



## Comparison of the effect of elevated CO<sub>2</sub> on an invasive species (*Centaurea solstitialis*) in monoculture and community settings

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### Abstract

The ongoing increase in atmospheric CO<sub>2</sub> concentration ([CO<sub>2</sub>]) is likely to change the species composition of plant communities. To investigate whether growth of a highly invasive plant species, *Centaurea solstitialis* (yellow starthistle), was affected by elevated [CO<sub>2</sub>], and whether the success of this species would increase under CO<sub>2</sub> enrichment, I grew the species in serpentine soil microcosms, both as a monoculture and as a component of a grassland community. *Centaurea* grown in monoculture responded strongly to [CO<sub>2</sub>] enrichment of 350 μmol mol<sup>-1</sup>, increasing aboveground biomass production by 70%, inflorescence production by 74%, and midday photosynthesis by an average of 132%. When grown in competition with common serpentine grassland species, *Centaurea* responded to CO<sub>2</sub> enrichment with similar but nonsignificant increases (+69% aboveground biomass, +71% inflorescence production), while total aboveground biomass of the polyculture increased by 28%. *Centaurea*'s positive CO<sub>2</sub> response in monoculture and parallel (but non-significant) response in polyculture provoke questions about possible consequences of increasing CO<sub>2</sub> for more typical California grasslands, where the invader already causes major problems.

### Introduction

The ongoing increase in atmospheric [CO<sub>2</sub>] may cause changes in the species composition of ecosystems, either by altering the global climate (Chapin et al. 1995; Harte & Shaw 1995) or more directly, by favoring certain photosynthetic pathways (Arp et al. 1993) or changing the magnitude and timing of resource availability within ecosystems (Field et al. 1996; Leadley et al. 1999; Owensby et al. 1999). Invasive species that can exploit the new environmental conditions may gain footholds in previously inhospitable ecosystems (Dukes & Mooney 1999). Although several researchers have examined the CO<sub>2</sub> responses of individually-grown invasive species (e.g., Smith et al. 1987; Sasek & Strain 1988; Huxman et al. 1998), few studies have focused on the responses of biological invaders in community settings (Dukes 2000).

California's grasslands were overrun by Eurasian annual grasses shortly after the arrival of Spanish settlers (Frenkel 1970). These aliens thoroughly dominate most California grasslands today. Outcrops of nutrient-poor and heavy metal-rich serpentine soils that occur along the Coast Range and the Sierra Nevada provide important exceptions to this dominance. Serpentine grasslands largely exclude alien species, and as a result harbor many species of native forbs and perennial bunchgrasses that are outcompeted on more fertile soils, and many endemic species (Kruckeberg 1984). However, these safe havens for natives are vulnerable to perturbation. Several researchers have demonstrated that fertilization of serpentine grasslands can lead to increases in the dominance of Eurasian grasses (Hobbs et al. 1988; Huenneke et al. 1990; Chiariello & Field 1996). Alien grasses are also thought to become more dominant in

wet years (Hobbs & Mooney 1991). Such increases in the abundance of alien species on these grasslands might eventually threaten the native plant species, and would more immediately affect endemic insect species that depend on native plants (Murphy & Ehrlich 1989; Weiss 2000). The exclusion of invasive plants from serpentine grasslands is thus critical to the preservation of elements of California's native grassland biodiversity.

The rise in atmospheric [CO<sub>2</sub>] is likely to alter resource availability in these serpentine grasslands, which could affect their susceptibility to invasion. By decreasing the transpiration rates of resident plants, elevated [CO<sub>2</sub>] increases late-season water availability in typical California grasslands (Fredeen et al. 1997). Carbon dioxide enrichment may also influence the water budget of California's serpentine grasslands, which have much shallower soils and a lower water holding capacity than the region's typical grasslands. Although no differences in moisture have been detected in shallow layers of serpentine soil (Field et al. 1997; Fredeen et al. 1997), deep-rooted species that grow through the summer on this substrate respond strongly to elevated [CO<sub>2</sub>] (Field et al. 1996), suggesting greater water availability in deep soil. Elevated [CO<sub>2</sub>] also accelerates net N mineralization in serpentine grasslands, potentially increasing N availability to plants (Hungate et al. 1997). Plants that can exploit these resources will gain a competitive advantage as atmospheric [CO<sub>2</sub>] increases.

The Mediterranean forb *Centaurea solstitialis* L. (yellow starthistle) is currently invading grasslands of western North and South America, and is established on four other continents (Maddox & Mayfield 1985; Maddox et al. 1985). *Centaurea* is a deep-rooted annual that flowers during the dry summer months, after most other mediterranean-climate grassland species have set seed. California's ecosystems have been particularly susceptible to invasion by this species; in 1997, more than 9 million hectares of the state were estimated to be infested (Pitcairn et al. 1998). This invasion has changed the value, appearance, and functioning of the state's rangelands. Because *Centaurea* is toxic to horses (Cordy 1954) and is considered low quality forage by ranchers, concerted efforts are underway to reduce the weed's prevalence in California.

Although *Centaurea* invasions have reached the border of many patches of California's serpentine grassland, the alien rarely, if ever, spreads into serpentine communities. The mechanism that prevents *Centaurea* from invading serpentine grasslands is un-

known. The invasibility of more fertile California grassland by *Centaurea* has been linked to late-season water availability (Dukes 2001). I hypothesized that elevated [CO<sub>2</sub>] would: (1) increase water availability under grassland communities on serpentine soil, (2) stimulate *Centaurea* growth, and (3) favor *Centaurea* in serpentine grasslands. To test these hypotheses, I grew *Centaurea* in serpentine soil microcosms under ambient and elevated [CO<sub>2</sub>]. In one set of microcosms, I grew *Centaurea* without competitors to determine whether the invader could grow in serpentine soil, and to assess its physiological responses and potential maximum growth response to CO<sub>2</sub>. In a second set of microcosms, *Centaurea* competed with species typical of local serpentine plant communities, establishing the invader's likely response in the field. Regular measurements of soil moisture allowed a comparison of the extent to which [CO<sub>2</sub>] affected water availability in each of the microcosm types.

## Materials and methods

### *Study site and design*

This study was part of the Jasper Ridge CO<sub>2</sub> experiment, which took place at Jasper Ridge Biological Preserve (JRBP), near Woodside, CA, USA (37°24' N, 122°14' W, 105 m elevation). The site has a Mediterranean climate, with cool, wet winters and warm, dry summers. This experiment was one of a suite of experiments that were conducted in 20 large (1.3 m square) open-top chambers supplied with either ambient air or ambient air plus about 350 μmol mol<sup>-1</sup> CO<sub>2</sub> (mean enrichment for the chambers was 352 μmol mol<sup>-1</sup> over the course of the experiment; mean daily standard error for enriched chambers was 2.2 μmol mol<sup>-1</sup>; Field et al. 1996). Each chamber housed 24 or more experimental microcosms. Microcosms for this experiment were placed in 12 of the open-top chambers. The microcosms were contained in 24 polyvinyl chloride pots, which stood 0.95 m tall by 0.2 m in diameter. Each pot contained 79 cm of crushed rock-based subsoil topped with 15 cm of serpentine topsoil, to simulate the soil profile found in serpentine grassland at JRBP (Field et al. 1996). The pots and soil columns had been used to grow serpentine plant communities in the year before this experiment; pots were placed in the same CO<sub>2</sub> environment they had experienced the previous year. Before the start of the present experiment, the top 13 cm of topsoil from each pot was

removed, pooled with that from all other pots (of both [CO<sub>2</sub>] treatments), and mixed thoroughly. All pots were then refilled with this single batch of homogenized topsoil. Soils were amended with 3 g m<sup>-2</sup> N, P, and K (each microcosm received 0.696 g of Osmocote 14-14-14 slow-release fertilizer pellets; Grace Sierra Horticultural Products Company, CA, USA), an amount calculated to replace the nutrients bound in plant tissue that was removed in the previous year's experiment. With this nutrient amendment, above-ground productivity in the polyculture microcosms closely paralleled the 1995-6 productivity of serpentine grasslands at JRBP (see below; C.B. Field et al., unpublished data).

I sowed all microcosms on October 19, 1995. Twelve microcosms received only *Centaurea solstitialis* seeds, and 12 microcosms received seeds of eight species; seven commonly found on serpentine soils in JRBP, and *Centaurea* (Table 1). Seeding densities were selected using criteria of Chiariello & Field (1996) in order to create polycultures that closely resembled nearby serpentine grassland communities in plant density and functional group representation. Because local serpentine grasslands are dominated (in terms of % cover) by annual species and experience frequent soil disturbance from gophers (Hobbs & Mooney 1995), and because *Centaurea* invades via short-distance seed dispersal (Roché 1992), these polycultures simulated the environment that invading *Centaurea* achenes experience in the field. Six replicate monoculture and polyculture microcosms were distributed among five open-top chambers at each CO<sub>2</sub> concentration (at each concentration, four chambers contained one randomly-placed replicate of each treatment, a fifth chamber contained two replicate monoculture microcosms, and a sixth chamber contained two replicate polyculture microcosms).

At JRBP, seasonal precipitation averages 667 mm, with most of the rain typically falling in January and February. The first significant storms generally arrive in October or November. The 1995-1996 growing season started later than usual, with the first significant rains falling on December 4, but was otherwise fairly typical. From December through May, monthly precipitation totals were 204, 251, 190, 72, 37, and 40 mm. No rain fell after May.

Microcosms were weeded regularly during the growing season to remove unsown seedlings germinating from the soil seed bank. In monocultures, *Centaurea* was thinned to 6-8 individuals per microcosm in the first week of March 1996, and thinned to the 3

largest individuals on April 15. *Centaurea* seedlings in the polycultures were counted to determine establishment rates on February 7, but this treatment was never thinned. *Centaurea* seeds failed to germinate in one elevated-[CO<sub>2</sub>]-exposed polyculture microcosm. This microcosm was omitted from all analyses of data concerning establishment, biomass and reproductive output.

#### *Measurements and analyses*

I measured soil moisture of five monoculture and five polyculture microcosms in both ambient and elevated [CO<sub>2</sub>] treatments using time-domain reflectometry. These measurements were made along two pairs of vertically oriented stainless steel waveguides, which extended to depths of 43.5 and 88.5 cm below the soil surface. I used pre-existing calibration curves for serpentine soil microcosms (Field et al. 1997) to convert readings from a cable tester (1502B, Tektronix, OR, USA) to soil moisture values.

On 6 and 31 May 1996, I measured photosynthesis, transpiration, and stomatal conductance of *Centaurea* plants in the monoculture treatments. In each microcosm, I took measurements on one young, fully expanded leaf from each of two plants. Measurements were made under each treatment's standard operating conditions with a closed gas exchange system (LI-6200, Li-Cor Inc., NE, USA). Reliable gas exchange measurements could not be obtained from *Centaurea* plants in the polyculture treatment because leaves of many individuals were too small for the gas exchange chamber.

From mid-May until mid-July, I periodically measured heights of bolting shoots in the *Centaurea* monocultures. I counted inflorescences (defined for the purposes of this study as stem termini that had reached floral bud stage 1 or beyond, as described by Maddox (1981)) of all *Centaurea* plants at the final harvest. Plants in monocultures were harvested on September 14 and plants in polycultures were harvested from 21-25 September. Tissue was dried at 65 °C for at least 48 hours before weighing. Aboveground biomass of *Centaurea*, *Hemizonia congesta*, and all other species (pooled) was recorded for each polyculture microcosm. *Hemizonia* biomass was recorded because *Hemizonia* and *Centaurea* (which are both in the Asteraceae) have similar phenologies and rooting patterns and thus might be expected to respond similarly to changes in resource availability.

Table 1. Species and seeding densities ( $\text{m}^{-2}$ ) used in the monoculture and community microcosms.

Species	Native?	Growth form <sup>a</sup>	Sowing density	Target density <sup>b</sup>
Polycultures				
<i>Plantago erecta</i>	Yes	EF	2640	2390
<i>Lasthenia californica</i>	Yes	EF	3567	1433
<i>Vulpia microstachys</i> var. <i>pauciflora</i>	Yes	AG	1051	955
<i>Hemizonia congesta</i> ssp. <i>luzulifolia</i>	Yes	LF	796	159
<i>Bromus hordeaceus</i>	No	AG	1050	955
<i>Lotus wrangelianus</i>	Yes	AL	223	223
<i>Nassella pulchra</i>	Yes	PG	478	159
<i>Centaurea solstitialis</i>	No	LF	796	159
Monocultures				
<i>Centaurea solstitialis</i>	No	LF	796	96

<sup>a</sup>Key: AG, annual grass; AL, annual legume; EF, early-flowering annual forb; LF, late-flowering annual forb; PG, perennial grass.

<sup>b</sup>Target density of surviving plants. Nomenclature follows Hickman (1993).

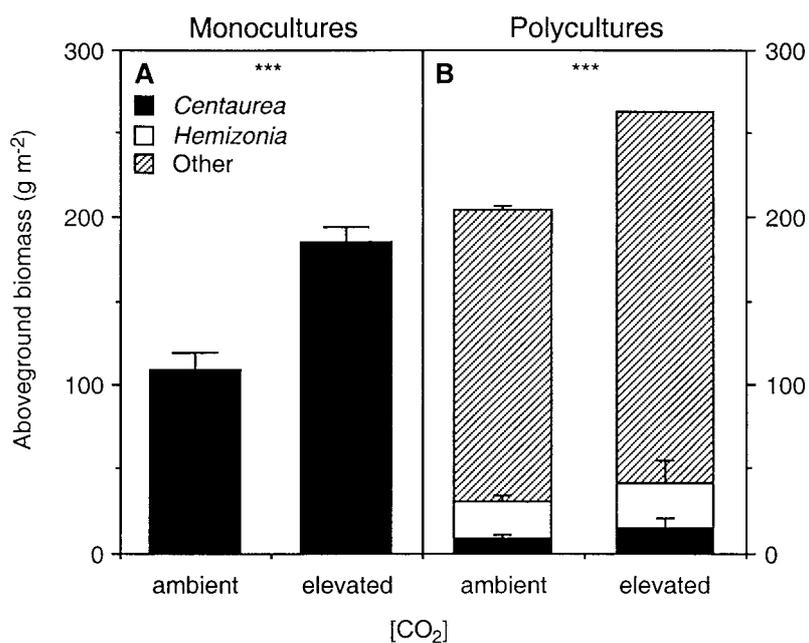


Figure 1. Average aboveground biomass production of *Centaurea* (black sections), *Hemizonia* (white sections), and other species (hatched sections) in **A** *Centaurea* monocultures and **B** serpentine polycultures under ambient and elevated [CO<sub>2</sub>] ( $n = 6$  except for serpentine communities grown in elevated [CO<sub>2</sub>], for which  $n = 5$ ). Bars represent standard error of the sums of all sections below. Standard error of total community grown in elevated [CO<sub>2</sub>] is too small to appear. Key: \*\*\*,  $P < 0.001$  (comparison of total aboveground biomass in microcosms grown in ambient and elevated [CO<sub>2</sub>]).

Values from the various measurements of *Centaurea* individuals were either pooled (e.g., plant heights, biomass) or averaged (e.g., gas exchange data) to obtain a single value for each microcosm before statistical analysis. Differences among treatments were analyzed with unpaired t-tests, or, in the case of soil moisture, height, and gas exchange measurements, with repeated measures ANOVA (SuperANOVA, Abacus Concepts, Inc., CA, USA).

## Results

### Monocultures

Elevated  $[\text{CO}_2]$  increased total aboveground biomass production by 70% in the monocultures ( $P = 0.0003$ , Figure 1A). Reproductive biomass rose by 91% ( $P = 0.0003$ , Figure 2C), and high- $[\text{CO}_2]$ -grown plants initiated 74% more inflorescences ( $P = 0.002$ , Figure 2A). Elevated  $[\text{CO}_2]$  also appeared to hasten and increase stem elongation. The sum of heights of *Centaurea* plants in elevated- $[\text{CO}_2]$ -exposed microcosms was marginally greater than that of plants in ambient-air-exposed microcosms over four measurement dates (repeated measures ANOVA:  $\text{CO}_2$  effect,  $P = 0.057$ ; Date,  $P = 0.0001$ ,  $\text{CO}_2 \times \text{date}$  interaction,  $P = 0.90$ ; Figure 3).

Elevated  $[\text{CO}_2]$  increased *Centaurea* photosynthesis (A) by an average of 132% over the two measurement dates, but did not affect transpiration (E) or stomatal conductance (repeated measurement ANOVA, photosynthesis:  $\text{CO}_2$  effect,  $P = 0.0015$ ; Date,  $P = 0.11$ ,  $\text{CO}_2 \times \text{date}$  interaction,  $P = 0.23$ ; conductance:  $\text{CO}_2$  effect,  $P = 0.65$ ; Date,  $P = 0.003$ ,  $\text{CO}_2 \times \text{date}$  interaction,  $P = 0.85$ ; transpiration:  $\text{CO}_2$  effect,  $P = 0.52$ ; Date,  $P = 0.0001$ ,  $\text{CO}_2 \times \text{date}$  interaction,  $P = 0.89$ ; Figure 4). This discrepancy led to an average increase in instantaneous midday water-use efficiency (A/E) of 135% in the  $\text{CO}_2$ -enhanced treatment.

Shallow (0–43.5 cm depth) soil in elevated- $[\text{CO}_2]$ -exposed monocultures was consistently wetter than shallow soil in ambient air monocultures (average volumetric soil moisture content across measurement dates: ambient, 17.3%; elevated, 20.7%. Repeated measures ANOVA:  $\text{CO}_2$  effect,  $P = 0.012$ ; Date,  $P = 0.0001$ ,  $\text{CO}_2 \times \text{date}$  interaction,  $P = 0.44$ ; Figure 5). Moisture in deep (43.5–88.5 cm depth) soils was increased by elevated  $[\text{CO}_2]$  only during the latter portion of the measurement period (average volumetric soil moisture content across measurement dates:

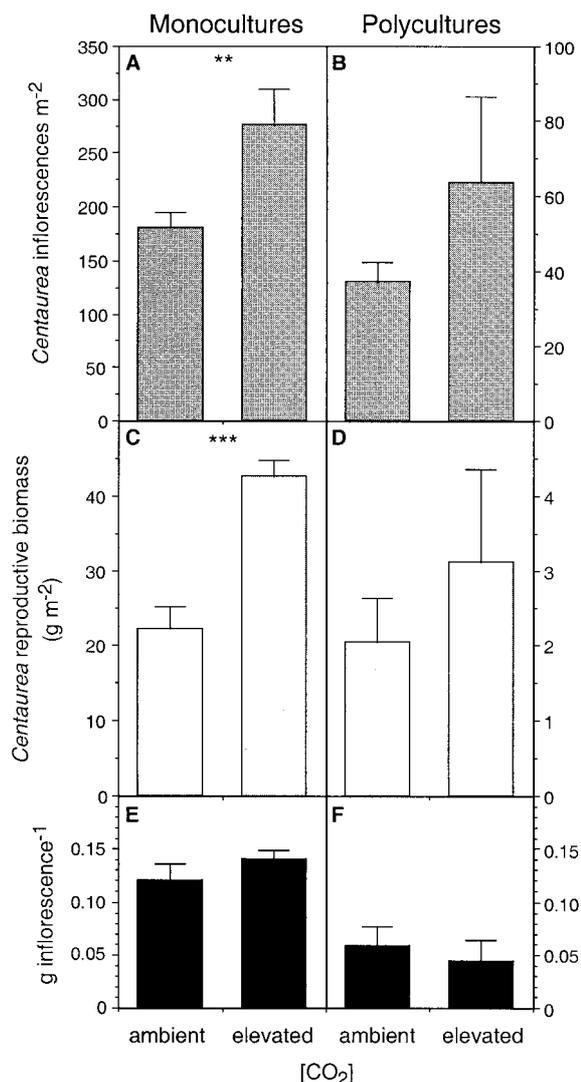


Figure 2. Reproductive output of *Centaurea* grown in ambient and elevated  $[\text{CO}_2]$ . Number of initiated *Centaurea* inflorescences (A and B), total reproductive biomass (C and D), and inflorescence biomass (E and F). Left-hand panels show values from *Centaurea* monocultures, and right-hand panels show values for *Centaurea* grown in serpentine polycultures (mean  $\pm$  standard error,  $n = 6$  except for serpentine polycultures grown in elevated  $[\text{CO}_2]$ , for which  $n = 5$ ). Note differences in scales between left- and right-hand axes. Key: \*\*,  $P < 0.01$ , \*\*\*,  $P < 0.001$ .

ambient, 11.4%; elevated, 13.0%. Repeated measures ANOVA:  $\text{CO}_2$  effect,  $P = 0.66$ ; Date,  $P = 0.0001$ ,  $\text{CO}_2 \times \text{date}$  interaction,  $P = 0.013$ ; Figure 5).

### Polycultures

Aboveground biomass of polycultures increased 28% under elevated  $[\text{CO}_2]$  (Figure 1B,  $P = 0.0002$ ).

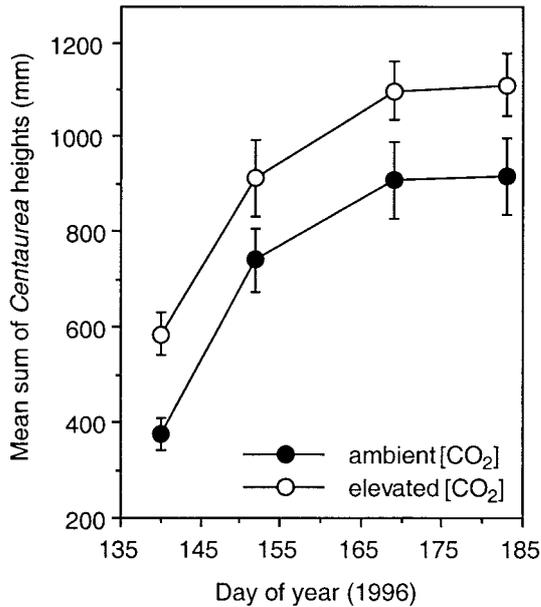


Figure 3. Average sums of heights of *Centaurea* individuals grown in monoculture under ambient (closed circles) and elevated (open circles) [CO<sub>2</sub>] (mean  $\pm$  standard error,  $n = 6$  for each treatment).

CO<sub>2</sub> enrichment was associated with nonsignificant increases in *Centaurea* establishment (20%; mean number of established plants  $\pm$  SE: ambient,  $6.0 \pm 1.2$ ; elevated,  $7.2 \pm 1.7$ ;  $P = 0.57$ ), total aboveground biomass (69%,  $P = 0.29$ , Figure 1B) and in the proportional contribution of *Centaurea* to community biomass (from 4.3% to 5.5%, a 29% change,  $P = 0.76$ ). Reproductive success of *Centaurea* increased nonsignificantly as measured by reproductive biomass (52%,  $P = 0.43$ , Figure 2D) and inflorescence production (71%,  $P = 0.24$ , Figure 2B).

Changes in aboveground (+19%,  $P = 0.63$ ) and reproductive biomass (-28%,  $P = 0.39$ ) of *Hemizonia* under elevated [CO<sub>2</sub>] were nonsignificant. However, CO<sub>2</sub> enrichment caused a significant increase (24%,  $P = 0.006$ ) in pooled aboveground biomass of all other species.

In general, soils in polyculture microcosms exposed to elevated [CO<sub>2</sub>] remained wetter than those in microcosms exposed to ambient air (Figure 5). In both shallow and deep soils, these differences were marginally significant (average volumetric soil moisture content across measurement dates, shallow soil: ambient, 16.9%; elevated, 18.8%. Deep soil: ambient, 8.1%; elevated, 12.3%. Repeated measures ANOVAs, shallow soil: CO<sub>2</sub> effect,  $P = 0.055$ ; Date,  $P = 0.0001$ , CO<sub>2</sub>  $\times$  date interaction,  $P = 0.27$ . Deep soil:

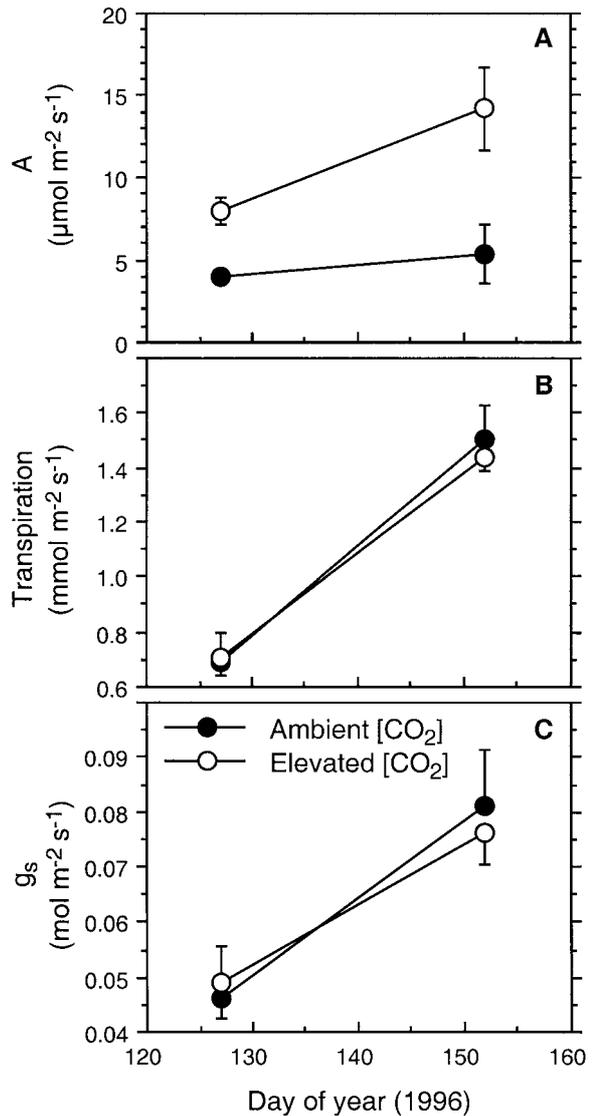


Figure 4. Mid-day leaf photosynthesis **B** transpiration and **C** stomatal conductance of *Centaurea* plants grown in monoculture at ambient (closed circles) and elevated (open circles) [CO<sub>2</sub>] (mean  $\pm$  standard error,  $n = 6$  on May 6,  $n = 5$  on May 31). Plants were in rosette form on May 6, and were bolting on May 31. For clarity, error in **B** and **C** is drawn in a single direction from each mean.

CO<sub>2</sub> effect,  $P = 0.090$ ; Date,  $P = 0.0001$ , CO<sub>2</sub>  $\times$  date interaction,  $P = 0.29$ . Figure 5).

#### Monoculture vs. polyculture comparisons

On an area basis, *Centaurea* produced more total biomass (+1597%,  $P < 0.0001$ ), reproductive biomass (+1090%,  $P < 0.0001$ ) and inflorescences (+485%,  $P < 0.0001$ ) in monocultures exposed to ambient air than in polycultures exposed to ambient air (Figures 1

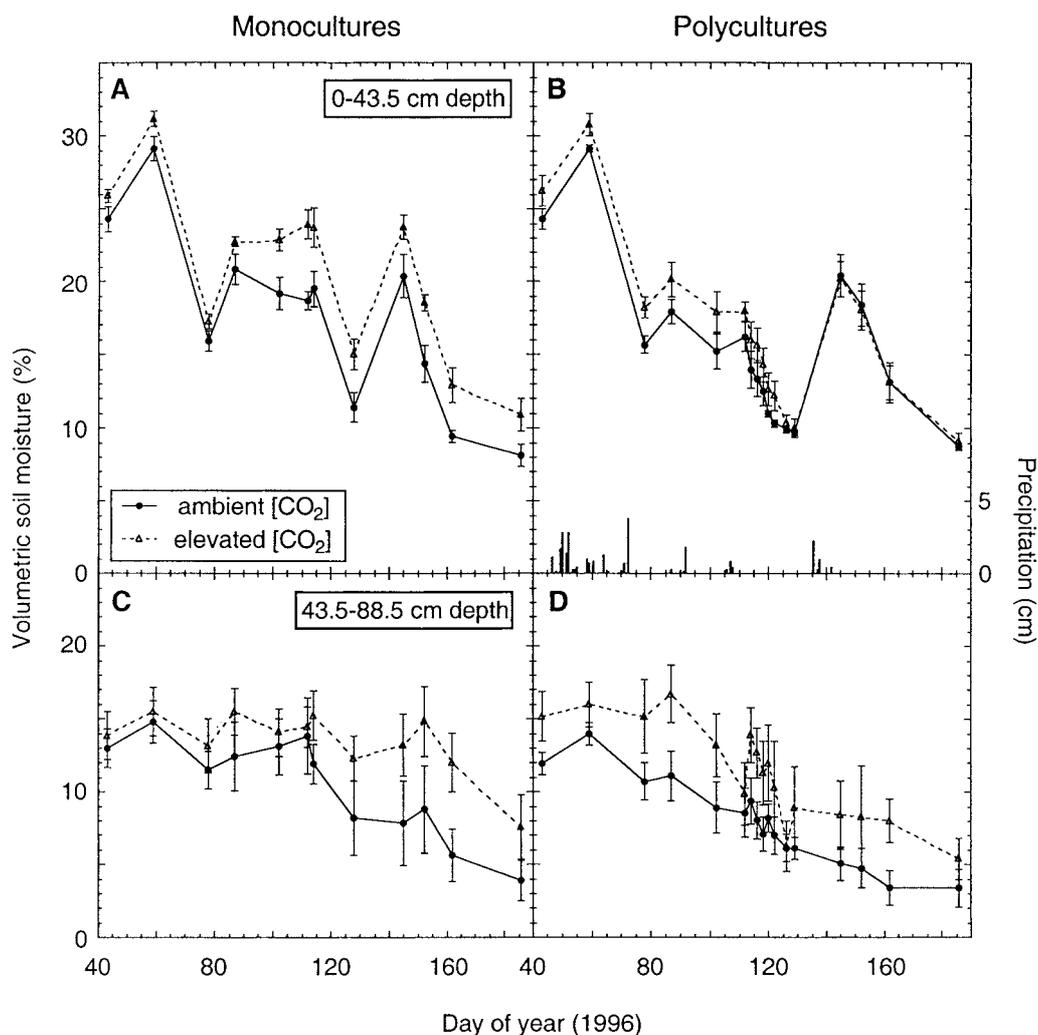


Figure 5. Volumetric soil moisture of **A** *Centaurea* monocultures and **B** serpentine polycultures in the shallow soil layer (0 to 43.5 cm depth), and **C** *Centaurea* monocultures and **D** serpentine polycultures in the deep soil layer (43.5 to 88.5 cm depth), exposed to ambient (closed circles, solid lines) and elevated (open triangles, dashed lines) [CO<sub>2</sub>] (mean  $\pm$  standard error,  $n = 5$  for each treatment). Vertical bars in **B** show daily precipitation totals outside the chambers.

and 2). In addition, individual seed heads were larger on *Centaurea* plants grown in monoculture (+209%,  $P < 0.02$ , Figure 2).

For a given CO<sub>2</sub> treatment and soil layer, polycultures and monocultures did not differ in soil moisture over the measurement dates (repeated measures ANOVA followed by Student–Newman–Keuls post-hoc test,  $\alpha = 0.05$ ).

## Discussion

It is clear from this study that *Centaurea solstitialis* can grow and reproduce on serpentine soil, and thus

may be able to invade serpentine refugia, given the right conditions. I have also demonstrated that, when grown in monoculture, *Centaurea* is highly responsive to elevated [CO<sub>2</sub>]. In the polyculture setting, however, *Centaurea*'s response to elevated [CO<sub>2</sub>] was apparently not strong enough to dramatically enhance its competitive ability relative to the species that are typically found in California's serpentine grasslands.

In the monocultures, *Centaurea* growth increased markedly under elevated [CO<sub>2</sub>]. I attribute this increase to at least two factors: (1) direct stimulation of photosynthesis; and (2) increased water availability (which may have allowed plants to maintain high

photosynthetic rates for a longer period of time). Leaf-level gas exchange measurements at two dates indicate that, late in the growing season, photosynthetic rates more than doubled under elevated  $[\text{CO}_2]$ . These gas exchange measurements did not expose differences in stomatal conductance or transpiration. However, soil was drier in ambient than in elevated  $[\text{CO}_2]$  microcosms on both dates (Figure 5). The drier soils may have suppressed stomatal conductance of plants in the ambient air treatment, masking potentially greater conductance at comparable soil moisture. In sandstone grasslands at Jasper Ridge, *Avena barbata* individuals grown in elevated  $[\text{CO}_2]$  had much lower early-season stomatal conductance than individuals grown in ambient air, but this difference disappeared late in the growing season (Jackson et al. 1994). Differences in leaf nitrogen concentrations ( $[\text{N}]$ ) can also cause differences in plant photosynthetic rates. I did not measure leaf  $[\text{N}]$  in conjunction with the photosynthesis measurements, so I can only speculate on this point. On the day of the second round of photosynthetic measurements (May 31), nine plants in the elevated  $[\text{CO}_2]$  treatment had started to form inflorescences, as opposed to five plants in the ambient  $[\text{CO}_2]$  treatment (no plants were forming inflorescences on the first measurement date). If N translocation from leaves to reproductive parts had begun, I would expect N concentrations in leaves to have declined most in the elevated  $[\text{CO}_2]$  treatment. Such a decline would likely cause a decrease in photosynthesis rates in the elevated  $[\text{CO}_2]$  treatment relative to the ambient treatment. In fact, I observed the opposite pattern, suggesting that differences in N translocation were not responsible for the observed patterns of gas exchange.

The consistent 1.5–4% difference in soil moisture between the two treatments in this study suggests that conductance and transpiration were lower under elevated  $[\text{CO}_2]$  over much of the growing season (before the gas exchange measurements were made), and that during this time, the difference in transpiration was proportionally greater than any difference in leaf area. Although it is likely that both the increase in water availability and direct stimulation of photosynthesis by elevated  $[\text{CO}_2]$  contributed to the increase in *Centaurea* growth, I am unable to compare the relative importance of these factors in this study.

Carbon dioxide enrichment did not dramatically increase *Centaurea*'s success in the model serpentine grassland community. Under ambient  $[\text{CO}_2]$ , *Centaurea* comprised only 4.3% of the serpentine polyculture. The invader tended to increase in abundance

under elevated  $[\text{CO}_2]$ , but remained a small fraction (5.5%) of total community biomass. The nonsignificant responses of aboveground growth, reproductive biomass, and number of initiated inflorescences indicate that, if elevated  $[\text{CO}_2]$  provides *Centaurea* a competitive advantage, that advantage is relatively small. Under field conditions, this might translate into greater aggressiveness as an invader, but with, at least in most sites, a slow increase in abundance. Notably, these nonsignificant increases closely paralleled significant changes in the same variables in monoculture-grown plants. The high intrinsic variability associated with studying the success of a single species in a community setting may have prevented detection of  $\text{CO}_2$  responses, despite substantial replication of the microcosms.

Variability within treatments may have similarly masked changes in the success of another late-season annual forb, *Hemizonia congesta*. In this study, aboveground biomass of *Hemizonia* increased nonsignificantly by 19% in elevated  $[\text{CO}_2]$ . In a previous microcosm study of serpentine plant polycultures, *Hemizonia* biomass production increased with marginal significance, and by a smaller margin, in response to  $\text{CO}_2$  enrichment (Chiariello & Field 1996).

Interannual variation in environmental conditions might also explain the nonsignificant responses of *Centaurea* and *Hemizonia* in polycultures in this study. Chiariello and Field conducted their microcosm study in 1993–1994, a much drier season than the present experiment, and productivity of their communities was lower than in the present experiment. It is possible that water was a more limiting factor for *Hemizonia* growth in 1993–1994 than in the 1995–1996 growing season, and that the water savings generated by  $\text{CO}_2$  enrichment were more critical for the summer growth of *Hemizonia*. Smith et al. (2000) observed striking interannual differences in the impact of  $\text{CO}_2$  on an invasive species in the Mojave Desert of North America. Success of the non-native annual grass *Bromus madritensis* ssp. *rubens* was strongly enhanced by  $\text{CO}_2$  enrichment in a very wet year, but unaffected in a dry year (in which annual species did not germinate). Similarly, the effects of  $\text{CO}_2$  on the success of *Centaurea* and other late-season annuals in serpentine grassland communities may vary widely depending on environmental conditions. In previous years, researchers at Jasper Ridge had observed large, statistically significant increases in growth of late-season annuals in field-based  $\text{CO}_2$  studies, on both serpen-

tine and more typical sandstone grasslands (Field et al. 1996).

Because this experiment took place in microcosms and over a single growing season, it would be imprudent to use its outcome to project the occurrence or absence of long-term shifts in the competitive balance of California's serpentine grasslands in response to elevated [CO<sub>2</sub>]. Results from this study suggest that, in the short run, the rise in [CO<sub>2</sub>] may not dramatically enhance *Centaurea*'s success in serpentine grasslands. However, *Centaurea*'s remarkably strong CO<sub>2</sub> response in monoculture and similar (though non-significant) response in polyculture provoke questions about the potential implications of increasing [CO<sub>2</sub>] for California's more fertile non-serpentine grasslands, where *Centaurea* has already caused major problems.

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