Photosynthesis, growth and density for the dominant species in a CO₂-enriched grassland

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Abstract. Although increased atmospheric CO₂ 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 CO₂ 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 CO₂ 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 CO₂ concentrations. Although specific leaf mass (leaf mass per unit leaf area) for Avena increased 20% in the field with elevated CO₂, 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 CO₂, with a 21% decrease in population density. For the relatively dry 1994 season Avena density was almost doubled in elevated CO₂, but increases in individual size and reproduction with CO₂ were small (6-18%). The primary effect of CO₂ in the drier year appears to have been greater Avena survival, rather than increased individual size.

Key words. Annual grassland, elevated CO₂, leaf nitrogen, photosynthesis, Avena reproduction.

INTRODUCTION

Short-term exposure of C₃ plants to elevated CO₂ generally leads to increased rates of leaf-level photosynthesis (Morison, 1990; Mooney et al., 1991). Photosynthetic responses are less consistent when the exposure to CO₂ 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 CO₂).

We showed previously that elevated CO₂ increased rates of photosynthesis approximately 70% for the dominant species (Avena barbata) in an annual grassland (Jackson et al., 1994). Increased photosynthetic rates with CO₂ 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 CO₂ concentrations of the treatments (i.e. chamber ambient vs. chamber + 350 p.p.m. CO₂). In this study we examine Avena photosynthesis at a range of atmospheric and internal CO₂ concentrations (Cᵣ and Cᵣ, respectively) in field and glasshouse experiments. We combine the results with assessments of leaf N in the field to examine photosynthetic regulation with a CO₂ 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.
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 C₄ 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 CO₂ were no-chamber controls, open-top chambers with ambient CO₂ and open-top chambers with ambient + 350 p.p.m. CO₂ (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 m² 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 CO₂ in high-CO₂ chambers. The experiments were performed the third season of CO₂ enhancement, and chamber CO₂ 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-CO₂ 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 CO₂ concentration (ambient or ambient + 350 p.p.m. CO₂) 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 CO₂ experiment (Malmsstrom, in prep.) involving the related cultivated oat, A. sativa L. Seedlings were germinated and grown in ambient or elevated CO₂ (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-m² plots. Approximately 400 plants were measured overall, and values within each 0.33-m² 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 CO₂ when compared at the same atmospheric CO₂ concentration (Fig. 1). Treatment differences were less than 10% for typical levels of the experiment (360–725 p.p.m. CO₂),
though always in the direction of slight downregulation in elevated CO₂. When compared at their respective growth CO₂ concentrations, plants in elevated CO₂ had photosynthetic rates 50% higher than plants at ambient CO₂ (17.3 and 11.4 µmol m⁻² s⁻¹, respectively). These rates, and the relative differences for plants in elevated and ambient CO₂, are quite similar to results from the previous growing season (Jackson et al., 1994).

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 CO₂; 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 CO₂ (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 CO₂. This prediction is in close agreement with the <10% reduction in photosynthesis observed for plants grown in elevated CO₂ (Fig. 1).

Leaf-level photosynthesis for A. sativa in the glasshouse showed similar relative responses to ambient and elevated CO₂ 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 CO₂ as a function of Cᵢ (Fig. 2a). When Cᵢ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ (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 CO₂ than in chamber controls, but in no case were the values significantly different (P > 0.10 in each case for the chamber comparisons).

Our data highlight the importance of population processes for predicting responses to atmospheric CO₂ (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 CO₂ 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 CO₂, approximately 10% higher with CO₂ (data not shown). In 1994, however, Avena produced over twice as many seeds in elevated CO₂ as in chamber controls (6500 and 3200 seeds m², respectively); this was despite smaller relative increases with CO₂ in the number of seeds produced per individual in 1994 than in 1993. Since Avena seed production in 1993 increased 10% in elevated CO₂, but Avena density was 87% greater in elevated CO₂ the following year, Avena plants in high CO₂ apparently had either greater survivorship in 1994 or began the year with seeds of higher quality than in ambient CO₂.

The large majority of studies on the biological consequences of elevated CO₂ have examined responses of ecosystem components, plants in pots or individual leaves. While the responses of these components are certainly...
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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 CO₂ 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 CO₂ was similar in successive wet and dry years, but CO₂-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 CO₂ 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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REFERENCES


