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Strong response of an invasive plant species (*Centaurea solstitialis* L.) to global environmental changes

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Abstract. Global environmental changes are altering interactions among plant species, sometimes favoring invasive species. Here, we examine how a suite of five environmental factors, singly and in combination, can affect the success of a highly invasive plant. We introduced *Centaurea solstitialis* L. (yellow starthistle), which is considered by many to be California's most troublesome wildland weed, to grassland plots in the San Francisco Bay Area. These plots experienced ambient or elevated levels of warming, atmospheric CO₂, precipitation, and nitrate deposition, and an accidental fire in the previous year created an additional treatment. *Centaurea* grew more than six times larger in response to elevated CO₂, and, outside of the burned area, grew more than three times larger in response to nitrate deposition. In contrast, resident plants in the community responded less strongly (or did not respond) to these treatments. Interactive effects among treatments were rarely significant. Results from a parallel mesocosm experiment, while less dramatic, supported the pattern of results observed in the field. Taken together, our results suggest that ongoing environmental changes may dramatically increase *Centaurea*'s prevalence in western North America.

Key words: *Centaurea solstitialis* (yellow starthistle); climate change; elevated CO₂; grasslands; invasive species; nitrogen deposition; rangelands; weed.

INTRODUCTION

Many ongoing global changes are expected to affect the success of invasive plant species (i.e., nonnative plant species that become widespread and locally or regionally dominant), because these species commonly share certain traits. For instance, a rapidly changing climate could favor invasive species through a variety of little-tested mechanisms relating to environmental tolerances, interspecific relationships, phenological plasticity, and seed dispersal distances (Dukes and Mooney 1999, Bradley et al. 2010, Willis et al. 2010). Regional increases in precipitation and nitrogen deposition can affect plant competition by increasing soil resource availability, to the advantage of many fast-growing invasive plant species (Brooks 2003, Scherer-Lorenzen et al. 2007, Blumenthal et al. 2009). Elevated CO₂ has been shown to preferentially benefit certain species in

competitive situations, but few studies have examined responses of invasive species in the field (Dukes 2000, Ziska and Dukes 2011).

As many aspects of the global environment change simultaneously, these changes may additively or interactively affect the success of invasive species. In regions where precipitation decreases, warming will compound the water stress experienced by plants. On the other hand, many plants growing under elevated CO₂ partially close their stomata, sometimes leading to water savings. The additional soil moisture could at least partially counteract increases in water stress due to warming or drought. With the wide variety of global changes currently occurring, predicting which combinations and interactions will be most consequential presents a challenge. Despite the potential importance of co-occurring environmental changes, few studies to date have examined invasive species' responses to more than one change at a time. Data from Williams et al. (2007) and Blumenthal et al. (2008) suggest interactions may

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occasionally be observed, but the frequency with which they will be important is unclear.

Native to the lands northeast of the Mediterranean Sea, *Centaurea solstitialis* (hereafter *Centaurea*) has now established populations on six continents (Maddox et al. 1985). The annual forb is poisonous to horses, and has spread rapidly through rangelands in large parts of western North America, leading to the release of at least seven biocontrol agents (Gutierrez et al. 2005). *Centaurea* is regarded by many as California's most troublesome wildland weed (Mackenzie 2004, Pitcairn et al. 2006).

We conducted two experiments to examine whether and how a suite of environmental changes, individually or in combination, might affect the success and impact of *Centaurea* in California grasslands. To assess *Centaurea*'s response to five environmental factors under field conditions, we seeded the species into the Jasper Ridge Global Change Experiment (JRGCE; Shaw et al. 2002, Dukes et al. 2005). The JRGCE has exposed California grassland to ambient and elevated levels of atmospheric CO₂, temperature, rainfall, and nitrate deposition, in all factorial combinations, since 1998. A small fire burned through the experimental site in summer 2003, adding a "burned" treatment to a subset of the plots. To assess the nature of *Centaurea*'s response to environmental changes under more controlled conditions, and its impact on other species, we created soil mesocosms that we seeded with either *Centaurea*, the annual grass *Avena barbata*, or both species, additively. Mesocosms of all three species combinations were grown outdoors under eight combinations of environmental conditions, featuring ambient and elevated levels of atmospheric CO₂, nitrate deposition, and phosphorus availability.

METHODS

Both experiments took place at the Jasper Ridge Biological Preserve, near Woodside, California, USA (37°24' N, 122°14' W, 120 m elevation). This region experiences a Mediterranean climate, with warm, dry summers and cool, wet winters. The local topsoil is a fine, mixed, thermic Typic Haploxeralf from the Francisquito series.

In the local grasslands, the dominant annual species typically germinate after the first heavy rains of the season, usually in October or November. The growing season for the dominant grasses lasts until May or June, when they set seed and senesce. *Centaurea* germinates with the other annuals, but survives through the summer, typically setting seed and dying in September or October.

Field experiment.—The JRGCE consists of 32 circular plots (2 m diameter), each divided into four quadrants. The July 2003 fire burned through two blocks in the central portion of the field site, leaving three blocks on either end of the site unburned. There were no clear differences in topography or productivity of burned and

unburned plots before the fire. After the fire, heaters were turned off in the burned area, such that the JRGCE comprised four blocks of burned grassland exposed to a factorial combination of ambient or elevated CO₂ (+300 ppm at the plot level), nitrate (+7 g N·m⁻²·yr⁻¹ as CaNO₃⁻ applied at the subplot level) and precipitation (+50% of ambient rainfall added shortly after each rain event plus a three-week extension of the rainy season, applied at the subplot level). The six unburned blocks experienced the original combinations of warming (+~1°C at the plot level via ceramic infrared heaters), CO₂, nitrate, and precipitation treatments. For analyses that included fire, we designated new experimental blocks based on hillslope position, proximity of plots to one another, and preexisting vegetation patterns. The 2003–2004 growing season was moderately dry, with an unusually dry spring. Thus, the precipitation treatment was relatively modest, and was concentrated during the winter.

Before the start of the 2003–2004 growing season, we added 10 *Centaurea* seeds to each of two circular exclosures (4.5 cm diameter) in each of the JRGCE's 128 quadrants (see Plate 1). Exclosures were placed near each other on small patches of soil (~144 cm²) that had been cleared of plant material and litter in May 2003. The exclosures, which consisted of clear plastic cylinders about 3 cm tall topped with white tulle netting to facilitate light penetration and airflow, protected seedlings of all species from herbivory by gastropods until February 2004, when the netting was removed.

A separate (unpublished) study outside the experimental plots confirmed that exclosures were necessary; by March of 2004, all *Centaurea* seedlings left unprotected (five locations) or surrounded by cylinders without netting (five locations) had been consumed or killed, while seedlings in exclosures survived. The cylinders were not always effective; herbivores completely consumed seedlings in one of the five control exclosures of the herbivory study, and in several cases exclosures in the main experimental area did not prevent the complete loss of seedlings. Nonetheless, *Centaurea* plants were present and even dominant in some areas within 100 m of the experiment, suggesting local patchiness in herbivore densities.

Where necessary in the experimental quadrants, we thinned *Centaurea* seedlings to four per exclosure in late January and early February and to a single plant per exclosure from late February through March. Other species were not disturbed.

We measured establishment by adding the numbers of thinned and harvested *Centaurea* plants in each quadrant. We used three measures to assess *Centaurea* growth in each quadrant: the average aboveground biomass of harvested plants, the maximum height of the harvested plants, and the maximum stem diameter of the harvested plants. *Centaurea* heights were measured on three dates during the growing season. On 15 May 2004, we measured stem diameters and cut all *Centaurea*

plants at the soil surface (see Plate 1). Tissue was oven dried (70°C) before weighing. Stem diameter is closely related to aboveground biomass but avoids some problems introduced to the other measurements by patchy deer herbivory shortly before the harvest date. In four quadrants where individual plants had been subjected to recent deer herbivory, biomass data were omitted from analyses. Herbivory was evident from observations and from unrealistically low measured aboveground biomass for a given stem diameter. Henry et al. (2006) reported resident species biomass responses based on the maximum biomass recorded in harvests of a 141-cm² quadrat from each plot on 20 April and 10 May 2004. Unlike the *Centaurea* enclosure areas, these harvest areas had not been cleared of litter from the previous year, except in the burned area.

We used two split-plot models (PROC MIXED; SAS Institute 1999) to test our results. Our original model included block, CO₂, warming, precipitation, and nitrate deposition, and a second model substituted fire for warming. Both models used the Satterthwaite method for determining denominator degrees of freedom. Quadrants with no surviving *Centaurea* plants were excluded from growth analyses. We transformed values as necessary to meet assumptions of the statistical analyses.

Mesocosm experiment.—In fall 2006, soil mesocosms were created by driving 50-cm sections of 19.7 cm (inner diameter) PVC pipe into grassland soil adjacent to the JRGCE (25 m from the nearest JRGCE plot), removing the pipe with an intact core of soil, and securing a cap with a drainage hole on the bottom. Seeds in the topsoil were eliminated by removing the top 3 cm of soil from the cores, spreading the topsoil on a concrete surface, and keeping the soil moist until no new germination was observed (three weeks). The soil was then turned over and allowed to dry out. After the topsoil was pre-germinated it was mixed and added to each mesocosm by hand, together with 24 seeds per mesocosm of *Centaurea solstitialis*, 120 seeds per mesocosm of *Avena barbata*, or both. Soil was then tamped with a wooden block. Seed numbers were based on typical field densities. Pots were watered by natural inputs of rain, beginning in October, and the experiment ran until the dominant plants reached maturity the following May, when all plants were harvested by cutting at the soil surface. Non-planted species that germinated were removed by hand. Three replicate mesocosms of each planting combination were created for each of eight treatments, featuring all combinations of ambient and elevated atmospheric CO₂ (700 ppm applied to groups of mesocosms via a free-air CO₂ enrichment-type infrastructure surrounded by partial chambers to stabilize concentrations), nitrate deposition (+6 g/m² as CaNO₃), and phosphate fertilization (+5.25 g/m² as superphosphate). We distributed mesocosms among 12 platforms that supported the CO₂ infrastructure for this and other experiments. Platforms measured 1.25 m on a

side and 0.5 m high, with pots resting on the platforms so that each pot could drain to its individual collection bottle on the ground. Each platform supported 20 pots from several simultaneous experiments, and was enclosed by an open-topped polyethylene chamber. Platforms were arranged in a 3 × 4 array, and the CO₂ treatment was applied in a checkerboard fashion, during the daytime only. Blocks consisted of rows of four platforms, such that two platforms within each block received elevated CO₂ and the other two did not. For each planting combination, each block contained one replicate of each of the eight treatments. Within any block, the four elevated CO₂ mesocosms for each planting combination were randomly assigned to two different platforms, as were the four ambient CO₂ mesocosms. We used a mixed model analysis (PROC MIXED; SAS Institute 1999) to separately test for treatment effects on *Avena* and *Centaurea*. The model includes CO₂, nitrate deposition, phosphorus availability, and competition, and uses the Satterthwaite method for determining denominator degrees of freedom, with random terms for block and platform effects.

RESULTS

Field experiment

We examined impacts of the environmental changes on *Centaurea* establishment, growth (measured as aboveground biomass, stem diameter, and height), leaf nitrogen, and shoot architecture. Burning doubled *Centaurea* establishment (+205%; $P = 0.0008$; Appendix A), and supplemental precipitation reduced establishment (−23%; $P = 0.04$). Establishment responded to nitrate deposition in a complex manner; nitrate reduced *Centaurea* establishment in ambient-temperature plots, but increased establishment in warmed plots. Under elevated CO₂, nitrate deposition decreased establishment in unburned plots, but increased establishment in burned plots (Appendices A, B).

Across all treatments, elevated CO₂ increased *Centaurea*'s aboveground biomass more than sixfold (Fig. 1a, b; Appendix B). In unheated quadrants, CO₂ increased shoot biomass more than sevenfold (755%; $P = 0.0054$), height by 171% ($P = 0.0102$), and stem diameter by 82% ($P = 0.0036$). In unburned quadrants, CO₂ caused marginally significant increases in shoot biomass (651%; $P = 0.0805$), height (104%; $P = 0.0965$), and stem diameter (76%; $P = 0.0732$). On average, CO₂ increased *Centaurea* growth in all twelve of the background treatments (Fig. 1a), and interactions between CO₂ and other factors were not significant in either analysis. *Centaurea* biomass varied widely under elevated CO₂: the largest plants grew much larger, but some plants in most background treatments remained relatively small, leading to the marginally significant results in unburned plots.

Nitrate deposition strongly increased *Centaurea* growth in analyses that did not include the burned plots (aboveground biomass, +327%, $P = 0.0050$; stem

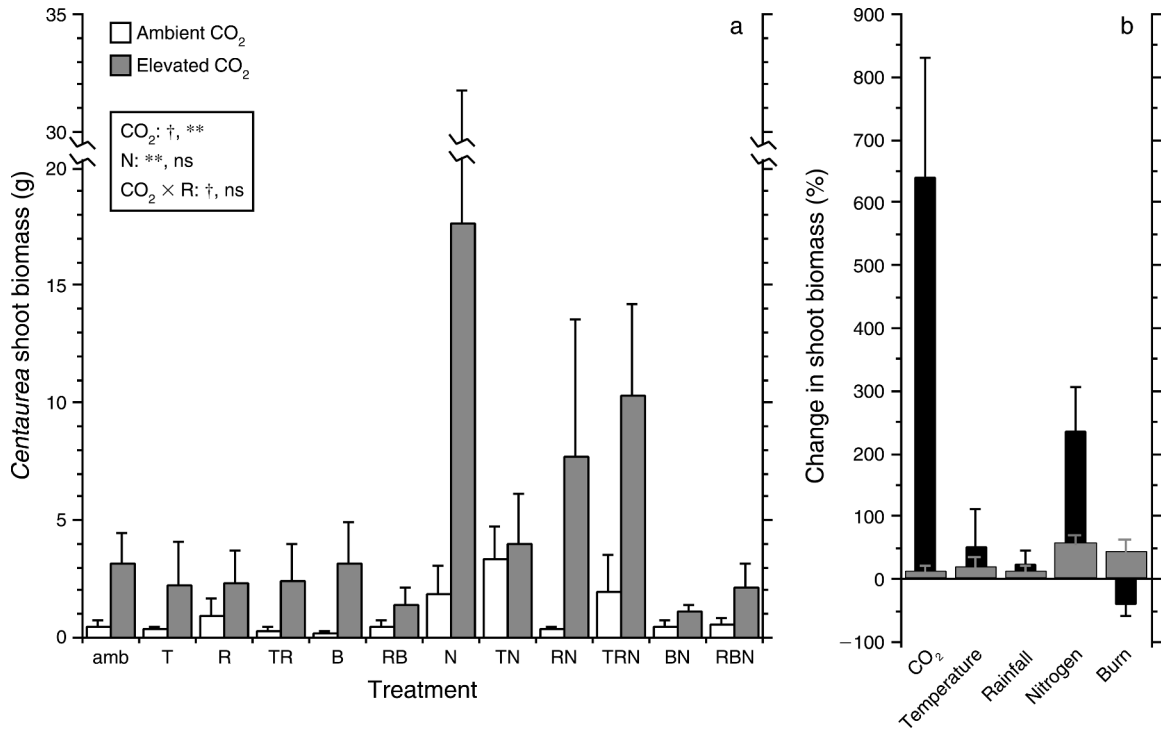


FIG. 1. Biomass responses of *Centaurea solstitialis* and the resident grassland community to environmental change treatments. (a) Mean (\pm SE) *Centaurea* shoot biomass by treatment. Key to treatments: amb, ambient; T, increased temperature; R, increased rainfall; N, nitrate deposition; B, burn. The inset box identifies significant and marginally significant treatment effects in analyses of either unburned (first symbol) or unwarmed treatments. In unburned treatments, $n = 3\text{--}6$ replicates; in burned treatments, $n = 3\text{--}4$ replicates. (b) Mean percentage response of *Centaurea* shoot biomass (narrow black columns; mean of responses across the background treatments) and aboveground biomass of resident species in earlier harvests (broad gray columns; computed from maximum biomass for each quadrant from two harvest dates, one week and four weeks before the *Centaurea* harvest) to the five experimental treatments across all treatment combinations (\pm SE of the response in individual combinations). For CO₂, rainfall, and nitrate deposition, $n = 12$ replicates. For temperature and burn responses, $n = 8$ replicates. For harvest information and greater detail on resident species responses, see Henry et al. (2006).

** $P < 0.01$; † $P < 0.10$; ns, $P > 0.1$.

diameter, +87%, $P < 0.0001$; height, +71%, $P = 0.0028$; Fig. 1; Appendix B). However, analyses that included the burned plots (and excluded the warmed plots) found no effect of nitrate on shoot biomass or height ($P > 0.10$; Appendix B), and only a marginally significant effect on stem diameter (+35%), suggesting the possibility of a nitrate by fire by warming interaction that we could not directly test. Burn by nitrate interactions were not significant, but a marginally significant interaction indicated stem diameters responded more to nitrate in warmed plots (+119%) than those at ambient temperature (+56%).

There was some suggestion that *Centaurea* grew less in the burned plots; stem diameters were 32% smaller ($P = 0.0423$), but shoot biomass and height were not significantly affected (Fig. 1; Appendix B). Warming and precipitation did not affect *Centaurea* shoot growth directly or through testable interactions.

Centaurea's growth responses to CO₂ and nitrate far exceeded those of the resident species (Fig. 1b). Periodic measurements of *Centaurea* leaf length and height

suggest that the response to nitrogen grew steadily over the course of the growing season, while the CO₂ response strengthened markedly in the last few weeks of the experiment (Appendix A).

Biomass responses of *Centaurea* to CO₂ did not appear to be caused by changes in shoot architecture or nutrient use efficiency; leaf:stem ratio and leaf percent N did not respond to CO₂ enrichment. Plants in burned plots had 27% lower leaf nitrogen concentrations. Leaf:stem ratios increased 106% with nitrate addition in ambient temperature plots, but decreased by 47% with nitrate addition in heated plots (Appendix B).

We explored whether differences in resident species composition among treatments might explain *Centaurea*'s strong responses to CO₂ and nitrate by estimating cover of all species in 8.9 cm diameter circles centered on the circles in which *Centaurea* was planted. Twelve species occurred in at least 12 quadrants across the experiment. *Centaurea* biomass in the circles was weakly positively correlated with relative cover (excluding *Centaurea*) of two of these species, but these species

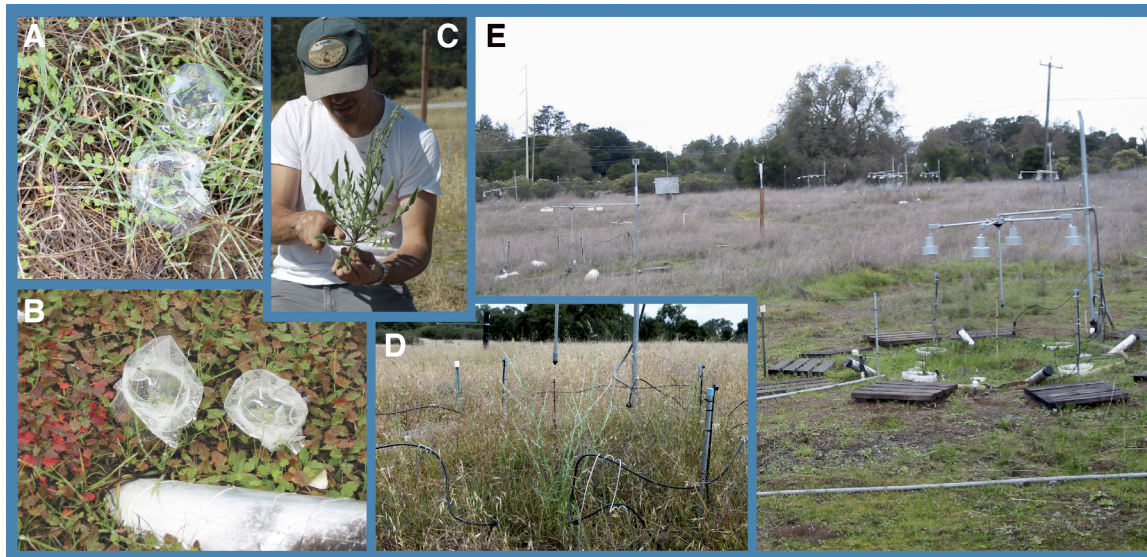


PLATE 1. Images of the field experiment. Exclosures in (A) unburned and (B) burned areas in December. (C) Harvesting *Centaurea solstitialis* and measuring stem diameters in May. (D) Elevated CO₂ plot with large *Centaurea* plants (foreground) in May. (E) Plots in the burned (right foreground) and unburned areas (background) in December. Photo credits: J. Dukes (A, B, E), N. Chiariello (C, D).

did not differ in cover with CO₂ or nitrate treatments. *Centaurea* biomass was negatively correlated with relative cover of one biennial species, *Crepis vesicaria*, and cover of *Crepis* was lower in plots receiving supplemental CO₂ ($P = 0.01$ in both tests). To examine whether this difference in *Crepis* abundance was responsible for the observed CO₂ effect, we conducted additional analyses of data from plots containing little or no *Crepis*. These analyses limited replication to the point that the results were no longer significant. However, the mean response of *Centaurea* growth to CO₂ remained virtually constant as analyses were restricted to plots containing less and less *Crepis* (Appendix A), suggesting that the effect of CO₂ on *Centaurea* biomass was not strongly influenced by differences in *Crepis* abundance among the plots.

Mesocosm experiment

In the outdoor mesocosms, supplemental CO₂ increased aboveground biomass of *Centaurea* (by 24%, $P < 0.01$; Appendix B), whether the species was grown alone or with *Avena*. Enhanced nitrate deposition had a small positive effect on *Centaurea* shoot growth, but only when the species was grown in monoculture (N × competition effect; $P < 0.01$). Competition with *Avena* strongly decreased shoot growth of *Centaurea* (by 84%; $P < 0.0001$).

Competition had a smaller effect on *Avena*; *Centaurea* did not affect *Avena* shoot growth under ambient CO₂ (Tukey-Kramer $P = 0.94$), but suppressed it under elevated CO₂ (by 33%; Tukey-Kramer $P = 0.04$; CO₂ × competition effect, $P = 0.02$). *Centaurea* also tended to suppress *Avena* growth under ambient nitrate deposition

(−27%), but not in mesocosms receiving additional nitrate (+1%). In general, supplemental nitrate increased shoot growth of *Avena*, and this stimulation thus tended to be strongest when *Avena* grew in mesocosms with *Centaurea* (average N effect, +68%, $P < 0.0001$; N × competition effect, $P = 0.0789$; N effect in monoculture, +45%; N effect in mixture, +102%). Phosphate addition had a small (+13%), marginally significant ($P = 0.0532$) effect on *Avena* shoot growth.

DISCUSSION

When grown in competition with other species, *Centaurea* benefited from CO₂ and nitrate deposition in both the mesocosm and field experiments. On a percentage basis, *Centaurea*'s CO₂ response in the field experiment exceeds those observed in other plant species in most (if not all) other field experiments to date. Data from the mesocosm experiment suggest that CO₂ can enhance the competitive effect of *Centaurea* on other species. Why might *Centaurea* have benefited so strongly from elevated CO₂, when the other grassland species did not?

Previous research in microcosms of a different grassland type suggests that *Centaurea* may benefit from elevated CO₂ through at least two mechanisms: increased photosynthetic rates and increased soil moisture availability (Dukes 2002a). Here, the lack of response of *Centaurea* and resident species to increased precipitation rules out soil moisture changes as a major contributor to the CO₂ response. *Centaurea*'s CO₂ response in our field experiment far exceeds responses observed in studies where *Centaurea* was grown without competition (monocultures in this study; Dukes 2002a,

Ziska 2003), or in single-year competition experiments with limited soil volumes (mixed culture mesocosms in this study and Dukes [2002a]). This suggests at least two factors may have contributed to *Centaurea*'s strong CO₂ response in the field: longer-term changes in the competitive environment and the unconstrained nature of the field setting.

Centaurea responded strongly to elevated CO₂ in the mesocosms, with greater shoot growth and enhanced impacts on *Avena*. However, these responses were much smaller than those we observed in the field, and we believe the mesocosms themselves probably constrained the magnitude of the response. The smaller soil volume available in mesocosms undoubtedly limited access of the deep-rooted *Centaurea* (Roché et al. 1994) to soil resources critical for growth (cf. Morghan and Rice 2006), and may thus have limited its CO₂ response in mixed culture; resource partitioning between *Centaurea* and annual grasses is constrained when rooting depth is limited (Sheley and Larson 1994, 1995). In the mesocosms that experienced ambient conditions, *Avena* and *Centaurea* appeared to partition resources less effectively than in an earlier competition study that took place in a wetter year and used larger pots (relative yield total [RYT] of 0.8 in this experiment, vs. ~1.3 in earlier study; RYT > 1 suggests resource partitioning [Dukes 2002b]). Thus, by allowing roots access to a greater soil volume, the field experiment would have allowed *Centaurea* to more effectively access resources that were inaccessible to its competitors, and this access may have been more beneficial or more pronounced under elevated CO₂. That is, elevated CO₂ may have allowed *Centaurea* in the field to access resources it could not otherwise have reached, and these extra resources may have allowed *Centaurea* to more fully express an inherently strong growth response to CO₂, in a positive feedback loop. Morgan et al. (2007) suggested a similar mechanism could have contributed to the strong response of the native sub-shrub *Artemisia frigida* to elevated CO₂ in North American shortgrass steppe.

We did not allow *Centaurea* to reach reproductive maturity in either experiment. However, reproductive biomass is tightly coupled to shoot biomass in this annual species (Dukes 2002b). Thus, the shoot biomass responses reported here reliably indicate *Centaurea*'s potential to maintain or increase population sizes.

The strong CO₂ and N responses we observed in the field were from a single year of study in which spring rainfall (on which *Centaurea* depends; Dukes 2001, Morghan and Rice 2006) was unusually low. Climatic variation and differences in herbivore population sizes may alter the strength of these responses by region and by year. However, the CO₂ and N responses were consistent across several climate-related background treatments, suggesting at least some robustness of the results across different climates or years. These responses were also supported by parallel (if muted) responses in the mesocosms in a separate year.

Although *Centaurea* growth in the field responded strongly to both CO₂ and N, it did not respond to warming or increased precipitation. We suggest two reasons for this insensitivity: the ideal climate of this location for *Centaurea*, and the relative subtlety of the treatments in this year. Jasper Ridge is near the center of *Centaurea*'s latitudinal distribution in North America, suggesting that the species can tolerate a fairly wide range of variation around the average climate at the site. Bioclimatic envelope models suggest that, even under a changing climate, the location will remain well suited for *Centaurea* (Bradley et al. 2009). Nonetheless, based on previous observations (e.g., Dukes 2001, Morghan and Rice 2006), we had expected supplemental precipitation to increase shoot growth. The dry spring meant that the precipitation treatment received less watering than usual; increasing precipitation by 50% did make soils wetter in the spring (Henry et al. 2006), but the difference would have been greater in a somewhat wetter year. The relatively small increases in soil moisture and canopy temperature caused by the JRGCE manipulations, combined with the likely insensitivity of *Centaurea* to moderate climatic deviations in this region of North America, would have limited the potential for responses of shoot growth to climate.

Grasslands are patchy on small scales, with physical disturbances such as those created by gophers often occupying a substantial fraction of the land. The high variability in growth of *Centaurea* plants under elevated CO₂ within many of the background treatments suggests that the species may respond most strongly in certain microsites within the grassland, such as those with little competition or those in which roots can grow rapidly, and may not respond in other, possibly more resource-limited microsites. Small-scale variation in herbivore populations may also strongly influence patterns of *Centaurea* abundance. In our study area, herbivore pressure evidently played a strong role in excluding *Centaurea*, and we depended on exclosures to protect the plants for much of the growing season. Neighboring areas of the grassland have large *Centaurea* populations, perhaps due to lower herbivory. In the context of this patchy environment, strong responses of *Centaurea* to CO₂, even on a subset of microsites, could lead to large increases in population sizes over time.

Centaurea establishment doubled in the post-fire treatment, where the litter layer had burned away, possibly as a consequence of increased light availability or a warmer microclimate. Shading by litter affects establishment success of many species in this grassland (Amatangelo et al. 2008). Similarly, increased precipitation may have reduced establishment as a result of (unmeasured) increases in shading by litter in this treatment. On average, increased precipitation increases grassland shoot biomass, which would typically result in more litter in the subsequent year. However, no significant increase in grassland shoot biomass was

detected in the year before this experiment (Dukes et al. 2005).

The response of *Centaurea* establishment to nitrate deposition depended on the warming, CO₂, and fire treatments. We speculate that competitive interactions between *Centaurea* and grass seedlings may have driven this complex pattern of responses. Nitrate suppressed establishment of *Centaurea* seedlings in unwarmed plots, but aided establishment in the heated treatment. Under elevated CO₂, nitrate deposition suppressed establishment in unburned plots, but boosted establishment in burned plots (Appendix A). In the case of both interactions, nitrogen may have favored fast-growing grasses in the cooler plots (unburned plots are more shaded), while increasing *Centaurea* growth rates under warmer conditions, such as in the burned area. These results suggest that the effect of nitrate on *Centaurea* establishment could be highly microsite dependent.

CONCLUSIONS

Given these results, we add *Centaurea* to a short but growing list of noxious (Mohan et al. 2006) and invasive (Smith et al. 2000, Belote et al. 2003, Hättenschwiler and Körner 2003) plants demonstrated to dramatically benefit from CO₂ in community settings, and to the longer list of invasives that benefit from increased N availability (Dukes and Mooney 1999, Scherer-Lorenzen et al. 2007, Blumenthal et al. 2009, Gonzalez et al. 2010). Atmospheric CO₂ concentrations are increasing by ~2 ppm/yr around the globe (Canadell et al. 2007). Nitrogen deposition rates vary spatially, but are already higher than our treatment levels at one sampling station in California (Fenn et al. 2003), and are expected to increase globally. Unless biocontrol agents become more effective at controlling *Centaurea* (Gutierrez et al. 2005), the weed's response to environmental changes is likely to heighten the challenge facing many North American land managers over the course of this century.

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APPENDIX A

Figures showing responses of *Centaurea solstitialis* establishment and height to environmental change treatments, and showing the effect of *Crepis vesicaria* abundance on CO₂ responses of *Centaurea* (*Ecological Archives* A021-085-A1).

APPENDIX B

Tables showing *P* values from mixed-model analyses of treatment effects on *Centaurea* in the field experiment, and of treatment effects on *Centaurea* and *Avena* shoot biomass in the mesocosm experiment (*Ecological Archives* A021-085-A2).