CO₂ alters water use, carbon gain, and yield for the dominant species in a natural grassland

Abstract: Global atmospheric CO₂ 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 CO₂ in a California annual grassland. Elevated CO₂ 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 CO₂ concentrations also resulted in greater midday photosynthetic rates (70% on average). The effects of CO₂ 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 CO₂, as estimated by instantaneous gas-exchange measurements and seasonal carbon isotope discrimination. Increases in CO₂ and photosynthesis resulted in more seeds per plant (30%) and taller and heavier plants (27% and 41%, respectively). Elevated CO₂ also reduced seed N concentrations (9%).

Key words: Annual grassland · *Avena barbata* · CO₂ · Reproduction · Water relations

Introduction

The concentration of CO₂ 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 CO₂ 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 CO₂ have been examined, the results have been somewhat contradictory (Dahman 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 CO₂ (Curtis et al. 1989; Arp and Drake 1991). In contrast, the tundra tussock grass *Eriophorum vaginatum* showed little growth response to elevated CO₂, 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 CO₂ (Morison 1993).

In this paper we present results from a high-CO₂ experiment in a California annual grassland, an ecosystem limited in part by water availability. Annual grasslands are uniquely suited to CO₂ 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 (37º29'N, 122º13'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. 1985). 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 µmol mol$^{-1}$ 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 l min$^{-1}$ of ambient air through each chamber (approximately ten air changes per minute), supplemented by 350 µmol mol$^{-1}$ 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. (1997).

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). Midday 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 (δ$^{13}$C, relative to the PDB standard) at the University of Utah's Stable Isotope Ratio Facility. Carbon isotope discrimination (A) was determined from the leaf carbon isotope ratio (δ$_{leaf}$) by:

$$A = \frac{(\delta_{leaf} - \delta_{atm})}{(1 + \delta_{atm})} \quad (1)$$

where δ$_{atm}$= -8.0% for the ambient CO$_2$ treatments; δ$_{leaf}$ 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 A and δ$_{atm}$ (the intercellular CO$_2$ concentration within the leaf) for a C$_3$ plant:

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

where $c_a$ is the CO$_2$ concentration in the atmosphere, a is the δ$^{13}$C fractionation due to diffusion (4.4%), and b is the net fractionation due to carboxylation (27%).

The instantaneous water-use efficiency (WUE, molar ratio of photosynthesis to transpiration) was related to $c_i$ and $c_a$ by:

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

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

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

with the information for respective $c_i$ and $c_a$ values obtained from A 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$^2$ 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.

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 midday 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 for four dates of the growing season (Table 1). Overall, in-