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Photosynthesis, growth and density for the dominant species in a CO_2-enriched grassland

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Abstract. Although increased atmospheric CO_2 frequently increases short-term photosynthetic rates, longer-term photosynthetic responses are more variable. Plant size, reproduction and ecosystem carbon gain are determined, in part, by such photosynthetic responses. Here we examine photosynthetic regulation for the dominant species in a grassland exposed to elevated CO_2 and examine whether the observed photosynthetic responses contribute to changes in growth, reproduction and plant density in the same grassland. *Avena barbata* in the field showed little evidence of photosynthetic downregulation with elevated CO_2 at the end of the growing season (differences between treatments $< 10\%$). Glasshouse studies also showed little evidence for downregulation of photosynthesis measured at various light and intercellular CO_2. concentrations. Although specific leaf mass (leaf mass per unit leaf area) for *Avena* increased 20% in the field with elevated CO_2, leaf nitrogen concentrations decreased 25%, resulting in an 11% reduction in leaf N on a leaf-area basis. For the relatively wet 1993 growing season, *Avena barbata* increased its size and reproduction approximately 30% in elevated CO_2, with a 21% decrease in population density. For the relatively dry 1994 season *Avena* density was almost doubled in elevated CO_2, but increases in individual size and reproduction with CO_2 were small (6–18%). The primary effect of CO_2 in the drier year appears to have been greater *Avena* survival, rather than increased individual size.

Key words. Annual grassland, elevated CO_2, leaf nitrogen, photosynthesis, *Avena* reproduction.

INTRODUCTION

Short-term exposure of C_3 plants to elevated CO_2 generally leads to increased rates of leaf-level photosynthesis (Morison, 1990; Mooney *et al.*, 1991). Photosynthetic responses are less consistent when the exposure to CO_2 is longer (months to years), either maintaining the full degree of increased photosynthesis (Arp & Drake, 1991; Körner & Diemer, 1994) or, in many cases, substantially downregulating the increase in photosynthesis (Tissue & Oechel, 1987; Delucia, Sasek & Strain, 1985; Sage, Sharkey & Seeman, 1989). In the majority of cases where down-regulation or acclimation occurs, the downward adjustment is not sufficient to overcome the effect of greater carbon supply (Cure & Acock, 1986). One possible consequence of increased photosynthesis can be an increase in plant biomass, as shown for 156 plant species surveyed by Poorter (1993, average biomass increase of 37% with a doubling of atmospheric CO_2).

We showed previously that elevated CO_2 increased rates of photosynthesis approximately 70% for the dominant species (*Avena barbata*) in an annual grassland (Jackson *et al.*, 1994). Increased photosynthetic rates with CO_2 also led to increased individual plant size and seed production in the field (Jackson *et al.*, 1994, average increases of approximately 30%). Photosynthetic comparisons in that study were made only at the growth CO_2 concentrations of the treatments (i.e. chamber ambient vs. chamber + 350 p.p.m. CO_2). In this study we examine *Avena* photosynthesis at a range of atmospheric and internal CO_2 concentrations (C_a and C_i, respectively) in field and glasshouse experiments. We combine the results with assessments of leaf N in the field to examine photosynthetic regulation with a CO_2-photosynthesis model (Luo, Field & Mooney, 1994). We then examine how the observed changes in photosynthesis contribute to changes in individual size, reproduction and density for the dominant species of the grassland across two growing seasons.

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METHODS

The field site was an annual sandstone grassland at the Jasper Ridge Biological Preserve near Stanford University, CA, U.S.A. (37°24′N, 122°13′W). The Mediterranean-type climate is characterized by cool, wet winters and warm, dry summers (Mooney *et al.*, 1986). The average precipitation from 1975–90 was 579 mm, with a minimum of 200 mm (1975–76) and a maximum of 1200 mm (1982–83). Precipitation for the 1993 and 1994 growing seasons was 905 mm and 433 mm. Species composition of the grassland is typical of cis-montane California, consisting primarily of C_3 Eurasian annuals, including *Avena*, *Bromus* and *Lolium* spp. (Gulmon, 1979). The soil at the site is sandstone-derived (Dibble Series, Lithic Xerochrepts; Kashiwagi, 1985) and the elevation is 200 m. No supplemental water or nutrients were added.

The three treatments (ten replicates per treatment) used to evaluate grassland responses to CO_2 were no-chamber controls, open-top chambers with ambient CO_2 and open-top chambers with ambient + 350 p.p.m. CO_2 (seasonal average of 720 μmol mol^{-1}). Each cylindrical open-top chamber was 1.0 m in height and 0.65 m in diameter (0.33 m^2 soil area); no-chamber controls were 0.65 m in diameter with a 0.02 m-tall aluminum ring at the soil surface. Individual blowers forced approximately 4500 l min^{-1} of ambient air through each chamber (roughly ten air changes minute^{-1}), supplemented by 350 μmol mol^{-1} CO_2 in high-CO_2 chambers. The experiments were performed the third season of CO_2 enhancement, and chamber CO_2 was maintained throughout the year. Further description can be found in Field *et al.* (1995) and Jackson *et al.* (1994).

Field measurements of leaf gas-exchange and plant size and reproduction were taken on the most common species of the grassland, *Avena barbata* Brot (Munz, 1968). Its density was approximately 1500 plants m^{-2} (Jackson *et al.*, 1994), comprising approximately 30% of community density and 40–50% of community biomass. Leaf gas-exchange measurements in the field were taken towards the end of the growing season, in the first 2 weeks of April, 1994. Photosynthesis-CO_2 relationships were measured with a LI-6200 (Li-Cor Inc., Lincoln, NE, U.S.A.) on fully expanded leaves of *A. barbata* in each field plot. The curves were measured in full sunlight at midday (approximately 1000–1500 μmol m^{-2} s^{-1}). Except for the leaf in the cuvette, the plant remained at its growth CO_2 concentration (ambient or ambient + 350 p.p.m. CO_2) while photosynthesis measurements were taken. To test the photosynthesis model of Luo *et al.* (1994), leaf N was measured with a Carlo-Erba NA 1500 on a subset of the leaves used for photosynthesis measurements.

In order to explore photosynthetic relationships in a situation allowing better environmental control, we also took advantage of a co-occurring glasshouse CO_2 experiment (Malmstrom, in prep.) involving the related cultivated oat, *A. sativa* L. Seedlings were germinated and grown in ambient or elevated CO_2 (daytime averages of approximately 380 p.p.m. and 700 p.p.m.) and day and night temperatures of 21°C and 13°C. Individual plants were grown in 10-cm diameter, 40-cm deep pots filled with no. 1 sand, supplemented by 2.0 g of 17-6-10 + minors time-release fertilizer (Osmocote, Grace Sierra). They were watered to field capacity daily and alternated between glasshouses weekly. A standard open system (Ball, 1987) was used to measure gas exchange on fully expanded *Avena* leaves. A variable intensity lamp (ILC Technology Inc., power supply with a UV-filter xenon lamp) supplied light to the chamber; light levels were continuously monitored adjacent to the leaves with a Ga-As photodiode.

For the 1993 field data, measurements of height, density and seed production for *Avena barbata* were taken as presented in Jackson *et al.* (1994). Methods for the 1994 field season were similar, with the following exceptions and clarifications. Height, density, and seed production were measured at the end of the growing season on all *A. barbata* plants within at least two randomly located 10-cm-diameter circles in each of the thirty 0.33-m^2 plots. Approximately 400 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 *A. barbata* plants (approximately 225 individuals in total). Limits on destructive harvests did not permit biomass determinations from >1 circle per plot.

RESULTS AND DISCUSSION

Rates of photosynthesis for *A. barbata* in the field were almost identical for plants in ambient and elevated CO_2 when compared at the same atmospheric CO_2 concentration (Fig. 1). Treatment differences were less than 10% for typical levels of the experiment (360–725 p.p.m. CO_2),

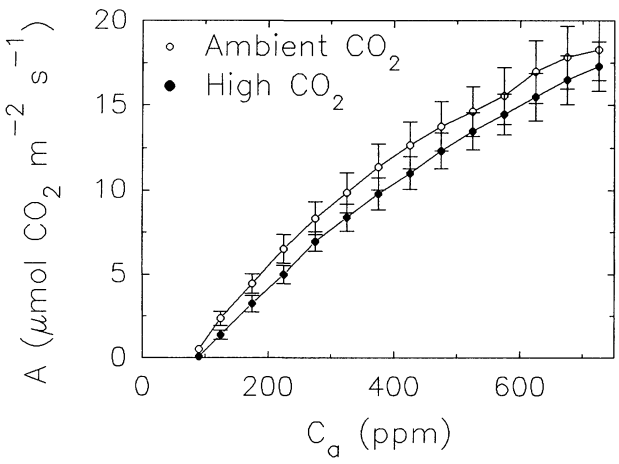

FIG. 1. Net photosynthesis (A) as a function of atmospheric CO_2 concentration (C_a) for *Avena barbata* leaves growing at ambient CO_2 (chamber controls) or elevated CO_2 (chamber + 350 p.p.m. CO_2; approximately 720 μmol mol^{-1} CO_2) (mean ± SE; n = seven plants for ambient, n = six plants for elevated; each plant from a different chamber). Gas-exchange measurements in the field were taken towards the end of the growing season (April, 1994) with a LI-6200 on fully expanded leaves of *A. barbata*. The curves were measured at midday in full sunlight (approximately 1000–1500 μmol m^{-2} s^{-1}). Except for the leaf in the cuvette, the plant remained at its operational CO_2 concentration while measurements were taken (ambient or ambient ± 350 ppm CO_2).

TABLE 1. Specific leaf mass (g m^{-2}), leaf N concentration (g N g^{-1}), and leaf N concentration by leaf area (g N m^{-2}) for *Avena barbata* plants in the field from open-top chambers with either ambient or ambient + 350 CO_2 (mean ± SE, $n = 3$ for ambient, $n = 7$ for elevated).

	Leaf properties		
CO_2 treatment	SLM (g m^{-2})	g N g^{-1} leaf	g N m^{-2} leaf
Ambient CO_2	55.8 ± 2.6	0.0194 ± .0026	1.10 ± 0.021
Elevated CO_2	67.2 ± 4.2	0.0145 ± .0007	0.97 ± 0.008

though always in the direction of slight downregulation in elevated CO_2. When compared at their respective growth CO_2 concentrations, plants in elevated CO_2 had photosynthetic rates 50% higher than plants at ambient CO_2 (17.3 and 11.4 μmol m^{-2} s^{-1}, respectively). These rates, and the relative differences for plants in elevated and ambient CO_2, are quite similar to results from the previous growing season (Jackson *et al.*, 1994).

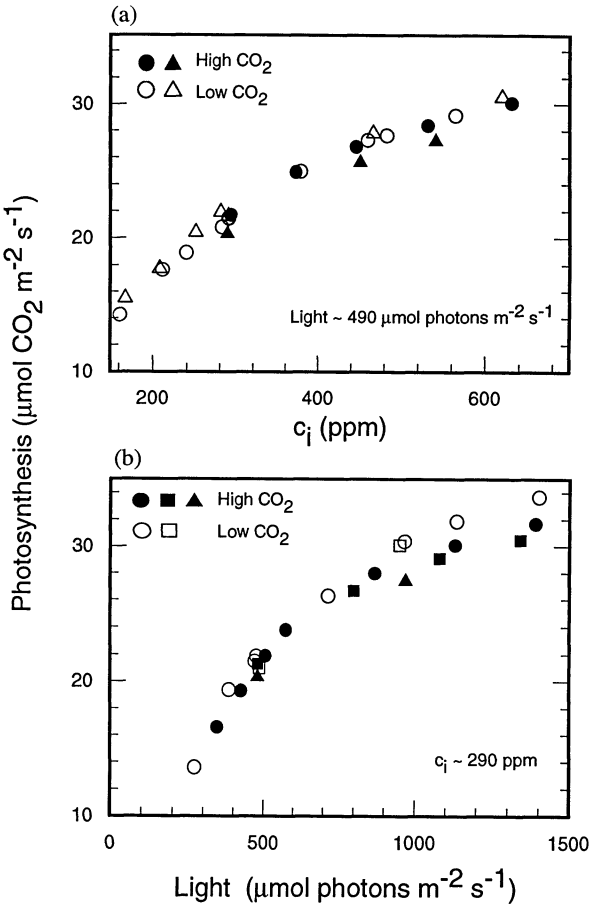

FIG. 2. Net photosynthesis as a function of internal CO_2 concentration (C_i) or light for leaves of *Avena sativa* grown at ambient or elevated CO_2 (daytime glasshouse averages of 380 and 700 p.p.m. CO_2, respectively). A standard open system (Ball, 1987) was used to measure gas exchange on fully expanded leaves. A variable intensity lamp (ILC Technology Inc., power supply with a UV-filter xenon lamp) supplied light to the chamber, and light levels were continuously monitored adjacent to the leaves with a Ga-As photodiode. Each open (ambient CO_2) or filled (elevated CO_2) symbol represents a different plant.

To link the photosynthesis data to potential changes in leaf nitrogen, we also examined leaf properties for *A. barbata* in the field. Specific leaf mass (SLM, leaf mass per unit leaf area) and leaf N concentrations changed in the directions expected with elevated CO_2; SLM increased 20% and leaf N concentration decreased 25% (Table 1, $P = 0.14$ and 0.06, respectively). Average leaf N on an area basis decreased 11% with CO_2 (Table 1), though differences were far from definitive ($P = 0.50$). These leaf N results are consistent with many studies from the literature (Stitt, 1991; Conroy & Hocking, 1993; Luo *et al.*, 1994). Based on our observed decrease in area-based N, the biochemical model of Luo *et al.* (1994) predicts a 7% downregulation in photosynthetic capacity for elevated CO_2. This prediction is in close agreement with the < 10% reduction in photosynthesis observed for plants grown in elevated CO_2 (Fig. 1).

Leaf-level photosynthesis for *A. sativa* in the glasshouse showed similar relative responses to ambient and elevated CO_2 as field-grown plants. At relatively low light (490 μmol photons m^{-2} s^{-1}), there was no evidence of photosynthetic down-regulation in elevated CO_2 as a function of C_i (Fig. 2a). When C_i was held constant at 290 p.p.m., photosynthetic rates for the two treatments were similar at a given irradiance (Fig. 2b), with a hint of down-regulation in elevated CO_2 at high light (> 1000 μmol photons m^{-2} s^{-1}).

Density, size, and reproduction for *A. barbata* in the field showed different dynamics for the wet and dry years of 1993 and 1994 (Fig. 3). In the wetter 1993, individual *Avena* plants were approximately 30% larger in elevated CO_2, with an equivalent increase in seed production (Fig. 3; $P = 0.001$, 0.17 and 0.02 for height, biomass and seed production, respectively). *Avena* density in 1993 was 21% lower in elevated CO_2 than in chamber controls, but the variation within treatments was high ($P = 0.54$ for the two chamber treatments). In contrast to 1993, *Avena* density in the drier year of 1994 was almost twice as great in elevated as in ambient CO_2 (an 87% increase, $P = 0.19$), but the increases in individual size and reproduction were diminished. Seed production, height, and individual biomass were 18%, 12%, and 6% higher in elevated CO_2 than in chamber controls, but in no case were the values significantly different ($P > 0.10$ in each case for the chamber comparisons).

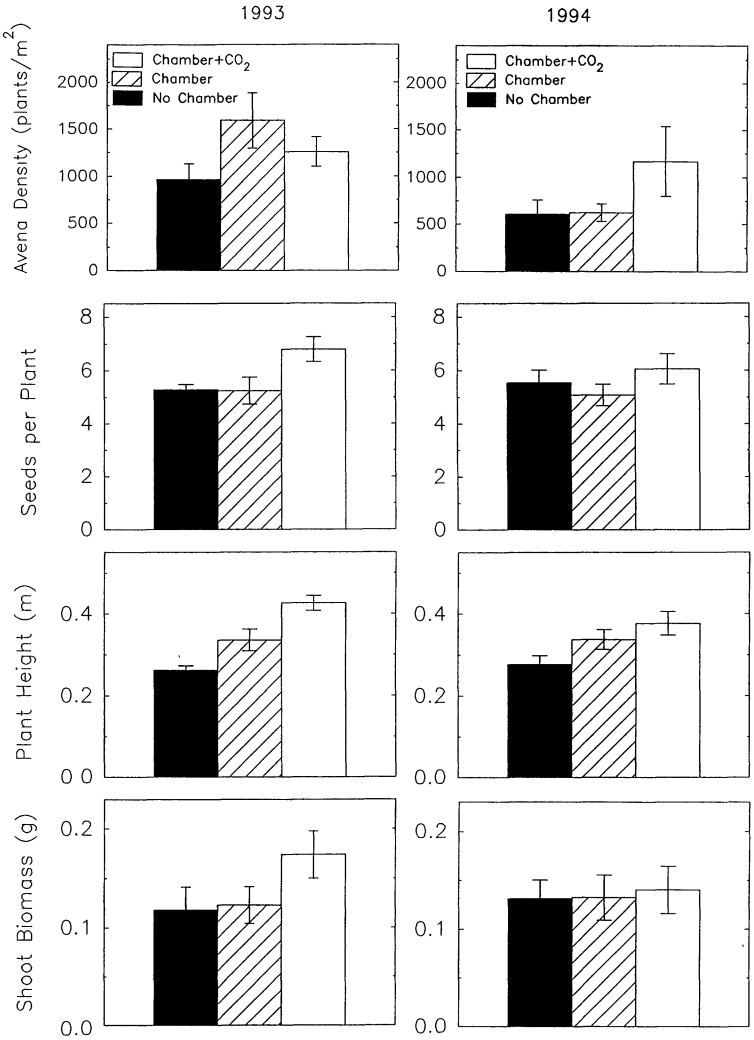

FIG. 3. Average density, seed number, height and shoot biomass (May, 1993 and 1994) for *Avena barbata* plants in no-chamber controls, chamber controls, and chamber + 350 p.p.m. CO_2 in the field (mean ± SE, $n = 9$ or 10 for each bar). Density, seed production, and height were measured at the end of the growing season on all *A. barbata* plants within at least two (1994) or three (1993) randomly located 10-cm-diameter circles in each of the thirty 0.33^2 plots. Approximately 1000 (1993) or 400 (1994) 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 each year and drying and weighing the *A. barbata* plants (approximately 250 individuals in total each year). Limits on destructive harvests did not permit biomass determinations from > 1 circle per plot. The 1993 results are from Jackson *et al.* (1994).

Our data highlight the importance of population processes for predicting responses to atmospheric CO_2 (Bazzaz *et al.* 1992). *Avena* density showed far more variation across years and treatments than any size or reproductive attribute we measured (Fig. 3). Density declined markedly in control treatments for the relatively dry 1994 season, falling to 40% of 1993 values in chamber controls ($P = 0.01$ by paired comparison). In contrast, *Avena* density in elevated CO_2 decreased only slightly in the drier 1994 (a 7% reduction from 1993, $P = 0.73$). The importance of density can also be seen by examining seeds produced on a population basis (*Avena* seeds per soil area), rather than per individual plant as presented in Fig. 3. There is essentially no persistent seed bank for *Avena* at Jasper Ridge, so seed production from the prior year provides the input for the current year. Average seed production in 1993 was 7600 and 8400 seeds m^{-2} in ambient and elevated CO_2, approximately 10% higher with CO_2 (data not shown). In 1994, however, *Avena* produced over twice as many seeds in elevated CO_2 as in chamber controls (6500 and 3200 seeds m^2, respectively); this was despite smaller relative increases with CO_2 in the number of seeds produced per individual in 1994 than in 1993. Since *Avena* seed production in 1993 increased 10% in elevated CO_2, but *Avena* density was 87% greater in elevated CO_2 the following year, *Avena* plants in high CO_2 apparently had either greater survivorship in 1994 or began the year with seeds of higher quality than in ambient CO_2.

The large majority of studies on the biological consequences of elevated CO_2 have examined responses of ecosystem components, plants in pots or individual leaves. While the responses of these components are certainly

important contributors to long-term ecosystem responses, scaling from leaf or plant to ecosystem is neither simple nor direct (Waring, 1993). Responses of ecosystem net primary production may sometimes qualitatively mirror patterns of leaf-level photosynthesis, as shown for arctic tundra (Tissue & Oechel, 1987), saltmarsh (Curtis *et al.*, 1989; Arp & Drake, 1991), and tallgrass prairie ecosystems (Owensby *et al.*, 1993; Knapp, Hamerlynck & Owensby, 1993). In many controlled-environment studies, however, the CO_2 response of growth is much greater for isolated plants than for plants in competition (Williams, Garbutt & Bazzaz, 1988; Bazzaz *et al.*, 1992). For the Jasper Ridge system, the stimulation of photosynthesis by CO_2 was similar in successive wet and dry years, but CO_2-induced changes in individual *Avena* biomass were much more pronounced for the wetter year of 1993. In contrast, total *Avena* production (the product of individual size and density) was relatively unchanged with CO_2 in 1993, despite larger individual plants; production substantially increased in the drier year of 1994 when individual growth responses were small. Ecosystem biomass for the Jasper Ridge system may be driven more by population-level factors than by individual plant growth responses.

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