend on the sex ratio of the alien's population since recruitment can be negatively affected by a limitation of pollen, which might occur when females are too abundant (Williams *et* al. 2000). However, no study has tested differences in invasiveness between plant sex forms.

Invasion success not only depends on the characteristics of alien species but also on invasibility, the ecosystem's intrinsic capacity to favour species' survival independently of their introduction rates (Lonsdale 1999). Invasibility depends both on abiotic and biotic factors. Yet it is not always clear which ecosystem characteristics favour or hinder the invasion of a particular alien species because performance of a species depends on multiple ecological factors (Hobbs & Humphries 1995). On one hand, soil nutrient pulses and climatic conditions are reported to favour ecosystem invasibility (Rejmánek 1989, Hobbs & Huenneke 1992, Bastl *et al.* 1997, Davis *et al.* 2000). Ecosystem invasibility may increase as there are more resources available to invaders (Davis *et al.* 2000) and decrease with environmental harness (Davis *et al.* 1999, Higgins *et al.* 1999). On the other hand, species-rich ecosystems are often predicted to be more resistant to plant invasions than species-poor ecosystems as a result of an efficient and complete use of all the available resources (Levine & D'Antonio 1999). In addition, disturbances can also promote invasions either through a reduction of vegetal cover or levels of competition, or through an increase in the availability of specific resources (Hobbs 1989, Hobbs & Humphries 1995).

Ruderal habitats, defined as rubbish or debris deposits are highly invaded (Lincoln *et al.* 1998). For example, in the alien flora of the Czech Republic 62.8 % of invasions occur in human-made habitats while 11.0 % have been recorded in seminatural habitats (Pysek *et al.* 2003). Similarly, in Spain from 637 naturalised plant species (13 % total flora), most of them (44.67 %) are found in ruderal and disturbed habitats (Vilà *et al*. 2001). Ruderal habitats are characterized by high propagule pressure and frequent disturbances, which increase their susceptibility to plant invasions with respect to unaltered habitats (Tyser & Worley 1992). However, despite differences in the degree of invasion between ruderal and non-ruderal habitats, the specific factors driving more successful invasions in ruderal habitats have not been analysed in detail. It would be necessary to relate invasion characteristics with the biotic and abiotic factors of these habitats.

Ruderal habitats are a common element in the Mediterranean landscape because of widespread modification by humans (Naveh & Vernet 1991). Most of the alien species that have been intentionally or accidentally introduced are able to successfully establish and invade ruderal habitats (Le Floc'h 1999) For example, *Cortaderia selloana* (Pampas grass), an invasive plant species native to South America, is invading disturbed and ruderal habitats of many Mediterranean coastal, riverine and marshland areas. Unfortunately, the specific biotic and abiotic drivers of successful invasions of *C. selloana* have not been explored. For this reason, after an initial assessment of *C. selloana* invasion in ruderal and non-ruderal habitats spread along the Catalan Mediterranean coastal strip (NE Spain) we compared if population characteristics and plant performance were associated to biotic and abiotic habitat factors in ruderal and non-ruderal habitats. In addition, we explored if female and hermaphrodite plants differed in their resource allocation and reproductive traits such as seed production and viability, panicle production and reproductive effort. We expected a better performance of *C. selloana* (e.g. high total plant density and recruitment) in ruderal habitats than in non-ruderal habitats. Performance should also be influenced by a high number of hermaphrodite plants because if females are too abundant, *C. selloana* populations will be limited by pollen availability, decreasing both seed production and seedling recruitment.

2.3 Material and methods

2.3.1 Field survey

From mid August to mid September 2004, at the stage of plant flowering, we conducted a survey of 27 *C. selloana* introduced populations in a Mediterranean coastal strip of Catalonia (NE Spain). Coordinates and altitude above sea level of each population were measured with a GPS. Mean annual temperature ranged from 15 to 17 ºC and mean annual rainfall varied from 400 to 700 mm. The habitat was classified "a priori" as ruderal (i.e. trampled areas, waste deposits, soil disturbed) or non-ruderal (i.e. old fields, grasslands, woodlands and marshes) (Table 1).

Table 1. *Cortaderia selloana* introduced populations surveyed in a Mediterranean coastal strip of Catalonia (NE Spain).

		UTM coordinates			
Code	**Location**	**X**	**Y**	**Altitude (m.a.s.l.)**	**Habitat**
1	Empordà I	510750	4679323	0	Non-ruderal
2	Empordà II	512231	4679854	1	Non-ruderal
3	Empordà III	507650	4671121	0	Non-ruderal
4	Empordà IV	509682	4676255	0	Non-ruderal
5	Blanes I	477828	4611642	32	Ruderal
6	Blanes II	482492	4614647	20	Ruderal
7	Blanes III	482928	4614957	20	Ruderal
8	Blanes IV	484952	4615929	23	Ruderal
9	Blanes V	489996	4617685	103	Ruderal
10	Blanes VI	492372	4618622	131	Ruderal
11	Blanes VII	484781	4620686	163	Ruderal
12	Mollet	434621	4599996	85	Ruderal
13	Parets	436127	4601152	73	Non-ruderal
14	Matadepera	419200	4605353	405	Non-ruderal
15	Terrassa I	419189	4599821	239	Ruderal
16	Terrassa II	420590	4599318	242	Ruderal
17	Sant Boi	420436	4577016	23	Ruderal
18	Llobregat I	419718	4570752	3	Non-ruderal
19	Llobregat II	419587	4569946	0	Non-ruderal
20	Llobregat III	420647	4570227	3	Non-ruderal
21	Llobregat IV	418715	4569935	0	Non-ruderal
22	Llobregat V	417996	4569770	0	Non-ruderal
23	Llobregat VI	418189	4570365	0	Non-ruderal
24	Llobregat VII	421225	4570632	5	Non-ruderal
25	UAB	424524	4594041	171	Ruderal
26	Calafell	379153	4560457	350	Non-ruderal
27	Vinaròs	287582	4485612	6	Non-ruderal

Populations were less than 35 km from the seashore and they were at least 1 km apart; the same distance chosen in a previous study that used herbarium records to determine the expansion history of *C. selloana* in California (Lambrinos 2001). A population was identified as a group of 5 or more plants present in an area where *C. selloana* could really spread. Therefore, populations situated in road sides or agricultural field margins were not included in our survey.

Vegetation characteristics of each invaded site were estimated by the point-intercept method conducted in one 50-m line transect in the centre of each population. We identified all functional groups (i.e. grasses, herbs, shrubs, vines and trees) found every 50 cm. Plant functional group richness (i.e. number of functional groups), total plant cover and percentage of bare ground was calculated in each site. In each site we randomly took 5 soil samples of the first 20 cm mineral soil with a 6 cm diameter drill. Soil samples of each site were pooled after air-drying on flat trays in the laboratory and we analysed total soil C, total N, $CaCO_3$, pH and texture. Total C and N was conducted with an elemental analyser of CE Instruments (NA2100 model). Organic carbon was calculated by substracting the C of calcium carbonate ($CaCO_3$) from the total C. Calcium carbonate was analysed following the pressure calcimeter method. pH was measured with a glass pH-meter in a soil suspension with water 1:2.5 (w:v). Texture was analysed following the pipet method (Gee & Bauder 1986). Percentage of macro-elements (i.e. particle size > 2-mm) was also determined by dividing the macroelements weight of the soil sample by the total weight of the sample.

In each site, we counted all *C. selloana* plants and measured the area of occupation with a GPS to estimate *C. selloana* density. When a population had more than 500 plants or when the invaded area was too large (> 4000 m^2) or highly impenetrable, *C. selloana* density was estimated by counting all plants inside two randomly chosen 20 x 20 m plots. We also randomly sampled 30 plants and measured their height, two perpendicular plant diameters, the number of panicles and determined their sex. Moreover, the sex and the number of panicles of 20 randomly chosen plants were additionally recorded. If the population had less than 30 plants, all plants were sampled. Plant volume (V) was estimated as $V = 2/3\pi R^2 H$, where “R” is the mean plant radius which was estimated with the two perpendicular diameters and “H” is its height.

Therefore, variables could be classified into population characteristics, plant characteristics, and abiotic and biotic site variables. Population characteristics included plant density, sex ratio (i.e. ratio between the number of female and hermaphrodite plants) and the proportion of juvenile plants, measured as the ratio between juvenile plants (i.e. had not produced panicles yet) and the total number of plants. Plant characteristics included plant volume, number of panicles per plant and reproductive effort (i.e. number of panicles/plant volume). Abiotic site variables referred to altitude and soil characteristics (i.e. total soil N, total organic C, pH, percentage of macroelements and percentages of sand, silt and clay). Finally, habitat type, total cover (without including *C. selloana*), percentage of bare ground and richness of plant functional groups were assembled into biotic site variables.

2.3.2 Seed production and viability

To compare seed production and viability of female and hermaphrodite plants, a field survey was conducted in Empordà I location (Table 1) in summer 2003. We identified the sex of all *C. selloana* individuals before seed formation. Fifty female and 50 hermaphrodite mature individuals of *C. selloana* were randomly selected in order to determine their seed production. From 25 randomly selected plants of each sex a panicle was collected and stored in a paper bag. A piece of panicle was collected from the remaining selected female and hermaphrodite plants and they were also stored in paper bags. Although panicle harvesting was done before seed dispersal, it was performed very carefully in order to avoid seed loss.

The whole collected panicles were air-dried at 70ºC to constant weight and weighed without the stem. The total number of seeds (Y) within a panicle was estimated by its dry weight (X) with the linear regressions obtained with the collected pieces of panicle: $Y = -80.30 + 3571.06X$, $n = 25$, $R^2 = 0.87$ ($F_{1, 23} = 158.67$, $P < 0.0001$) for female and $Y = 51.93 + 769.31X$, $n = 24$, $R^2 = 0.22$. ($F_{1, 22} = 6.33$, $P = 0.02$) for hermaphrodite plants.

To quantify differences in seed germination between female and hermaphrodite plants, 10 fresh panicles of 12 female and 12 hermaphrodite individuals of *C. selloana* from Empordà I location (Table 1) were collected. Ten seeds of each panicle per plant were placed in 5 cm Ø petri dishes on top of one layer of autoclaved filter paper in standard laboratory conditions. Petri dishes were moved twice a week to avoid position effects and to guarantee that all the dishes received the same amount of light and that were growing under homogeneous conditions. Paper filter was continuously maintained saturated with distilled water. Germination was recorded every day during one month and germinated seeds were subsequently removed from the petri dish. Seeds were considered as germinated when the radicle or coleoptile were visible.

2.3.3 Statistical analysis

Characteristics of habitats

In order to characterize both ruderal and non-ruderal habitats, unpaired t-tests were used to compare differences in abiotic and biotic variables. Total N was transformed as $1/(X)^{½}$ and total cover was log (1+X) transformed to meet the assumptions of parametric statistical analysis.

Demography of *C. selloana* invasion

An unpaired t-test was used to compare total plant density, sex ratio and JI/TI between ruderal and non-ruderal habitats. Differences between habitats in total plant volume, number of panicles per plant and reproductive effort were analysed with a nested ANOVA with habitat as a fixed factor and population nested within habitat as a random factor. Total plant density was log (X+1) transformed to homogenize variances.

To explore differences in resource allocation between female and hermaphrodite plants across all populations a nested ANOVA with sex as a fixed factor and population nested within sex as a random factor was used to compare plant volume, number of panicles and reproductive effort of both sexes.

Differences in seed production between both sexes were analysed with an unpaired t-test. A nested ANOVA with sex as a fixed factor and plant nested within sex as a random factor was used to analyse differences in percentage germination between female and hermaphrodite plants. Percentage germination was transformed as arcSin (1-X) to meet the assumptions of homogeneity of variance.

In order to find out if either plant density or the proportion of juvenile plants depended on the sex ratio, we conducted a regression analysis with sex ratio as the independent variable and plant density and the proportion of juvenile plants as dependent variables.

***C. selloana* invasion patterns related to biotic and abiotic variables**

In order to explore the invasion pattern of *C. selloana*, we conducted a Principal Components Analysis (PCA) in which we included *C. selloana* population variables and the biotic and abiotic habitat factors in order to detect correlations and to find out how *C. selloana* populations grouped. Previously, correlations between variables were tested by conducting a contingency table. When 2 variables were strongly correlated (i.e. correlation coefficient > 0.8) we only included one of them in the PCA. We also analysed the association between *C. selloana* demographic characteristics as dependent variables, and biotic and abiotic habitat factors as independent variables with a stepwise regression analysis. As mentioned before, plant density, total N and total cover were transformed in order to meet the assumptions of homogeneity of variances.

2.4 Results

2.4.1 Characteristics of habitats

Ruderal habitats were characterized by significantly having less total soil N, less soil organic C and a higher percentage of macro-elements than non-ruderal habitats (Table 2). Altitude, pH and percentages of sand, silt and clay did not significantly vary between ruderal and non-ruderal habitats.

Significant differences in total cover and percentage of bare ground were also found between habitats. Ruderal habitats had a lower total cover and a higher percentage of bare ground than non-ruderal habitats (Table 2). However, richness of plant functional groups and did not significantly vary between habitats.

Table 2. Biotic and abiotic habitat characteristics of ruderal and non-ruderal habitats invaded by *C. selloana* across a Mediterranean coastal strip.

	Ruderal	**Non-ruderal**	**t_{25}**	***P***
Altitude (m)	106.09 ± 26.69	58.19 ± 31.95	1.07	0.29
Total N (%)	0.08 ± 0.01	0.14 ± 0.02	2.87	0.008
Soil organic C (%)	0.73 ± 0.22	2.74 ± 0.24	5.79	0.0001
Macro elements (%)	39.1 ± 3.6	16.1 ± 4.8	3.52	0.002
pH	8.08 ± 0.12	8.23 ± 0.05	0.71	0.48
Sand (%)	62.21 ± 6.33	68.87 ± 4.14	0.92	0.37
Silt (%)	14.12 ± 3.75	11.92 ± 2.62	0.50	0.62
Clay (%)	21.46 ± 2.02	16.83 ± 1.64	1.79	0.09
Total cover (%)	51.7 ± 5.0	112.8 ± 12.5	3.89	0.0007
Bare ground (%)	44.5 ± 4.1	10.5 ± 2.5	7.53	< 0.0001
Richness of plant functional groups	3.0 ± 0.2	3.5 ± 0.3	1.43	0.17

2.4.2 Demography of *C. selloana* invasion

C. selloana populations in ruderal habitats had a significantly higher plant density and proportion of juvenile individuals than populations in non-ruderal habitats. Consequently, *C. selloana* plants in ruderal habitats were on average 1.6 times smaller than plants in non-ruderal habitats (Figure 1, Table 3). Although plant volume distribution of *C. selloana* had a reversed-J shape in both habitats, it was more skewed in non-ruderal than in ruderal habitats (Figure 2). Given the lower plant volume of *C. selloana* in ruderal habitats, panicle production was approximately 3 times and reproductive effort 2.7 times lower than in non-ruderal habitats (Figure 1, Table 3). Finally, only marginal significant differences were found for the sex ratio towards a hermaphrodite bias in ruderal (0.63 ± 0.18) compared to non-ruderal (1.03 ± 0.16) habitats ($t_{25} = 1.93$, $P = 0.07$).

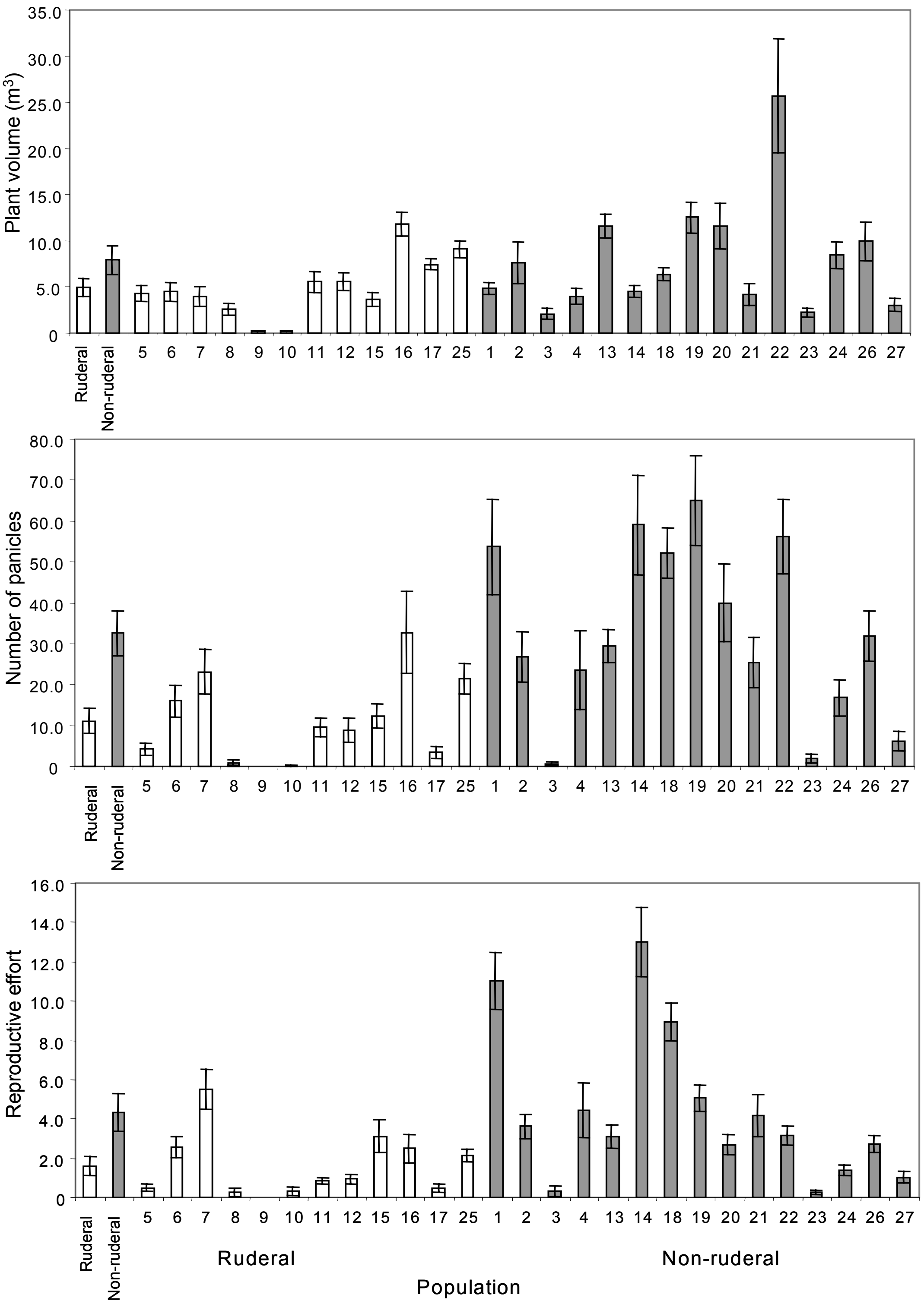

Figure 1. Plant volume, number of panicles per plant and reproductive effort (mean ± s.e.) of *C. selloana* in ruderal (white bars) and non-ruderal (black bars) habitats across a Mediterranean coastal strip. Each bar represents the mean of a population according to Table 1. The two initial left-hand bars of the histograms are the habitat means (i.e. the average of the population means for each habitat).

Table 3. *C. selloana* population and plant characteristics in ruderal and non-ruderal habitats across a Mediterranean coastal strip.

	Total density (plants/ha)	**Proportion of juvenile plants**	**Number of panicles**	**Plant volume (m^3)**	**Reproductive effort**
Ruderal	1429.8 ± 540.7	0.54 ± 0.09	11.0 ± 3.0	4.9 ± 1.0	1.6 ± 0.5
Non-ruderal	253.1 ± 63.4	0.24 ± 0.07	32.6 ± 5.5	8.0 ± 1.6	4.3 ± 1.0
(t_{25}, *P*)	(2.40, 0.02)	(2.64, 0.01)			
($F_{25,\,581}$, *P*)			(9.07, 0.001)	(7.54, <0.0001)	(15.40, 0.001)

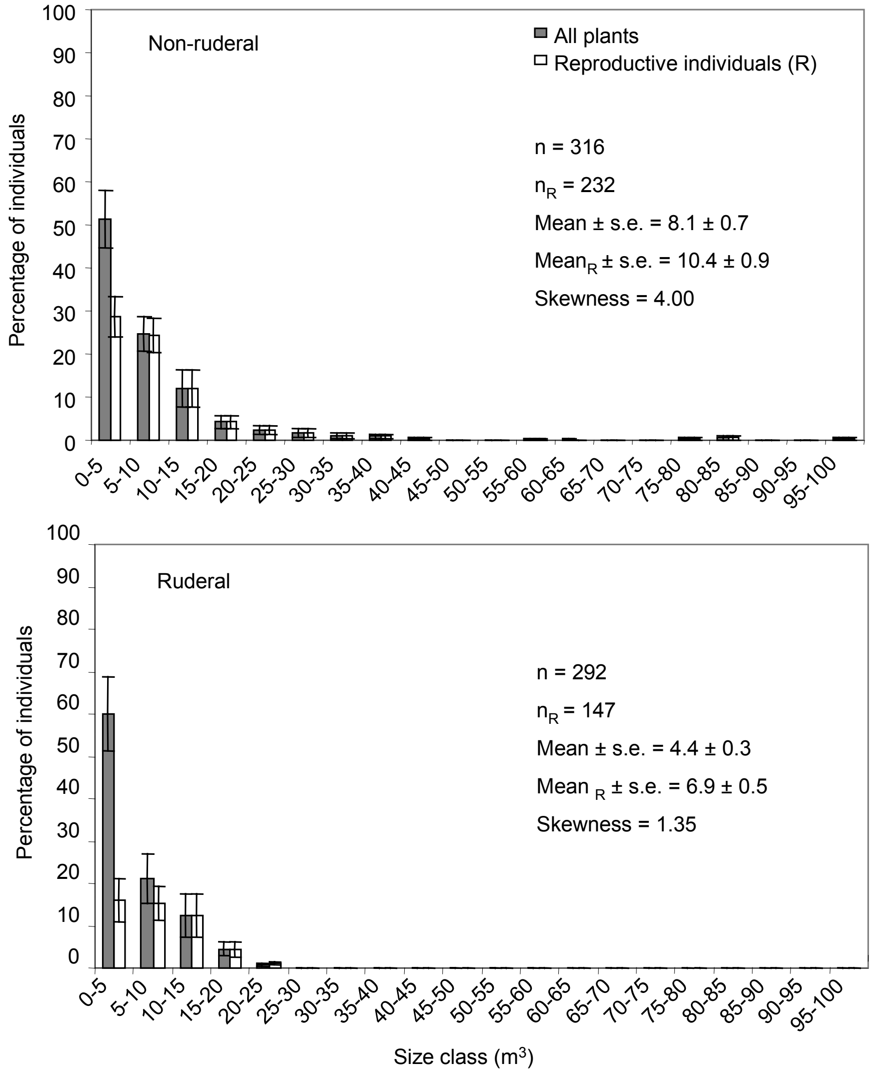

Figure 2. Plant size distribution (mean ± s.e.) of *C. selloana* invasion in non-ruderal and ruderal habitats across a Mediterranean coastal strip.

With respect to plant sex characteristics, no significant differences between female and hermaphrodite plants were found for plant volume ($F_{23, 319} = 1.30$, $P = 0.16$), the number of panicles ($F_{23, 457} = 1.53$, $P = 0.06$) and reproductive effort ($F_{23, 319} = 0.79$, $P = 0.74$). However, seed production of female panicles was significantly higher than seed production of hermaphrodite panicles ($t_{49} = 7.07$, $P < 0.0001$). Female panicles produced on average (± s.e.) 52539.9 ± 6517.0 seeds whereas hermaphrodite panicles produced 5015.1 ± 1037.2 seeds. Overall, a female plant produced 10.5 times more seeds than a hermaphrodite plant. Significant differences were also found between seed germination of female and hermaphrodite plants ($F_{1, 216} = 1296.66$, $P < 0.001$). Percentage germination of seeds from female plants (71.4 ± 3.1 %) was 5.1 times larger than that of hermaphrodite plants (14.0 ± 2.3 %). Moreover, percentage germination not only depended on sex but also on the mother plant ($F_{22, 216} = 54.29$, $P < 0.001$).

Finally, 18.7 % of the variation in plant density and 33.0 % in the proportion of juvenile plants was explained by the sex ratio ($F_{1, 25} = 12.29$, $P = 0.002$ and $F_{1, 25} = 5.76$, $P = 0.02$, respectively). As the sex ratio became biased towards the number of females, both the JI/TI and plant density decreased (Figure 3).

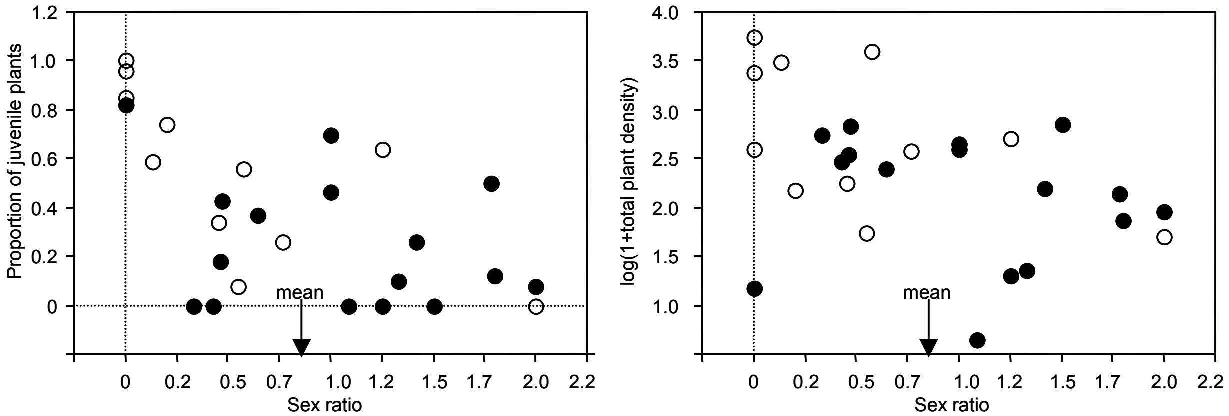

Figure 3. Correlation between the proportion of juvenile *C. selloana* plants and total plant density with the sex ratio (ratio between the number of females and the number of hermaphrodites) in non-ruderal (filled circles) and ruderal (open circles) habitats. The arrow indicates the mean sex ratio considering all populations.

2.4.3 *C. selloana* invasion patterns related to biotic and abiotic variables

The correlation matrix revealed that there was a strong, negative correlation between percentage of sand and either the percentage of silt (correlation coefficient = 0.97) or the percentage of clay (correlation coefficient = 0.91). Therefore, only the percentage of sand was used as a variable.

The PCA explained 50.90 % of the variance. In the first component (PCA_1), which explained the 33.61 % of the variance, *C. selloana* populations clustered as a response to habitat type (Figure 4).

The variability of population parameters explained by biotic and abiotic habitat factors ranged from 21.6 % to 55.8 %. With the overall model, plant density was positively correlated to the percentage of bare ground and it was negatively correlated with pH and richness of plant functional groups ($F_{3,\ 23} = 9.68$, $P = 0.0003$) (Table 4, Figure 5). The remaining 8 variables did not significantly contribute to explaining the variation in total plant density.

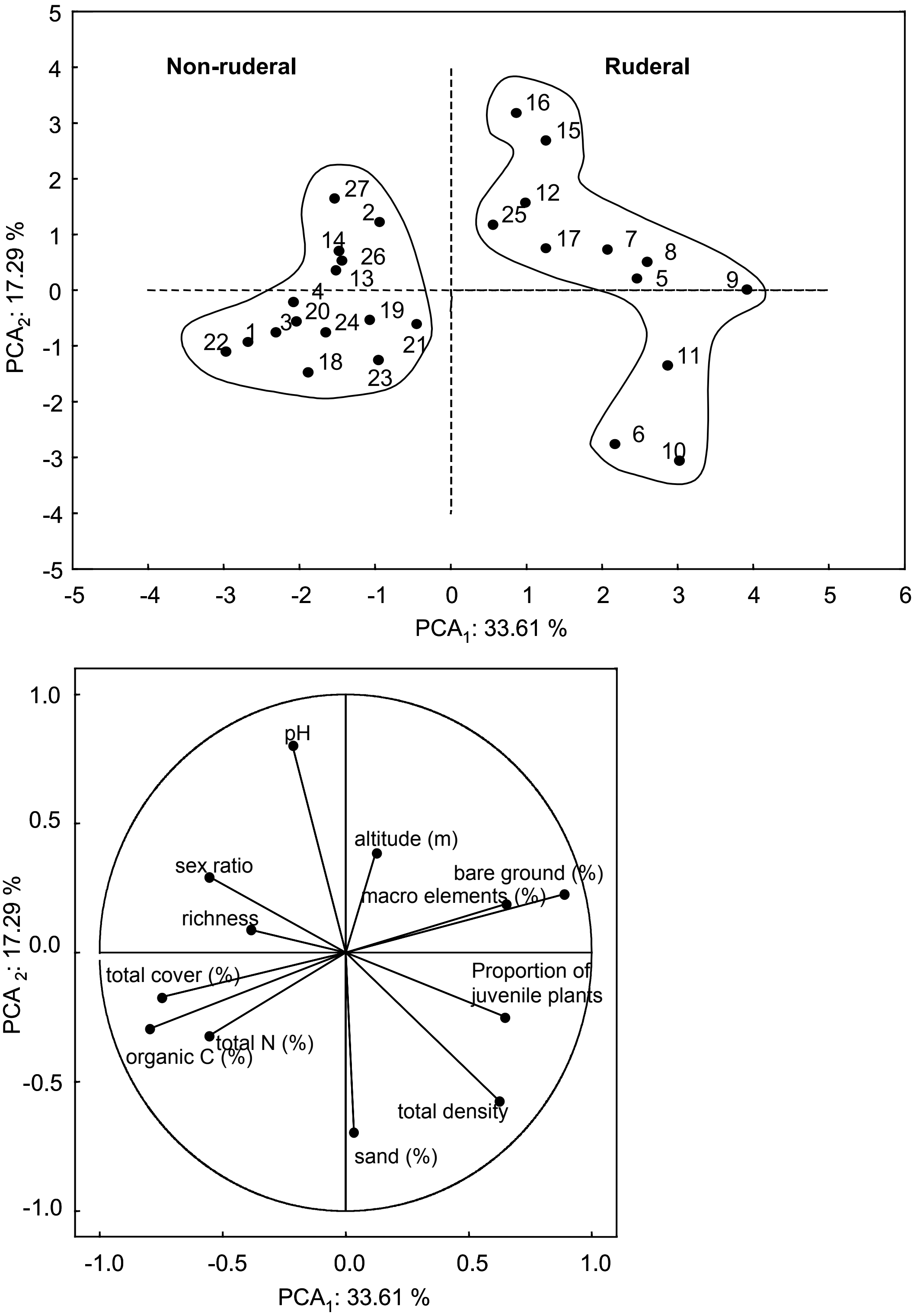

Figure 4. Projections of *C. selloana* populations and biotic, abiotic and population invasion variables in the factor-plane extracted with a PCA. Numbers indicate the population sampled according to Table 1.

Table 4. Stepwise regression between demographic parameters of *C. selloana* and biotic and abiotic significant habitat factors.

Dependent variable	**Predictors**	**Coefficient**	***F*-value**	**% var.[a]**
Plant density	Intercept	9.86	11.24	
	Percentage of bare ground	0.01	6.33	34.4
	pH	- 0.81	4.94	46.3
	Richness of plant functional groups	- 0.37	9.37	55.8
Proportion of juvenile plants	Intercept	0.18	4.09	
	Percentage of bare ground	0.01	8.17	21.6
Sex ratio	Intercept	1.14	39.56	
	Percentage of bare ground	- 0.01	4.90	40.5

[a] % var. = % cumulative variation explained.

The proportion of juvenile plants also depended positively on the percentage of bare ground ($F_{2, 24} = 8.17$, $P = 0.008$) (Table 4, Figure 5). Finally, of the 11 variables we considered, only the percentage of bare ground contributed significantly ($F_{1, 25} = 4.90$, $P = 0.04$) to explaining the variation in sex ratio (Table 4). As the percentage of bare ground increased, populations were less biased towards the number of female plants (Figure 5).

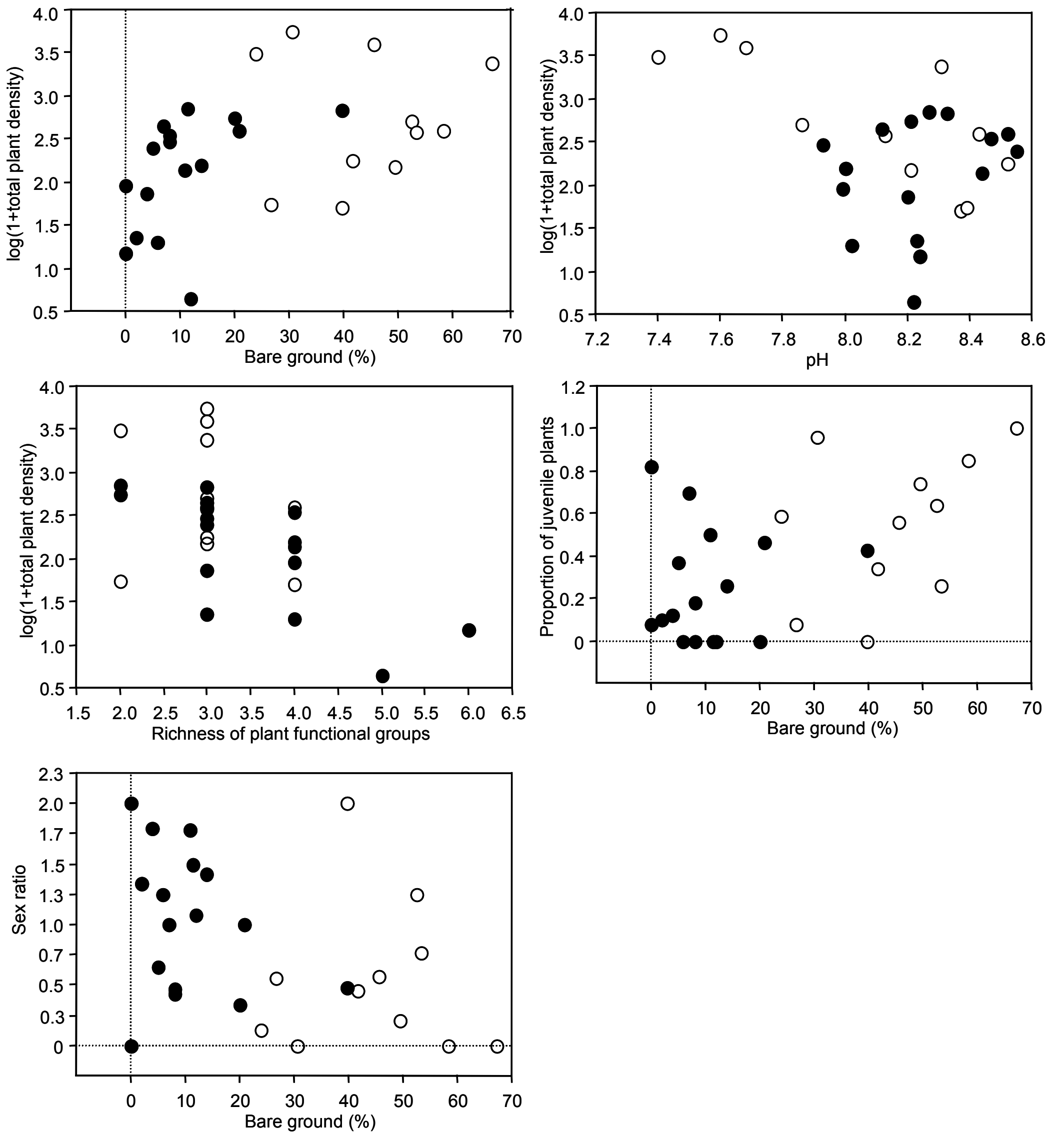

Figure 5. Significant relationships between *C. selloana* demographic variables and biotic and abiotic habitat factors in non-ruderal (filled circles) and ruderal (open circles) habitats.

2.5 Discussion

2.5.1 Association of invasion to habitat characteristics

Alien species abundance has been reported to be considerably high in ruderal habitats because they have been deeply modified by human activities (Vilà *et al.* 2001, Sobrino *et al.* 2002). In particular, disturbances, which often occur in ruderal habiats, can provide open windows for alien species to colonize and spread into new habitats through the creation of patches of open ground or a reduction in levels of competition

(Hobbs 1989, Hobbs & Huenneke 1992, Hobbs 2000). Abiotic and biotic characteristics of ruderal and non-ruderal invaded habitats differed considerably in their ecological characteristics: ruderal habitats had a lower soil nutrient content, a lower total plant cover and high percentages of macroelements and bare ground than that of non-ruderal habitats. Data obtained from north American herbarium records has revealed that *C. selloana* has frequently occupied non-ruderal habitats in southern California over the past 50 yr (Lambrinos 2001). However, *C. selloana* has also been reported to easily invade waste areas and open and disturbed areas (Harradine 1991). Therefore, we expected a better performance of this species in ruderal habitats. Our study along the Mediterranean coastal strip has revealed that although *C. selloana* invasion takes place both in ruderal and non-ruderal habitats, the most successfully invaded habitats are ruderal because populations in these habitats are bigger and have greater proportions of juvenile plants than populations in non-ruderal habitats. Therefore, *C. selloana* establishment in these habitats is higher. In addition, ruderal habitats had a substantial percentage of bare ground, which has been suggested to be a good predictor of ecosystem invasibility because it reflects the frequency and intensity of soil disturbance (Cronk & Fuller 1995). Therefore, these habitats were highly disturbed and were very susceptible to *C. selloana* invasion because *C. selloana* seeds could find safe-sites to germinate and establish, favouring seedling recruitment.

Total plant density also increased as richness of plant functional groups decreased. The role of diversity in determining ecosystem invasibility has long been discussed. At the local scale, species-rich communities are more resistant to invasion due to an effective and complete use of the available resources than species-poor communities. However, at the regional scale, observational analyses have found that the diversity of aliens matches patterns of native species diversity, because both groups of species respond to the same ecological factors varying at the large scale (Levine & D'Antonio 1999). There are several factors covarying with diversity such as low levels of competition or disturbances that can account for our results (Rejmanek 1989). As other alien species, *C. selloana* tolerates a wide range of environmental conditions (Bossard *et al.* 2000). However, we found that low pH values favoured *C. selloana* establishment. Moreover, it has also been suggested that *C. selloana* seedling establishment requires sandy soils (Bossard *et al.* 2000), yet we found that the percentage of sand did not influence the establishment of this species. Focussing on soil nutrients, it is widely accepted that nitrogen is a limiting resource for vegetation (Davis *et al.* 2000). Recent studies have found that soil nutrient levels can determine the invasibility of ecosystems. For example, it has been shown that plant invasions in a limestone grassland in Great Britain were highest in nutrient-rich sites (Burke & Grime 1996). Conversely, we found that *C. selloana* is successfully invading ruderal habitats in which soil N is lower than in non-ruderal habitats.

2.5.2 Association of invasiveness to sex form

Invasiveness may also depend on intrinsic demographic characteristics. Gynodioecious populations in which females are very abundant are predicted to be limited by pollen availability (Williams *et al.* 2000). Therefore, in *C. selloana* populations pollen limitation may constrain seedling recruitment if females are too abundant. Our results are consistent with this statement because the proportion of juvenile individuals was negatively correlated with the sex ratio suggesting that populations whose sex ratio was biased towards the number of females had a lower proportion of juvenile plants and consequently a lower potential to invade than populations with a lower number of females.

Sexual morphs in sexually dimorphic plant species allocate resources differently. In gynodioecious species, differences in fecundity between sexual morphs respond to an unbalanced contribution of genes to the next generation of both sexes because hermaphrodites contribute both with pollen and seeds whereas the contribution of females is restricted to seeds (McCauley & Taylor 1997, Molina-Freaner & Jain 1992, Williams *et al.* 2000). Consequently, if females are to be maintained in natural populations, they will need to compensate this disadvantage with an increase in reproduction success (Ashman 1992, Williams *et al.* 2000). However, the existence of compensatory advantages may differ between species. Some gynodioecious species do not show these differences between both sex forms. For example, it has been found that total investment in sexual biomass and vegetative characteristics of *Cucurbita foetidissima* populations of the south-western U.S. did not differ between hermaphrodite and female plants (Kohn 1989). Similarly, hermaphrodite and female plants of *Daphne laureola* populations in the south of Spain did not significantly differ neither in plant size nor in reproductive parameters (Alonso & Herrera 2001). Conversely, some other studies have found that females of the colonizing species *Trifolium hirtum* in California tend to produce more inflorescences and fruits than hermaphrodites (Molina-Freaner & Jain 1992). Moreover, females in other species such as *Chamaecrista fasciculate* redirect resources from reproduction to vegetative biomass (Williams & Fenster 1998). Our results for *C. selloana* confirm that female and hermaphrodite plants differ in their reproductive traits because although no differences in panicle production, plant volume and reproductive effort were found, both seed production and seed germination of female plants were considerably larger than that of hermaphrodite plants.

Using an average seed germination of 71.4 % and 14.0 % for female and hermaphrodite plants, respectively, the number of viable seeds on an individual panicle would be 13660 for females and 702 for hermaphrodites. Therefore, for a mature female plant, which produces on average 22.2 panicles, estimated viable seeds would be 303252, while for a mature hermaphrodite plant (24.4 panicles on average) it would be 17131. Consequently, the reproductive capacity of female *C. selloana* plants in populations which are not limited by pollen availability far exceeds hermaphrodite plants. Given the low seed production and viability of hermaphrodite plants it can be assumed that hermaphrodites act almost like pollen parents and therefore, behave as a subdioecious species (Connor 1973).

2.5.3 Conclusions

Overall, *C. selloana* performance was considerably better in ruderal habitats than in non-ruderal habitats because the abiotic and biotic conditions of ruderal habitats were more suitable for the invasion of this species. Specifically, the existence of high percentages of bare ground, low pH values and low richness of plant functional groups in these habitats increased the recruitment and survival of new seedlings. As regards sexual morphs, although resource allocation of female *C. selloana* plants did not differ from that of hermaphrodites, we found that *C. selloana* populations in ruderal habitats were not biased towards a greater number of females even though this could favour recruitment, considering the high amounts of viable seeds produced by female plants. This feature, however, is only an advantage if pollen is readily available. Finally, as long as disturbances occur in ruderal habitats, the creation of new patches of open ground will be guaranteed, allowing this species to become established and increasing the invasive potential of its populations.

2.6 Acknowledgements

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3. Historical land-use legacy and *Cortaderia selloana* invasion in the Mediterranean region

3.1 Abstract

Two major components of global change: land-use changes and intentional or accidental species introduction are threatening the conservation of native species worldwide. In particular, Mediterranean coastal areas are highly susceptible to the invasion of alien species and they also have experienced major changes in land-use such as agricultural abandonment and urbanization. However, there has been little research done which quantitatively links biological invasions and the components of land-use changes (i.e. number, types, trajectory and direction of the changes). We analysed the current distribution and abundance of *Cortaderia selloana* (Schultes et Schultes fil.) Asch. et Graebner, an alien ornamental species, in 332 fields in Aiguamolls de l'Empordà (Catalonia, NE Spain) and related the patterns of invasion to spatiotemporal data on land-use changes from 1956 to 2003. Our aim was to determine which land-uses had been more susceptible to *C. selloana* invasion during the last 5 years and to find out which components of land-use changes triggered invasion. We found that 22.30 % of the fields are currently invaded. In the last 5 years, fields have triplicated the total density of *C. selloana*. The presence of *C. selloana* decreases with the distance from urban areas. Invasion is over-represented in pastures and old-fields, and it has increased with time since abandonment. The presence of *C. selloana* was also associated to fields that had experienced many changes in land-use in the last 46 years. The most heavily invaded fields were those that were pastures in 1956 and are now old fields in 2003. On average, the largest plants are found in agricultural field margins and in fields that had a disturbed land-use either in 1956 or in 2003. Furthermore, pastures had the lowest proportion of reproductive plants. Overall, current *C. selloana* patterns of invasion can be explained by the historical legacy of land-use changes.

Keywords: agricultural fields, alien plant, GIS, global change, land-use changes, land-use history, Mediterranean Basin, old-fields, Pampas grass, pastures.

3.2 Introduction

Biodiversity is mainly being threatened by two components of global change: mobility and land-use change. The mixing of the globe's biota due to the breakdown of the global biogeographic barriers (Vitousek 1994, Mooney & Hobbs 2000),is potentially the factor of greatest impact on worldwide biodiversity (Sala *et al*. 2000). Biological invasions are escalating due to firstly the increasing number of intentional or accidental introductions of alien species caused by biotic change, and secondly due to land-use changes which provide open windows to the colonization and spread of new arrivals (Vitousek 1994, Pysek 1998, Mack & Lonsdale 2001).

Changes in land-use can be defined as land transformations from one ecosystem "state" to another in terms of ecosystem structure, composition and function (Hobbs 2000). Many observational analyses have reported that land-use changes increase biological invasions since the most heavily invaded land-use types are those which directly or indirectly suffer major environmental changes or are "less natural". Despite this evidence, there has been little research studying the historical factors, such as previous land-uses, that may enhance invasions through their influence on the initial characteristics of a site and through the colonization of the first stages of succession. Therefore, to study how land-use changes interact with invasions and to find out which factors trigger invasions it is necessary to link both phenomena in a spatiotemporal way (Vilà *et al.* 2003). For example, if within a particular land-use there are differences in the distribution or abundance of an alien species, analysis of the spatiotemporal sequence of land-use changes might relate these differences to successional stages or to differences in the parameters (i.e. components) describing land-use changes. Such parameters are the number of different land-uses, the trajectory and the direction of the land-use changes which could lead to a final degradation or to a final restoration state.

Land-use changes are paramount in the history of the Mediterranean Basin since its landscape has long been modified by human activities (Naveh & Vernet 1998). During the last 10,000 years, forest practices, livestock grazing and fire have profoundly changed its landscape (Thornes 1996). Nowadays, these traditional activities have gradually become nonviable and have resulted in rural depopulation. In addition, there have been many intentional and accidental species introductions in the Mediterranean Basin (Le Floc'h 1991). Agricultural, ruderal and coastal habitats are commonly invaded by alien plants (Vilà *et al.* 2001). Specifically, coastal areas are highly susceptible to the invasion of alien species due to their mild climate, the existence of highly disturbed habitats and the human use of alien ornamental plant species which increase the alien propagule pressure (Sobrino *et al.* 2002). Therefore, Mediterranean areas are excellent study areas to focus on the relationship between land-use changes and patterns of plant invasion.

We studied the link between the distribution, abundance and performance of *Cortaderia selloana* (Pampas grass), an invasive plant species native to South America, and land-use changes during 1956-2003 in coastal areas of the *Parc Natural dels Aiguamolls de l'Empordà* (Catalonia, NE Spain) in order to test (a) which land-uses have been more susceptible to *C. selloana* invasion, (b) which land transformation components trigger invasion, (c) if time since agricultural abandonment increase invasion and finally, (d) if there is an association between the presence of urbanized areas and invasion. We expected old fields to be the most highly invaded type of land-use because land abandonment may have created open sites that could have enhanced invasion (Burke & Grime 1996, Bastl *et al.* 1997, Parker & Reichard 1998). We also expected that the more changes in land-use which have occurred within a field, the more invaded it would be due to more landscape disturbances promoting invasion (Hobbs 2000, Aragón & Morales 2003). Moreover, alien species have been reported to significantly increase along a successional gradient (Rose 1997) and to decrease as the distance to the potential focus of invasion (e.g. urban areas) decreases (Rose 1997, Roy *et al.* 1999, Aragón & Morales 2003, Vilà *et al.* 2003).

3.3 Material and Methods

3.3.1 Study site

The study site was located in La Rubina (UTM quadrat 31T EG17), a protected wetland area of the *Parc Natural dels Aiguamolls de l'Empordà* (Catalonia, NE Spain). The climate is Mediterranean with mild, wet winters and hot dry summers. Mean monthly temperatures for the coldest (January) and the hottest (August) months are 10.3 ºC and 26.3 ºC, respectively. The mean annual precipitation is 739.4 mm (Clavero *et al.* 1996, http://www.meteocat.com). Soil comprises silt and clay, occasionally mixed with sand.

La Rubina is an agricultural zone of private ownership within the protected wetland. Land division is quite regular as a result of Mendizabal's disentitlement that took place in the XIXth century. Consequently, the area is mainly formed of small uniform sized fields (15m x 160m approximately, 2,400 m^2) surrounded by 2 m wide water channels bordered by *Tamarix* spp., *Salix* spp. and *Phragmites australis* as dominant species. The majority of the fields are crops of forage herbs and grasses such as lucerne (*Medicago sativa*) and barley (*Avena sativa*). Pastures, which mainly consist of grasslands with *Festuca arundinacea*, *Elymus pungens*, *Trifolium pratense*, and halophytic communities dominated by *Juncus acutus*, are the second most abundant land-uses. However, land abandonment has increased during the last decades. In addition, this area has experienced important changes since 1956 due to the launching of mass tourism which has been characterized by an increase in housing development and the rapid appearance of tourist resorts (1956 is the first year from which historical data is available). Currently, the study fields are surrounded by highly urbanized areas (i.e. campsites and resorts) in which *C. selloana* has been planted as an ornamental.

3.3.2 Surveys of fields invaded by *C. selloana*

Detailed surveys among 332 fields of La Rubina were conducted in the summer of 1998 and 2003. In 1998 all *C. selloana* plants found within each invaded field were counted. In 2003 we also counted all *C. selloana* plants in fields where less than 50 individuals were found. If more than 50 individuals were found within a field, three randomly placed 15 m x 15 m plots were established and all the individuals within plots were surveyed. In the 2003 survey, the height and two perpendicular plant diameters at the base of plants were measured for all *C. selloana* plants counted. To estimate aboveground biomass we approximated the shape of *C. selloana* to a part of a semisphere (V) whose formula is $V = 2/3\pi R^2 H$, where "R" is the mean species radius which was estimated with the two perpendicular diameters and "H" its height. In addition, we also noted if the plants were reproductive by the presence of flowering panicles.

Therefore, for 2003 we have several components of invasibility for each field: the probability for *C. selloana* to established itself (the frequency of invaded fields), total plant density, density of flowering plants, mean plant biomass and reproductive individuals/total individuals ratio (hereafter referred to as RI/TI) for each field.

We compared *C. selloana* density between 1998 and 2003 with a Wilcoxon Signed Rank Test as *C. selloana* total density did not follow a normal distribution neither in 1998 nor in 2003. We made a simple regression with the density from 1998 and 2003 to test if the slope of the regression was significantly different from 1 and to find out if the invasion of *C. selloana* had increased or decreased during this period of time. In addition, we analysed the invasion patterns graphically with log-transformed data (density +1) because most plant densities were low or zero either in 1998 or in 2003.

3.3.3 Land-use/history analysis

Land-uses of the 332 fields and surrounding area of La Rubina were determined through the examination of aerial photographs (1:22000 and 1:18000) and ortho-photo maps (1:5000) from the years 1956, 1970, 1987, 1996 and 2002. For each year, fields were classified in five land-use-categories: (1) agricultural, (2) pasture, (3) old field, (4) urban development (i.e. with buildings), and (5) unknown. The last category refers to the cases in which we could not determine clearly their status due to the low quality of the images. Land-use classification was done according to the brightness of the colour of the fields and to the presence or absence of clear margins after field checking.

We classified each field according to the following components of land-use history: (1) land-use changes during 1956-2002 (considering 0 and 1-or-more changes), (2) trajectory of the land-use change (comparing land-use at the beginning and at the end of the time series) and (3) direction of the land-use change considering pastures and old fields as semi-natural and agricultural or urban developed land-uses as disturbed. For example, a field that has gone through the following sequence: old field (1956) -

pasture (1970) - pasture (1984) - agricultural (1996) - agricultural (2002), has undergone more than one land-use change, it has been altered from an old field land-use (1956) to a agricultural land-use (2002) and it has changed from semi-natural land-use to disturbed.

3.3.4 Linking distance to urban areas to *C. selloana* invasion

We analysed the association between the percentage of invaded fields in 2003 and the distance to urban areas. Urban settlements of the study area were digitised and converted into raster format; with a pixel of 1m. Maps of distance to each pixel in the study area to the nearest urban pixel were then obtained using MiraMon, an in-house developed GIS (Pons 2001). The mean distance of each field to urban areas was obtained by combining the distance map and a polygon layer with the field boundaries, and by calculating the mean value of pixels of the distance map falling into each field. We tested if there was a relationship between the distance to urban areas and both the presence and total density of *C. selloana* per field by a logistic regression and the Spearman rank correlation test, respectively.

3.3.5 Linking land-uses of 1998 and 2003 to *C. selloana* invasion

We tested if *C. selloana* invasion in each land-use was not biased towards the most abundant land-use by matching field surveys of 1998 and 2003 with their most contemporary land-use maps (1996 and 2002 respectively). We compared, then, the observed frequency of invaded fields per land-use with their expected frequency according to the relative proportion of land-uses by means of a χ^2 goodness-of-fit analysis (Vilà *et al*. 2003). Total plant density in 1998 and 2003, density of flowering plants, mean plant biomass and RI/TI per field in 2003 were also tested among land-uses with ANOVA tests, or with Kruskall-Wallis analysis when data did not follow a normal distribution. The Scheffé test was used to analyse pair-wise differences.

3.3.6 Linking land-use history (1956 - 2003) to *C. selloana* invasion

Likewise for land-uses, we compared each land-use history component defined between 1956 and 2003, to determine if the observed number of invaded fields within each category of land-use history was significantly different from its relative frequency by a $\chi 2$ goodness-of-fit analysis.

Differences in *C. selloana* total density, density of reproductive plants, mean plant biomass and RI/TI between the number of land-use changes were compared by a t-test or a Mann-Withney U test. Differences in trajectory and direction of the land-use change were compared with an ANOVA, or alternatively with a Kruskal Wallis test when data were not normally distributed.

Furthermore, an ANOVA was used to test the differences in *C. selloana* density among a successional series according to the abandonment age of each invaded field, classified as follows: (1) still agricultural, (2) abandoned during the last 7 to 16 years, and (3) abandoned during the last 33 to 46 years.

For those components of land-use changes which were significant on a certain invasibility component, we tested if significance was not affected by time since abandonment and the distance to urban areas by a General Linear Model (GLM) analysis, with invasibility components as dependent variables and components of land-use changes, distance to urban areas and time since abandonment as independent variables. Unfortunately, we could not include all land-use change components in the analysis and identify interactions because of unbalanced data and small sample size. Moreover, a previous contingency table analysis detected strong correlations between land-use history components.

3.4 Results

3.4.1 Patterns of *C. selloana* invasion

The percentage of invaded fields increased 1.85 times during 5 years (from 12.05% in 1998 to 22.30% in 2003), at a mean rate of 0.37 fields/year. On average, total plant density was significantly higher in 2003 than in 1998 (Z-value = 5.07, $P < 0.001$). Comparing all the fields that had been invaded once, either in 1998 or in 2003, the mean total density of *C. selloana* changed from 31.86 ± 12.51 in 1998 to 91.62 ± 27.01 individuals/ha in 2003, approximately a 3 fold increase during the study period.

As regards *C. selloana* total density, there has been a definite increase from 1998 to 2003 since the majority of points are situated above the diagonal line whose equation ($Y = X$) represents no increase in density (Figure 1). There is a significant simple linear correlation between invasion in 1998 and invasion in 2003 ($Y = 43.88 + 1.50X$, $R^2 = 0.5$; $F_{1, 80} = 74.35$, $P < 0.0001$) and the slope of the line of best fit is significantly different from 1 ($t_{79} = 2.87$, $P = 0.003$). There were 42 fields without *C. selloana* in 1998 which were invaded in 2003. There were also 8 fields invaded in 1998 that were not invaded in 2002. The instances of decrease in *C. selloana* total density are probably due to human elimination of the plant.

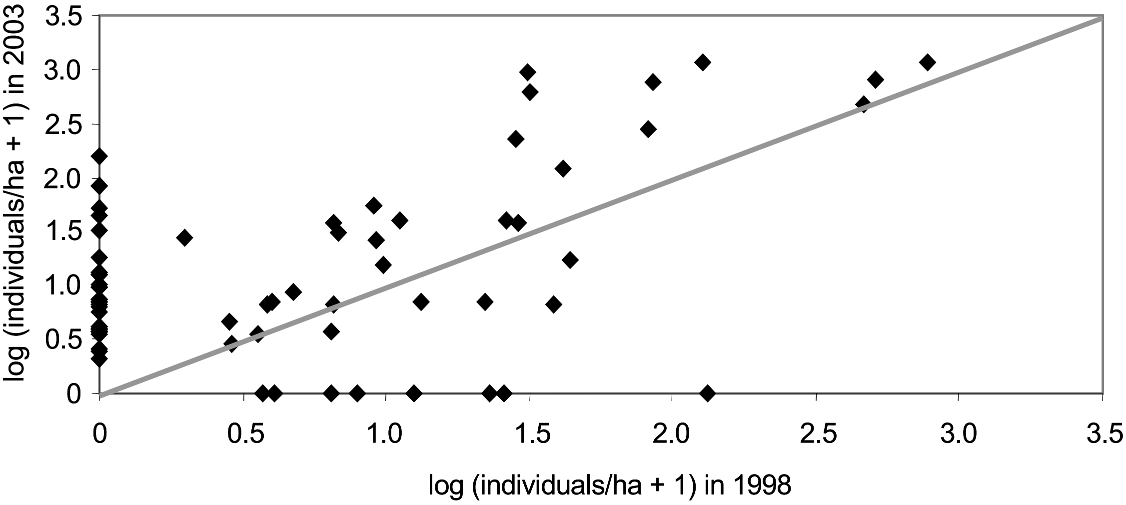

Figure 1. *C. selloana* invasion patterns between 1998 and 2003. The diagonal line represents no increase in density.

3.4.2 Invasion and distance to urban areas

The presence/absence of *C. selloana* in the fields of La Rubina varied significantly with the distance from urban areas ($\chi^2 = 19.31$, $P < 0.0001$). The number of invaded fields decreased as the distance from urban areas increased. The majority of the invaded fields were located less than 200 m from urban areas (Figure 2).

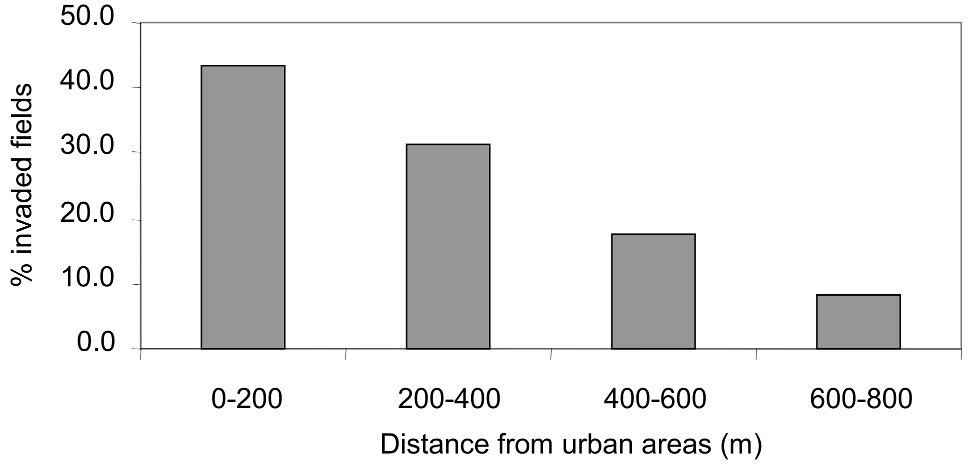

Figure 2. Relationship between the percentage of invaded fields and the distance from urban areas.

However, there was no significant relationship between *C. selloana* total density and the distance from urban areas (Spearman correlation coefficient r = 0.034, P = 0.77).

3.4.3 Linking land-uses with *C. selloana* invasion

From 1956 to 1987 pastures were the most important land-use (>60%) (Fig 3 A). In 1996 the percentage decreased considerably to 26.5% and since then it has not varied. In contrast, the percentage of agricultural fields has changed from 19.0% in 1987 to 66% in 1996. The percentage of old fields has increased steadily with time but it has always been smaller compared to pastures and agricultural fields. The appearance of buildings has also slightly increased from 0% in 1956 to 0.6% in 2002. The percentage of non-classified fields (unknown) has decreased through time due to better resolution of the images (Figure 3 A).

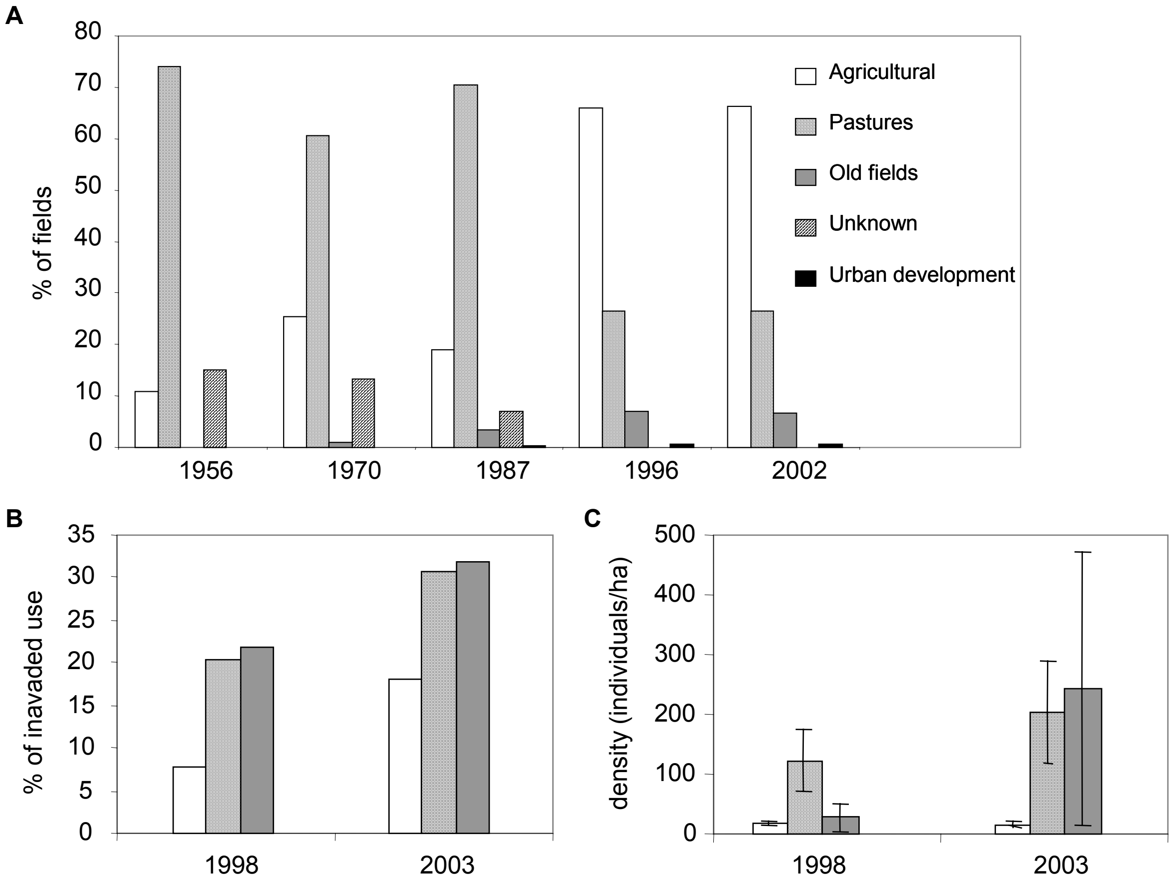

Figure 3. A) Land-uses in 1956, 1970, 1987, 1996 and 2002. B) Percentage of *C. selloana* invading land-uses in 1998 and 2002. C) *C. selloana* density per land-use in 1998 and 2002.

Focussing on 1996 and 2002, the most invaded land-uses were old fields followed by pastures. The percentage of invaded agricultural fields, pastures and old fields has increased 2.3, 1.5 and 1.5 times, respectively (Figure 3 B). Furthermore, during this short period of time, *C. selloana* density has increased in pastures and old fields, these being more highly invaded than agricultural fields (Figure 3 C).

The analysis of the association between *C. selloana* invasion and land-use demonstrates that this distribution is not random (Table 1). Observed and expected distributions of *C. selloana* invasion were significantly different both in 1998 and in 2003 (χ^2 test = 11.64, df = 2, P = 0.003 and χ^2 test = 6.84, df = 2, P = 0.03, respectively). *C. selloana* invasion in pastures and old fields were over-represented for both years whereas in agricultural fields it was under-represented.

Table 1. Observed and expected numbers of invaded and non-invaded fields for the three invaded land-uses for the years 1998 and 2003.

Land-use	**Observed**		**Expected**	
1998	Invaded	Non-invaded	Invaded	Non-invaded
Agricultural	17	202	26.5	192.4
Pastures	18	70	10.7	77.3
Old fields	5	18	2.8	20.2
2003				
Agricultural	40	180	49.3	170.7
Pastures	27	61	19.7	68.3
Old fields	7	15	4.9	17.1

The *C. selloana* total density was significantly different between the three land-use types both in 1998 and in 2003 ($F_{2, 37} = 3.52$; $P = 0.04$ and $F_{2, 47} = 6.26$; $P = 0.004$, respectively) (Figure 3 C). In 1998 pastures were the most invaded land-use (122.3 ± 52.1 individuals/ha) followed by old fields (27.0 ± 24.7 individuals/ha) and agricultural fields (16.3 ± 3.4 individuals/ha). By contrast, in 2003 the mean *C. selloana* total density was higher in old fields (242.2 ± 228.5 individuals/ha) followed by pastures (204.2 ± 84.8 individuals/ha). Agricultural fields were the least invaded land-use type (15.9 ± 4.4 individuals/ha). Mean total density of reproductive plants in 2003 did not significantly differ between land-uses (H = 2.3; df = 2; $P = 0.32$).

In 2003, *C. selloana* biomass was significantly different among land-uses ($F_{2, 724} = 19.8$; $P < 0.0001$). Plants in agricultural fields were larger than in pastures and old fields. No significant differences were found between plant biomass of pastures and old fields (Schefe-test, $P = 0.6$). The biomass distribution of *C. selloana* in pastures (Figure 4 B) and old fields (Figure 4 C) was a reversed-J shape, with more than 50% of individuals concentrated in the first volume category (0-5 m^3). However, in agricultural fields (Figure 4 A), the biomass distribution was less skewed. For all land-uses the biggest individuals were all mature. However, in old fields plants with less biomass had a higher fertility than in the other two land-uses. There were significant differences in RI/TI between land-uses (H = 6.74; df = 2; $P = 0.03$): RI/TI was higher in old field and agricultural fields (0.93 ± 0.49 and 0.91 ± 0.36, respectively) than in pastures (0.67 ± 0.91).

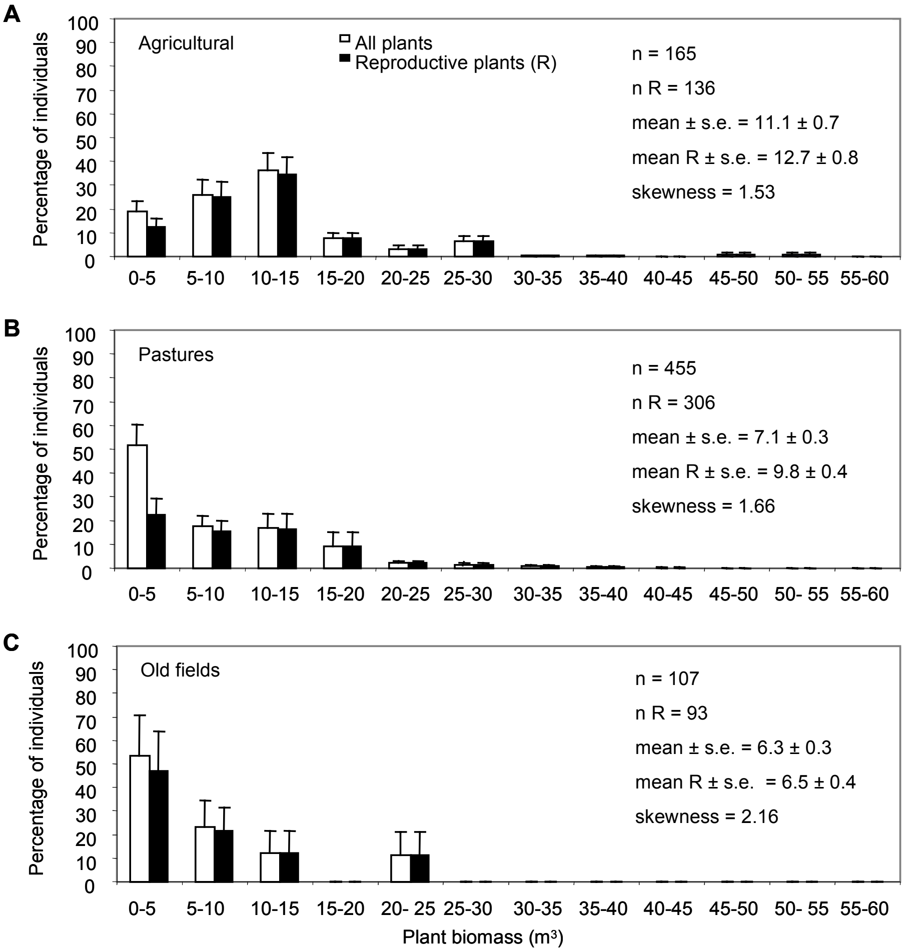

Figure 4. Size distribution of *C. selloana* for the different invaded land-uses.

3.4.4 Linking land-use changes history with *C. selloana* invasion

C. selloana total density increased significantly along succession ($F_{2, 71} = 3.76$, $P = 0.03$). Fields that were abandoned at least 33 years ago were the most dense (210.1 ± 85.1 individuals/ha), followed by fields that were abandoned from 7 to 16 years ago (63.1 ± 43.1 individuals/ha). Fields that have not been abandoned were the least invaded (13.4 ± 3.5 individuals/ha). However, fields that were abandoned from 7 to 16 years ago are the most invaded (44.44 %), followed by fields that were abandoned from 33 to 47 years ago (31.71 %). Again, fields that had not been abandoned were the least invaded (18.35 %).

The χ^2 test confirms that there was a significant association between the presence of *C. selloana* and land-use changes during 1956-2002 ($\chi^2 = 12.50$, df = 1, *P* = 0.0004). Invaded fields that have suffered one or more land-use changes were over-represented (16.17 %) whereas fields that remained stable (with no land-use changes) during this period of time were under-represented (9.36 %). However, neither the trajectory of the land-use change nor the direction of the land-use were associated with *C. selloana* invasion ($\chi^2 = 3.97$, df = 6, *P* = 0.68 and $\chi^2 = 2.76$, df = 3, *P* =0.43, respectively) (Table 2).

Table 2. Observed and expected numbers of invaded and non-invaded fields among the four components of land-use history.

Land-use component	**Observed**		**Expected**	
Land-use changes:	Invaded	Non-invaded	Invaded	Non-invaded
0	22	110	33.7	98.3
≥ 1	38	65	26.3	76.7
Trajectory of the land-use change:				
Pasture → agricultural	31	93	31.7	92.3
Pasture → pasture	21	50	18.1	52.9
Pasture →old field	4	7	2.8	8.2
Pasture → urban development	0	19	0.5	1.5
Agricultural → old field	0	2	0.3	0.7
Agricultural → agricultural	3	3	5.6	16.4
Agricultural →pasture	1	1	1.0	3.0
Direction of the land-use change:				
Disturbed → semi-natural	1	4	1.3	3.7
Semi-natural→ semi-natural	24	55	20.1	58.9
Semi-natural → disturbed	31	95	32.0	94.0
Disturbed → disturbed	3	19	5.6	16.4

The preliminary approach revealed that *C. selloana* total density did not differ significantly with land-use changes ($t_{43} = 1.10$; *P* = 0.28). Conversely, it significantly depended on the trajectory of the land-use change ($F_{4, 40} = 3.47$; $P = 0.02$). Fields that have changed from pastures to old fields and fields that have remained as pastures were the most highly invaded. Significant differences in *C. selloana* total density also appeared related to the direction of the land-use change ($F_{3, 41} = 4.72$; $P = 0.006$). Fields that have remained as semi-natural were the most invaded (Table 3).

Table 3. *C. selloana* density, density of reproductive individuals, plant volume and reproductive individuals/total individuals ratio for each component of land-use history. Values are mean ± s.e. Asterisks indicate that standard error could not be calculated since in these categories there was only one field. DRI = Density of Reproductive Individuals. RI/TI = reproductive individuals/total individuals ratio.

Components of land-use	**Density (ind/ha)**	**DRI (ind/ha)**	**Volume (m^3)**	**RI/TI**
Land-use changes:				
0	132.1 ± 80.5	31.9 ± 12.2	9.8 ± 2.1	0.71 ± 0.11
≥1	73.6 ± 41.0	14.9 ± 3.1	10.3 ± 0.7	0.88 ± 0.04
Trajectory of land-use change:				
Pasture → agricultural	16.9 ± 4.6	13.7 ± 3.4	11.1 ± 0.6	0.91 ± 0.04
Pasture → pasture	178.7 ± 86.0	35.2 ± 11.9	8.1 ± 1.5	0.65 ± 0.11
Pasture → old field	579.0 ± 576.5	18.9 ± 16.3	4.9 ± 1.4	0.93 ± 0.07
Agricultural → agricultural	2.6 ± 1.1	2.6 ± 1.1	21.3 ± 9.4	1.00 ± 0.00
Agricultural → pasture	24.7 *	16.5 *	3.8 *	0.67 *
Direction of land-use change:				
Disturbed → semi-natural	24.7 *	16.5 *	3.8 *	0.67 *
Semi-natural → semi-natural	228.8 ± 97.7	33.2 ± 10.5	7.7 ± 1.3	0.69 ± 0.10
Semi-natural → disturbed	16.9 ± 4.6	13.7 ± 3.4	11.1 ± 0.6	0.91 ± 0.04
Disturbed → disturbed	2.6 ± 1.1	2.6 ± 1.1	21.3 ± 9.4	1.00 ± 0.00

The density of reproductive individuals did not differ significantly among any of the components of land-use history ($Z = 0.22$; $P = 0.83$ for the number of land-use changes, $Z = 0.22$; $P = 0.83$ for the number of land-uses types, $H = 3.48$; df = 4; $P = 0.48$ for the trajectory of the land-use change and $H = 3.15$; df = 3; $P = 0.37$ for the direction of the land-use change). Mean *C. selloana* biomass did not vary significantly between land-use changes (t_{43} = 0.30; P = 0.76). Conversely, significant differences appeared considering the trajectory of the land-use change ($F_{4, 40}$ = 5.07; P = 0.002) and the direction of the land-use change ($F_{3, 41}$ = 6.50; P = 0.001). Mean plant biomass was higher in fields that were agricultural both in 1956 and in 2003 (21.3 ± 9.4 m^3) and in fields whose direction of the land-use change consisted in having a disturbed land-use both in 1956 and in 2003 (21.3 ± 9.4 m^3). No significant differences in RI/TI appeared considering the number of land-use changes (Z = 1.63; P = 0.10), the trajectory of the land-use change (H = 7.20; df = 4; P = 0.13) nor the direction of the land-use change (H = 6.70; df = 3; P = 0.08, Table 3).

The contingency table analysis on land-use change components revealed that the trajectory and direction of land-use changes were strongly correlated (χ^2 = 135.00; df = 12; $P < 0.0001$). Therefore, we only considered the trajectory of land-use changes as the explanatory variable and determined the effect of this land-use component, distance to urban areas and time since abandonment on *C. selloana* density and plant biomass. The GLM revealed that the trajectory of land-use changes was the only independent parameter that had a significant effect on *C. selloana* total density ($F_{3, 37}$ = 3.30; P = 0.03). Specifically, it explained 35.0 % of the variation. By contrast, *C. selloana* total density did not depend either on the time since abandonment ($F_{2, 37}$ = 1.93; P = 0.16) or on the distance to urban areas ($F_{1, 37}$ = 0.13; P = 0.72). Similarly, 42.5 % of the variation in plant biomass was significantly explained by the trajectory of land-use changes ($F_{3, 37}$ = 5.05; P = 0.005) while time since abandonment and the distance to urban areas had no significant effect on plant biomass ($F_{2, 37}$ = 2.74; P = 0.08 and $F_{1, 37}$ = 0.001; P = 0.97, respectively).

3.5 Discussion

Some species when introduced into a new area tend to spread from their initial focus of introduction. This process is mainly characterized by an increase in population numbers caused by changes in demographic rates and a simultaneous increase in the area occupied by the population due to the dispersal of propagules (Parker & Reichard 1998). The high increase in the percentage of invaded fields and the increase in *C.*

selloana density that has taken place between 1998 and 2003 reflects that the species is expanding fast despite the fact that landowners may have tried to deter its spread. Such management practices have not counterbalanced the constant influx of propagules arriving from nearby tourist resorts that have proliferated since the late 1960s (Saurí *et al.* 2000).

Many studies have found that the number of alien species decreases as the distance from the potential focus of invasion increases (Rose 1997, Aragón & Morales 2003, Vilà *et al.* 2003). Moreover, it is also known that urban areas can be regarded as potential focuses of invasion due to their high richness of alien species (Roy *et al.* 1999). Our results show that *C. selloana* presence decreases as the distance from urban areas increases which is also in accordance with patterns of invasion of *Opuntia maxima* and *Pittosporum undulatum*. The former is an ornamental alien species also invading coastal areas located less than 200 m from urban settlements (Vilà *et al.* 2003). The latter is an Australian native species that is invading bushland areas of northern Sydney and whose density in young (12-13 yr) and middle-aged (26-50 yr) sites decreases with distance to urban and suburban edges (Rose 1997). However, its density does not depend on the distance from urban areas. This suggests that while the presence of the first propagules to a site depends on the focus of invasion, population growth depends on local site characteristics.

Cortaderia selloana populations in pastures and old fields are not evenly distributed in size since more than 50% of their individuals are situated in the smallest biomass class and bigger individuals are far less abundant. In contrast, agricultural fields are less invaded, plants are on average larger, small individuals are no longer the most abundant biomass class and population distribution is not as skewed to the right as in pastures and old fields. The different biomass distribution in agricultural fields may be caused by the environmental conditions of field margins where *C. selloana* invasion is restricted since agricultural margins are unmanaged areas. Except in pastures, most individuals are mature, indicating that invasion in pastures is at a more initial stage than that occurring in old fields or agricultural fields.

La Rubina has experienced a major land-use change from 1956 to 2003. From 1956 to 1987 agriculture was a secondary land-use. This was probably caused by the fact that as in other Mediterranean regions traditional agriculture became progressively economically unviable during the 1960s (Debussche *at al*. 1999; Grove & Rackham 2001). After 1987 most fields shifted from pastures to modern agricultural lands and since 1996 this has been the most abundant land-use. Land-uses practically have not changed during the period 1996-2002. *C. selloana* invasion was not biased towards the most abundant land-use neither in 1996 nor in 2002 although field margins where *C. selloana* invasion is restricted are more likely to be invaded due to their ruderal characteristics. Moreover, agricultural fields are not the most successfully invaded land-use (*C. selloana* density has not changed during these years). Old fields and pastures have been the most successfully invaded land-uses: *C. selloana* total density in the former has experienced a nine-fold increase during the last 5 years and in the latter pastures a nearly two-fold increase.

Several techniques have been developed for modelling species distribution and occurrence at regional scales in spatially explicit contexts. A logistic regression model has explored the importance of environmental factors in explaining the current distribution and the future spread of species that are invading the Cape Pensinsula. In particular, elevation and rainfall have been predicted to be the most important factors for determining the frequency of the invasive species *Acacia Cyclops* and *Pinus pinaster*. The modelling of their spread has revealed that their distribution will increase significantly, covering a large area of the Cape Peninsula (Higgins *et al*. 1999). Another study modelled the interactions between environment, plant traits and disturbances of pine invasions in the southern hemisphere. Results showed that all these determinants of invasion success significantly influenced the rate of invasion of pine trees (Higgins & Richardson 1998). However, none of these models considered that the current distribution of invasive species can also reflect land-use legacy. We have found that land-use changes trigger the invasion of *C. selloana*. Changes in land-use are usually associated to landscape disturbances that may represent an open window to the invasion of alien species (Hobbs 2000, Aragón & Morales 2003), yet the majority of studies analyse land-use changes from a static point of view (but see Vilà *et al.* 2003). These results are consistent with those obtained for *Opuntia stricta* and *O. maxima* distribution in Cap de Creus (NE Spain) where they have invaded the habitats that had experienced more changes during a 20-year period.

The trajectory of land-use change influenced invasion even when time since abandonment and distance to urban areas were included in the model, reinforcing the role of land-use history on invasion. *C. selloana* total density was higher in fields that were pastures in 1956 and old fields in 2002. This high proliferation of *C. selloana* may be caused by the fact that pastures and old fields are stable environments since they have not been cultivated at least since 1956. Consequently, the longer a field is abandoned, the more *C. selloana* total density increase.

Our analysis of the land-use history of La Rubina has revealed that between the years 1956 and 2002 some of the agricultural fields have become pastures and old fields. Abandonment of these agricultural fields may have provided an open window to the invasion of *C. selloana*. In addition, it is known that this species produces a large amount of seeds (Connor & Edgar 1974, Lambrinos 2002) which could take advantage of land abandonment. Consequently, this species could have successfully established itself in these fields and increased its density through time. Our results show that fields that have been abandoned for a long time are much more invaded than fields that have been recently abandoned. This is also consistent for the invasion of *P. undulatum* into urban bushland areas (northern Sydney) since the abundance and basal area of this species increases significantly along a successional gradient (Rose 1997). However, time since abandonment had no significant effect on *C. selloana* total density when we considered this variable together with the distance from urban areas and the trajectory of land-use changes.

Finally, the direction of the land-use also influenced the performance of *C. selloana.* Plants were bigger in fields that had been disturbed since 1956. This occurred particularly in agricultural fields, since their margins offer the invader special conditions which promote growth. In addition, our results suggested that these results were not influenced by the distance from urban areas and time since abandonment.

Land-use history and time since abandonment have been proved of major importance in determining the species composition of a particular area (Aragón & Morales 2003). In addition, land-use changes have been tightly linked to biological invasions through alterations in ecosystem dynamics that provide opportunities for species colonization and population expansion (D'Antonio & Vitousek 1992, Hobbs

2000). However, it has been reported that there is little research which links both phenomena in a spatiotemporally explicit way (Thomson *et al*. 1993). Our study is not only useful to describe the present distribution of an invasive species but also to test if differences in its present distribution are due to past land-use changes and if differences within a particular land-use can be linked to different successional stages. We have shown that invasion is not biased towards the most abundant land-use and that land-use legacy has a strong influence on invasion patterns.

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4. The role of successional stage, vegetation type and soil disturbance on *Cortaderia selloana* invasion

4.1 Abstract

Ecosystems are dynamic hence their invasibility (i.e. susceptibility to invasion) could vary with time along succession. However, different plant-plant interaction outcomes (i.e. facilitation, tolerance and inhibition) can lead to differences in invasibility between successional stages. It is widely known that disturbances enhance invasibility and therefore young seral stages are predicted to be more susceptible to biological invasions than later seral stages. Unfortunately, there is scarce research focussing on the mechanisms of species invasion along succession.

We studied the establishment and performance of *Cortaderia selloana* (Schultes et Schultes fil.) Asch. et Graebner, an alien South American ornamental species that is invading many parts of the world, to test the hypothesis that early successional stages are the most susceptible to *C. selloana* invasion and that soil microdisturbances will increase invasion at any point of succession. For this purpose, we monitored survival and growth of transplanted *C. selloana* seedlings in disturbed and non disturbed plots throughout a successional gradient (i.e. 1 - > 10 yr), in different vegetation types and within the area of influence of coexisting species with similar growth form.

Despite seedling survival was being extremely low in all treatments, our results revealed that early successional stages were not the most easily invaded communities since we found no significant differences in *C. selloana* percentage survival along the successional gradient. This result, suggested that none of the plant-plant interaction outcomes ruled *C. selloana* invasion. Invasibility neither depended on the invaded vegetation type or on the coexisting species with similar growth form. However, we found a facilitating effect from *P. australis*, a native coexisting species, on the growth of *C. selloana* seedlings. *P. australis* cover might protect *C. selloana* seedlings from excessive light since all *C. selloana* seedlings in plots where *P. australis* had been clipped died in a short period of time despite having a high soil moisture. Finally, *C. selloana* survival and seedling biomass was enhanced by soil disturbance at any seral stage. Overall, this study contributes to linking ecosystem invasibility and succession ecology by focussing on the several ways that resident species can facilitate, inhibit or tolerate the establishment of new species.

Keywords: additional experiments, invasibility, facilitation, microdisturbance, removal experiments, successional mechanisms.

4.2 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, Mack & Lonsdale 2001). It is widely known that ecosystems vary in their invasibility (i.e. susceptibility to invasion). Invasivility depends on several biotic factors such as the competitive abilities of the native species, the presence of effective herbivores, pathogens and mutualists in the recipient community, and environmental factors such as the region's climate and disturbance regimes (Maron & Connors 1996, Lonsdale 1999, 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 and Wilson 2001).

It has been found that disturbances *per se* or alterations of disturbance regimes can increase community invasibility (Hobbs & Humphries 1995, Hobbs 2000, D'Antonio & Corbin 2003). It has also been predicted that invasibility declines during the course of succession (Rejmánek 1989, Lepart & Debussche 1991, Hobbs & Huenneke 1992). Moreover, most alien species are by their nature ruderals, r-strategists (Heywood 1989). Therefore, "pioneer communities" will exhibit a higher number and proportion of invaders than successionally more advanced stages. Theoretical models support this idea (Rejmánek 1989) but there are contradictory field data supporting it. On the one hand, it has been observed that vegetation types occurring at the end of succession are rarely invaded (Lepart & Debussche 1991), but on the other hand, mid-successional stages have also 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 seral changes in species: 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 themselves 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 latter 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). 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 the establishment and performance of *Cortaderia selloana* (Schultes et Schultes fil.) Asch. et Graebner, a tussock perennial grass native to South America. It was introduced to Europe as an ornamental and is now invading old fields, coastal and riparian areas. Our main hypothesis is that early successional stages will be the most susceptible to *C. selloana* invasion. Therefore, we hypothesise that *C. selloana* invasion will be ruled by the successional mechanism of facilitation. In addition, we want to find out if *C.* selloana invasion of latter successional stages can be modulated by vegetation type. We expect that *C. selloana* invasion will not depend on vegetation types provided that local soil microdisturbances take place.

4.3 Material and Methods

4.3.1 Study site

The study site 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. In the last centuries, humans have changed the original landscape of Delta del Llobregat from wetlands to pine forests and agricultural lands, and in recent decades industrial and urban areas have also proliferated. 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 inland which could include humid, dry or salty environments ranging from high sand contents to textures more rich in silt or clay, creates special microhabitats that determine its vegetation (Gurri 1998, Orta *et al*. 1992).

Our research was conducted in 3 areas within the Delta: (i) in an agricultural-old field matrix in the west of the Delta (hereafter agricultural-old field matrix), (ii) in a shore of a lagoon in Prat del Llobregat (hereafter Prat del Llobregat) and (iii) in an old-field in the area of Remolar-Filipines close to Barcelona airport (hereafter old-field of Remolar-Filipines). The soil is basically sandy and the water table level is located at approximately 50 cm from the soil surface (Domènech *personal observation*). 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).

4.3.2 Establishment on 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: (a) fields with some annual grasses and herbs that had been abandoned 2 to 3 years ago (hereafter referred to as < *5*), (b) fields with perennial grasses and shrubs that had been abandoned 5 to 10 years ago (hereafter referred to as < *10*) and (c) fields that were abandoned at least 10 years ago, consisting in more mature communities formed by *Phragmites australis* (hereafter referred to as > *10P*) and *Juncus acutus* (hereafter referred to as > *10J*). In addition, we included one field that had been abandoned just before the experiment (hereafter referred to as < *1*). We could not find more replicates for < *1* since obtaining permission from land-owners to conduct experiments was very difficult. Data obtained from this field was only used in the seedling survival analysis. All successional stages, except < *1*, were replicated 10 times, but at the beginning of the experiment we lost 2 < *5* fields because they were cultivated, and 1 > *10P* field and 4 > *10J* fields due to a large wildfire.

Vegetation characteristics of each field were estimated by the point-intercept method conducted in one 25-m line transect in each field. Differences in vegetation characteristics between successional stages were analysed with ANOVA and subsequent multiple-comparisons with 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 < *5* fields were the less diverse (Scheffé-test, $0.0001 < P > 0.05$) and had the lowest total cover (Scheffé-test, $0.0001 < P \geq 0.03$). Species richness at this stage was only significantly lower than species richness of < *10* fields (Scheffé-test, $P = 0.003$) (Table 1).

In each field, four 50 x 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 x 90 cm area. Sixteen 3 month old seedlings of *C. selloana* that had emerged and were grown outdoors in trays filled with gardening soil at Universitat Autònoma de Barcelona (UAB) campus, were planted in each plot with a distance of 10 cm from each other. In disturbed plots seedlings were planted within the 50 x 50 cm area, and the remaining 40 cm frame area was as 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) has been proved to be a good estimator of plant biomass (Y) through the allometric regression $Y = 0.0003X - 0.00009$, $n = 67$, $r^2 = 0.76$. No significant differences were found among the planted seedlings in leaf number both between field stages ($F_{3,\ 58} = 2.02$, $P = 0.12$) and between treatments ($F_{1,\ 58} = 0.32$, $P = 0.57$). Similarly, for total leaf length there were also no significant differences either between field stages ($F_{3, 58} = 2.44$, $P = 0.07$) or between treatments ($F_{1, 58} = 2.38$, $P = 0.13$). These seedling measures were repeated at the end of the experiment in January 2004.

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. A survival analysis was used to compute the product-limit (Kaplan-Meyer) estimations of mean survival time of *C. selloana* seedlings in each successional stage with and without disturbance. Differences were analysed with a Gehan-Wilcoxon test. A Scheffé-test was used to examine pair-wise comparisons. The effect of successional stage and soil disturbance on *C. selloana* percentage survival at the end of the experiment were analysed with a Kruskal-Wallis analysis and a Mann-Whitney U test, respectively, since data did not follow a normal distribution. At the end of the experiment no seedlings planted in non disturbed plots apart from < *10* survived. Therefore, differences in final leaf length and the number of leaves in the other non-disturbed plots could not be calculated. Differences in successional stage for these 2 variables were analysed with a one factor ANOVA. Both variables were transformed as ln (x+2) and ln (x+1) to meet the assumptions of parametric statistical analysis.

4.3.3 Establishment in different vegetation types

In order to determine if there were differences in vegetation invasibility to *C. selloana* invasion within late successional stages we selected 30 > 10 old-fields from the same agricultural-old field matrix. Old-fields were grouped into three categories according to the dominance of their vegetal cover: (a) *P. australis* cover (> *10P*), (b) *J. acutus* cover (> *10J*) and (c) herb cover (> *10H*). All the dominant plant species belonged to the same life-form, monocotyledonous perennials, as in the previous experiment. We had 10 replicates for each vegetal cover (Table 1). Diversity was significantly different among vegetation types ($F_{2, 18} = 5.59$, $P = 0.01$): > *10H* fields had the highest diversity. However, species richness ($F_{2, 18} = 2.98$, $P = 0.08$) and total cover ($F_{2, 18} = 2.32$, $P = 1.23$) did not significantly differ among the three vegetation types (Table 1).

Table 1. Vegetation characteristics (mean ± s.e.) within each successional stage in the agricultural-old-field matrix in Delta del Llobregat.

Stage	Species richness	Diversity (H')	Total cover (%)	Dominant species (% cover)
< *5*	2.6 ± 0.4	0.98 ± 0.11	74.3 ± 6.10	*Plantago coronopus* (13.8) *Aster squamatus* (8.5)
< *10*	5.6 ± 0.7	2.08 ± 0.13	148.7 ± 13.70	*Torilis nodosa* (29.1) *Agrostis stolonifera* (24.3)
> *10P*	4.0 ± 0.3	1.60 ± 0.11	164.6 ± 11.60	*Phragmites australis* (43.9) *Plantago coronopus* (17.46)
> *10J*	5.0 ± 0.3	1.95 ± 0.09	200.9 ± 5.08	*Agrostis stolonifera* (34.39) *Juncus acutus* (16.9)
> *10H*	5.8 ± 0.7	2.20 ± 0.15	169.3 ± 14.62	*Torilis nodosa* (31.2) *Agrostis stolonifera* (27.5)

In each field, four 50 x 50 cm experimental plots separated by at least 1 m were established. In two randomly chosen ones we applied a soil disturbance treatment by manually raking the first 25 cm of a 90 x 90 cm area. Sixteen 6 months seedlings of *C. selloana* that had germinated and grown outdoors at UAB campus were planted in each plot. In disturbed plots, seedlings were planted within the 50 x 50 cm area, and the outside 40 cm frame remained as a buffer zone. At the beginning of the experiment total seedling leaf length and number of leaves were measured from a random sample of 5 disturbed and non disturbed plots from each vegetation type. Seedlings had on average 2.4 ± 0.1 leaves and total leaf length measured 5.05 ± 0.19 cm. These measures did not significantly vary either between vegetation types ($F_{2,24} = 0.12$, $P = 0.88$ for number of leaves and $F_{2,24} = 1.27$, $P = 2.99$ for total leaf length) or soil disturbance ($F_{1,24} = 3.13$, $P = 0.09$ for number of leaves and $F_{1,24} = 2.93$, $P = 0.10$ for total leaf length).

Seedling survival was monitored once a month from March to October. Within each field we calculated the mean percentage survival for each pair of disturbed and non disturbed plots and therefore, we compared the mean percentage survival in disturbed and non-disturbed plots of each field along the successional gradient. A survival analysis (Kaplan-Meyer) was used to estimate mean survival times and percentage survival at the end of the experiment with a Kruskal Wallis, and a Mann-Whitney U test to analyse the effect of vegetation type and disturbance, respectively. At the end of the experiment, in October 2004 we measured the number of leaves of surviving seedlings. After this, plants were cut and weighed after drying at 70ºC to constant weight. Neither the dry weight nor the number of new leaves followed a normal distribution. Therefore, a Kruskal Wallis test and a Mann-Whitney U test were used to test differences between the three vegetation types and differences due to the effect of disturbance, respectively.

In order to characterize the microenvironmental conditions of the vegetation where *C. selloana* seedlings were planted, 4 random measures of soil moisture by a Time Domain Reflectometry (TDR) and 4 perpendicular Photosynthetic Active Radiation (PAR) measures were taken in each field on 16th June and 13th July. Mean soil moisture and mean PAR in each field were calculated with these values, without considering disturbed and non-disturbed plots. Differences between vegetation types in both variables were tested with a Repeated Measures ANOVA. Differences within each vegetation type were analysed with a Scheffé-test.

Additionally, we established two 15 x 15 cm plots in each field centred on an area of 30 x 30 cm that had manually been disturbed as described before, the remaining 15 cm frame was left as a buffer area. Several pieces of panicles from female plants containing an average of 4243.2 ± 170.5 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 following regression: $Y = 3571.1X – 80.3$, $r^2 = 0.87$, $n = 25$. Plots were sampled at fifteen-day intervals for two months and each time emerged *C. selloana* seedlings were pulled. Mean percentage of germination was calculated for each pair of plots and differences between the three vegetation types was analysed with a one-factor ANOVA analysis with vegetation type as a fixed effect. We did not study *C. selloana* seedling emergence on non disturbed plots because a previous study conducted in seasonal wetlands, *C. jubata* grasslands, dune scrub and maritime chaparral reported that *C. selloana* germination was very low in non disturbed plots (Lambrinos 2002).

4.3.4 Effect of P. australis on establishment

Many late successional stages invaded by *C. selloana* are dominated by *P. australis*. Therefore, in order to determine the neighbouring effect of this species on *C. selloana* invasion we established in May 2002, 36 50 x 50 cm experimental plots in the Prat del Llobregat study site which was dominated by *P. australis*. Half of the plots were randomly chosen and the stems of *P. australis* 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. Twelve 3 month old seedlings of *C. selloana* that had germinated and were grown outdoors in trays filled with gardening soil at the UAB campus were planted inside each plot with a 10 cm separation between seedlings. Seedlings had on average 3.7 ± 0.1 leaves and total leaf length measured 28.4 ± 0.8 cm. There were no significant differences between the initial sites of transplanted seedlings in control and in plots where *P. australis* had been clipped ($Z = 0.29$, $P = 0.77$ for the number of leaves and $t_{34} = 0.34$, $P = 0.74$ for total leaf length, respectively). These seedling measures were repeated at the end of the experiment in October 2002. Seedling survival was monitored twice in June, September and October 2002.

A survival analysis was performed in order to estimate the product limit (Kaplan-Meyer) seedling mean survival time. Percentage survival and the number of leaves did not follow a normal distribution, consequently a Mann-Whitney U test was used to compare seedlings planted in *P. australis* plots and seedlings planted in clipped *P. australis* plots. The final total leaf length was analysed with an unpaired t-test.

To characterise the environmental conditions where *C. selloana* seedlings were growing, 4 measures of PAR at perpendicular direction and 4 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 and differences between treatments on the mean values of PAR and soil temperature were analysed with an unpaired t-test.

4.3.5 Establishment beneath *J. acutus*, *P. australis* and *C. selloana*

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 of Remolar-Filipines invaded by *C. selloana*. We considered the fields 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 australis* (53.60%), *Juncus maritima* (19.61%) and *J. acutus* (9.15%). In addition, 6 15 x 15 m plots were randomly established in order to determine *J. maritimus* (955.5 ± 197.0 individuals/ha) and *C. selloana* (192.6 ± 81.68 individuals/ha) density. Height and two perpendicular diameters were measured for 20 individuals of *C. selloana* and *J. maritimus* in order to quantify their volume (7.6 ± 0.9 m^3 and 2.8 ± 0.5 m^3, respectively). This experiment was conducted with *J. acutus* and *P. australis* because they belonged to the same life form, monocotyledonous perennials, as *C. selloana*. In addition, *J. acutus* was chosen instead of the more abundant *J. maritimus* because it had a larger plant biomass. Therefore, it was more similar to *C. selloana*. Density and cover of *C. selloana* was lower than that of *J. maritimus* and *P. australis* but *C. selloana* plants had a substantially larger plant biomass.

Sixty 50 x 50 cm experimental plots were established beneath the area of influence of *C. selloana* (15 plots), beneath *J. acutus* (15 plots) and beneath *P. australis* (30 plots). In 15 randomly chosen plots beneath *P. australis* (hereafter referred as *P. australis* clipped plots) we cut aboveground biomass as in the previous experiment. Sixteen 3 month old seedlings of *C. selloana* were planted in each plot. Seedlings had on average 2.6 ± 0.03 leaves and total leaf length measured 14.2 ± 0.2 cm. These measures did not significantly differ between seedlings planted beneath each species ($F_{3,56} = 1.01$, $P = 0.39$ for the number of leaves and $F_{3,56} = 1.22$, $P = 0.31$ for total leaf length, respectively).

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. A survival analysis (Kaplan-Meyer) was used to estimate mean survival time of seedlings. Differences were analysed with a Gehan-Wilcoxon test and pair-wise comparisons were established with a Scheffé-test. Percentage survival at the end of the experiment (June 2004) did not follow a normal distribution, therefore data was analysed with a Kruskal Wallis analysis. In addition, plants were harvested and weighed after drying at 70ºC to constant weight to obtain their final biomass. Differences were analysed with ANOVA with plot type as a fixed effect.

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 *J. acutus*, *C. selloana* and *P. australis* 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 was conducted 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. Soil properties were analysed with a Kruscal-Wallis test since they did not follow a normal distribution.

Four measures of PAR at perpendicular directions and 4 random soil moisture measures by a TDR were taken 2 times in each plot during summer 2003. Mean PAR and mean soil moisture were calculated for each plot. Both variables were analysed with a Repeated Measures ANOVA, differences within each treatment were analysed with a Scheffé-test. Soil moisture was log-transformed to meet the assumptions of homogeneity of variance.

4.4 Results

4.4.1 Establishment on a successional gradient

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 2003 (Figure 1). No significant effect of successional stage was found on percentage survival ($H = 0.27$, d.f. = 3, $P = 0.97$) whereas significant differences were found between disturbed (3.1 ± 1.5 %) 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 ($\chi^2 = 109.12$, d.f. = 4, $P < 0.0001$) and also between disturbed and non disturbed plots ($\chi^2 = 13.12$, d.f. = 1, $P < 0.0003$). Mean survival time of the < *1* year old field was the highest (Scheffé-test, $P < 0.0001$). For disturbed plots, mean survival time of fields from successional stage < *1* was higher than < *5*, < *10* and > *10P* fields (Scheffé-test, $P < 0.001$, $P = 0.005$ and $P = 0.004$, respectively). Mean survival time of < *10* fields was higher than > *10J* (Scheffé-test, $P = 0.003$). Furthermore, < 5 fields had a higher mean survival time than > *10J* and > *10P* (Scheffé-test, $P = 0.0004$ and $P = 0.03$, respectively) (Table 2).

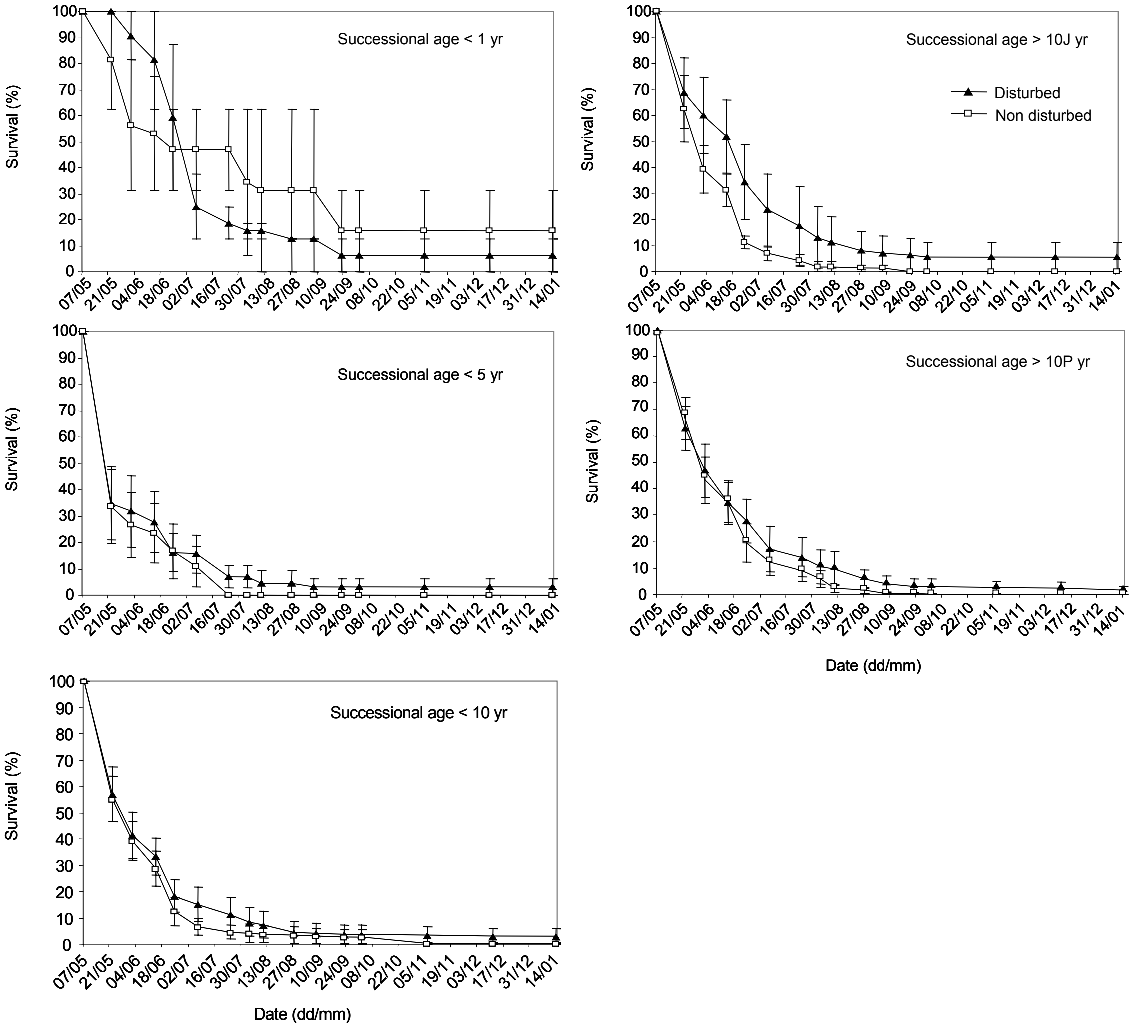

Figure 1. *C. selloana* seedling survival in fields of different successional stages in disturbed and non disturbed plots along the sampling period in an agricultural-old-field matrix in Delta del Llobregat. “J” = dominated by *J. acutus* and “P” = dominated by *P. australis*.

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 > *10J* fields (Scheffé-test, $0.001 < P \leq 0.03$) (Figure 2A). 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, $0.007 < P \leq 0.03$) (Figure 2B). This comparison could not be established with non disturbed plots because at the end of the experiment non-disturbed plots of < *10* fields were the only successional stage with alive seedlings.

Table 2. Product-limit (Kaplan-Meyer) estimations of survival time (mean ± s.e.) of *C. selloana* seedlings transplanted in fields of different successional stages in an agricultural-old-field matrix in Delta del Llobregat. Values within columns followed by different lower-case letters are significantly different between treatments according to a Scheffé-test. "J" = dominated by *J. acutus* and "P" = dominated by *P. australis*.

	Survival time (days)	
Successional stage	**Non-disturbed**	**Disturbed**
< 1	69.19 ± 8.71 a	60.75 ± 6.01 a, d
< 5	23.87 ± 1.57 b	26.81 ± 1.91 c
< 10	29.10 ± 2.04 b	33.36 ± 2.23 b, c
> 10P	31.35 ± 1.62 b	41.45 ± 2.86 a
> 10J	26.25 ± 1.70 b	44.44 ± 3.06 b, d

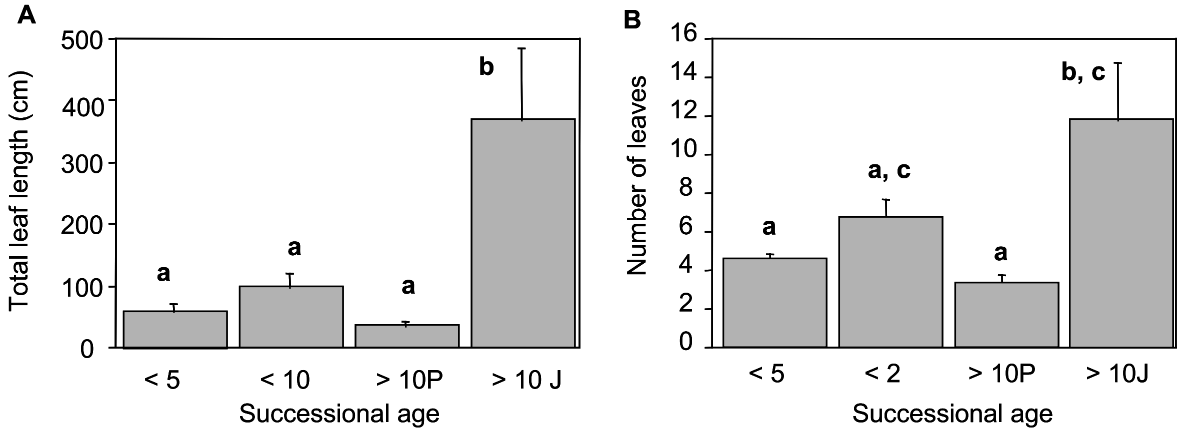

Figure 2. Total leaf length and production of leaves (means + s.e.) of disturbed plots along a successional gradient in an agricultural-old-field matrix in Delta del Llobregat. A Scheffé-test was used to establish pair-wise comparisons. "J" stands for *J. acutus* and "P" stands for *P. australis*.

4.4.2 Establishment in different vegetation types

Vegetation types did not receive different PAR ($F_{2, 27} = 1.17$, $P = 0.33$) and obviously PAR measures were significantly higher at the second sampling which took place in July ($F_{1, 27} = 116.59$, $P < 0.0001$). However, there was no significant interaction between vegetation types and sampling date ($F_{2, 27} = 3.23$, $P = 0.05$) (Table 3). 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 3).

Table 3. PAR and soil moisture (mean ± s.e.) in *P. australis*, *J. acutus* and herbs vegetation types in an agricultural-old-field matrix in the west of Delta del Llobregat.

Vegetation type	**16th June** **PAR**	**Soil moisture (%)**	**13th July** **PAR**	**Soil moisture (%)**
P. australis	1502.6 ± 81.3	19.7 ± 2.5	902.9 ± 47.9	18.2 ± 2.4
J. acutus	1514.2 ± 71.8	23.3 ± 3.2	749.6 ± 62.9	21.6 ± 2.8
Herbs	1294.9 ± 69.8	15.5 ± 2.4	873.4 ± 94.8	14.9 ± 2.0

Of the 1903 seedlings we planted only 3.9 % remained alive by the end of the experiment (Figure 3). Percentage survival of C. selloana seedlings was not significantly different between vegetation types ($H = 0.73$, d.f. = 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 (6.6 ± 1.7 %) than percentage survival in non disturbed plots, which was extremely low (0.7 ± 0.3 %).

Significant differences were found in mean survival time between vegetation types ($\chi^2 = 6.30$, d.f. = 2, P = 0.04) and also considering soil disturbance ($\chi^2 = 45.80$, d.f. = 1, P < 0.0001). Regarding non disturbed plots, C. selloana seedlings beneath J. acutus had a longer survival time than beneath herbs (Scheffé-test, P = 0.0007) or beneath P. australis (Scheffé-test, P = 0.001). However, when establishing pair-wise comparisons between vegetation types in disturbed plots no significant differences appeared (Table 4).

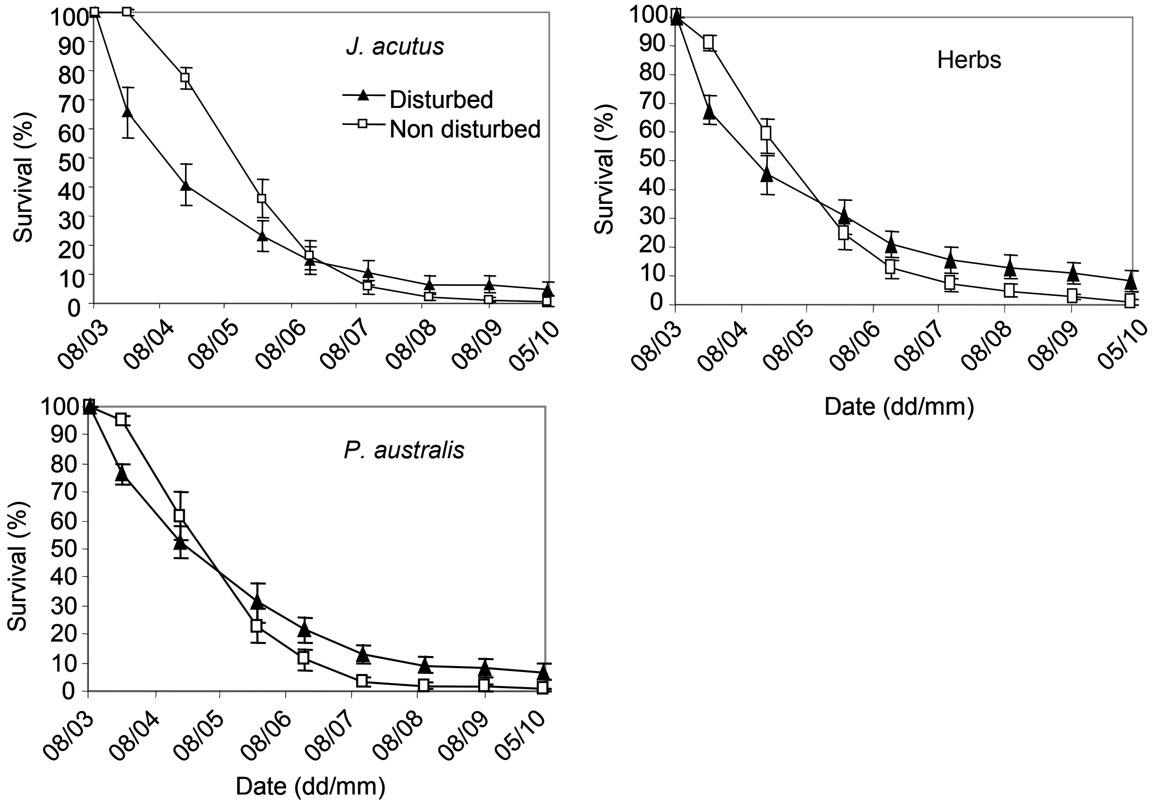

Figure 3. Survival (mean ± s.e.) of *C. selloana* transplanted seedlings in *J. acutus*, *P. australis* and herb vegetation types and effect of soil disturbance in an agricultural-old-field matrix in Delta del Llobregat.

Table 4. Product-limit (Kaplan-Meyer) estimations of survival time (mean ± s.e.) of *C. selloana* seedlings in three different vegetation types in an agricultural-old-field matrix in Delta del Llobregat. Values within columns followed by different lower-case letters are significantly different between treatments.

	Survival time (days)	
Vegetation type	**Non disturbed**	**Disturbed**
P. australis	73.15 ± 1.95 b	76.28 ± 3.22 a
J. acutus	84.34 ± 2.03 a	65.48 ± 3.20 a
Herbs	72.93 ± 2.35 b	72.59 ± 3.58 a

Seedling dry weight did not significantly vary between vegetation types (H = 1.27, d.f. = 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 (0.160 ± 0.280 g).

The percentage of germination of C. selloana seeds was 13.5 ± 9.6 % in J. acutus vegetation type, 12.6 ± 3.9 % in herb vegetation type and 10.7 ± 3.8 % in P. australis vegetation type. However, it was not significantly different between the three vegetation types ($F_{2, 27}$ = 0.12, P = 0.88).

4.4.3 Effect of *P. australis* on establishment

P. australis clipped plots received a significantly higher PAR (1004.1 ± 142.9) than *P. australis* plots (508.6 ± 92.5) (t_{34} = 2.90, *P* = 0.006). However, mean soil temperature at 2 cm in *P. australis* clipped plots was not higher (25.3 ± 0.6 ºC) than in plots with *P. australis* (24.9 ± 0.5 ºC) (t_{34} = 0.43, *P* = 0.67).

Of the 432 seedlings we planted only 13.9 % remained alive until the end of the experiment. *C. selloana* percentage seedling survival in *P. australis* clipped plots (12.7 ± 4.4 %) was not significantly different (Z = 0.11, *P* = 0.91) than in plots with *P. australis* (17.6 ± 6.5 %) (Figure 4). Survival time also did not differ between treatments (79.35 ± 2.88 days and 83.01 ± 2.92 days, respectively) (χ^2 = 2.42, d.f. = 1, *P* = 0.12).

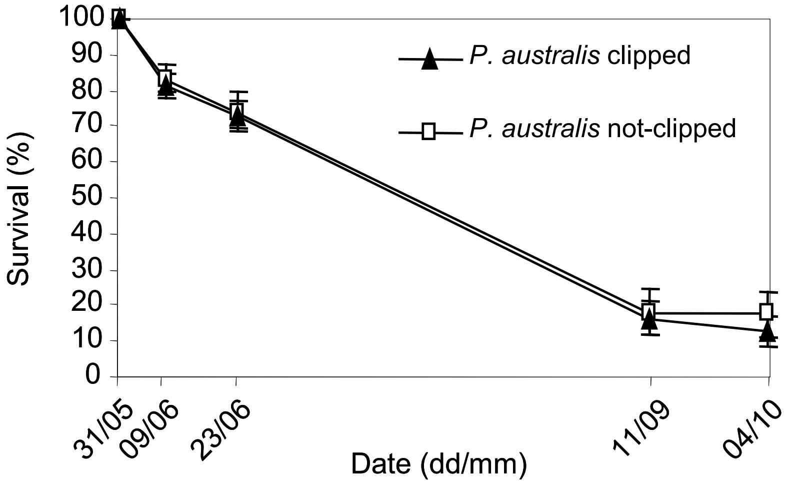

Figure 4. Survival (mean ± s.e.) of transplanted *C. selloana* seedlings beneath *P. australis* and where *P. australis* aboveground biomass was clipped in the shore of a lagoon in Prat del Llobregat.

Seedlings of plots with *P. australis* produced 0.2 ± 0.2 leaves during the course of the experiment and seedlings of plots without *P. australis* 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 *P. australis* were longer (67.4 ± 7.5 cm) than seedlings of *P. australis* clipped plots (35.8 ± 7.9 cm).

4.4.4 Establishment beneath *J. acutus*, *P. australis* and *C. selloana*

Soil under *C. selloana* was not significantly different from soil under *J. acutus* and *P. australis* for all the soil properties studied (Table 5)

Treatments received significantly different PAR ($F_{3,\ 55}$ = 47.13, P <0.0001): PAR values were the highest in plots where *P. australis* had been clipped (Scheffé-test, $0.0001 < P \leq 0.02$) (Table 6). Measures of PAR were not significantly changed 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).

Table 5. Soil properties (mean ± s.e.) beneath *C. selloana*, *J. acutus* and *P. australis* in an old-field invaded by *C. selloana* in Remolar-Filipines.

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

Table 6. PAR and soil moisture measures (mean ± s.e) beneath *J. acutus*, *P. australis* and *C. selloana* in an old-field invaded by *C. selloana* in Remolar-Filipines. 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**
J. acutus	514.0 ± 72.8 a	652.2 ± 98.1 a	13.64 ± 1.29 a	8.60 ± 0.88 a
C. selloana	621.7 ± 131.7 a	652.7 ± 152.4 a	15.49 ± 1.39 a	11.64 ± 1.33 a, b
P. australis	1315.8 ± 122.3 b	1165.8 ± 139.5 a	21.28 ± 2.20 a	17.69 ± 2.20 b
P. australis clipped	2152.7 ± 70.1 c	2142.0 ± 69.1 b	20.52 ± 2.10 a	12.13 ± 2.14 a, b

Soil moisture also varied significantly between treatments ($F_{3,\ 55}$ = 3.67, *P* = 0.02). In general, plots with *P. australis* and plots where *P. australis* 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 6) (Scheffé-test, 0.20 ≤ *P* ≤ 1.00), significant differences appeared at the second sampling date. Soil moisture beneath *C. selloana* and *J. acutus* was the lowest. Moreover, soil moisture of *P. australis* plots was higher than soil moisture of *J. acutus* plots (Scheffé-test, *P* = 0.02) (Table 6).

Of the 960 *C. selloana* seedlings we planted, only 2.5 % remained alive by the end of the experiment. All seedlings where *P. australis* was clipped died before the end of the experiment (Figure 5). However, there were no significant differences in percentage survival of *C. selloana* seedlings between the three remaining treatments (H = 2.28, d.f. = 2, *P* = 0.32): percentage survival beneath *C. selloana* was 4.2 ± 2.2 %, 3.3 ± 2.1 % beneath *J. acutus* and 2.5 ± 1.8 % beneath *P. australis*. Mean seedling survival time varied significantly between treatments (χ^2 = 384.20, d.f. = 3, *P* < 0.001). Seedlings beneath *C. selloana* had the longest survival time and seedlings in *P. australis* clipped plots had the lowest value (Scheffé-test, 0.0001 > *P*). Final biomass of plants varied significantly between treatments ($F_{2,\ 21}$ = 6.76, *P* = 0.005): seedlings beneath *P. australis* produced the highest biomass and seedlings beneath *J. acutus* and *C. selloana* produced the lowest (Table 7).

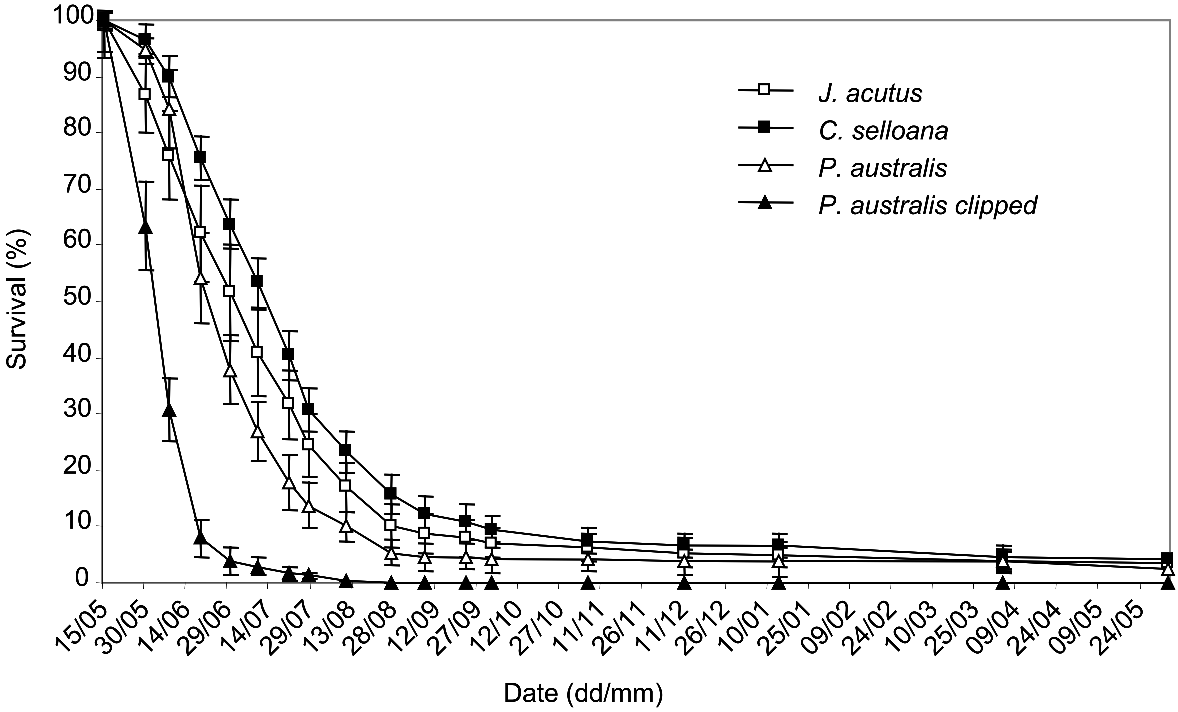

Figure 5. Survival (mean ± s.e.) of *C. selloana* seedlings transplanted beneath *J. acutus*, *C. selloana*, *P. australis* and *P. australis* clipped in an old-field invaded by *C. selloana* in Remolar-Filipines in Delta del Llobregat.

Table 7. Product-limit (Kaplan-Meyer) estimations of survival time and final dry biomass (mean ± s.e.) of *C. selloana* seedlings transplanted in plots beneath *C. selloana*, *J. acutus*, *P. australis* and *P. australis* clipped in an old-field invaded by *C. selloana* in Remolar-Filipines in Delta del Llobregat. Values followed by different lower-case letters are significantly different between treatments within a variable.

Treatments	**Survival time (days)**	**Final biomass (g)**
C. selloana	79.10 ± 4.87 a	0.032 ± 0.016 a
J. acutus	68.85 ± 5.43 a, d	0.008 ± 0.004 a
P. australis	58.45 ± 4.78 b, d	0.170 ± 0.066 b
P. australis clipped	20.92 ± 0.86 c	

4.5 Discussion

It is generally agreed that during the course of succession there is a decline of invasibility (Rejmánek 1989, Lepart & Debussche 1991). Specifically, young successional stages are often predicted to be more susceptible to invasions than latter successional stages since they are less complex communities (Crawley 1989). In addition, the most likely mechanism to provide a window of time in which invasions can occur is facilitation: species may not establish at the very beginning of succession due to a lack of their required resources and they can neither establish at later stages since natural enemies may be too abundant (Crawley 1989). However, our results reveal that early successional stages are not more invaded than latter stages since we did not find differences in *C. selloana* seedling performance along the successional gradient, which contrasts with the high invasibility of mid-successional stages found by Bastl *et al*. (1997). Consequenly, neither the facilitation model of succession nor the tolerance model can account for our results. Neither can our results be explained by the inhibition model of succession (Connell & Slatyer 1977, Ward & Jennings 1990) otherwise we would have found that early native colonizers prevented *C. selloana* invasion at the beginning of succession, but late seral species and *C. selloana* invasion would have been promoted at the end of succession.

Furthermore, ecosystem invasibility not only depends on vegetation succession but also on vegetation types. For instance, grasslands have been reported to be less invaded than other vegetation types (Huenneke *et al*. 1990, Burke & Grime 1996). By contrast, we found that within latter successional stages invasibility did not depend on vegetation type since communities dominated either by *P.* australis, *J. acutus* or herbs did not differ in their resistance to invasion. This result is consistent with the absence of differences found in *C. selloana* germination in disturbed plots in these vegetation types, showing that invasibility was the same for the three vegetation types. In addition, this lack of significant differences can be used to infer that the different microenvironmental conditions of each successional stage or vegetation type also did not affect *C. selloana* invasion.

The continued existence of species or communities often require some type of disturbance. There is overwhelming evidence that different types of disturbance promote biological invasions either through a reduction of vegetal cover or levels of competition or through an increase in the availability of specific resources (Hobbs & Huenneke 1992, Hobbs & Humphries 1995, Davis *et al.* 2000). Our results are consistent with this statement since soil microdisturbances increased seedling survival and growth during succession and in different vegetation types. Moreover, the mean survival time of *C. selloana* seedlings in a < 1 yr field was higher than later seral stages, indicating that the absence of any plant cover enhanced *C. selloana* invasion. Consequently, although some alien species, like *C. selloana*, may seem to be unsuccessful invaders due to their low capability of invading different successional stages or different vegetation types, disturbances can increase their potential to invade (Hobbs & Huenneke 1992). Therefore, the pattern we observe suggests that although timing in succession plays an important role in biological invasions (Crawley 1989), the chance of finding safe sites to get established, which may be provided by disturbances, might also be of vital importance in determining the invasibility of ecosystems.

However, localized soil disturbances are not the only factor that can promote plant invasions. *P. australis* has been traditionally clipped in the studied areas to promote its regeneration and we suspected that this management action could enhance *C. selloana* invasion through a reduction of competition. *P. australis* has widely been reported to inhibit the germination or establishment of other species through the modification of biotic and abiotic factors (Chambers *et al.* 1999, Keller 2000, Meyerson *et al.* 2000). For this reason, we expected a higher percentage survival and a better performance of *C. selloana* seedlings in plots where *P. australis* had been clipped.

On the contrary, we found a facilitative effect of *P. australis* on *C. selloana* establishment. Percentage survival in plots where *P. australis* had been clipped rapidly fell during the first month after transplanting and none of these seedlings remained alive by the end of the experiment. Moreover, *P. australis* clipping decreased mean survival time of *C. selloana* seedlings with respect to plots where this species had not been clipped. These effects were probably caused by the high amount of PAR that seedlings received in these plots due to the absence of vegetal cover. During the experiment in Prat del Llobdregat seedlings of *P. australis* plots also benefited from the *P. australis* cover and consequently produced a greater total leaf length than the other seedlings. In the old-field of Remolar-Filipines we could not check for this pattern because no seedlings of plots where *P. australis* had been clipped survived. Seedlings beneath *P. australis* produced a higher final biomass than seedlings beneath *C. selloana*. However, although *J. acutus* and *C. selloana* have a similar structure, seedlings beneath *J. acutus* did not experience the same effect and produced less biomass. The facilitative role of some natives on aliens has been found in other studies. For example, the native nitrogen-fixing shrub, *Lupinus arboreus*, favours the invasion of the alien *Bromus diandrus* in California coastal prairies (Maron & Connors 1996).

Overall, we should consider that although *C. selloana* survival was very low both in a successional gradient and in different vegetation types, we have proved that soil disturbance enhances *C. selloana* invasion at any point of succession. Furthermore, some native species such as *P. australis* even can protect *C. selloana* seedlings and promote their growth. Our study suggests that there might be other factors that possibly promote *C. selloana* invasion. In fact, a high production of small seeds is one of the characteristics that have been related to successful invaders (Bazzaz 1986, Baker 1965). *C. selloana* produces large amounts of small wind-dispersed seeds (10^6 seeds per mature plant for females and 10^5 for hermaphrodites; Connor & Edgar 1974, Lambrinos 2002) 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 (Domènech *unpublished data*). It should be highlighted that this 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).

4.6 Acknowledgements

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

5.1 Abstract

Of the species intentionally or accidentally introduced to new habitats only a few succeed in establishing themselves. Success depends on species traits as well as on the characteristics of the invaded community. Alien species have been reported to have a superior competitive ability than native species of the recipient communities. However, their competitive abilities have rarely been compared simultaneously at the same life-history stage and for the same functional group of species. Resource pulses of soil nutrients and water can also provide the triggering conditions for invasions to start. Alien species' resistance and adjustment to water stress might largely determine the success of invasions in Mediterranean ecosystems because biomass production is controlled by water availability rather than by nutrients. Two outdoor pot experiments were conducted to test the hypotheses that the alien perennial tussock grass *Cortaderia selloana* is a superior competitor and it is more resistant to water stress than the two coexisting native species of the same functional group, *Festuca arundinacea* and *Brachypodium phoenicoides*. We found that the relative aboveground biomass of *C. selloana* was not affected by either intra or interspecific competiton. However, when considering the alien's relative impact, *C. selloana* did not reduce the growth of the target native species more than it could be reduced by growing with other native species. Moreover, with regard to native species resistance, the effect of one native species on the other native was not greater than its effect on the alien *C. selloana*. Although both *C. selloana* and *B. phoenicoides* performed in a similar way under water stress conditions (i.e. specific leaf area, relative above and belowground biomass decreased and shoot-root biomass ratio increased). However, the alien species' capacity to adjust to water stress, indicated by the root-shoot ratio, was slightly better than that of *B. phoenicoides*. Moreover, *F. arundinacea* was the most severely affected species by water stress. Overall, *C. selloana* is not a superior competitor than the coexisting native species. However, it seems to be more resistant to water stress because as water become scarce *C. selloana* maximizes water uptake and minimizes water losses more than *B. phoenicoides* and, especially, *F. arundinacea*.

Keywords**:** alien plant, *Brachypodium phoenicoides*, *Festuca arundinacea*, intraspecific competition, interspecific competition, Relative Interaction Index, resistance to invasion.

5.2 Introduction

The intentional or accidental introductions of alien species are the causes of biological invasions which pose a major threat to the conservation of biodiversity worldwide (Vitousek 1994, Davis 2003, Keane & Crawley 2002). Despite this, only a few introduced species succeed in establishing in the recipient community (Holdgate 1986, Parker & Reichard 1998), depending on the biotic and environmental characteristics of the recipient community as well as on the biological attributes of the invader (Lonsdale 1999).

On the one hand, some alien 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 species is introduced, competition for limited resources is one of the first interactions the species has with the recipient community (Vilà & Weiner 2004). Field observations and experiments have proved that the threat alien species pose on the persistence of native species is usually driven by the competition effect of the alien species on natives (Parker & Reichard 1998, Levine *et al*. 2003). However, most studies are biased because they have focussed on highly aggressive invaders competing with less vigorous species of dissimilar life form or life-history stage (Vilà *et al*. 2004). Furthermore, when analysing competitive abilities of alien species, the competitive effect that the native species have on the alien should be simultaneously compared (Vilà & Weiner 2004).

On the other hand, it has also been argued that resource pulses (e.g. soil nutrients and water) provide the triggering conditions for invasions to start (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 & 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 & Chesson 2002). Alien species resistance and adjustment to water stress are important for invasion to occur in Mediterranean ecosystems where climate is characterized by hot, dry summers and biomass production of native species is controlled by water availability rather than by light and nutrients (Piñol *et al*. 1995). Furthermore, competition for water is very common in Mediterranean ecosystems (Vilà & 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. Consequently, in order to determine which plant strategy (i.e. competitive, stress tolerant and ruderal) (Grime 1982) rules the success of plant invasions in Mediterranean ecosystems it is necessary to quantify both the importance of the competitive abilities of alien species simultaneously with that of native species, and in addition, 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 tussock perennial grass native to South America which was introduced to Europe as an ornamental. It is now is invading the Mediterranean old fields and grasslands of Catalonia (NE Spain) dominated by other 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* possesses traits that allow it to take advantage of low water resources and that it is a better competitor than coexisting native species of the same functional group. We conducted two outdoor pot experiments to test the following hypotheses: (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 viceversa, and (2) *C. selloana*'s performance will not be as severely affected by water stress as will the performance of the other two coexisting native perennial grasses.

5.3 Material and Methods

5.3.1 Study species

Festuca arundinacea is a perennial grass native to Europe frequently found in humid grasslands. Leaves are rolled in the bud, blades are 3 to 12 mm wide and 10 to 60 cm long. Leaf margins are rough and cutting to the touch. Basal leaves are broad and dark-green. Its maximum growth takes place during spring and autumn and its deep and extensive root system helps it to withstand drought conditions. At the beginning of its development it basically spreads by erect tillers which end with inflorescences that form compact panicles. F. arundinacea flowers in spring and seed mature in early summer. It is adapted to a wide range of soil and climatic conditions (Tutin et al. 1980, Bolòs & Vigo 2001, http://aggie-horticulture.tamu.edu).

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. It makes simple, rigid and erect stems. Leaves are also rigid and their length ranges from 10 to 40 cm. *B. phoenicoides* is considered as an essential species for ecological succession in pastures since it establishes during the initial stages and allows the entrance of other species, thus letting succession lead to more complex communities (Tutin *et al*. 1980, Bolòs & Vigo 2001, http://biodiver.bio.ub.es).

The 3 species (see *Introducció general* for information on *C. selloana*) 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 (Bossard *et al*. 2000) and its maximum plant volume ranges from 45 to 55 m^3 whereas *F. arundinacia* and *B. phoenicoides* can reach only from 40 to 60 cm in height and the diameter of the tussock is from 5 to 10 times smaller than that of *C. selloana* (Domènech *unpublished data*).

5.3.2 Plant material

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

5.3.3 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 ºC and 673.1 mm, respectively (http://www.meteocat.com).

In order to determine the mean initial above and belowground biomass of the three target species we weighed the leaves and roots from 20 seedlings of each species after air-drying at 70ºC 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 between species ($F_{2, 55} = 38.00$, $P < 0.0001$), being the largest in *F. arundinacea* (Fisher's PLSD test, $P < 0.0001$). Belowground biomass was 0.0019 ± 0.0001 g for *B. phoenicoides*, 0.0009 ± 0.0001 g for *C. selloana* and 0.0021 ± 0.0002 g for *F. arundinacea*. Belowground biomass was also significantly different between species ($F_{2, 55} = 26.46$, $P < 0.0001$), being the largest in *F. arundinacea* (Fisher's PLSD test, $P < 0.0001$).

Nine competitive treatments which included all possible pair-wise combinations of intraspecific and interspecific competition and no competition were replicated 12 times, as follows: (1) 2 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) 2 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) 2 seedlings of *B. phoenicoides* per pot (B:B) and finally, (9) one seedling of *B. phoenicoides* per pot (B).

Pots were watered every two days to avoid water stress and were randomly moved every 15 days to guarantee that all the plants were growing under the same environmental conditions. On July 2004, once the majority of plants had occupied all the pot volume and started to produce panicles, plants were collected and weighed after air-drying at 70ºC to constant weight. 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 seedlings aboveground biomass we calculated the relative aboveground growth (RAG) of each species as: $(B_{t1} - B_{t0})/ B_{t0}$, where B_{t1} = biomass at harvesting time and B_{t0} = estimated biomass before treatment.

Differences in the RAG of each species growing alone, under intraspecific competition and under interspecific competition were compared with a 4 level one-factor ANOVA. Only one plant per pot was randomly selected to evaluate the effect of intraspecific competition. Fisher's PLSD test was used to establish pair-wise comparisons. According to our hypothesis of C. selloana being a superior competitor than the native species, we expected C. selloana RGA 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 & Weiner (2004). First, with regard to the alien species impact we tested if 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, focussing 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 (CI) indices such as the relative CI (RCI) and the log response ratio (ln RR) (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:

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

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 absence of inter- or intra-specific interactions.

Unpaired t-tests were used to compare the mean effect of *C. selloana* on *B. phoenicoides* (RII B:C) with the mean effect of *F. arundinacea* on *B. phoenicoides* (RII B:F), and the mean effect of *C. selloana* on *F. arundinacea* (RII F:C) with the mean effect of *B. phoenicoides* on *F. arundinacea* (RII F:B). Similarly, unpaired t-tests were also used to compare the mean effect of *B. phoenicoides* on *F. arundinacea* (RII F:B) with the mean effect of *B. phoenicoides* on *C. selloana* (RII C:B), and the mean effect of *F. arundinacea* on *B. phoenicoides* (RII B:F) with the mean effect of *F. arundinacea* on *C. selloana* (RII C:F). 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 was larger than the effect of a native on the other native. Second, with regard to the native's resistance, we would expect RII C:F and RII C:B to be less negative than RII B:F and RII F:B, indicating that the negative effect of a native species on the other native was larger than the effect on the alien.

5.3.4 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 placed on benches in an open greenhouse which consisted of a plastic cover shelter sustained by a metallic structure. Therefore the greenhouse excluded rainfall, allowing for the control of watering during the experiment, but it did not change the other environmental conditions.

Before starting the experiment, all pots were watered to excess and allowed to drain during a night. Species were randomly assigned to one of the following water stress treatments following the same protocol as a previous study conducted with *C. selloana* and *C. jubata* seedlings (Stanton & Di Tomaso 2004): (1) a fully watered treatment (hereafter “control”) which was used as an indicator of unstressed growth; (2) an intermediate drought stress (hereafter “moderately stressed”) in which at the beginning of the experiment plants were withheld water for 6 days, watered every day during the successive 8 days and not watered during the successive 31 days; (3) a sustained drought treatment (hereafter “severely stressed”) in which plants did not receive water for the course of the experiment. Each treatment was replicated 12 times. The final number of pots was 108 (3 water stress treatments x 3 species x 12 replicates). Pots were randomly moved once a week in order to guarantee that all the plants were growing under the same conditions.

In order to detect if the watering treatments had been homogeneous among species, at the end of the experiment (45 days after planting), we measured soil moisture with a TDR in a subsample of 7 pots per treatment and per species. At the end of the experiment 3 leaves of 3 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 LICOR (Li-cor, Lincoln, NE, USA). Leaves were weighed after air-drying at 70ºC to constant weight, and the mean specific leaf area (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 70ºC to constant weight and weighed to measure final above and belowground biomass. As for the competition experiment, in order to correct for the initial differences in above and belowground biomass we calculated the relative growth of each species as: $(B_{t1} - B_{t0})/ B_{t0}$, where B_{t1} = biomass at harvesting time and B_{t0} = estimated biomass before treatment. We also calculated the root-shoot biomass ratio (R/S ratio) for each plant as the ratio between below and aboveground biomass.

Differences between water stress treatments and species on SLA, above and below ground relative growth (RAG and RBG, respectively) and R/S ratio were analysed with a 2-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*. Pair-wise differences between stress treatments and between species were analysed with a Fisher's PLSD test. Data was transformed when necessary to meet the assumptions of homogeneity of variances and to fit a normal distribution of data.

In order to quantify the effect of moderate and severe water stress treatments on species performance compared to control conditions, we calculated the Relative Interaction Index (RII) for all the measured plant variables. A negative RII would indicate a negative effect of a particular water stress treatment in seedling performance with respect to the control treatment, a positive RII would indicate that water stress treatments increased seedling performance, finally RII = 0 would indicate no effect of any of the water stress treatments.

5.4 Results

5.4.1 Competition experiment

RAG of *C. selloana* and *F. arundinacea* seedlings was not significantly affected by any of the four competition treatments: ($F_{3, 40} = 1.81$, $P = 0.16$ and $F_{3, 31} = 0.41$, $P = 0.75$; respectively) (Figure 1). However, significant differences were found for *B. phoenicoides* ($F_{3, 42} = 5.04$, $P = 0.005$). ARG of *B. phoenicoides* seedlings in competition with *C. selloana* (Fisher's PLSD test, $P = 0.006$) and with *F. arundinacea* (Fisher's PLSD test, $P = 0.01$) was significantly lower than under intraspecific competition (Figure 1).

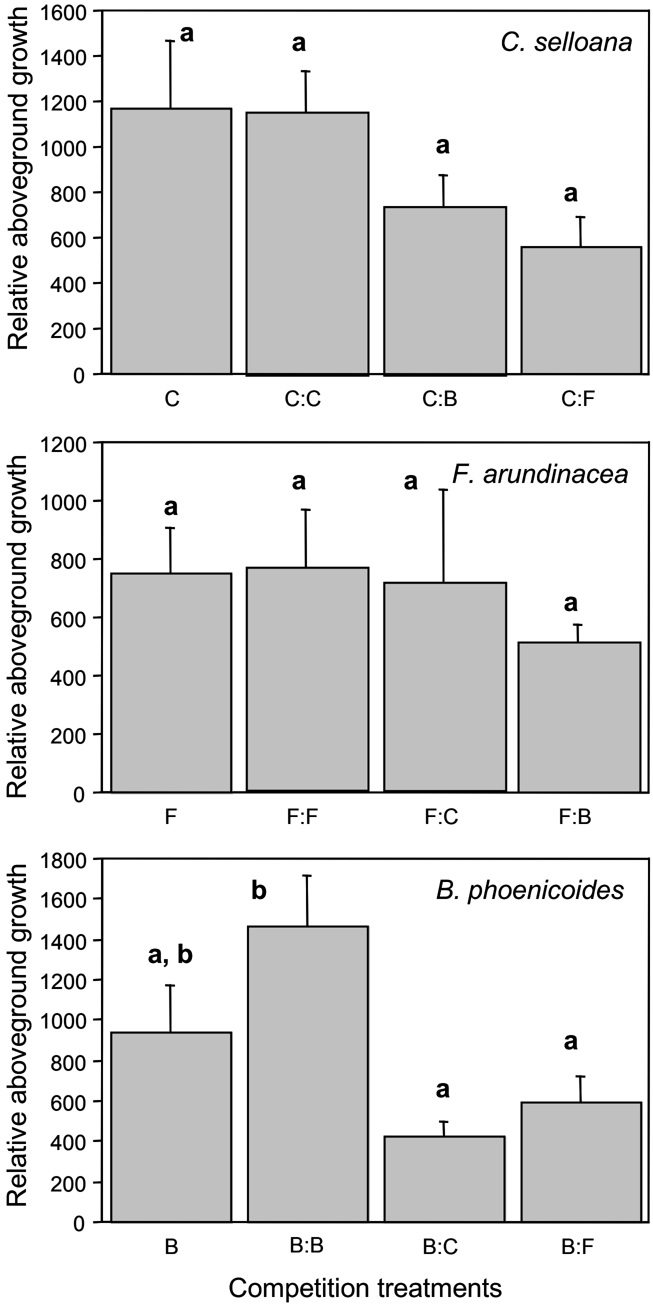

Figure 1. Aboveground relative growth (mean + s.e.) of *C. selloana* (C), *F. arundinacea* (F) and *B. phoenicoides* (B) in 4 competition treatments: growing alone, under intraspecific competition and under interspecific competition. Different lowercase letters above columns indicate significant differences between competition treatments according to Fisher's test.

Regarding the alien species impact, we found negative values of RII either when *C. selloana* was growing with *B. phoenicoides* or with *F. arundinacea*, indicating that the alien *C. selloana* competed with the two native species. 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 neither significantly larger than the effect of *B. phoenicoides* on *F. arundinacea* (t_{16} = 0.81, *P* = 0.43). When focussing on the native species resistance to the alien, significant differences appeared. The effect of *B. phoenicoides* on *C. selloana* was significantly larger than the effect of *B. phoenicoides* on *F. arundinacia* (t_{20} = 2.36, *P* = 0.03). 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) (Figure 2).

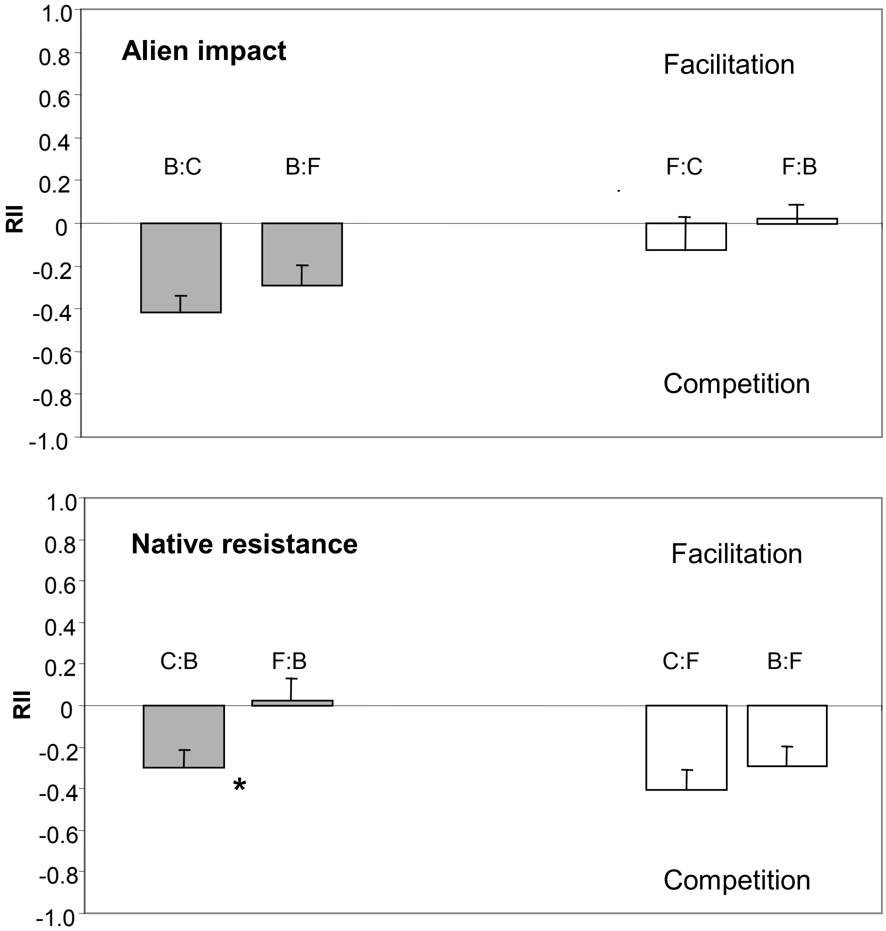

Figure 2. Relative Interaction Indices (RII) (mean + s.e.) comparison using the alien's species impact and native's species resistance approaches. Positive RII indicate a facilitative effect between species and negative RII indicate competition between species. Asterisk indicate significant differences (*P* < 0.05). "C" = *C. selloana*, "B" = *B. phoenicoides* and "F" = *F. arundinacea*.

5.4.2 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, there were no significant differences between the three target species ($F_{2, 54} = 2.75$, $P = 0.07$). The highest soil moisture was measured in control/non-stressed pots (36.30 ± 1.43 %), followed by moderately stressed pots (9.72 ± 0.81 %) and severely stressed pots (5.98 ± 0.51 %). Consequently, moderate and severe water stress caused 73.22 % and 83.5 % reduction in soil moisture with respect to control treatment. The interaction between 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 ($F_{2, 18} = 20.44$, $P < 0.0001$). *F. arundinacea* SLA was significantly higher than in the other 2 species (Fisher's PLSD test, $P < 0.0001$) and there were no significant differences between *B. phoenicoides* and *C. selloana* (Fisher's PLSD test, $P = 0.15$). The highest SLA was measured in control plants (Fisher's PLSD 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: *F. arundinacea* SLA was only reduced by severe water stress. In contrast, 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 (Fig 3 A).

The RAG was also significantly different between species ($F_{2, 98} = 17.57$, $P < 0.0001$) and treatments ($F_{2, 98} = 427.87$, $P < 0.0001$). *F. arundinacea* significantly produced more aboveground biomass than *B. phoenicoides* (Fisher's PLSD test, $P = 0.02$) and *C. selloana* (Fisher's PLSD test, $P = 0.0006$). RAG of *C. selloana* was significantly lower than that of *B. phoenicoides* (Fisher's PLSD test, $P < 0.0001$). RAG was the highest in the control water stress treatments and the lowest in the severe water stress treatments (Fisher's PLSD test, $P < 0.0001$). The interaction between species and water stress treatments was also significant ($F_{4, 98} = 8.90$, $P < 0.0001$): RAG 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 RAG was considerably larger than that experienced by *C. selloana* and *B. phoenicoides* (Figure 3 B).

The same pattern was observed for RBG: 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 RBG with respect to the control treatment than the moderate treatment (Fisher's PLSD test, $P < 0.0001$). *F. arundinacea* produced the highest RBG, especially in the control water stress treatment, but this species was again the most affected by moderate and severe water stress treatments (Figure 3 C).

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 PLSD test, $P < 0.0001$) and it was significantly lower in *B. phoenicoides* than in *C. selloana* (Fisher's PLSD 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 ($F_{4, 98} = 10.47$, $P < 0.0001$). 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 (Figure 3 D).

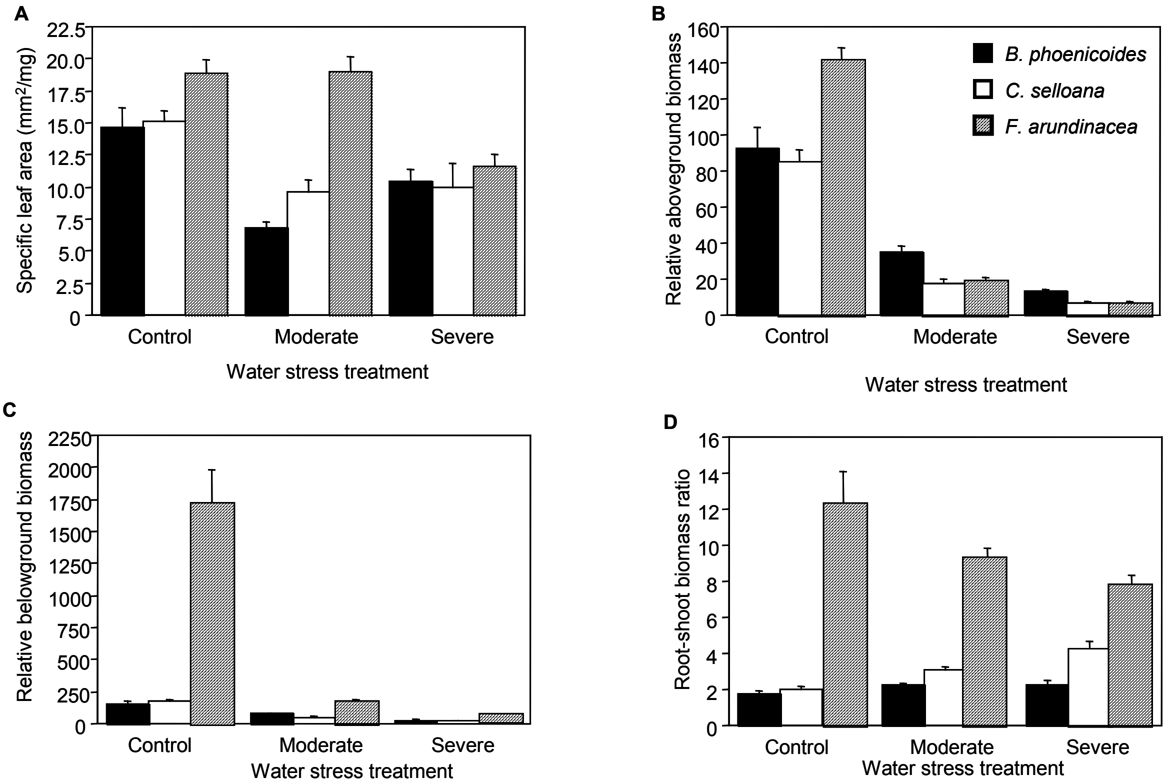

Figure 3. Effect of water stress on A) specific leaf area, B) relative aboveground biomass growth, C) relative belowground biomass and D) root-shoot ratio (mean + s.e.) in the alien *C. selloana* and in the natives *B. phoenicoides* and *F. arundinacea*.

Overall, the effect of moderate and severe water stress compared to the control/non-stress treatment indicate that the most negatively affected species for all variables was *F. arundinacea* followed by *C. selloana* except for R/S ratio where the intensity of the change was larger in *C. selloana* than in *F. arundinacea* (Table 1).

Table 1. Effect of moderate and severe water stress on the Relative Interaction Index (RII) on the three target species. "SLA" = specific leaf area, "RAG" = relative aboveground biomass, "RBG" = relative belowground biomass and "R/S" = root-shoot biomass ratio.

	RII							
	Effect of moderate stress on:				**Effect of severe stress on:**			
	SLA	**RAG**	**RBG**	**R/S**	**SLA**	**RAG**	**RBG**	**R/S**
B. phoenicoides	- 0.37	- 0.45	- 0.34	+ 0.12	- 0.17	- 0.75	- 0.69	+ 0.13
C. selloana	- 0.23	- 0.66	- 0.54	+ 0.21	- 0.21	- 0.86	- 0.74	+ 0.36
F. arundinacea	+ 0.003	- 0.76	- 0.82	- 0.14	- 0.24	- 0.91	- 0.94	- 0.22

5.5 Discussion

Interspecific competition has been reported to play an important role in determining the likelihood of plant invasions (Crawley 1990). In particular, alien species are hypothesised to be superior competitors than native species as a result of different evolutionary histories (Baker 1965, Holdgate 1986, Roy 1990, Keane & Crawley 2002). However, this statement should be carefully considered since the native species chosen to perform competitive experiments with alien species usually tend to be rare or endemic natives that are clearly threatened by the abundance of the alien (Huenneke & Thompson 1994). Furthermore, most experiments do not inform us if at the individual level the alien species performs better in competition than the native species. Our competition experiment between the alien *C. selloana* with the two native species *F. arundinacia* and *B. phoenicoides* of the same functional group at the same life-history stage, revealed that the alien *C. selloana* does not take advantage of growing with the two natives *F. arundinacea* or *B. phoenicoides*. Therefore, we reject our hypothesis that *C. selloana* is a better competitor than the native species.

Furthermore, when testing the hypothesis that an alien species is a better competitor than a native species it has rarely been attempted to consider at the same time both the invader's relative impact and the native species' relative resistance to the invader (Vilà & 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* posed on *F. arundinacea* and *B. phoenicoides*, respectively. With regard to native species resistance, we expected that the 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. phoeincoides* reduced the growth of *C. selloana* whereas it facilitated *F. arundinacia* growth. Therefore, at the individual level *C. selloana* seems not to have the potential to displace any of the two native species and to resist competition posed by the native species.

C. selloana's invasive potential in Mediterranean ecosystems has been related to a great water-use efficiency, to a high water capture when water is not limiting and to tolerance to water stress (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 & DiTomaso 2004). Our water stress experiment only partially support these results. *C. selloana* was not as affected by moderate and severe water stress treatments as *F. arundinacea*. However, the reduction in aboveground and belowground biomass experienced by *C. selloana* due to moderate and severe water stress was similar to that of *B. phoenicoides*. Consequently, our results do not suggest a better performance of *C. selloana* under water stress than the coexisting native species.

The capacity to increase the root-shoot biomass as water becomes a limiting factor can determine plant survival specially for Mediterranean species (Specht *et al.* 1983, Broncano et al. 1998, Sardans *et al.* 2004). Mediterranean plants are expected to have a higher root-shoot biomass than *C. selloana* because in its native range this species grows in relatively damp soils where water is not a limiting factor (http://www.issg.org). However, in stress conditions, root-shoot biomass of *C. selloana* increased more than *B. phoenicoides*, indicating that *C. selloana* seem to maximize water uptake by increasing belowground biomass and to minimize water losses by decreasing aboveground biomass (Matsuda *et al.* 1989, Poorter & 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.

Furthermore, responsiveness to favourable or unfavourable conditions of native and alien species can be measured with potential relative growth rates which have been strongly correlated with specific leaf area (Lake & Leishman 2004). Therefore, if an alien species has a better resistance to water stress than a native species it should experience a lower reduction in its specific leaf area. Previous studies have found that invasive species have a larger specific leaf area than native species (Baruch & Goldstein 1999, Grotkopp *et al*. 2002, Lake & Leishman 2004). Although specific leaf area of *F. arundinacea* plants under control water treatment was the highest, our results proved again that *C. selloana* was less affected in this parameter by severe water stress than *F. arundinacea*.

To summarize, the alien *C. selloana* seems to display little competitive advantage or resistance to competition when growing with other native species. In addition, *C. selloana* does not always perform better under moderate or severe water stress, yet the analysis of the root-shoot biomass suggest that *C. selloana* has the greatest capacity to increase the root-shoot biomass when water is scarce, which can be an advantage during the driest Mediterranean season. According to the plant strategies proposed by Grime (1982), our results suggest that *C. selloana* follows a stress tolerant strategy rather than a competitive strategy. It should also be taken into account that in seedling transplant experiments *C. selloana*'s invasive potential seems to be mainly related to a ruderal strategy that allows this species to benefit from disturbances (Domènech *chapter 4*). The species is thus not predominantly limited to one of Grime's strategies.

5.6 Acknowledgements

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6. *Cortaderia selloana* seed germination under different ecological conditions

6.1 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 such as the production of seeds which are able to germinate in a wide range of environmental conditions. Although some invaders tolerate different environments, the abiotic characteristics of the recipient community also determines invasive success of alien species provided they have a better performance under changes in the availability of certain resources such as water, compared to native plants. Finally, the absence of soil pathogens that negatively affect the alien species' seed germination may also favour invasions.

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 *C. selloana* 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. In addition, we expected that seed germination would not be affected by soil pathogens. 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 this constrained seed germination to approximately 60 %. Finally, seed germination decreased in sterilized soil. 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. Finally, soil microorganisms appear to have a positive effect on germination.

Keywords: alien species, germination test, light, natural enemies, soil textural gradient, water availability.

6.2 Introduction

During the last few centuries there has been a considerable transfer of the Earth's biota due to multiple intentional or accidental species introductions caused by human activities such as the trade boom or the massive alteration of the landscape (Vitousek 1994, Mack & Lonsdale 2001). The resulting biological invasions are a major cause of biodiversity loss because they are causing the extinction of native species and modifying ecosystem functions (Vitousek 1994, Keane & Crawley 2002, Davis 2003). However, not all the introduced alien species succeed in establishing in the recipient community (Holdgate 1986, Parker & Reichard 1998). Among other factors, invasion success depends on the biological attributes of the invader, on resource availability, on the invaded environment and on the lack of natural enemies (Lonsdale 1999).

Some successful invaders produce copious amounts of seeds which disperse widely and germinate in a wide range of environmental conditions (Holdgate 1986, Noble 1989, Gordon 1998, Goergen & Daehler 2001, Cadotte & Lovett-Doust 2001), yet not all successful invaders display these characteristics (Baker 1965) and even the same species can differ in its fecundity depending on ecological conditions and resources available in the recipient community.

The abiotic environment of the recipient community can constrain invasive success if the ecological conditions are not suitable for seed germination and seedling establishment of the alien species (Shea & Chesson 2002). 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 textures. In addition, it has been reported that invader species might have a superior response to resource pulses compared to native plants (Shea & Chesson 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 & Laurenroth 1995). Finally, the lack of natural enemies in the recipient community can also trigger the invasive success of alien species (Lonsdale 1999, Maron & Vilà 2001). Specifically, it has recently been suggested that absence of soil pathogens may favour alien plant species recruitment success at early stages of invasion (Mitchell & Power 2003, Reinhart *et al*. 2003).

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 (Bossard *et al*. 2000, Lambrinos 2002), but little is known about the abiotic and biotic factors that may favour its seed germination. For this reason, we conducted an array of germination tests with to determine if *C. selloana* seed germination is able to tolerate a wide range of environmental conditions such as different degrees of shading, different soil textures and several grades of water availability. Moreover, we also expected that seed germination would be improved by the absence of soil pathogens.

6.3 Material and Methods

6.3.1 Effect of shading on *C. selloana* germination

To test the effect of shading on seed germination we constructed three cubes of 50 x 50 x 50 cm and covered them with three different woven materials that filtered light allowing sunlight penetration of 50 %, 30 % and 5%. Each cube contained fifteen 5 Ø petri dishes with 10 *C. selloana* seeds from female plants placed on one layer of autoclaved filter paper. We also studied seed germination in fifteen uncovered 5 cm Ø 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. Each treatment was separated 1 m from each other in order 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 were 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 arcSin (1-X) to meet the assumptions of homogeneity of variances.

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

Seed germination of female plants 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 it was obtained 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).

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

	Soil texture			
Soil fractions (%)	**Coarse clay**	**Sandy-clay-loam**	**Sandy loam**	**Sandy**
Sand (2000 < Ø < 20 µm)	45. 0	60.0	75.0	90.0
Silt (2 < Ø < 20 µm)	31.1	22.6	14.1	5.7
Clay (Ø < 2 µm)	23.9	17.4	10.9	4.3

Each experimentally made soil was placed in 2-litre pots that were progressively watered for two weeks and homogenized once they were dry in order to contribute to soil structuring. Twenty five seeds from female plants were placed on 12 cm Ø 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.

6.3.3 Effect of water stress and soil sterilization on *C. selloana* germination

To test the effect of water stress on *C. selloana* germination we applied three watering treatments: (i) a fully watered control/non-stressed treatment in which petri dishes were sprayed with distilled water every day in order to maintain them constantly moist, (ii) an intermediate water stress treatment in which petri dishes were sprayed with water every day during the first five weeks, (iii) a severe water stress treatment in which petri dishes were only sprayed with water during the first three weeks. Each petri 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. Each treatment was replicated 20 times.

We studied germination in sterilized soil with half of the petri dishes of each water stress treatment by using gardening soil which had been autoclaved in order to eliminate all soil microorganisms. 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 soil sterilization and water stress was analysed after two months, when no seed germination under moderate and severe stress was observed, with a two-way ANOVA. A Scheffé test was used for pair-wise comparisons between watering and sterilization treatments.

6.4 Results

6.4.1 Effect of shading on *C. selloana* germination

Shading had a significant effect on percentage germination ($F_{3, 56} = 7.57$, $P = 0.0002$). Percentage germination of seeds which received 100 % light was the lowest (Scheffé test, $0.001 \leq P \geq 0.003$), but it was only reduced by approximately 20 %. There were not significant differences between the other treatments (Figure 1).

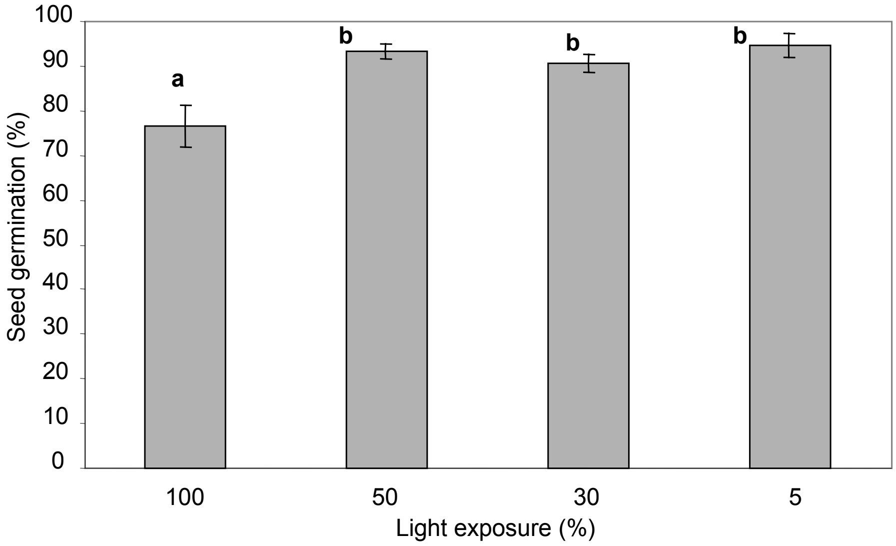

Figure 1. Mean percentage germination (± s.e.) of *C. selloana* seeds on a light exposure gradient. Different letters above columns indicate significant differences between light exposure treatments ($P < 0.05$).

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

Percentage germination of *C. selloana* seeds was significantly different along the soil texture gradient ($F_{3, 36} = 8.52$, $P = 0.0002$). Percentage germination increased as the soil was enriched with sand (Figure 2). Percentage germination of *C. selloana* seeds in sandy texture was significantly higher than percentage germination in coarse clay and sandy-clay-loam textures (Scheffé test, $0.0003 \leq P \geq 0.02$).

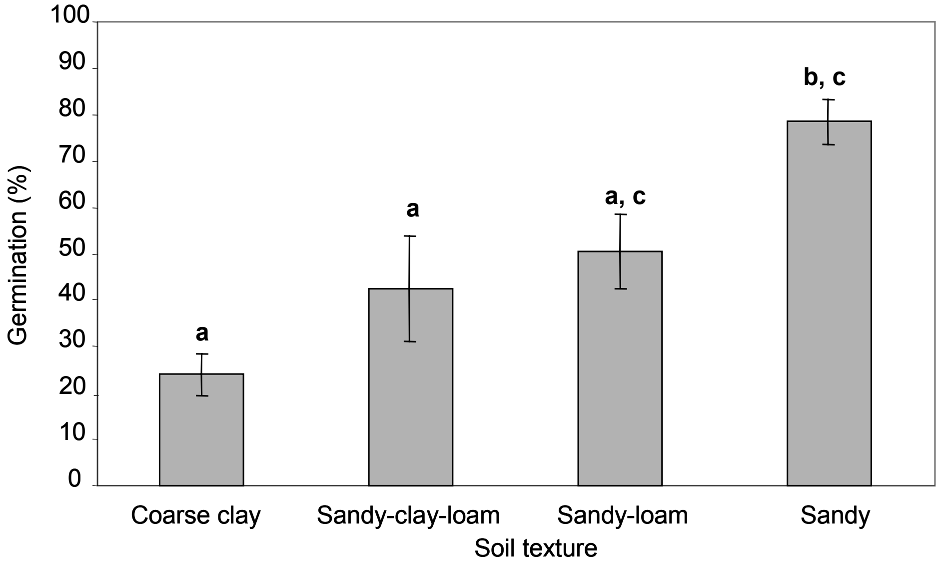

Figure 2. Mean percentage germination (± s.e.) of *C. selloana* seeds on four experimentally made textures. Different letters above columns indicate significant differences between soil textures ($P < 0.05$).

6.4.3 Effect of water stress and soil sterilization on *C. selloana* germination

Water stress had a significant negative effect on percentage germination of *C. selloana* seeds ($F_{2,\ 54} = 70.13$, $P < 0.0001$). Intermediate and severe water stress treatments significantly reduced percentage germination with respect to control/non-stressed water treatment to 45 % and 60 %, respectively (Scheffé test, $P < 0.0001$). Percentage germination of *C. selloana* seeds under moderate water stress was also significantly higher than percentage germination under severe water stress (Scheffé test, $P = 0.0004$).

The general effect of soil sterilization on percentage germination was also significant ($F_{1,\ 54} = 12.28$, $P = 0.0009$): it significantly reduced percentage germination (Figure 3). The interaction between water stress and soil sterilization was not significant ($F_{2,\ 54} = 1.80$, $P = 3.60$).

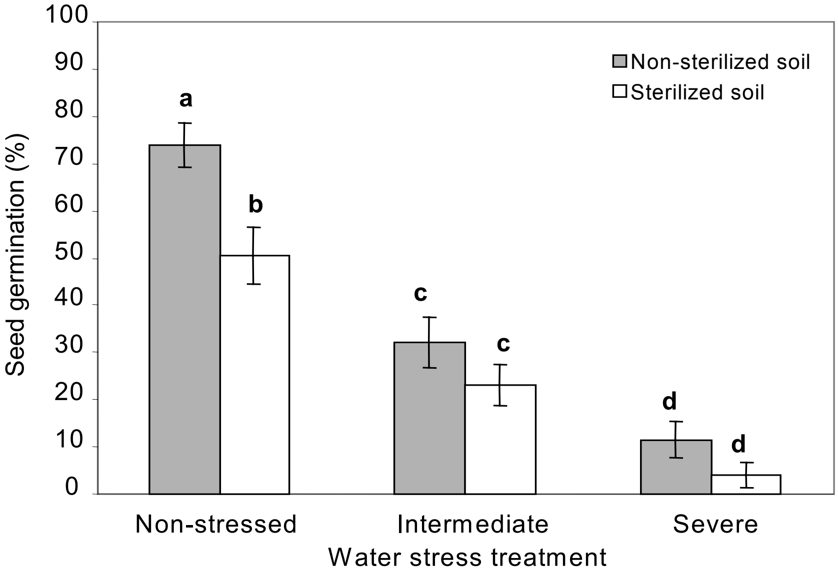

Figure 3. Mean percentage germination (± s.e.) of *C. selloana* seeds under control/non-stressed, intermediate and severe drought and soil sterilization. Different letters above columns indicate significant differences between water stress and soil sterilization treatments ($P < 0.05$).

6.5 Discussion

Successful invaders have been reported to produce large amounts of seeds, to tolerate a wide range of environmental conditions and to escape from natural enemies (Holdgate 1986, Noble 1989, Gordon 1998). For example, *Pennisetum setaceum* is an alien perennial grass which produces from two to nine times more seeds than its native competitor *Heteropogon contortus*. In addition, *P. setaceum* has higher germination rates than the native and can grow both in disturbed and undisturbed environments and tolerates competition with other species (Goergen & Daehler 2001). Similarly, a comparative ecological study of closely related alien and native species in Australia revealed that the alien *Senecio madagascariensis* had superior germination rates both under high light and dark conditions compared to the native *S. latus* (Radford & Cousens 2000). Moreover, seedlings of the alien S*enecio inequidens* have been reported to be less predated and to be superior competitors than seedlings from the native *S. malacitanus* (Garcia 2004).

C. selloana usually invades areas where there is a high percentage of bare ground as a result of frequent disturbances (Harradine 1991, Domènech *chapter 2*), therefore we expected *C. selloana* seed germination to not tolerate shading. On the contrary, we found that shading significantly improved seed germination by 16.2 %. By contrast, seed germination of the congener *C. jubata* is 3.3 times higher in high light than under dark conditions (Drewitz & DiTomaso 2004).

Previous germination tests have 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). However, it is said that *C. selloana* seedling establishment requires sandy soils (Bossard *et* al. 2000). This is consistent with our results because we have found 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 has revealed that *C. selloana* is invading habitats whose soil has more than 60 % sand (Domènech *chapter 2*). Conversely, we have found that this species also germinated in soils which contained lower percentages of sand. We also suspected that *C. selloana* seed germination would not be severely affected by water stress, as it had been previously found that *C. selloana* seedlings can resist moderate and sever water stress (Bossard *et al*. 2000, Domènech *chapter 5*). Our results support this hypothesis because although water stress significantly reduced *C. selloana* seed germination, seeds still germinated under intermediate and severe water stress. Finally, escape from soil pathogens has been proposed as favouring alien plant success (Keane & Crawley 2002, Mitchell & Power 2003, Reinhart *et al*. 2003). However, we found the opposite result probably because soil sterilization had eliminated all microorganisms from the introduced range that could have either a positive or a negative effect on *C. selloana* seed germination. This suggests that the negative effect of certain soil microorganisms might be lower than the positive effect of others.

Overall, *C. selloana* seed germination is increased under shaded conditions, in sandy soils, in the absence of water stress and with soil microorganisms. However, this species has the ability to germinate under all the conditions studied. Therefore, it can be concluded that the invasive success of *C. selloana* can be attributed 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 *chapter 2*) which disperse widely and have the potential to invade a wide variety of new environments, especially when they find the most suitable conditions to germinate.

6.6 Acknowledgements

We thank L. Marco for helping to maintain the germination tests. Funding was provided by the REN2000-0361/GLO project from the Ministerio de Ciencia y Tecnología.

7. Conclusions

7.1 Conclusions generals

1. *Cortaderia selloana* és capaç d'augmentar considerablement la seva densitat i colonitzar espais seminaturals en un període de temps relativament curt. Per exemple, en els darrers 5 anys el nombre de camps envaïts a la Rubina (Parc Natural dels Aiguamolls de l'Empordà) ha augmentat 1.5 cops i la densitat de *C. selloana* s'ha triplicat.

2. Les zones envaïdes per *C. selloana* tendeixen a concentrar-se prop de zones urbanes i complexes turístics que actuen com a fonts de la invasió, essent les pastures i els camps abandonats els usos del sòl més susceptibles a la invasió de *C. selloana*. Per contra, els camps cultivats no són envaïts per aquesta espècie ja que les pràctiques agrícoles impedeixen el seu establiment tot restringint-lo als marges dels camps. Malauradament, els camps de conreu poden ser alhora un focus important d'invasió quan són abandonats o transformats en pastures. La densitat de la població està positivament correlacionada amb l'edat d'abandonament.

3. Hi ha una associació positiva entre la presència de *C. selloana* i el nombre de canvis d'usos del sòl. La resta d'atributs de la història dels usos del sòl, direcció i trajectòria dels canvis d'usos, no estan relacionats amb la presència de *C. selloana*. Però la trajectòria dels canvis d'usos del sòl sí està relacionada amb la densitat de *C. selloana*: els camps que han romàs com a pastures al llarg dels anys i les pastures que han esdevingut camps de conreu en el passat són els usos més envaïts.

4. Experiments de trasplantament al camp han demostrat que la invasió de *C. selloana*, mesurada com el percentatge de supervivència i creixement de les plàntules, no depèn de l'estadi successional en què es trobi la vegetació. L'establiment mitjà de plàntules de *C. selloana* és baix (2.0 %) tant en estadis inicials que teòricament haurien de ser els més susceptibles a la invasió, com en els intermitjos o en els estadis més avançats. En conseqüència, els mecanismes

de successió de facilitació, tolerància i inhibició no semblen explicar el procés d'invasió d'aquesta espècie.

5. En els estadis successionals més avançats, la invasió de *C. selloana* tampoc depèn del tipus de vegetació existent. L'establiment d'aquesta espècie és també baix (3.9 %) i no difereix entre comunitats dominades per *Phragmites australis*, *Juncus acutus* o herbassars. A més, tampoc s'ha trobat diferències en la germinació de llavors de *C. selloana* en parcel·les pertorbades situades en aquests tres tipus de comunitats, fet que suggereix que les condicions microambientals que es donen en aquests tipus de vegetació no afecten la invasió.

6. En canvi, les pertorbacions dels hàbitats afavoreixen clarament l'establiment de *C. selloana* i la seva expansió. Així doncs, els hàbitats ruderals, que sovint són pertorbats per l'acció de l'home, presenten una elevada proporció d'individus juvenils i per tant un gran reclutament de nous individus en comparació als hàbitats no ruderals. A més, s'ha comprovat que les micropertorbacions del sòl augmenten l'establiment, la supervivència i el creixement de *C. selloana*. Per tant, aquesta espècie podrà envair qualsevol estadi successional o tipus de vegetació sempre i quan hi hagi alguna pertorbació que redueixi la coberta vegetal i augmenti la disponibilitat de recursos.

7. La supervivència i el creixement de les plàntules de *C. selloana* es veu reduïda considerablement per l'estassada de *P. australis* que sovint es du a terme com a mesura de gestió per promoure'n la seva regeneració. En conseqüència, es pot concloure que la presència de *P. australis* facilita l'establiment de *C. selloana.*

8. L'èxit de la invasió de *C. selloana* es pot atribuir a la seva capacitat de germinar en un ampli ventall de condicions ecològiques. Malgrat la germinació es veu afavorida per l'ombra, textures del sòl amb un elevat contingut de sorra i elevades disponibilitats d'aigua, *C. selloana* també germina en condicions menys favorables com per exemple 100 % d'insolació, textures argiloses i en disponibilitat molt baixa d'aigua. Altrament, l'esterilització del sòl disminueix la germinació d'aquesta espècie com a conseqüència que aquest tractament

probablement elimina tots els microorganismes del sòl de la zona d'introducció, tant els que l'afecten de manera positiva com els que l'afecten negativament.

9. *C. selloana* és una espècie ginodioica, i com a tal s'espera que les plantes femella tinguin mecanismes per compensar el fet que únicament transmeten els seus gens mitjançant la producció de llavors. Tan la producció de llavors com la seva viabilitat és més elevada en les plantes femella que no pas en les hermafrodites. En canvi, la grandària de les plantes, la producció de panicles i l'esforç reproductiu no varien en funció del sexe de la planta.

10. El potencial d'invasió de les poblacions de *C. selloana* depèn també de la proporció de sexes de la població ja que la proporció de femelles està negativament correlacionada amb la proporció de plantes juvenils. Llavors, les poblacions que tinguin una proporció de sexes esbiaixada cap al nombre de femelles estaran limitades per la disponibilitat de pol·len i tindran per tant una menor proporció d'individus juvenils que les poblacions que tenen proporcions no esbiaixades cap al nombre de femelles.

11. *C. selloana* no és competitivament superior a les espècies natives *B. phoenicoides* o *F. arundinacea* del mateix grup funcional i en el mateix estadi de desenvolupament. Hi ha 3 evidències que ho corroboren: (a) el creixement no és millor en competència interespecífica que en competència intraespecífica*,* (b) l'efecte de *C. selloana* en les espècies natives no és significativament diferent del que les natives tenen en l'espècie exòtica i (c) l'efecte d'una espècie nativa en l'altra no és més gran que l'efecte d'aquestes en l'espècie exòtica.

12. *C. selloana* és més resistent a l'estrès hídric que aquestes dues espècies natives. Quan *C. selloana* és sotmesa a un estrès hídric moderat o sever maximitza la captació d'aigua mitjançant l'increment de biomassa subterrània i minimitza la pèrdua d'aigua mitjançant la reducció de la biomassa aèria. *B. phoenicoides* es comporta de manera similar, però en aquest cas, l'increment de la relació biomassa subterrània/aèria és menor. Per contra, *F. arundinacea* es comporta de manera totalment oposada, indicant que aquesta espècie és la més afectada per la manca d'aigua.

13. En general, tot i que *C. selloana* no és una espècie molt competitiva, està millor adaptada a la sequera que les espècies natives, fet que pot suposar un avantatge durant les estacions més seques típiques del clima mediterrani. Per tant, considerant les estratègies proposades per Grime (1982), els resultats suggereixen que *C. selloana* és més estrès tolerant que no pas competitiva, tot i que cap de les dues estratègies és predominant. Tant en l'inventari com en els experiments de camp s'ha trobat que el potencial d'invasió de *C. selloana* està principalment associat a una estratègia ruderal que li permet beneficiar-se de les pertorbacions les quals en faciliten el seu establiment. Les taxes de germinació i la supervivència de les plàntules són baixes, però estan compensades per la producció d'una gran quantitat de llavors sobre tot en les plantes femenines.

7.2 General conclusions

1. *Cortaderia selloana* is capable of considerably increasing its density and colonizing seminatural areas in a relatively short period of time. For example, the number of invaded fields in la Rubina (Parc Natural dels Aiguamolls de l'Empordà) has increased 1.5 times during the last 5 years, and *C. selloana* density has suffered a 3 fold increase.

2. Invaded fields cluster near urban areas and tourist resorts which act as *C. selloana* invasion sources. Moreover, pastures and old fields are the most susceptible land-uses to *C. selloana* invasion. Oppositely, agricultural fields are the least invaded because agricultural practices hinder *C. selloana* establishment by restricting it to field margins. However, these plants can also be a focus of invasion once fields have been abandoned or transformed into pastures. Density of *C. selloana* populations is positively correlated with time since abandonment.

3. There is a positive association between *C. selloana* presence and the number of land-use changes. The other land-use attributes, direction and trajectory of land-use changes, are not correlated with *C. selloana* presence. However, there is a significant association between the trajectory of land-use changes and *C.*

selloana density: fields that have remained as pastures through years and pastures that have become agricultural fields are the most invaded land-uses.

4. Seedling transplant experiments have revealed that *C. selloana* invasion, measured as percentage survival and growth of *C. selloana* seedlings, does not depend on the successional stage. Mean *C. selloana* seedling establishment is low (2.0 %) both in initial stages, which should be the most susceptible to invasion, in mid-successional stages and in successionally more advanced stages. Consequently, neither the facilitation model of succession nor the tolerance or inhibition models seem to explain the invasion process of this species.

5. In the most advanced successional stages, *C. selloana* invasion does not depends on the vegetation-type. Its establishment is also low (3.9 %) and no significant differences were found between communities dominated by *Phragmites australis*, *Juncus acutus* and grasslands. In addition, *C. selloana* seed germination in disturbed plots does not differ between these vegetation-types, suggesting that the microenvironmental conditions of these vegetation-types do not affect its invasion.

6. However, habitat disturbances clearly favour *C. selloana* establishment and its spread. Ruderal habitats, which are frequently disturbed by human activities, have a high proportion of juvenile individuals and consequently a high seedling recruitment compared to non-ruderal habitats. Furthermore, it has been found that soil microdisturbances increase *C. selloana* establishment, survival and growth. Therefore, this species will be able to invade any successional stage or vegetation type provided that there are disturbances that decrease vegetal cover and increase nutrient availability.

7. *C. selloana* seedling survival and growth is considerably reduced by the clipping of *P. australis*, a management action carried out to promote its regeneration. This result suggests that *P. australis* enhances *C. selloana* invasion.

8. *C. selloana* invasive success can be related to its capacity to germinate under a wide range of ecological conditions. Although seed germination is favoured by shaded conditions, soil textures with a high percentage of sand and high water availability, *C. selloana* seeds also germinate in less favourable conditions such as 100 % light, soil textures with low sand content and low water availability. In addition, soil sterilization reduces percentage germination because it eliminates all soil microorganisms from the introduced range that can have either a positive or a negative effect.

9. *C. selloana* is a gynodioecious species and we consequently expected that female plants would have compensatory mechanisms because they only contribute genes to the next generation by seeds. Both seed production and viability of female plants is higher than that of hermaphrodite plants. However, plant volume, panicle production and reproductive effort do not vary in relation to sex.

10. The invasive potential of *C. selloana* populations also depends on the sex ratio of each population because this variable is negatively correlated with the proportion of juvenile plants. For this reason, *C. selloana* populations whose sex ratio is biased towards the number of females will be limited by pollen availability and they will have a lower proportion of juvenile individuals than populations whose sex ratio is not biased towards the number of females.

11. *C. selloana* is not a better competitor than the native species of the same functional group and life history stage, *Brachypodium phoenicoides* and *Festuca arundinacea*. There are 3 evidences that support this statement: (a) *C. selloana* plant growth under interspecific competition is not higher than under intraspecific competition, (b) *C. selloana* effect on the native species is not significantly different than the effect that native species have on the exotic species, and (c) the effect of a native species on the other is not larger than the effect of these species on the exotic.

12. *C. selloana* is more resistant to water stress than the 2 native species. Under moderate or severe water stress, *C. selloana* maximizes water uptake by

increasing the belowground biomass, and it minimizes water losses by reducing the aboveground biomass. *B. phoenicoides* behaves in a similar way, yet the increase in the root-shoot ratio is lower than that of *C. selloana.* Oppositely, *F. arundinacea* decreases its root-shoot ratio, indicating that this species is the most affected by water stress.

13. Overall, although *C. selloana* does not seem to be an effective competitor, it is better adapted to drought conditions than the native species, which can be an advantage during the driest Mediterranean seasons. Therefore, according to the plant strategies proposed by Grime (1982), our result suggest that *C. selloana* follows a stress tolerant strategy rather than a competitive strategy, yet none of these strategies predominate. Both in the field surveys and in the transplant experiments we have found that *C. selloana* invasive potential is basically related to a ruderal strategy. This strategy allows *C. selloana* to take advantage of disturbances which enhance its establishment. Percentage germination and seedling survival under field conditions are low, but they are compensated by a large production of seeds, specially in female plants.

8. References

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8.2 Web sites

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