

COMPETITIVE EFFECTS OF THE ALIEN INVASIVE *CENTAUREA SOLSTITIALIS* L. ON TWO CHILEAN *BACCHARIS* SPECIES AT DIFFERENT LIFE-CYCLE STAGES

EFECTOS COMPETITIVOS DE LA ALOCTONA INVASORA CENTAUREA SOLSTITIALIS L. SOBRE DOS ESPECIES CHILENAS DE BACCHARIS EN DIFERENTES ESTADOS DEL CICLO DE VIDA

Susana Gómez-González^{1,2}, Lohengrin A. Cavieres^{1,2},
Patricio Torres¹ & Cristian Torres-Díaz¹

¹Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile; ²Instituto de Ecología y Biodiversidad (IEB), Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile.
sgomez@udec.cl

ABSTRACT

Several studies have revealed a variety of mechanisms of invasion of alien plant species. However, little is known on how those mechanisms and their associated effects on native species change across different life-cycle stages. Under controlled conditions, we assessed the interactions between the alien invasive species *Centaurea solstitialis* L. (Asteraceae) and two pioneer native species to the Chilean matorral; *Baccharis linearis* (Ruiz et Pav.) Pers. and *B. paniculata* DC. (Asteraceae). Competitive effects of the invader on natives were evaluated by combining different life-cycle stages: seed-seed, plant-seed, and plant-plant. Seed germination of *C. solstitialis* was explosive and much faster than that of the native species. The presence of *C. solstitialis* (individuals or seeds) did not affect negatively the seed germination of the two *Baccharis* species. However, the presence of *C. solstitialis* plants significantly decreased the total biomass of *Baccharis* plants. Thus, the effect of *C. solstitialis* on *Baccharis* species depended on the life-cycle stage at which the interactions occurred. In the Chilean matorral, the early emergence of *C. solstitialis* could be an important invasion mechanism, enabling established plants to competitively displace late emerging seedlings of *Baccharis* species. The huge abundance of *C. solstitialis* in some disturbed matorrals suggests that seedling establishment of these two pioneer species could be limited.

KEYWORDS: Allelopathy, matorral, Mediterranean, seed germination, yellow starthistle.

RESUMEN

Varios estudios han revelado una variedad de mecanismos de invasión en las plantas alóctonas. Sin embargo, aún se conoce poco sobre cómo tales mecanismos y sus efectos asociados cambian a través de diferentes estados del ciclo vida. En este estudio evaluamos, bajo condiciones controladas, el resultado de las interacciones competitivas entre la especie invasora *Centaurea solstitialis* L. (Asteraceae) y dos especies pioneras nativas del matorral chileno; *Baccharis linearis* (Ruiz et Pav.) Pers. y *B. paniculata* DC. (Asteraceae). Estas interacciones fueron evaluadas combinando diferentes estados del ciclo de vida: semilla-semilla, planta-semilla y planta-planta. La germinación de *C. solstitialis* fue explosiva, siendo mucho más rápida que la de las especies nativas. La presencia de *C. solstitialis* (plantas o semillas) no disminuyó la germinación de las especies nativas de *Baccharis*. Sin embargo, la presencia de plantas establecidas de *C. solstitialis* disminuyó significativamente la biomasa de las plantas de *Baccharis*. Entonces, el efecto de *C. solstitialis* sobre las especies de *Baccharis* varió en función del estado del ciclo de vida en el cual las interacciones ocurrieron. En el matorral chileno, la emergencia temprana y explosiva de *C. solstitialis* podría ser un importante mecanismo de invasión, ya que aquellas plantas prontamente establecidas podrían desplazar competitivamente a las plántulas de *Baccharis* que emergen más tarde. La enorme abundancia de *C. solstitialis* en algunas zonas de matorral sugiere que el establecimiento de plántulas de estas dos especies pioneras podría estar siendo limitado.

PALABRAS CLAVE: Alelopatía, matorral, mediterráneo, germinación, abrepño amarillo.

INTRODUCTION

The negative impact of alien invasive plants on native species populations, communities, and ecosystems is widely recognized (Mack *et al.* 2000), and much research has been done on eluding the mechanisms that allow alien plant species to become dominant in the recipient community (Levine 2000, Levine *et al.* 2003, Coleman & Levine 2007). However, less investigation has been focused on how different mechanisms interact across different life-cycle stages of invasive and native species to explain the invasion success (e.g. Orr *et al.* 2005, Widmer *et al.* 2007, Ens & Frens 2008, Muoghalu 2008).

Regarding the effects at the plant neighbourhood scale, many studies have shown that invasive plant species can reduce around 50% of the native plant species' performance in terms of biomass or relative growth rate (for review see Vilá & Weiner 2004). Those studies are generally focused on plant-plant interactions, where the negative effects of the invaders on natives are mainly caused by competition for soil resources (Gordon *et al.* 1989, Welker *et al.* 1991) or by allelochemicals released by the invasive species (Callaway & Aschehoug 2000, Vivanco *et al.* 2004). In addition, alien invasive plants can also affect native species by inhibiting the establishment of new individuals (i.e., seedlings) by different mechanisms (Yurkonis *et al.* 2005). For example, some invasive species release allelochemicals that inhibit the seed germination of some native species (i.e., plant-seed interactions, Bais *et al.* 2003, Jefferson & Pennacchio 2003, Prati & Bossdorf 2004).

Although seed-seed interactions could play an important role on explaining the alien success, little attention has been paid to interactions between alien and native species at the seed stage. Seed germination and seedling emergence can be affected by the presence of heterospecific seeds in the seed bank (Bergelson & Perry 1989, Lortie & Turkington 2002), where chemicals leached by seeds may be involved (Bergelson & Perry 1989, Murray 1998, Latta & Bazzalo 1999, Casini & Olivero 2001). Invasion success can also be related to a high germination capability of the invader. Early emergence produces a competitive advantage since early germinated individuals can monopolize resources and attain sufficient biomass for a successful establishment (Miller 1987, Wilson 1988, Verdú & Traveset 2005). Thus, since the importance of the competitive effects of alien plants on native

species could differ across their life cycle, a comprehensive understanding of the invasion mechanisms should explore the results of interactions at different life-cycle stages.

Centaurea solstitialis L. (Asteraceae) is an annual or biennial species native to Eurasia that has invaded successfully different regions of the world (Hiero *et al.* 2006). In Chile, *C. solstitialis* is distributed across the Mediterranean region of the country (central Chile), and it has been catalogued as a serious weed generating negative impacts on agricultural crops (Matthei 1995). *Centaurea solstitialis* is generally found on roadsides and old fields, but it has also been observed to grow densely on native shrublands (hereafter the matorral). The Chilean matorral has undergone intense human disturbances since the Spaniard colonization (grazing, burning, clearing, etc.). Disturbed matorrals are savannah-like vegetation where shrub clumps of *Acacia caven* (Molina) Molina and *Baccharis* spp. are surrounded by grasslands of weedy native and alien species. In some disturbed matorral stands, *C. solstitialis* is the dominant species in the herbaceous layer, covering around 40% (Gómez-González, unpublished data). Although the impact of *C. solstitialis* on native matorral species is unknown, its huge abundance in the herbaceous layer might affect the recruitment of native pioneer shrubs. Field and lab experiments suggest that European forbs can limit the colonization of open areas by *Baccharis* spp. in the matorral of central Chile (Martínez & Fuentes 1993) and also in shrublands of northern California (Williams *et al.* 1987, Williams & Hobbs 1989). According to the successional model proposed by Armesto & Pickett (1985) for the Chilean matorral, *Baccharis* species are key elements for the secondary succession because established individuals in open areas could act as "facilitators" of other late successional species, favouring the regeneration of the vegetation after a disturbance. Hence, it is important to evaluate whether the presence of *C. solstitialis* negatively affect the seedling emergence and performance of *Baccharis* species, and to detect the life-cycle stage of the invader at which it has the stronger effects. This information could be useful for future management and restoration of matorral areas currently invaded by *C. solstitialis*.

In this study we take the following questions into consideration: i) which are the competitive effects of *C. solstitialis* on *Baccharis* species at

different life-cycle stages? and ii) in what kind of interaction (seed-seed, plant-seed or plant-plant) is the invader more harmful for *Baccharis* species? To answer these questions we evaluated under controlled conditions the competitive interactions between *C. solstitialis* and two *Baccharis* species: *B. linearis* (Ruiz et Pav.) Pers. and *B. paniculata* DC. (Asteraceae). We performed pair-wise experiments to explore: 1) seed-seed effects, 2) plant-seed effects, and 3) plant-plant effects. These experiments involved almost the whole life cycle of *C. solstitialis* and the early life-cycle stages of *Baccharis* species, in order to simulate the natural situation in which the invader might affect the seedling establishment of these two pioneer native species.

MATERIALS AND METHODS

STUDIED SPECIES

Centaurea solstitialis is a facultative winter annual species (sometimes biennial or short-lived perennial from a tap root). It produces rosette leaves that lie close to the ground, and erect stems 0.15-2 m in height. *Centaurea solstitialis* has a large taproot that grows to soil depths of 1 m or more (Sheley *et al.* 1993). The yellow flowerheads produce two types of achenes (hereafter seeds); most of them (75-90%) have a short pappus but some achenes have no pappus (mainly at the periphery of the flowerhead). Large plants can produce nearly 75,000 seeds with 87.6 to 95.2% of viability (Maddox 1981, Benefield *et al.* 2001). In *C. solstitialis* infestations, seed density in the soil can range from 3,000 to 10,000 seeds per square meter (Sheley & Larson 1994, DiTomaso *et al.* 1999), and seedbank longevity can be as long as 10 years (Callihan *et al.* 1993).

Baccharis linearis and *B. paniculata* are 0.4-3 m tall dioecious shrubs, densely branched, with 2-10 white flowerheads at the top of the branches. These *Baccharis* species produce great numbers of achenes, but seed viability is relatively low (30-50%, Gómez-González, personal observation). It has been reported that seed density in the soil can range from 212 to 707 and from 500 to 2,400 seeds per square meter for *B. paniculata* and *B. linearis* respectively (Martínez & Fuentes 1993, Gutiérrez *et al.* 2000). Achenes are wind-dispersed and seedlings tolerate high irradiance and drought, and consequently, they successfully establish in cleared areas of the matorral (Armesto & Pickett 1985). Seed dispersal and

seedling emergence occur simultaneously to that of *C. solstitialis* (late summer and late autumn respectively), so *Baccharis* spp. are interacting with this invader both at the seed (within the seedbank before rains) and the seedling stages.

SEED COLLECTIONS

During January 2004, we collected seeds of *C. solstitialis*, *B. linearis* and *B. paniculata* in Quebrada de la Plata (33°29'S; 70°52'W), Province of Santiago, Central Chile. Seed collection was carried out across several disturbed matorral stands which were located along a 5 km trail in Quebrada de la Plata. Seeds of at least 50 plant individuals of each species were collected. Seeds were carried to the laboratory, where we carefully observed all seeds with a binocular microscope (Zeiss). Then, only seeds that looked healthy and filled with an embryo (regarded as viable seeds) were selected for the experiments. All maternal lines were pooled and represented in the seed set used for the experiments.

EXPERIMENT 1. SEED-SEED INTERACTIONS

To evaluate possible allelopathic effects at the seed stage, we performed germination trials where seeds of each *Baccharis* species were germinated under the following conditions: i) 30 seeds in absence of other seeds (control), ii) 30 seeds in presence of 30 conspecific seeds (i.e., 60 seeds of the same species), and iii) 30 seeds in presence of 30 *C. solstitialis* seeds. In addition, 30 seeds of *C. solstitialis* were germinated in each of the following conditions: i) in absence of other seeds (control) and ii) in presence of conspecific seeds. This last treatment (conspecific interaction) was added to distinguish inter-specific effects from density dependant effects. Each treatment was replicated four times. In all treatments, we placed the seeds on Petri dishes with filter paper and distilled water (2.5 ml aprox.).

Seed germination trials were carried out in a growth-chamber with a photoperiod of 16 h light and 8 h darkness and a thermoperiod of 12 h at 10°C and 12 h at 20°C. This thermoperiod simulate the temperature conditions during the fall season, when seedling emergence begins for all these species. Every two days and over a total period of 28 days, emerged seedlings were checked and petri-dishes were randomly re-positioned inside the chamber. All petri-dishes were watered when needed. We considered a seed germinated when cotyledons were visible. For each species and treatment, we calculated the following parameters of germination:

1. The coefficient of velocity of germination $CV = 100 \cdot \sum Ni / (\sum Ni \cdot Ti)$ with Ni being the number of seeds newly germinated on day i , and Ti the number of days needed for germination, $i = 1 \dots 28$.

2. The final percentage of germination $FG = (\sum Ni) \cdot 100 / N$ with Ni being the number of seeds newly germinated on day i , and N the total number of tested seeds, $i = 1 \dots 28$.

EXPERIMENT 2. PLANT-SEED INTERACTIONS

To evaluate competitive effects of established individuals on seed germination, we sowed 30 seeds of each *Baccharis* species in the following conditions: i) absence of plant individuals (control), ii) presence of one *C. solstitialis* individual, and iii) presence of one conspecific individual. Additionally, we sowed 30 seeds of the invasive species in: i) absence of *Baccharis* individuals (control), ii) presence of one *B. linearis* individual, iii) presence of one *B. paniculata* individual, and iv) presence of one conspecific individual. We established four replicates for each species and treatment. We obtained all plant individuals from the seeds germinated as in the experiment 1. After germination, the seedlings (of the same age) were transplanted in 500 ml pots filled with commercial organic soil (C/N = 40, pH 5.0-8.5). After 1 month of growing, we sowed 30 seeds of the corresponding treatment on each pot. Seeds were sown equidistant to the plant shoot at 2 cm depth. We randomly placed the pots within a greenhouse. Every four days, all pots were randomly redistributed in order to avoid any effect of micro-environmental differences inside the greenhouse. Every two days, and over a total period of 28 days, all samples were watered and the number of seedlings emerged were recorded. We considered that a seedling was emerged from the soil when the cotyledons were visible. For each species and treatment, we calculated the final percentage of seedlings emerged and the velocity of emergence as described in the experiment 1 (*FG* y *CV* respectively).

EXPERIMENT 3. PLANT-PLANT INTERACTIONS

To evaluate competitive interactions between established individuals, we planted one individual of each *Baccharis* species in the following conditions: i) absence of other individuals (control), ii) presence of one *C. solstitialis* individual, and iii) presence of one conspecific individual. Additionally, one *C. solstitialis* plant was grown: i) in absence of other individuals (control), ii) in presence of one

conspecific individual. This last treatment (conspecific interaction) was added to distinguish inter-specific effects from density dependant effects. Each treatment was replicated 10 times.

All plant individuals were obtained from seedlings emerged at the same time and they were grown in pots as described in the experiment 2. After three months of growth, we harvested all plants. At this time, *C. solstitialis* individuals were adults while *Baccharis* species were yet saplings. Each individual was separated into roots and shoots and dried in an electric oven at 60°C for 3 days. For each plant individual we calculated the root, shoot and total dry biomass, and the root-shoot ratio. In the case of the intraspecific competition treatments, where two conspecific individuals shared the same pot and individual roots were undistinguishable, the root biomass per individual was estimated as the total root biomass within the pot divided by two.

DATA ANALYSIS

Statistical analyses were performed using the softwares R 2.8.0 (R Development Core Team 2008) and STATISTICA 6.0 (StatSoft, Inc. 2001).

Differences among treatments in the *FG* were analyzed by means of generalized linear mixed models (GLMM), fitted by the Laplace approximation (Raudenbush *et al.* 2000, Crawley 2007). In these models, the dependent variable was the *FG* (data expressed as proportion, binomial errors). Independent variables were the treatment (control, presence of competitor) as fixed factor and the block (Petri dishes and pots for the experiment 1 and 2 respectively) as random factor. Wald-Z tests were used to assess the null hypothesis of no treatment effect (i.e., estimated parameters equal zero). We used Mann-Whitney *U* tests to explore the effect of the presence of competitor on the velocity of germination (*CV*) of each species. Additionally, these analyses (GLMM and Mann-Whitney *U* tests for the *FG* and the *CV* respectively) were used to evaluate species-specific differences in the germination capability by taking into account only the control treatments. We analyzed biomass data (experiment 3) with one-way ANOVA and Tukey tests, after the logarithmic transformation of the data. These analyses were unbalanced due to the lose of three samples. P-values < 0.05 were regarded as statistically significant.

RESULTS

GERMINATION CAPABILITY OF THE SPECIES

Centaurea solstitialis showed almost 100% of seed germination in only 4 days (Fig.1). In contrast, *Baccharis* species showed significantly slower germination (lower CV) than the invader (Mann-Whitney *U*-test, *C. solstitialis* vs. *B. linearis*, $P=0.02$, *C. solstitialis* vs. *B. paniculata*, $P=0.02$, Fig. 1). Further, the final germination (FG) of *C. solstitialis* was significantly greater than that of both *Baccharis* species (GLMM, *C. solstitialis* vs. *B. paniculata*, $P<0.001$, *C. solstitialis* vs. *B. linearis*, $P=0.03$, Fig.1).

SEED-SEED INTERACTIONS

Treatments did not affect the final germination of any of the three studied species (FG, Table I, Fig. 2). That is, neither the presence of seeds of the same species nor the presence of heterospecific seeds affected their final germination. Furthermore, there were no significant differences in the velocity of germination between treatments in the most of the cases, except for *C. solstitialis* seeds, which emerged significantly slower in presence of *Baccharis* seeds compared to the control (Table I, Fig. 2).

PLANT-SEED INTERACTIONS

The presence of a conspecific or heterospecific plant individual did not significantly affect the germination (FG and CV) of the species in the most of the cases (Table II, Fig. 3). Only *B. paniculata* showed higher CV when seeds emerged in the presence of a *C. solstitialis* plant compared to the control (Table II, Fig. 3).

PLANT-PLANT INTERACTIONS

Root, shoot and total biomass of *C. solstitialis* were not significantly affected by intra- or interspecific competition (Fig. 4a-c). Indeed, compared to the control, the invader reduced its biomass by only 11.3% and 7.8% in presence of *B. paniculata* and *B. linearis* respectively. Nevertheless, the root-shoot ratio of the invader did significantly increase due to competition with a conspecific individual as well as with *Baccharis* spp. (Fig. 4d).

In contrast, the presence of *C. solstitialis* decreased the root, shoot and total biomass of *Baccharis* species without changing their root-shoot ratio (Fig. 4a-d). Specifically, the total biomass of *B. paniculata* and *B. linearis* was 25% lower in presence of *C. solstitialis* than without competition (Fig. 4c), although this effect was not significant

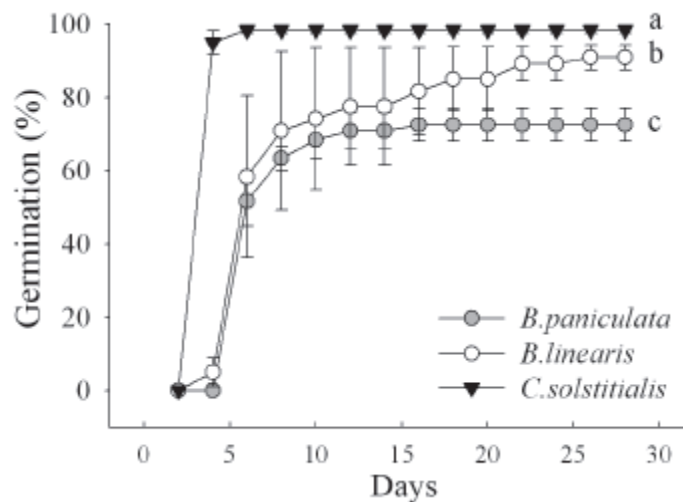


FIGURE 1. Comparison among the germination curves of the three studied species (regarding only the control treatment of the experiment 1). Mean values \pm SE are shown, $n=4$. Different letters denote significant differences in the FG among species (GLMM, Wald Z-test, $P < 0.05$).

FIGURA 1. Comparación de las curvas de germinación de las tres especies de estudio (considerando sólo el tratamiento control del experimento 1). Se muestran los valores medios \pm EE, $n=4$. Letras diferentes denotan diferencias significativas en el FG entre las especies (GLMM, prueba Wald Z-test, $P < 0,05$).

(Tukey test, *B. linearis*: alone vs. +C, $P=0.06$; *B. paniculata*: alone vs. +C, $P=0.06$, Fig. 4c). However, there was a significant biomass reduction (around 40%) in both *Baccharis* spp. in presence of *C. solstitialis* compared to when they grew with a

conspecific individual (Fig. 4c). It must be noted that *Baccharis* species showed a tendency to increase their biomass in the presence of a conspecific individual compared to the control (growing alone) (Fig. 4c).

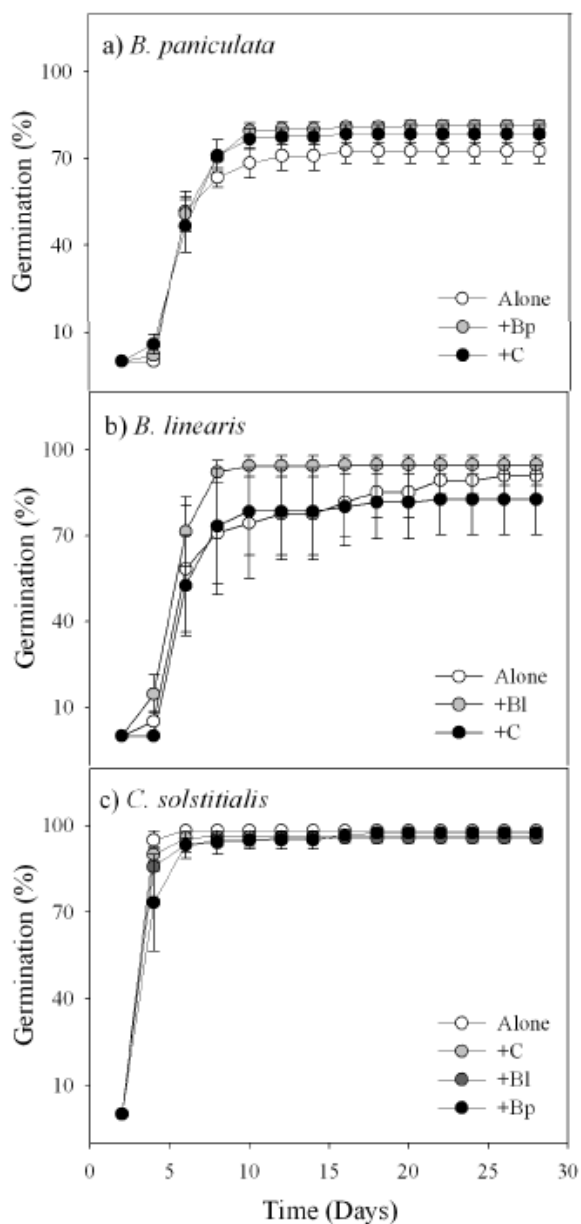


FIGURE 2. Germination curves of *B. paniculata* (a), *B. linearis* (b) and *C. solstitialis* (c) under the treatments of seed-seed interaction (experiment 1). Mean values \pm SE are shown, $n = 4$. See treatment codes in Table I.

FIGURA 2. Curvas de germinación de *B. paniculata* (a), *B. linearis* (b) y *C. solstitialis* (c) bajo los tratamientos de interacción entre semillas (experimento 1). Se muestran los valores medios \pm EE, $n = 4$. Ver códigos de los tratamientos en la Tabla I.

TABLE I. Effect of the presence of hetero- and conspecific seeds (experiment 1) on the final germination (*FG*) and the velocity of germination (*CV*) of the studied species. Treatments: Alone: germination in the absence of other seeds; +C: presence of *C. solstitialis* seeds; +Bp: presence of *B. paniculata* seeds; +Bl: presence of *B. linearis* seeds. Significant P-values are highlighted in bold ($P < 0.05$, Wald Z-test for *FG* and Mann-Whitney *U*-test for *CV*). β : Estimated coefficient in the GLMM. SE: Standard Error.

TABLA I. Efecto de la presencia de semillas hetero- y coespecíficas (experimento 1) sobre la germinación final (*FG*) y la velocidad de germinación (*CV*) de las especies estudiadas. Tratamientos: Alone: germinación en ausencia de otras semillas; +C: presencia de semillas de *C. solstitialis*; +Bp: presencia de semillas de *B. paniculata*, +Bl: presencia de semillas de *B. linearis*. Valores de P significativos son marcados en negrita ($P < 0,05$, prueba Z de Wald para *FG* y prueba *U* de Mann-Whitney para *CV*). β : Coeficiente estimado en el GLMM. SE: Error Estándar.

Experiment 1: seed-seed effects					
Focus species	FG			CV	
	β (SE)	Wald-Z	P	Z	P
<i>C. solstitialis</i>					
Alone vs. +Bp	-0.41 (0.92)	-0.45	0.65	2.02	0.04
Alone vs. +Bl	-0.94 (0.85)	-1.11	0.27	2.02	0.04
Alone vs. +C	-0.94 (0.85)	-1.11	0.27	0.86	0.39
<i>B. paniculata</i>					
Alone vs. +C	0.31 (0.30)	1.05	0.29	-0.29	0.77
Alone vs. +Bp	0.49 (0.26)	1.89	0.06	0.58	0.56
<i>B. linearis</i>					
Alone vs. +C	-0.45 (1.01)	-0.45	0.65	0.29	0.77
Alone vs. +Bl	0.69 (0.66)	1.05	0.29	-0.58	0.56

TABLE II. Effect of the presence of hetero- and conspecific individuals (experiment 2) on the final germination (*FG*) and the velocity of germination (*CV*) of the studied species. Treatments: Alone: emergence in the absence of plant individuals; +C: presence of a *C. solstitialis* individual; +Bp: presence of a *B. paniculata* individual; +Bl: presence of a *B. linearis* individual. Significant P-values are highlighted in bold ($P < 0.05$, Wald Z-test for *FG* and Mann-Whitney *U*-test for *CV*). β : Estimated coefficient in the GLMM. SE: Standard Error.

TABLA II. Efecto de la presencia de individuos hetero- y coespecíficos (experimento 2) sobre la germinación final (*FG*) y la velocidad de germinación (*CV*) de las especies estudiadas. Tratamientos: Alone: emergencia en ausencia de plantas establecidas; +C: presencia de un individuo de *C. solstitialis*; +Bp: presencia de un individuo de *B. paniculata*; +Bl: presencia de un individuo de *B. linearis*. Valores de P significativos son marcados en negrita ($P < 0,05$, prueba Z de Wald para *FG* y prueba *U* de Mann-Whitney para *CV*). β : Coeficiente estimado en el GLMM. SE: Error Estándar.

Experiment 2: plant-seed effects					
Focus species	FG			CV	
	β (SE)	Wald-Z	P	Z	P
<i>C. solstitialis</i>					
Alone vs. +Bp	0.49 (0.30)	1.62	0.10	0.00	1
Alone vs. +Bl	0.15 (0.41)	0.36	0.71	0.00	1
Alone vs. +C	0.49 (0.30)	1.59	0.11	-0.58	0.56
<i>B. paniculata</i>					
Alone vs. +C	0.58 (0.32)	1.79	0.07	-2.02	0.04
Alone vs. +Bp	-0.60 (0.51)	-1.23	0.22	-1.73	0.08
<i>B. linearis</i>					
Alone vs. +C	-0.27 (0.52)	-0.52	0.61	-1.41	0.16
Alone vs. +Bl	-0.66 (0.61)	-1.08	0.28	0.00	1

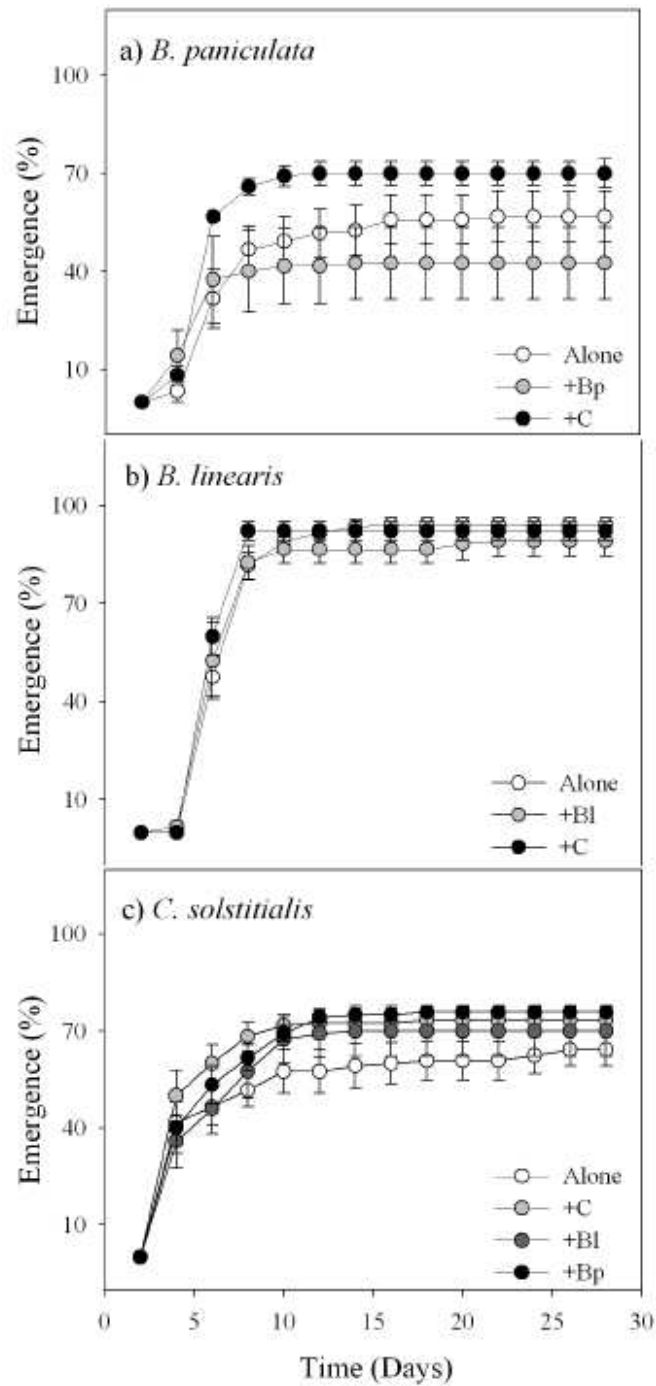


FIGURE 3. Emergence curves of *B. paniculata* (a), *B. linearis* (b) and *C. solstitialis* (c) under the treatments of plant-seed interaction (experiment 2). Mean values \pm SE are shown, $n = 4$. See treatment codes in Table II.

FIGURA 3. Curvas de emergencia de *B. paniculata* (a), *B. linearis* (b) y *C. solstitialis* (c) bajo los tratamientos de interacción planta-semilla (experimento 2). Se muestran los valores medios \pm EE, $n = 4$. Ver códigos de los tratamientos en la Tabla II.

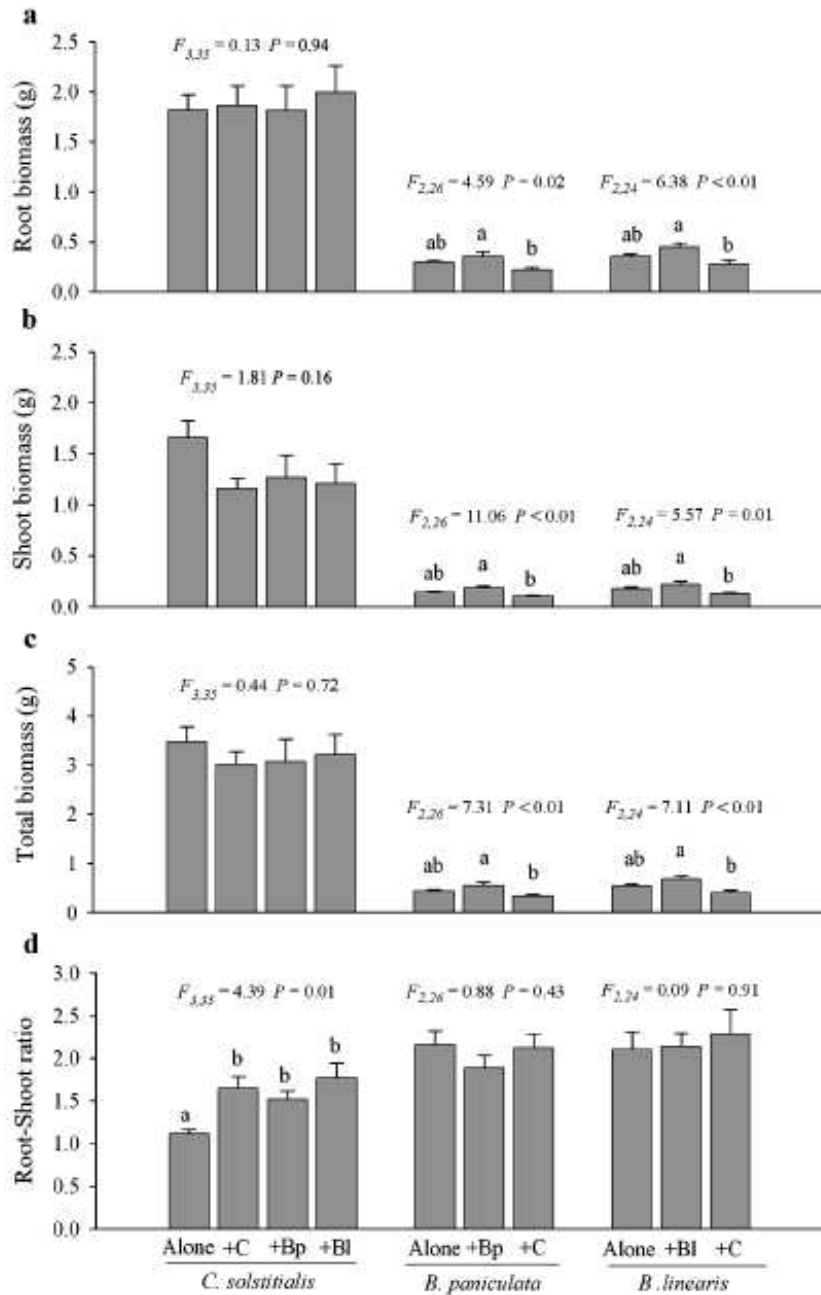


FIGURE 4. Effect of plant-plant interaction (experiment 3) on the average root biomass (a), shoot biomass (b), total biomass (c), and root-shoot ratio (d) per plant of the studied species. Treatments: Alone: growing without competition; +C: growing with *C. solstitialis*; +Bp: growing with *B. paniculata*; +Bl: growing with *B. linearis*. Mean values \pm SE are shown, $n = 10$. Different letters indicate significant differences among treatments ($P < 0.05$, Tukey test post-ANOVA).

FIGURA 4. Efecto de la interacción planta-planta (experimento 3) sobre el promedio de la biomasa de raíces (a), la biomasa de tallos (b), y la razón raíz-tallo (d) por planta de las especies estudiadas. Tratamientos: Alone: creciendo sin competencia; +C: creciendo con *C. solstitialis*; +Bp: creciendo con *B. paniculata*; +Bl: creciendo con *B. linearis*. Se muestran los valores medios \pm EE, $n = 10$. Letras diferentes denotan diferencias significativas entre tratamientos ($P < 0,05$, prueba de Tukey post-ANOVA).

DISCUSSION

Under the controlled conditions of our experiments, we found that *C. solstitialis* produced different effects on *Baccharis* species depending on the life-cycle stage at which plant interactions occurred. At the seed stage, while there were no allelopathic effects of the invader on *Baccharis* spp., *C. solstitialis* seeds did emerge later in presence of *B. linearis* seeds. The presence of established *C. solstitialis* individuals did not affect negatively the seed germination of the natives. Instead of this, seed germination of *B. paniculata* was accelerated in presence of one *C. solstitialis* individual. However, established *C. solstitialis* individuals reduced the performance (biomass) of both native *Baccharis* species.

SEED GERMINATION CAPABILITY AND SEED-SEED ALLELOPATHIC EFFECTS

Centaurea solstitialis had higher velocity of germination than *Baccharis* species. After only 4 days, 95% of *C. solstitialis* seeds emerged, whereas *Baccharis* species did not reach 10% of germination. These differences in the germination rate could be explained by the differences in their life history, since *C. solstitialis* is an annual herb and *Baccharis* species are shrubs. However, it has been found that the germination rate of *C. solstitialis* is much higher than that of many other matorral species independently of their life history, including weedy natives and alien grasses (Sierra-Almeida & Cavieres, unpublished data).

In *C. solstitialis*, the early emergence together with its elevated seed production and viability (Maddox 1981, Benefield *et al.* 2001) could be traits associated with its successful invasion in the Chilean matorral and also in other Mediterranean-type ecosystems (Piper 2001). In Mediterranean-type ecosystems early emergence is particularly important because seedlings that emerge earlier can produce an important amount of below-ground biomass before the onset of summer drought (Verdú & Traveset 2005). In the Chilean matorral, most of the species (including *C. solstitialis*) emerge during the fall after the first rains (Figuroa & Jaksic 2004) and hydric resources for seedlings establishment are available for a very short time. Hence, the massive and fast germination of *C. solstitialis* could be an advantageous trait for the occupation of available sites and early resources uptake. Indeed, we have observed that this high germination result in

extremely dense seedling populations in the matorral. In ecosystems from eastern Washington, Talbott (1987) reported seedling densities approaching 27,000 individuals per square meter, and Piper (2001) has pointed out that *C. solstitialis* effectively eliminates the emergence or growth of competing vegetation at high densities. Thus, future investigation should be destined to explore whether *C. solstitialis* is limiting the seedling emergence of *Baccharis* species in the field. This process is probable to occur in those disturbed matorrals that are highly invaded by this species.

On the other hand, seed germination of *C. solstitialis* was delayed by the presence of *Baccharis* seeds. Other studies have also shown allelopathic effects among seeds (Latterra & Bazzalo 1999, Casini & Olivero 2001). This effect could be mediated by allelopathic compounds accumulated in the seed coat. Kuti *et al.* (1990) showed that some potent phytotoxic compounds (roridins and baccharinoids) are accumulated in the seed coat of several *Baccharis* species. These allelochemicals interact with the gibberellic acid and thus inhibit the germination of other species (Kuti *et al.* 1990). Since the seed density of *Baccharis* species is relatively high in the soil seed bank of the matorral (500 to 2,400 seeds per square meter, Gutiérrez *et al.* 2000), the explosive emergence of *C. solstitialis* might be counteracted in some way.

One limitation of our experiment on seed-seed interactions was the fact that we did not test the viability of the non-germinated seeds, and thus the final percentage of germination might have been underestimated in some cases. However, we found high values of germination (over 70%) for all species and treatments, indicating that the studied species do not seem to show seed dormancy as a strategy (Baskin & Baskin 1998). Therefore, it is probably that the most of the remaining non-germinated seeds were not viable.

PLANT-PLANT COMPETITIVE EFFECTS

According to Vilá & Weiner (2004), the study of competitive interactions between invasive and native species should include both the effect of the invader on the native and the effect of the native on the invader (native species resistance), because the invasion success results from the balance of both effects. In our experiment, *C. solstitialis* had negative effects on the biomass of *Baccharis* species but not *vice versa*. This competitive superiority could be

due to differences in the life history between the invader and *Baccharis* species. However, Quin *et al.* (2007) reported the same results when they performed greenhouse experiments to evaluate the competitive interactions between *C. solstitialis* and five herbaceous species natives to California grasslands. Widmer *et al.* (2007) suggest that *C. solstitialis* success in California is not fully explained by its life history traits (i.e., prolific seed production, high seed viability, deep-root system, etc.), because those traits are also present in its native range. In fact, Widmer *et al.* (2007) showed that *C. solstitialis* has changed the resource allocation in the invaded range, since seeds have larger reserve of starch compared to its native range. As consequence, seedlings are larger in the invaded range and it could give these plants an early competitive advantage against native plants (Widmer *et al.* 2007). This support the hypothesis that *C. solstitialis* has evolved in the invaded range, increasing its competitive ability (EICA hypothesis, Blossey & Nötzold 1995). Thus, the negative effects of *C. solstitialis* on *Baccharis* species seems not to be caused only by differences in their life history traits, but maybe also by the higher competitive ability that *C. solstitialis* acquires after evolving in the invaded range.

As suggested by Callaway *et al.* (2006) and Quin *et al.* (2007), unlike other invasive *Centaurea* species, *C. solstitialis* does not appear to be allelopathic. Our results indicated that the presence of *C. solstitialis* plants did not affect negatively the seed germination of both *Baccharis* species, and its effect on established *Baccharis* plants was not lethal. Instead of allelopathy, our results and the recent evidence indicate that the success of *C. solstitialis* is mediated by below-ground competition (Quin *et al.* 2007). When *C. solstitialis* competed with the *Baccharis* species the total biomass did not change but the root:shoot ratio increased. In other words, *C. solstitialis* modified resource allocation in presence of *Baccharis* species, producing a greater proportion of roots. This is a plastic response that might allow *C. solstitialis* to be drought tolerant in spite of the presence of competitors (Karcher *et al.* 2008). Furthermore, it is well known that root growth of *C. solstitialis* is very fast during the winter and the beginning of spring, reaching depths up to 1m (Sheley *et al.* 1993). In California, Enloe *et al.* (2004) found that soils of plant communities dominated by *C. solstitialis* are significantly drier than those dominated by native grasses. Thus, we suspect that *C. solstitialis* could out-compete *Baccharis* seedlings through its ability of reaching the deeper soil layer before the dry season,

and also through the plasticity of root:shoot allocation. Light-mediated competition might also play an important role in reducing *Baccharis* performance. In our experiment, *C. solstitialis* showed high growth rate and *Baccharis* plants were rapidly shaded. Shading can be strong in matorral areas dominated by *C. solstitialis*; because the high seedling density at the onset of the rainy season is added to the presence of old stalks that remain standing from the last summer.

The importance of evaluating the competitive effects of *C. solstitialis* on seedling emergence and performance of *Baccharis* species resides in the fact that these species are key elements in the natural recover of the matorral after a disturbance (Armesto & Pickett 1985). Martínez & Fuentes (1993) have shown that some European forbs (e.g., *Erodium cicutarium* and *Trifolium* sp.) can limit the colonization of open areas by *Baccharis* spp. in the matorral of central Chile. The role of alien grasses and forbs in suppressing native shrubland re-establishment has been also reported in California shrublands (Williams *et al.* 1987, Williams & Hobbs 1989, Eliason & Allen 1997) and more recently in neotropical savannas (Hoffmann & Haridasan 2008). Hence, in those matorral areas in which *C. solstitialis* is dominant (around 40% cover), the natural succession could be modified if the seedling establishment of *Baccharis* spp. is limited by competition with the invader (Eliason & Allen 1997). However, more research including field experiments are needed to evaluate this hypothesis.

An unexpected result was that the biomass of both *Baccharis* species showed certain tendency to increase under conspecific competition compared to control (growing alone). A possible reason for this pattern is that conspecific neighbours could have protected each other from desiccation. Facilitation among conspecific plants of the same age is a kind of interaction that can be relevant for the seedling establishment of plant species in some arid and semiarid ecosystems (Goldberg *et al.* 2001, Franks 2003). Then, it would be interesting to assess whether seedling survival of these *Baccharis* species are really being facilitated by conspecifics in the matorral, since they may better resist *Centaurea* invasion at high densities.

To conclude, our results and available evidence suggest that different mechanisms could be involved together in the invasion success of *C. solstitialis* in recipient communities. At the seed stage, early emergence could be an important invasion mechanism to displace native species by means of site pre-emption, especially in Mediterranean environments where soil

resources are available for a very short time. Then, the high competitive ability of established individuals and the plasticity of root:shoot allocation could allow *C. solstitialis* to monopolize soil resources, reducing their neighbours' growth. Regarding the effects of *C. solstitialis* on the studied *Baccharis* species, we propose that competition at the stage of seedling establishment would be the key process in limiting their natural recruitment in the Chilean matorral.

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