

## Resistance to *Centaurea solstitialis* invasion from annual and perennial grasses in California and Argentina

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**Abstract** A common explanation for *Centaurea solstitialis* invasion in California is that it occupies an “empty niche” created by the replacement of native perennial grasses by exotic annual grasses and concomitant increases in soil water availability. This hypothesis, however, cannot explain *C. solstitialis* invasion into perennial-dominated grasslands of central Argentina. We assessed invasibility of annual versus perennial grass communities in these regions

through parallel field experiments where we created grass plots and, after one year of establishment, measured effects on water and light, and added *C. solstitialis* seeds in two successive trials. Additionally, we removed vegetation around naturally occurring *C. solstitialis* in both regions, and examined the performance of Californian and Argentinean *C. solstitialis* individuals when growing under common conditions simulating climate in California and Argentina. In California, both grass types offered high resistance to *C. solstitialis* invasion, water was generally greater under perennials than annuals, and light was similarly low beneath both types. In Argentina, invasibility was generally greater in annual than perennial plots, water was similar between groups, and light was much greater beneath annuals. Removal experiments showed that competition from annual grasses in California and perennial grasses in Argentina greatly reduce *C. solstitialis* performance. Additionally, Californian and Argentinean individuals did not exhibit genetic differentiation in studied traits. Our results suggest that dominant plant functional groups in both California and Argentina offer substantial resistance to *C. solstitialis* invasion. The success of this species might be tightly linked to a remarkable ability to take advantage of disturbance in both regions.

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## Introduction

Contemporary biological invasions are unique in that immigrants lack an evolutionary history with members and abiotic components of the recipient community (Callaway et al. 2005); however, there are commonalities in factors that influence immigrations from regional species pools (Tilman and Pacala 1993; Chesson 2000). These commonalities make classic community theory valuable for understanding invasions (Shea and Chesson 2002; MacDougall et al. 2009). According to niche-centered ideas on the coexistence of species in the same trophic level (Chesson 2000), different responses to resource opportunities between resident and non-resident species are crucial for the establishment and population growth of immigrants. Differences between these groups include variations in spatial and temporal resource utilization, responses to climatic fluctuations, colonization-competition tradeoffs, and adaptations to natural versus anthropogenic disturbance regimes (Chesson 2000; Shea and Chesson 2002). In invasion ecology, related ideas have long been synthesized in the “empty niche” hypothesis (Elton 1958), according to which exotics invade because they take advantage of resources that are not used by the residents.

The introduction of the same species into different regions that vary substantially in abiotic and biotic conditions offers an unparalleled, yet poorly exploited (but see Lambrinos 2002; Shea et al. 2005), opportunity to examine processes that influence the performance of exotics, and thus advance our understanding of the mechanistic nature of invasions. *Centaurea solstitialis* L. (yellow starthistle, Asteraceae), a ruderal annual native to western Eurasia and introduced around the world (Maddox et al. 1985), is one of the most abundant and widely distributed exotics in two regions with contrasting climates and dominant plant functional groups, northern California and central Argentina (Hierro et al. 2006). California has a Mediterranean-type climate with summer drought and winter rain (Major 1988) and grasslands dominated by Eurasian annual grasses (Heady 1988); central Argentina, on the other hand, has a continental climate with predominantly summer rain and grasslands dominated by native perennial bunchgrasses (Cano et al. 1980; Online Resource 1). One of the leading hypotheses for the

invasion of *C. solstitialis* in California is that the widespread replacement of native perennial grasses by Eurasian annual grasses has left, as a result of the shallow root system and early senescence of annuals, substantial resource pools of soil moisture (Borman et al. 1992; Holmes and Rice 1996; Dyer and Rice 1999) that can be accessed by the deep taproots of *C. solstitialis* (Roché et al. 1994). In contrast to the annuals, the deep root systems of the original perennial grasses have been hypothesized to access these deeper and longer lasting water resources and thus compete more effectively with *C. solstitialis* than annual grasses. In support of this proposition, Dukes (2002) found that annual grasses partitioned belowground resources with *C. solstitialis* and exerted weaker competitive effects on the invader than perennial grasses in experimental microcosms. This pattern of exotic annuals paving the way for *C. solstitialis* in California cannot explain, however, the rampant invasion of *C. solstitialis* in the perennial grasslands that dominate central Argentina. Furthermore, in field experiments, Hierro et al. (2006) found that the establishment of *C. solstitialis* in undisturbed vegetation was higher in perennial grass communities in Argentina than in annual grass communities in California. Thus, the hypothesis that *C. solstitialis* is promoted by the absence of native perennial grasses in California requires further exploration. Also, the success of *C. solstitialis* in a region dominated by communities that according to this hypothesis should offer substantial resistance to its invasion suggests, among other possibilities, that Californian and Argentinean populations could differ in their abilities to invade communities.

Here, we assessed the invasibility of annual versus perennial grass communities to *C. solstitialis* in parallel field experiments conducted in the annual grasslands of northern California and the perennial-dominated grasslands of central Argentina. In addition, we examined the possibility that divergent selective forces between northern California and central Argentina or random founder effects have resulted in different levels of invasiveness (i.e., ability to invade) in *C. solstitialis* populations (Sakai et al. 2001). Community invasibility in both regions was evaluated by creating experimental plots composed of either annual or perennial grasses, measuring their effects on resource availability, and invading them with *C. solstitialis* seeds. We further explored

the invasibility of plant communities in California and Argentina by removing neighbors around naturally occurring *C. solstitialis* individuals and measuring the performance of the invader in the presence and absence of intact local plant communities. Differences in invasiveness degree were assessed by comparing the performance of Californian and Argentinean individuals growing under common conditions, simulating rainfall patterns in California and Argentina.

## Materials and methods

### Experimental grass plots and seed additions

We created plots composed of either annual or perennial grasses at the campuses of the University of California at Davis and the National University of La Pampa, Santa Rosa, Argentina (see Online Resource 2 and 3). Plots were 0.50 m × 0.50 m in size, and each of them was separated by 1 m (n = 20 per functional type). Experimental plots of annual grasses included the Eurasian natives *Bromus diandrus* and *B. hordeaceus* in California, and the Argentinean natives *B. brevis* and *Hordeum euclaston* in Argentina. Experimental plots of perennial grasses were built with the Californian natives *Nassella pulchra* and *Elymus glaucus* in California, and the Argentinean natives *N. tenuis* and *Piptochaetium napostaense* in Argentina. These grass species are among the dominants within each functional type in each region (Heady 1988; Rúgolo de Agrasar et al. 2005). An equal mix of the two annual species was sown in experimental plots at a density of 6,000 seeds per m<sup>2</sup> (Heady 1958; Gordon and Rice 1993; Holmes and Rice 1996; Dukes 2001) in autumn in both regions—November 2002 in California and March 2003 in Argentina. Perennial grasses were grown from seeds in greenhouses for three months and then transplanted into field plots (Holmes and Rice 1996; Dyer and Rice 1999) also in November 2002 and March 2003, totaling 25 transplants per plot. Throughout the study, plots were weeded of other species as necessary to maintain the original experimental species composition. To prevent mortality of the transplants, plots with the young perennial grasses were lightly watered to keep the surface soil moist in July and August 2003 in California and until January 2004 in

Argentina. Plots with annual grasses were not watered because water additions could have initiated early germination and thus altered the natural dynamics of annual grasslands. We assumed this watering would not affect subsequent soil moisture readings because it ceased one and two years before recording soil moisture in our first and second seed addition experiment (see below), respectively. After one year of grasses establishment, we used these plots to conduct a seed addition experiment designed to assess the susceptibility of annual versus perennial grasslands in both northern California and central Argentina to *C. solstitialis* invasion (see Online Resource 4). After two years of establishment, we conducted a second seed addition experiment, and included procedural control plots, 0.5 m × 0.5 m in size, with no vegetation present (n = 10 per region) to the experimental design to assess *C. solstitialis* invasion without competitors. These plots can also be viewed as a mimic for disturbance to vegetation in grasslands. Because we did not conduct reciprocal invasion trials, in which *C. solstitialis* plots received seeds of annual or perennial grasses, our design precludes evaluating whether the outcome of species interactions would result in coexistence, multiple stable states, or exclusion of grasses.

We started the second seed addition experiment in October 2004 in California and April 2005 in Argentina, matching the primary emergence period of *C. solstitialis* (Sheley and Larson 1994; Hierro et al. 2006). We added seeds of *C. solstitialis* into half of the annual and perennial grass plots (n = 10 per community type and region), leaving the other half of the plots without seeds to assess the effects of the seedbank and dispersal and be able to measure light and soil moisture (see below) without the influence of the invader. In all cases, *C. solstitialis* seeds were added shortly before a rain, and in California, that rain was the first one of the season. To better understand the recruitment dynamics of *C. solstitialis* in annual versus perennial grass plots, we invaded individual plots in each treatment with either 0, 200, 400, 800, 1600, 3200, or 6400 locally collected pappus seeds (Clark et al. 2007; Poulsen et al. 2007). These additions are within the range of the estimated seed production in invaded sites in California (500 seed m<sup>-2</sup> to 27,200 seed m<sup>-2</sup>, Pitcairn et al. 2002), and they likely saturated the system with seeds (Clark et al. 2007; Poulsen et al. 2007). The treatments of 0,

**Table 1** Percent cover of plants, litter, and bare ground at the time of invading experimental plots with *C. solstitialis* seeds in northern California and central Argentina

Region	Plot type	Plants	Litter	Bare ground
Northern California	Annual grasses	100 ± 0	0	0
	Perennial grasses	97 ± 2	0.5 ± 0.5	3 ± 2
Central Argentina	Annual grasses	44 ± 7	34 ± 4	23 ± 5
	Perennial grasses	98 ± 1	2 ± 1	0

Values are means ± 1 SE of 10 plots per functional type in each region

200, and 400 seeds, which were expected to show larger variation in recruitment than treatments with higher number of seeds were replicated twice in each functional group treatment and control, while all other seed number treatment had a single replicate. The establishment of annual grasses in Argentina was poor and much lower than in California (Table 1); consequently, at the time of adding *C. solstitialis* seeds, all plots with annual grasses in Argentina were re-seeded with the same seed density used previously (after Dukes 2001). We did not reseed plots in California because they received large amounts of seed naturally from the established experimental species. After invading plots with *C. solstitialis* seeds, we measured photosynthetically active radiation (PAR) at 0.02 m from the soil surface and near the center of all plots with a LI-250 (LI-COR) light meter in late fall (December and June) and late winter (March and September) in both regions. *Centaurea solstitialis* forms a rosette during the winter; thus, PAR sampling dates were intended to measure light experienced by seedlings. Simultaneously, we measured PAR at 0.02 m from the soil surface in the open spaces next to experimental plots (full PAR) to calculate proportional PAR as PAR in experimental plots/full PAR. In addition, we measured volumetric water content from 0.10 m to 1.20 m-deep in both regions using polyvinyl chloride (PVC) pipes installed in the center of plots and the same Frequency Domain Reflectometer (Troxler [Triangle Park, North Carolina], Sentry 200-AP) in late summer (August and March). These soil moisture measures were not calibrated, and as a consequence, they do not express absolute values, but serve well for comparative purposes within a region. At the peak of *C. solstitialis* flowering, during the summer following the addition of seeds, we determined the number of plants established, dry aboveground biomass (mean

of a maximum of five randomly selected individuals), and number of capitula (mean of the same individuals used for biomass).

#### Removal of natural vegetation

We further explored the general importance of competition from resident species on *C. solstitialis* invasion in California and Argentina by conducting a plant removal experiment at three sites in each region (see Online Resource 5). At each site, in the fall of 2002 in California (November) and that of 2003 in Argentina (April), we randomly selected 15 groups composed of three naturally established *C. solstitialis* seedlings, each seedling separated by approximately 1 m ( $n = 135$  seedlings per region). All selected seedlings had three leaves and were similar in size. Within groups, we randomly assigned one of the following three treatments to a seedling: (1) removal of all vegetation within a 0.25 m radius of the seedling ( $n = 45$  plots per region), (2) removal of only other *C. solstitialis* plants within a 0.25 m radius of the seedling ( $n = 45$ ), and (3) no removal ( $n = 45$ ). Since *C. solstitialis* seedlings can occur at very high densities in these regions, treatment (2) was meant to exclude intraspecific competition and better quantify effects of local plant communities on *C. solstitialis* performance in each region. After approximately eight months of growth in California and nine months in Argentina, we measured survival (proportion of plants found alive), dry aboveground biomass, and number of capitula of *C. solstitialis* adults. We repeated these activities from December 2003 to August 2004 in California and April 2004 to January 2005 in Argentina. In this second year, we also measured the total aboveground biomass of surrounding vegetation in treatments (2) and (3) at the end of the experiment to quantify the aboveground

competitive environment experienced by *C. solstitialis* in each region.

### Common garden

In a final experiment, we explored both the possibility that populations of the invader from California and/or Argentina have undergone local genetic differentiation and the effects of regional rainfall patterns on the invader's performance. Pappus seeds were collected from six populations in each region (see Online Resource 6) in summer 2002 and used for the experiment in November 2003. Upon collection, we determined the mass of 50 seeds per population. Individual plants of *C. solstitialis* were grown from seed in 0.10 m diameter by 1 m tall PVC pipes filled with a 1:1 mixture of sterile natural soil and sterile sand. Each of the 12 populations was replicated with five individuals. We grew plants in a growth chamber (Environmental Growth Chambers [Chagrin Falls, Ohio], GCW 36) simulating the average climatic conditions in Davis, California, and Santa Rosa, Argentina (see Online Resource 1). Initial conditions simulated October in California and April in Argentina (see Online Resource 7 for details on chamber periodic adjustments). Rainfall annual means and seasonal patterns vary substantially between California and Argentina; therefore, we applied two water treatments to populations from both regions. We used a total of 120 plants in this experiment (2 regions\*6 populations\*5 plants\*2 water treatments). Plants were harvested as they senesced, upon which we determined total dry biomass, capitula number, root:shoot ratio, and relative growth rate (RGR).

### Statistical analyses

#### *Experimental grass plots and seed additions*

Differences in proportional PAR amongst experimental plots with annuals, perennials, and no vegetation in fall and winter in both regions were assessed with a Generalized Linear Model fit to a Binomial distribution, where the effects of experiment (seed addition I or II), region, plot type (nested within region), and season were tested. Post-hoc comparisons were conducted with Tukey LSD contrast test. Generalized Linear Models were also used to test for effects of grass functional group and soil depth on

soil moisture in these plots. Given that soil depth measurements differed between regions in the first year (see Online Resource 4) and they were taken at different times (including seed addition I and II), analyses were conducted separately for each region, and grass group and soil depth were nested within time. When significant grass group effects were detected at  $\alpha P < 0.05$ , post-hoc t-tests were used to identify the specific depths at which grass functional groups differed. Finally, the relationship between the number of seeds added to plots in the fall and the number of adult *C. solstitialis* plants present in them in the summer was assessed by fitting polynomial (linear and quadratic), exponential rise to maximum, power, and logarithm models and selecting significant ( $P < 0.05$ ) models based on the highest  $R^2$  and lowest standard error of the estimate ( $S_{y,x}$ ) depicted by the analysis. Excepting polynomial models, the presence of zeros in the data prevents assessment; to overcome this limitation, 0.5 was added to both the dependent and independent variable. The slopes of linear models (annual vs perennial plots in California; see "Results") were compared with *t* test. In addition, aboveground biomass (modeled as Normal) and fecundity (modeled as Poisson) of *C. solstitialis* plants amongst open, annual grass, and perennial grass plots were compared by combining data from invaded plots and conducting a Generalized Linear Model for each response variable with plot type nested within region. Post-hoc comparisons were conducted with Tukey LSD.

#### *Removal of natural vegetation*

Comparisons of *C. solstitialis* survival, size, and fecundity among removal treatments within each region and year ( $n = 3$  sites) were conducted using Generalized Linear Mixed Models fit to Binomial, Normal, and Poisson distributions, respectively. In these models, site was treated as a random factor and removal treatment as a fixed factor. Post-hoc comparisons were conducted with Tukey LSD.

#### *Common garden*

Seed mass between Californian and Argentinean populations were compared with a Generalized Linear Model fit to a Normal distribution, where origin was treated as a fixed factor and population

( $n = 6$ ) was nested within origin. Effects of climate, origin, and their interaction on *C. solstitialis* total biomass, root:shoot ratio, number of capitula, and RGR were also evaluated with a Generalized Linear Model fit to Normal, Binomial, Poisson, and Binomial distributions, respectively. In addition, seed mass was included as a covariate to control for potential maternal effects derived from differences in seed size between Californian and Argentinean populations (see Results).

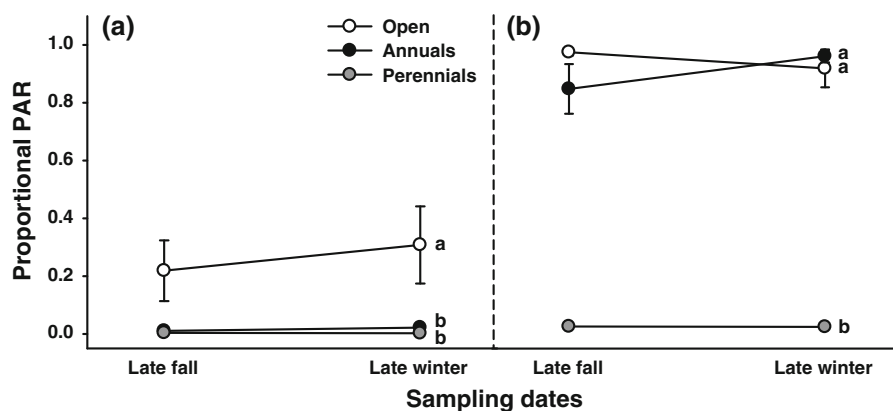
## Results

### Experimental grass plots and seed additions

Proportional PAR in California was almost identical in annual and perennial grass plots, but in Argentina, it was much higher under annual than under perennial grasses ( $\chi^2_{\text{experiment } 1} = 0.762$ ,  $P = 0.383$ ;  $\chi^2_{\text{region } 1} = 89.393$ ,  $P < 0.001$ ;  $\chi^2_{\text{plot type(region) } 4} = 100.647$ ,  $P < 0.001$ ;  $\chi^2_{\text{season } 1} = 2.072$ ,  $P = 0.150$ ; Fig. 1). In fact, proportional PAR in plots with annual grasses was as high as that in plots with no vegetation in Argentina. Soil water content was higher under perennial than under annual grasses at the end of the dry season in California and similar between plant functional types in Argentina (Table 2; Fig. 2). Soils in California were around 10% wetter under perennial than annual grasses at 10 cm to 50 cm-deep, and showed no significant differences at greater depths

(see Online Resource 8). Results for PAR and soil moisture in this experiment were consistent with those obtained in our previous invasion of experimental plots (see Online Resource 4).

In California, the number of *C. solstitialis* adults in the summer increased linearly with the number of seeds added in the fall in plots with both annual ( $y = 0.282 + 0.0008x$ ,  $R^2 = 0.693$ ,  $S_{x,y} = 1.109$ ,  $F_{1, 8} = 18.080$ ,  $P = 0.003$ ) and perennial ( $y = -0.035 + 0.0003x$ ,  $R^2 = 0.923$ ,  $S_{x,y} = 0.206$ ,  $F_{1, 8} = 95.822$ ,  $P < 0.001$ ) grasses (Fig. 3). Although very low for both functional types, the slope of the regression line for annuals was significantly higher than that for perennials ( $t_{18} = 2.465$ ,  $P = 0.024$ ). Low establishment of *C. solstitialis* in this experiment matches results from our first seed addition, in which no *C. solstitialis* established in neither annual nor perennial experimental plots (see Online Resource 4). In addition, there were no differences in size and fecundity of *C. solstitialis* between annual and perennial grass plots (Online Resource 9). In Argentina, *C. solstitialis* establishment increased up to the treatment of 3200 seeds and then it reached plateau in annual grass plots ( $y = 73.851(1 - e^{-0.0007x})$ ,  $R^2 = 0.758$ ,  $S_{x,y} = 16.346$ ,  $F_{1, 8} = 24.986$ ,  $P = 0.001$ ). In contrast, no *C. solstitialis* plant established in perennial grass plots; perhaps because of dry conditions in 2005. In both regions, number of plants increased exponentially with number of seeds in plots with no vegetation (California:  $y = 48.406(1 - e^{-0.030x})$ ,  $R^2 = 0.514$ ,  $S_{x,y} = 20.836$ ,  $F_{1, 8} = 8.447$ ,  $P = 0.020$ ;



**Fig. 1** Proportional photosynthetic active radiation (PAR) during *C. solstitialis* seedling stage in plots with annual grasses, perennial grasses, and no vegetation (open) in parallel seed addition experiments in **a** northern California and **b** central

Argentina. Circles are means  $\pm 1$  SE of 10 plots. Different letters indicate statistical differences ( $P < 0.05$ ) between treatments according to Tukey LSD test



**Table 2** Output of GLMs for soil moisture in annual and perennial grass plots in parallel field experiments in northern California and central Argentina

Region	Statistics	P
Northern California	$\chi^2_{\text{time } 3} = 0.714$	0.870
	$\chi^2_{\text{grass group}(\text{time}) 4} = 188.640$	<0.001
	$\chi^2_{\text{soil depth}(\text{time}) 4} = 12.328$	0.015
	$\chi^2_{\text{grass group} \times \text{soil depth } 1} = 91.981$	<0.001
Central Argentina	$\chi^2_{\text{time } 3} = 467.152$	<0.001
	$\chi^2_{\text{grass group}(\text{time}) 4} = 4.643$	0.326
	$\chi^2_{\text{soil depth}(\text{time}) 4} = 176.823$	<0.001
	$\chi^2_{\text{grass group} \times \text{soil depth } 1} = 1.963$	0.161

Argentina:  $y = 147.111(1 - e^{-0.002x})$ ,  $R^2 = 0.983$ ,  $S_{x,y} = 8.015$ ,  $F_{1,8} = 465.470$ ,  $P < 0.001$ ), and the invader was the largest and most fecund in this experimental treatment (see Online Resource 9).

Removal of natural vegetation

The mean size of individual *C. solstitialis* plants was 10 and six times greater when growing alone than with competitors under the relatively favorable rainfall conditions of 2002–2003 in California and 2004–2005 in Argentina, respectively (Fig. 4). In addition, differences in plant size were also apparent between plots without intraspecific competition and the controls during this season in Argentina. Drought in 2003–2004 in California and Argentina reduced *C. solstitialis* growth, but plants were still larger in

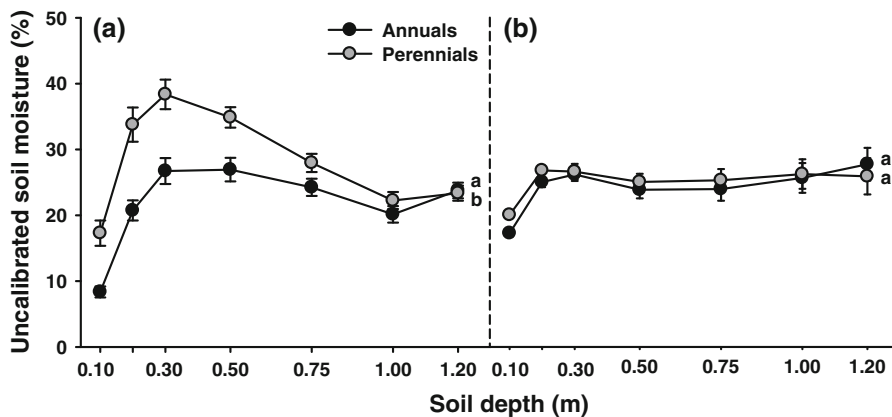
plots without competitors in both regions. The number of capitula produced by the invader closely followed observations for aboveground biomass (see Online Resource 10). In contrast, we did not detect significant differences in the survival of *C. solstitialis* plants among treatments. The aboveground competitive environment experienced by target *C. solstitialis* plants was greater in the perennial grasslands of Argentina than in the annual grasslands of California (see Online Resource 11).

Common garden

*Centaurea solstitialis* seeds from northern California populations were heavier than those from central Argentina [ $0.0020 \pm 0.0004$  and  $0.0015 \pm 0.0003$ , respectively;  $\chi^2_{\text{origin } 1} = 366.804$ ,  $P < 0.001$ ;  $\chi^2_{\text{population}(\text{origin}) 10} = 349.023$ ,  $P < 0.001$ ]. In contrast, Californian and Argentinean populations were similar in all other studied traits. Plants grew larger and allocated more biomass to roots under simulated climatic conditions of northern California, but produced more capitula under those of central Argentina (Fig. 5; Online Resource 12). In turn, *C. solstitialis* grew at similar rates under both climatic conditions.

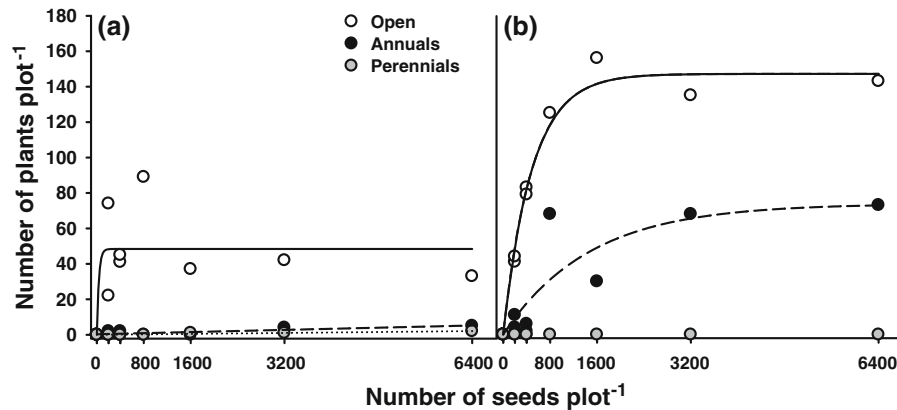
Discussion

Consistent with one of the earliest ideas in invasion biology, that invaders occupy “empty niches” and thus have access to resources that are not used by the



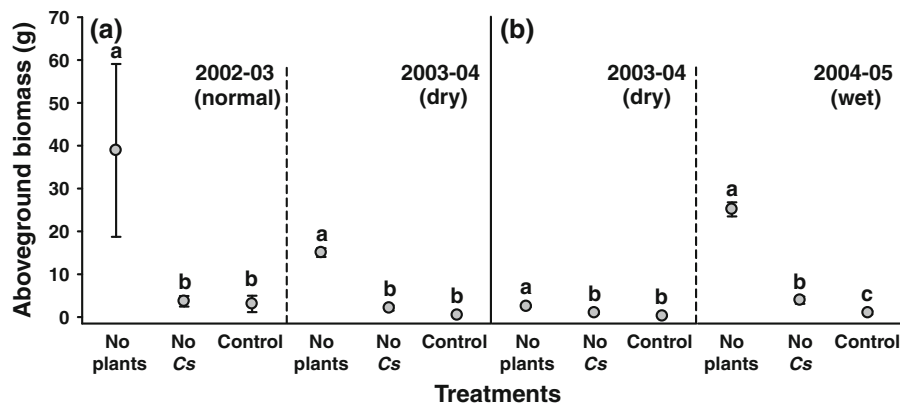
**Fig. 2** Soil moisture dynamics in late summer in annual vs. perennial grass plots in parallel seed addition experiments in **a** northern California and **b** central Argentina. Circles show

means  $\pm$  1 SE of 10 plots; in some cases SE are within the diameter of the circles. Different letters indicate statistical differences ( $P < 0.05$ ) between treatments



**Fig. 3** The relationship between the number of *C. solstitialis* seeds added to plots and *C. solstitialis* establishment in plots with vegetation experimentally removed (open), annual

grasses, or perennial grasses in **a** northern California and **b** central Argentina. No *C. solstitialis* established in plots with perennials in Argentina



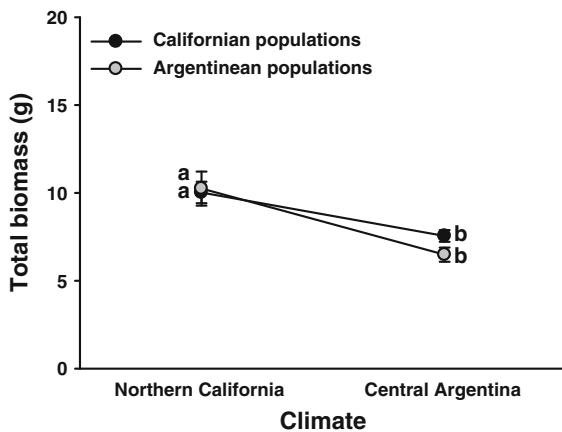
**Fig. 4** Aboveground biomass of mature *C. solstitialis* individuals in plots where all vegetation surrounding these individuals was removed (no plants), only other *C. solstitialis* neighbors were removed (no Cs), and no vegetation was removed (control) over two consecutive years in **a** northern California and **b** central Argentina. The 2003–2004 season was drier than the historic rainfall mean in both regions (dry);

rainfall in the 2002–2003 season in California was close to that mean (normal), and that in the 2004–2005 season in Argentina was above the historic mean (wet). Circles are means  $\pm$  1 SE of three sites; in some cases SE are within the diameter of the circles. Different letters indicate statistical differences ( $P < 0.05$ ) among treatments as determined by Tukey LSD test

locals (Elton 1958), the success of *C. solstitialis* in California has been related to the widespread replacement of native perennial by exotic annual grasses and concomitant increases in soil water availability below 0.50 m depth late in the growing season (Borman et al. 1992; Holmes and Rice 1996; Dyer and Rice 1999). Our results offer only limited support to this hypothesis. A higher number of *C. solstitialis* plants established in plots composed of annual grasses than in those of perennial grasses when invaded with a range of seed numbers, but the number of plants established and slopes of linear

regressions were very low, indicating that both annual and perennial grass communities offer substantial biotic resistance to this invader in California. Also, no *C. solstitialis* individual established in either annual or perennial plots in our first seed addition experiment and the size and fecundity of the invader did not differ between functional groups in none of the seed addition trials conducted in this region. Additionally, soil moisture was greater under annual grasses than under perennial grasses only at 1.20 m-deep in our first trial, when no *C. solstitialis* plant established in either annual or perennial grass plots.





**Fig. 5** Total biomass of Californian and Argentinean *C. solstitialis* plants at the end of a reciprocal common garden experiment simulating climate conditions in northern California and central Argentina. Circles are means  $\pm$  1 SE of six populations in each region; in some cases SE are within the diameter of the circles. Different letters above bars indicate significant differences ( $p < 0.05$ ) between treatments

These soil water results suggest that in sites with deep soils in California, dominant annual grasses may develop extensive root systems and use surface as well as deep water in the soil profile. The young age of our perennial grasses, and consequently a potentially reduced root development, may have also influenced our soil water measurements; importantly, however, perennial grasses were highly resistance to the invasion of *C. solstitialis* in our experimental plots. Finally, findings from plant removal experiments also showed that competition from naturally established annual grasses in California can greatly reduce the growth and fecundity of the invader. Taken together, our results raise the possibility that annual grasses in northern California provide higher competitive resistance to invasion by *C. solstitialis* than previously considered.

Interestingly, hypotheses for invasion by *C. solstitialis* in California have not been synthesized with those proposed for how recruitment of deep-rooted native perennial grasses in this region is limited. Water depletion in the upper 0.30 m of the soil and reduction of light by annuals have been suggested as mechanisms inhibiting recruitment of the native perennial grasses that used to cover California (Holmes and Rice 1996; Dyer and Rice 1999; Enloe et al. 2004). Light intensity at the soil surface during the winter has also been shown to be a crucial factor

for the invasive success of *C. solstitialis* (Roché et al. 1994; DiTomaso et al. 2003). PAR in our experimental plant communities in California was very low under both annual and perennial grasses and surface soils were drier in plots with annuals. These results suggest that the same mechanisms by which exotic annuals may suppress the recruitment of deep-rooted native grasses (but see Seabloom et al. 2003) may also limit the invasion of a deep-rooted exotic herb in California.

In the other studied region, central Argentina, experimental native annual grasses were indeed more susceptible to the invasion of *C. solstitialis* than native perennial grasses, but annuals increased light availability, not water availability. In addition, annual grasses are rare in the natural grasslands of this region (Cano et al. 1980), and thus they cannot explain the widespread invasive success of *C. solstitialis*. As in California, results from seed addition trials were confirmed by those from our complementary experimental approach, as plant removals indicated that dominant perennial grasses exert strong competitive effects against the invader in central Argentina.

Low establishment and performance levels of *C. solstitialis* in plots with annuals and perennials in California and in those with perennials in Argentina contrasted with the high success of the invader in non-vegetated plots in seed addition and plant removal experiments in both regions. These findings are consistent with previous comparisons between these regions on the invasion success of *C. solstitialis* (Hierro et al. 2006), and reinforce the notion that the success of this species in both northern California and central Argentina is greatly dependent on the conditions created by disturbance, among which high light availability seems of paramount importance.

Our common garden provided no evidence for a genetically based differentiation in the invasiveness of *C. solstitialis* in California versus Argentina. Instead, simulated rainfall patterns prompted a plastic response in which individuals from both regions grew larger and allocated more biomass to roots under the Mediterranean conditions of northern California, but were more fecund under those of central Argentina. This plasticity could play a substantial role in the success of *C. solstitialis* in divergent environments (Richards et al. 2006, Keller and Taylor 2008). In turn, we detected a 33% increase in seed mass in

Californian populations relative to Argentinean populations. Seed size has been proposed to influence seedling establishment (Buckley et al. 2003; Widmer et al. 2007, and references therein); however, recent greenhouse experiments suggest that individuals from Argentina are stronger intraspecific competitors than those from California (Lortie et al. 2009). Additional common gardens, where plant communities are invaded with Californian and Argentinean seeds, are needed to examine the ecological significance of increased seed size in Californian populations.

Our study shows that dominant plant functional groups in both northern California and central Argentina offer high competitive resistance to *C. solstitialis* invasion. Together with previous findings (Hierro et al. 2006), our work suggests that the widespread distribution and high abundance of *C. solstitialis* in California and Argentina may be more contingent on the remarkable ability of the invader to take advantage of conditions created by disturbance than on the nature of the functional group that dominates grasslands in these regions. The ability of *C. solstitialis* to exploit disturbed sites has been shown to be superior to that of other congeneric ruderals (Gerlach and Rice 2003). Further comparisons of life history traits, disturbance responses, enemy effects, and competitive capabilities between *C. solstitialis* and local ruderals may help to improve our understanding of its invasion success. More generally, given that numerous invaders are ruderals, such an approach may shed light on how exotic ruderals commonly perform better than native ruderals in disturbed environments.

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