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R. B. Jackson · O. E. Sala · C. B. Field · H. A. Mooney

CO_2 alters water use, carbon gain, and yield for the dominant species in a natural grassland

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Abstract Global atmospheric CO_2 is increasing at a rate of 1.5–2 ppm per year and is predicted to double by the end of the next century. Understanding how terrestrial ecosystems will respond in this changing environment is an important goal of current research. Here we present results from a field study of elevated CO_2 in a California annual grassland. Elevated CO_2 led to lower leaf-level stomatal conductance and transpiration (approximately 50%) and higher mid-day leaf water potentials (30–35%) in the most abundant species of the grassland, *Avena barbata* Brot. Higher CO_2 concentrations also resulted in greater midday photosynthetic rates (70% on average). The effects of CO_2 on stomatal conductance and leaf water potential decreased towards the end of the growing season, when *Avena* began to show signs of senescence. Water-use efficiency was approximately doubled in elevated CO_2, as estimated by instantaneous gas-exchange measurements and seasonal carbon isotope discrimination. Increases in CO_2 and photosynthesis resulted in more seeds per plant (30%) and taller and heavier plants (27% and 41%, respectively). Elevated CO_2 also reduced seed N concentrations (9%).

Key words Annual grassland · *Avena barbata* CO_2 · Reproduction · Water relations

R. B. Jackson (✉) · O. E. Sala · H. A. Mooney
Department of Biological Sciences,
Stanford University,
Stanford, CA 94305 USA

O. E. Sala
Department of Ecology, Faculty of Agronomy,
University of Buenos Aires, Av San Martín 4453,
Buenos Aires, Argentina

C. B. Field
Carnegie Institution of Washington, 290 Panama Street,
Stanford, CA 94305, USA

Introduction

The concentration of CO_2 in the atmosphere has increased 30% since the beginning of the industrial revolution and is predicted to double by the end of the next century (Keeling 1986; Schlesinger 1991). Such concentrations of atmospheric CO_2 are unprecedented over the last 160,000 years (Barnola et al. 1987), and probably over the last 10 million (Gammon et al. 1985; Van Der Burgh 1993). A major goal of current research is to understand how terrestrial ecosystems will respond in this changing environment (Tissue and Oechel 1987; Curtis et al. 1989; Bazzaz 1990).

For the few natural ecosystems where *in situ* responses to CO_2 have been examined, the results have been somewhat contradictory (Dahlman 1993). *Scirpus olneyi* growing in an estuarine marsh showed increased primary productivity and no evidence of photosynthetic downregulation after four years of field exposure to high CO_2 (Curtis et al. 1989; Arp and Drake 1991). In contrast, the tundra tussock grass *Eriophorum vaginatum* showed little growth response to elevated CO_2, and it downregulated photosynthesis to pre-treatment rates after only 3 weeks of exposure (Tissue and Oechel 1987). Plant productivity in these ecosystems is not generally limited by water availability, yet the interaction between plant growth and water use is fundamental to understanding the response of biological systems to increased atmospheric CO_2 (Morison 1993).

In this paper we present results from a high-CO_2 experiment in a California annual grassland, an ecosystem limited in part by water availability. Annual grasslands are uniquely suited to CO_2 research, since the low year-to-year buffering of carbon allows changes to be detected rapidly, and high plant densities allow tractable, well-replicated experiments. We monitored the most common species of the grassland, *Avena barbata* Brot., which makes up 30% of the community by number and an even greater proportion by biomass. The variables measured included stomatal conductance, transpiration, photosynthesis, leaf water potential, plant size, density, and the number and quality of seeds produced.

Materials and methods

The study site was an annual sandstone grassland at the Jasper Ridge Biological Preserve (37°24′ N, 122°13′ W) near Stanford University (McNaughton 1968). The species composition is typical of grasslands in cis-montane California, consisting almost entirely of Eurasian annuals, including *Avena*, *Bromus*, and *Lolium* spp. (Gulmon 1979). The climate at the site is characterized by cool, wet winters and warm, dry summers (Mooney et al. 1986). The elevation is 200 m and the average annual precipitation from 1975 to 1990 was 579 mm, though the 1992–1993 growing season was substantially wetter than average. No supplemental water or nutrients were added.

Three field treatments (ten replicates per treatment) were used to evaluate responses to elevated CO_2: no-chamber controls, open-top chambers with ambient CO_2, and open-top chambers with ambient +350 (a seasonal average of 723 μmolmol^{-1} CO_2). Each cylindrical open-top chamber was 1 m tall and 0.65 m in diameter (0.33 m^2 soil area), while no-chamber controls were a 0.65-m wide ring at the soil surface. Individual blowers forced 4500 lmin^{-1} of ambient air through each chamber (approximately ten air changes per minute), supplemented by 350 μmolmol^{-1} CO_2 in high-CO_2 chambers. The experiments were performed the second growing season of CO_2 enhancement, and chamber CO_2 was maintained throughout the year. A more comprehensive description of the methods and rationale for the experiment can be found in Field et al. (1995).

We monitored the most common species of the grassland, *Avena barbata*. Its density as estimated from ninety 10-cm diameter rings was approximately 1500 plants m^{-2} (5000 plants m^{-2} for all species); it makes up approximately 30% of community density and 40–50% of community biomass. Measurements were initiated in mid-March when the plants were of sufficient size, and continued through senescence in mid-May. Physiological measurements were taken on the most recent fully-expanded leaf of *Avena* plants selected randomly in each field plot (values for multiple leaves within a plot were averaged), and neither leaves nor plants were used more than once during the season. Stomatal conductance, transpiration, and photosynthesis were measured with a closed gas-exchange system (LI-6200, Li-Cor Inc., Lincoln, NE) at the treatment's operational CO_2 concentration. Leaf conductances and transpiration on additional days were obtained with a steady-state porometer (LI 1600, Li-Cor Inc., Lincoln, NE). Mid-day leaf water potentials were measured with a pressure chamber (Scholander et al. 1965).

Leaf material for isotopic analysis was collected on three dates (12 March, 13 April and 7 May 1993) from the most recent fully-expanded leaves of three random *Avena* plants within each plot. The leaves were oven-dried at 70° C, ground to a fine powder, and analyzed for their carbon isotope composition ($\delta^{13}C$, relative to the PDB standard) at the University of Utah's Stable Isotope Ratio Facility. Carbon isotope discrimination (Δ) was determined from the leaf carbon isotope ratio (δ_{leaf}) by

$$\Delta = \frac{(\delta_{air} - \delta_{leaf})}{(1 + \delta_{air})} \quad (1)$$

where δ_{air}=−8.0‰ for the ambient CO_2 treatments; δ_{air} in elevated CO_2 was −21.3‰, −21.0‰, and −20.7‰ as averaged through 12 March, 13 April and 7 May, respectively (the isotopic composition of high-CO_2 air was monitored twice a month during the growing season). Farquhar et al. (1989) derived the following equation for the relationship between Δ and c_i (the intercellular CO_2 concentration within the leaf) for a C_3 plant:

$$\Delta = a + (b - a)\frac{c_i}{c_a} \quad \text{or} \quad \frac{c_i}{c_a} = \frac{(\Delta - a)}{(b - a)} \quad (2)$$

where c_a is the CO_2 concentration in the atmosphere, a is the ^{13}C fractionation due to diffusion (4.4‰), and b is the net fractionation due to carboxylation (27‰).

The instantaneous water-use efficiency (A/E, or the molar ratio of photosynthesis to transpiration) is also related to c_i and c_a by

$$A/E = \frac{(c_a - c_i)}{(1.6\Delta w)} \quad (3)$$

where Δw is the leaf to air vapor concentration gradient. The ratio of water-use efficiencies for two leaves experiencing the same Δw is therefore

$$\frac{(A_1/E_1)}{(A_2/E_2)} = \frac{(c_{a1} - c_{i1})}{(c_{a2} - c_{i2})} \quad (4)$$

with the information for respective c_i and c_a values obtained from Δ and Eq. 2.

Measurements of *Avena* height, density, and seed production were taken at the end of the growing season on all *Avena* plants within three randomly located 10-cm-diameter circles in each of the thirty 0.33-m^2 plots (ten replicates per treatment). Approximately 1000 *Avena* plants were measured overall, and values within each 0.33-m^2 plot were averaged. Average shoot biomass was obtained by harvesting one 10-cm-diameter circle per plot and drying and weighing the *Avena* plants (287 plants overall); limits on destructive sampling did not allow biomass determinations from >1 circle per plot. Fruit and seed weights were obtained from four fruits per plot on 20 May 1993 (one seed per fruit in *Avena*). Each set of four seeds was subsequently dried at 75° C, ground to a fine powder, and assessed for N and C concentrations with a Carlo-Erba NA 1500 elemental analyzer.

Avena seed production, fruit and seed weights, and seed N and C concentrations were analyzed by one-way ANOVA. The number of *Avena* plants available for biomass determination was quite limited, because we were not able to harvest more than one 10-cm diameter circle per plot. However, there were no limitations on the number of non-destructive estimates of height. Therefore, in order to assess treatment effects upon plant size, we used both an integrative multivariate ANOVA of height and mass (Wilks' lambda, Johnson and Wichern 1988) and two univariate ANOVA. *Avena* density was analyzed by nonparametric Kruskal-Wallis test due to large variability within and among replicates and non-normal distribution of the data.

Results

Elevated CO_2 decreased mid-day stomatal conductance by 50% and 65% compared to *Avena* leaves in chamber and no-chamber controls (Fig. 1A), with similar reductions in transpiration (Fig. 1B). Midday leaf water potentials were up to 36% higher in elevated CO_2 until late in the growing season, when relative differences in stomatal conductance and leaf water potentials decreased (Fig. 1C).

Rates of *Avena* mid-day photosynthesis were on average 70% greater in elevated CO_2 than in chamber controls (Fig. 1D). Differences were smaller early in the growing season, when the soil was the wettest. As the season progressed and low-CO_2 plants reduced midday conductances, relative differences in photosynthesis increased and high-CO_2 leaves had rates more than double those in chamber controls (Fig. 1D). Even on the first sampling date when mid-day photosynthetic rates were similar, high-CO_2 plants had greater rates of photosynthesis later in the afternoon when stomata in all treatments began to close (data not shown).

The instantaneous water-use efficiency (WUE, molar ratio of photosynthesis to transpiration) of *Avena* plants was roughly double the WUE of control treatments on four dates of the growing season (Table 1). Overall, in-

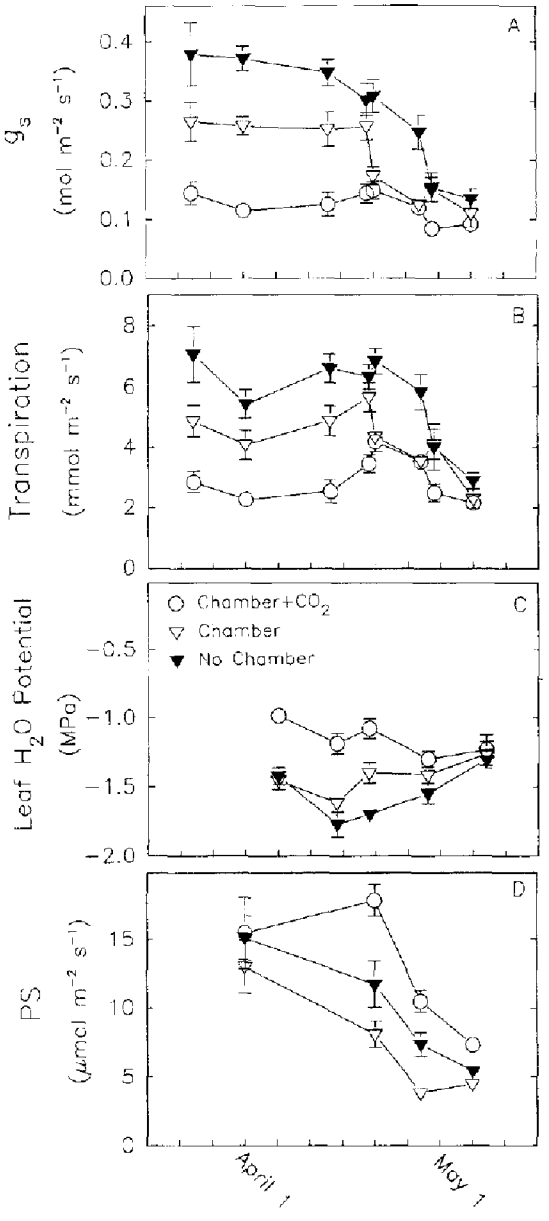

Fig. 1A Mid-day leaf stomatal conductance, **B** transpiration, **C** water potential and **D** photosynthesis for *Avena* plants in no-chamber controls (*solid triangles*), chamber controls (*open triangles*), and chamber +350 (*open circles*) (approximately 700 μmolmol^{-1} CO_2) (mean±SE, n=6–10). Physiological measurements were initiated in mid to late March, when the plants were of sufficient size, and continued through plant senescence in mid May. Measurements were taken on the most recent fully-expanded leaf of random *Avena* plants in each field plot (10 plots per treatment, multiple plants averaged for a given plot)

stantaneous WUEs in high CO_2 were 2.2 times greater than either control treatment when averaged across the season (Table 1). Carbon isotope discrimination (Δ) provides a reliable estimate of WUE that is integrated temporally over the period of leaf construction (Ehleringer 1989). Values of Δ were similar for treatments (Table 2), and correspond to c_i/c_a ratios of 0.72–0.77 (Table 2, Eq. 2). Since c_a in elevated CO_2 was approximately twice the ambient c_a, and the c_i/c_a ratios were similar for all treat-

Table 1 Average instantaneous mid-day water-use efficiency (A/E, mmol CO_2 mol^{-1} H_2O) on four dates of the 1993 growing season for *Avena* plants from no-chamber controls, chamber controls, and chamber +350 μmol CO_2. High-CO_2 plants were 2.2 times more water-use efficient than plants from both control treatments when averaged over the growing season

Treatment	Date			
	30 March	20 April	27 April	5 May
No-chamber	2.78	1.72	1.27	1.89
Chamber	3.18	1.86	1.09	1.97
Chamber+CO_2	6.79	4.26	2.97	3.40

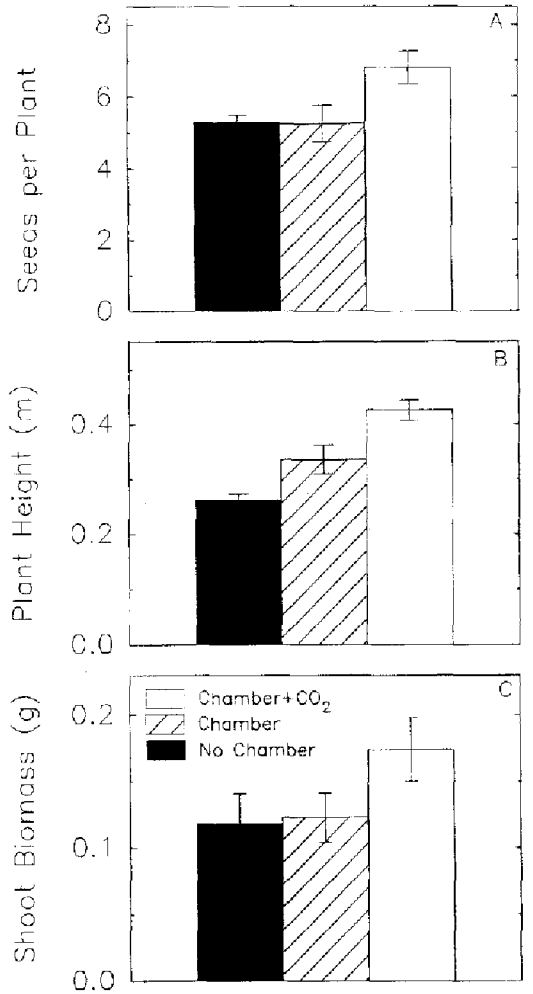

Fig. 2A The average seed number, **B** height, and **C** shoot biomass for individual *Avena* plants in no-chamber controls (*solid bars*), chamber controls (*shaded bars*), and chamber +350 (*open bars*) (approximately 700 μmolmol^{-1} CO_2) (mean±SE, n=10 for each bar). Measurements of height and seed numbers were taken at the end of the growing season on all *Avena* plants within three random 10-cm-diameter circles in each of the thirty 0.33-m^2 plots (ten replicates per treatment). Approximately 1000 individuals were measured overall, but values within each 0.33-m^2 plot were averaged. Average shoot biomass was obtained by harvesting one 10-cm wide ring per plot and drying and weighing the *Avena* plants (287 plants total); limits on destructive sampling did not allow biomass sampling from >1 ring

Table 2 Leaf carbon isotope composition ($^{13}\delta C$), discrimination (Δ), the ratio of intercellular to atmospheric CO_2 concentrations (c_i/c_a), and relative water use efficiency on three dates of the 1993 growing season for *Avena* plants from no-chamber controls, chamber controls, and chamber +350 μmol CO_2 (mean±SE, n=5 for all values). The carbon isotope composition of the air (δ_{air}) was −8.0‰ for the ambient CO_2 treatments; δ_{air} in elevated CO_2 was −21.3‰, −21.0‰, and −20.7‰ as averaged through 12 March, 13 April and 7 May, respectively (the isotopic composition of high-CO_2 air was monitored twice a month during the growing season). See Eq. 1 in the Methods for the definition of Δ

	Treatment	Date		
		12 March	13 April	7 May
δ_{leaf}	No-chamber	−28.5±0.18	−28.5±0.20	−28.7±0.13
	Chamber	−28.6±0.24	−28.9±0.12	−28.6± 0.41
	Chamber+CO_2	−42.2±0.80	−42.4±0.30	−42.1±0.45
Δ	No-chamber	20.6±0.18	20.6±0.20	20.9±0.13
	Chamber	20.8± 0.24	21.1±0.12	20.8±0.42
	Chamber+CO_2	21.3±0.81	21.8±0.31	21.7±0.46
c_i/c_a	No-chamber	0.72	0.72	0.73
	Chamber	0.72	0.74	0.73
	Chamber+CO_2	0.75	0.77	0.77
Relative WUE	No-chamber	1.0	1.1	1.0
	Chamber	1	1	1
	Chamber+CO_2	1.8	1.8	1.7

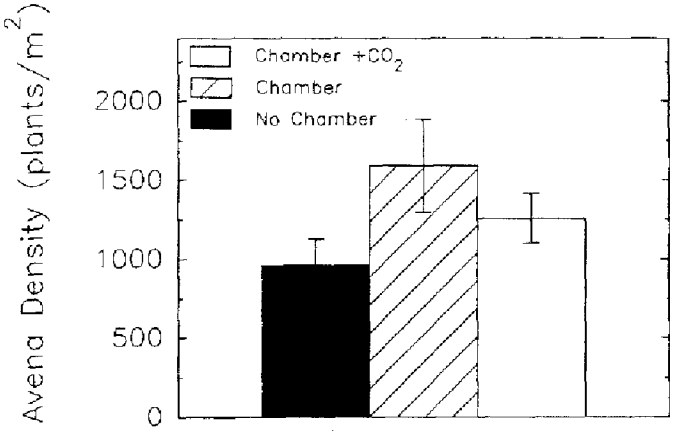

Fig. 3 Average density of *Avena* plants in no-chamber controls (*solid bars*), chamber controls (*shaded bars*), and chamber +350 (*open bars*) (mean±SE, n=10 for each bar). Density was measured in three random 10-cm-diameter circles in each of the thirty 0.33-m^2 plots (ten replicates per treatment), and the three estimates per plot were averaged to avoid pseudoreplication. Plant density varied substantially within and among plots, and was not significantly different among treatments (P>0.15 by Kruskal-Wallis test of the three treatments)

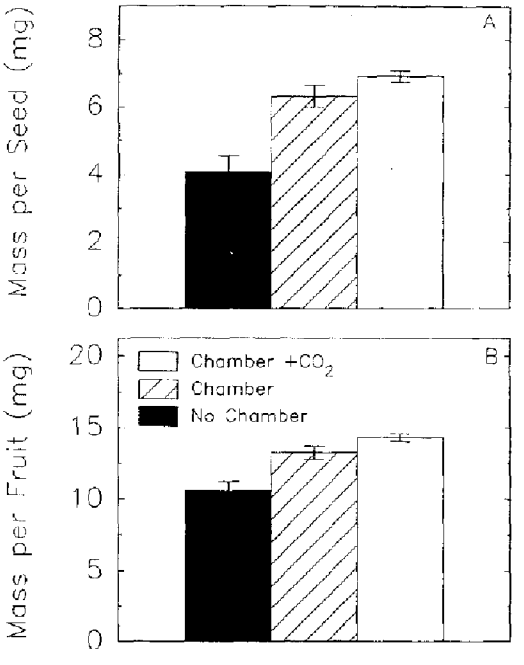

Fig. 4 **A** Average mass per seed and **B** mass per fruit for *Avena* plants from no-chamber controls (*solid bars*), chamber controls (*shaded bars*), and chamber +350 (*open bars*) (mean±SE, n=10 for each bar). Four seeds/fruits were randomly selected from each plot, dried at 75° C, and weighed. Elevated CO_2 increased seed and fruit weights by 9% relative to chamber controls, but differences were not significant (P>0.14 for both). Average seed and fruit mass in the no-chamber treatment were significantly smaller than in either chamber treatment (P<0.01)

ments (Table 2, Eq. 2), the drawdown of CO_2 within the leaf (c_i−c_a) was approximately twice as large in elevated CO_2 as in ambient CO_2. By Eq. 4, we conclude that the integrated WUE was almost twice as great in elevated CO_2 as in ambient CO_2 (Table 2). The seasonal estimate of WUE from carbon isotope discrimination was 1.8, in close agreement with our estimate of 2.2 from gas exchange measurements.

To be important in an evolutionary context to plants, physiological changes must ultimately lead to changes in plant fitness. *Avena* plants in the high-CO_2 treatment produced 1.5–1.6 times more seeds on average than in either of the ambient-CO_2 treatments (Fig. 2A, P=0.02), an increase of approximately 30%. High-CO_2 *Avena* plants also were significantly larger than ambient-CO_2 plants (Fig. 2B and 2C, P<0.0005 by multivariate ANOVA, P<0.001 and P=0.17 individually for univariate ANOVAs of height and biomass). High-CO_2 plants were 27% taller and 41% heavier on average than plants from

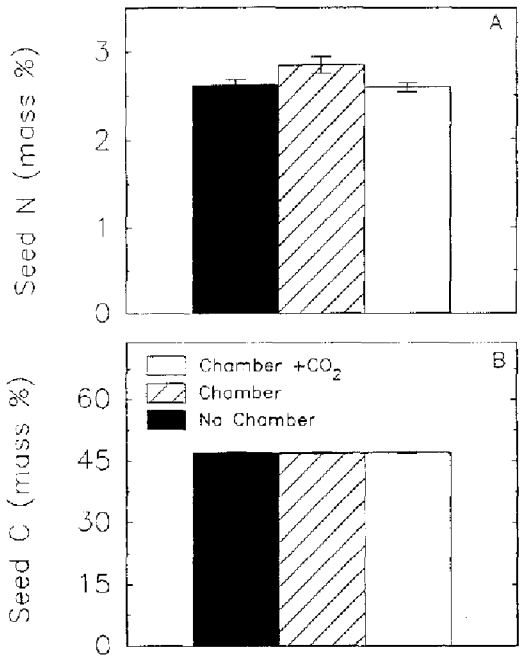

Fig. 5 **A** Seed nitrogen and **B** carbon concentrations for *Avena* plants from no-chamber controls (*solid bars*), chamber controls (*shaded bars*), and chamber +350 (*open bars*) (mean±SE, n=10 for the chamber treatments, n=7 for the no-chamber treatment). The N concentration of seeds was 2.84% in chamber controls but only 2.59% in elevated CO_2, a significant reduction of 9% (P=0.04). The carbon concentration of seeds was unchanged by CO_2 (P=0.72, 47% C for all treatments)

chamber controls, and 63% taller and 48% heavier than plants from no-chamber controls. *Avena* density was 21% lower in chamber controls than in elevated CO_2 (Fig. 3), but estimates varied substantially within and among replicates and were not significantly different (P=0.54 for the two chamber treatments, P=0.19 for the three treatments). This interaction between plant size and density is potentially quite important, since there was no evidence for an increase in biomass at the ecosystem level (Field et al., in preparation).

Avena seeds from elevated CO_2 were 9% heavier on average than in chamber controls (Fig. 4A), but the means were not significantly different (P=0.14). Average seed and fruit mass in the no-chamber treatment were significantly smaller than in either chamber treatment (Fig. 4, P<0.01). The N concentration of seeds was 2.84% in chamber controls but only 2.59% in elevated CO_2 (Fig. 5A), a significant reduction of 9% (P=0.04). The carbon concentration of seeds was unchanged by CO_2 (Fig. 5B, P=0.72, 47% C for all treatments).

Discussion

Water-use efficiency (mmol CO_2 mol^{-1} H_2O) of *Avena* plants was approximately doubled in elevated CO_2, as estimated from gas-exchange measurements and carbon isotope discrimination. Leaf c_i/c_a ratios were maintained at 0.72–0.77 in ambient and elevated CO_2 treatments, with slightly higher values in elevated CO_2. The tendency to maintain similar c_i/c_a ratios with increasing atmospheric CO_2 results in decreased stomatal conductance and transpiration on a leaf-area basis (Long and Hutchin 1991). Morison (1993) discusses a few cases where large increases in flux-based WUE (as defined above) may not result in the same increase in yield-based WUE (defined as total dry matter produced/total evapotranspiration). A system where H_2O availability was not limiting to plants, or that had multiple interacting stresses (Chapin et al. 1987), might be expected to show smaller increases in yield-based WUE than would be predicted solely from leaf-level fluxes. In addition, the dynamics of stomatal conductance only partially account for the dynamics of canopy water loss (Jarvis and McNaughton 1986).

One of the primary responses of plants to elevated CO_2 is to reduce stomatal conductance and transpiration (Smith et al. 1987; Garbutt et al. 1990; Radoglou et al. 1992; Morison 1993). CO_2 may also increase plant biomass and leaf area in many cases. If leaf area increases proportionally more than stomata close, plants may use water more quickly in elevated CO_2, despite greater water-use efficiency. For our system, stomatal conductance and transpiration in high CO_2 were reduced approximately 50% compared to chamber controls (Fig. 1A, B). We found evidence suggesting an increase in average individual plant size (30–40%, Fig. 2) and a possible decrease in *Avena* density (20%, Fig. 3). The net result was a 34% increase in soil moisture by the end of the growing season (Fredeen et al., in prep.). This increase in soil water could have resulted in a longer growing season, but this appeared not to be the case. There were no apparent differences in *Avena* leaf senescence (the proportion of brown-to-total leaf length) in early May (P>0.50, average leaf senescence 79%).

A number of other studies have examined physical and physiological responses of plants to elevated CO_2 (e.g., Williams et al. 1988; Larigauderie et al. 1988; Bazzaz and Miao 1993). Most have found a decrease in stomatal conductance with increased CO_2 (Morison 1993). Decreased stomatal conductance frequently results in lower transpiration and higher leaf water potentials (e.g., Garbutt et al. 1990; Tyree and Alexander 1993), as reported here. There is much more variability across systems in photosynthetic responses (Tissue and Oechel 1987; Arp and Drake 1991). Furthermore, growth and reproduction are more variable still, as a result of the increasing number of factors and complexity of interactions affecting these processes (e.g., Rogers et al. 1983; Williams et al. 1988; Woodward et al. 1991). Here we present results from a natural system which is decidedly water-limited, and showed decreases in stomatal conductance and transpiration and increases in photosynthesis and water use efficiency. These physiological changes in elevated CO_2 were translated to changes in plant size and reproduction.

Predicting the consequences of global change on terrestrial ecosystems presents a tremendous challenge, es-

pecially since experiments with artificial and natural systems have yielded a broad range of responses (Tissue and Oechel 1987; Curtis et al. 1989; Idso et al. 1991; Norby et al. 1992; Körner and Arnone 1992). Our current CO_2 study links changes in water use and carbon gain at the leaf level to increased size and reproduction in a California annual grassland. Such changes have the potential to alter species composition and equilibrium plant density. The impact of these changes at the ecosystem level will depend on the complex interactions of different biological and climatic processes.

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