Photosynthesis Research **43**: 263–271, 1995.

Regular paper

Contrasting leaf and 'ecosystem' CO_2 and H_2O exchange in *Avena fatua* monoculture: Growth at ambient and elevated CO_2

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Received 28 November 1994; accepted in revised form 20 March 1995

Key words: elevated CO_2, 'ecosystem' gas-exchange, photosynthetic water-use efficiency, *Avena fatua*

Abstract

Elevated CO_2 (ambient + 35 Pa) increased shoot dry mass production in *Avena fatua* by ~ 68% at maturity. This increase in shoot biomass was paralleled by an 81% increase in average net CO_2 uptake (A) per unit of leaf area and a 65% increase in average A at the 'ecosystem' level per unit of ground area. Elevated CO_2 also increased 'ecosystem' A per unit of biomass. However, the products of total leaf area and light-saturated leaf A divided by the ground surface area over time appeared to lie on a single response curve for both CO_2 treatments. The approximate slope of the response suggests that the integrated light saturated capacity for leaf photosynthesis is ~ 10-fold greater than the 'ecosystem' rate. 'Ecosystem' respiration (night) per unit of ground area, which includes soil and plant respiration, ranged from −20 (at day 19) to −18 (at day 40) μmol m^{-2} s^{-1} for both elevated and ambient CO_2 *Avena*. 'Ecosystem' below-ground respiration at the time of seedling emergence was ~ −10 μmol m^{-2} s^{-1}, while that occuring after shoot removal at the termination of the experiment ranged from −5 to −6 μmol m^{-2} s^{-1}. Hence, no significant differences between elevated and ambient CO_2 treatments were found in any respiration measure on a ground area basis, though 'ecosystem' respiration on a shoot biomass basis was clearly reduced by elevated CO_2. Significant differences existed between leaf and 'ecosystem' water flux. In general, leaf transpiration (E) decreased over the course of the experiment, possibly in response to leaf aging, while 'ecosystem' rates of evapotranspiration (ET) remained constant, probably because falling leaf rates were offset by an increasing total leaf biomass. Transpiration was lower in plants grown at elevated CO_2, though variation was high because of variability in leaf age and ambient light conditions and differences were not significant. In contrast, 'ecosystem' evapotranspiration (ET) was significantly decreased by elevated CO_2 on 5 out of 8 measurement dates. Photosynthetic water use efficiencies (A/E at the leaf level, A/ET at the 'ecosystem' level) were increased by elevated CO_2. Increases were due to both increased A at leaf and 'ecosystem' level and decreased leaf E and 'ecosystem' ET.

Introduction

Anthropogenic CO_2 production, primarily from fossil fuel combustion, is resulting in rising CO_2 concentrations in the earth's atmosphere (Conway et al. 1994) and CO_2 levels are predicted to double from preindustrial levels by the middle of the next century (Houghton et al. 1990). Large uncertainties exist as to how elevated CO_2 will impact the earth system, or whether terrestrial plants, viz. photosynthesis and enhanced carbon storage, will mitigate the rate of rise in global atmospheric CO_2 (Tans et al. 1990). With respect to photosynthesis, there are some compelling reasons to believe that plants might be able to slow or halt the rise in atmospheric CO_2. First, 90 to 95% of the worlds plants possess a photosynthetic metabolism (C3) which is CO_2 limited under current atmospheric CO_2 concentrations. At the leaf level, net photosynthesis in C3 plants typically increases with increasing CO_2 to at least double current concentrations. Second, elevated CO_2 stimulates photosynthesis and growth in a broad range of agricultural (see Kimball 1983) and tree crops (Idso et al. 1993). The response of natural 'ecosystems' to elevated CO_2 has received much less attention but appears to be less substantial: Stimulation of biomass production has ranged from small or transient in tundra (Oechell and Strain 1985; Oechel et al. 1994) to slightly greater for tallgrass prairie (Owensby et al. 1993) to modest in a high productivity salt marsh community (Drake 1989), relative to agricultural crop responses.

We are currently investigating the effects of a doubling of the atmospheric CO_2 concentration on individual and 'ecosystem' properties in serpentine and sandstone annual grassland in cis-montane central California. Our results suggest that there is a poor correspondence between stimulation of leaf level photosynthesis and plant biomass in the dominant biomass species (*Avena barbata* and *A. fatua* make up ~ 2/3 of the biomass in the sandstone grassland), relative to much lower stimulation of photosynthesis and biomass at the 'ecosystem' level. Specifically, increases in leaf level net photosynthesis (70%) and plant biomass (41%) have been observed (Jackson et al. 1994), while at the 'ecosystem' level, only modest increases in net CO_2 uptake (17%) (Fredeen et al. 1995a) and even smaller increases in biomass production (Field et al. 1995) were measured.

There are many possible reasons for the poor correspondence between the stimulation of leaf-level photosynthesis and that of the 'ecosystem'. First, belowground respiration can be stimulated by elevated CO_2 (Luo et al. 1995). Second, as leaf area indices increase, an increasing fraction of leaf elements operate at subsaturating light intensities. Finally, nutrient limitations, common in most terrestrial 'ecosystems' (Vitousek and Howarth 1991), typically restrict growth and leaf expansion before photosynthesis per unit of leaf area (Natr 1972, 1975), and alter biomass partitioning patterns to favor non-photosynthetic plant parts (Bloom et al. 1985). Based on the preceding mechanisms and empirical results from CO_2 enrichment studies, an emerging paradigm is that resource limitations restrict the overall growth stimulation from elevated CO_2 (e.g. Mooney et al. 1991; Field et al. 1992). Our first objective was to test the idea that the limited response of *Avena* at the 'ecosystem' level in the field has been due to limitations in resources such as water, which was provided at high levels in this study.

A second objective was to explore the relationship between leaf and 'ecosystem' level CO_2 and H_2O exchange. Measurements of leaf level CO_2 exchange are often easier to accomplish than 'ecosystem' measurements, especially in communities with extensive canopies. However, it is often more difficult to understand the significance of a leaf level response in the context of the entire 'ecosystem' because few studies have actually compared leaf and 'ecosystem' CO_2 and H_2O exchange rates. For this study, we chose a relatively simple system; monocultures of *Avena fatua* (a dominant annual in the sandstone grassland community at the Jasper Ridge Preserve, Stanford, CA, USA) and grew them in relatively large and well-watered soil volumes (14 dm^3) in temperature controlled phytocells at either ambient or elevated (ambient + 35 Pa) CO_2 concentrations.

Materials and methods

Growth conditions

A uniform greenhouse potting mix (~ 3 : 2 : 1 : 1 mixture of soil : peat : perlite : vermiculite) was used to fill 28 tubes constructed of 0.95 meter lengths of 20 cm inside diameter PVC pipe. All tubes were brought to field capacity on 6/24/93 and again on 7/15/93 to allow for pregermination of unwanted propagules and for soil nutrient equilibration. On 30 July, 1993, 14 tubes were randomly assigned to either an ambient or elevated (ambient + 35 Pa) CO_2 phytocell. A general description of these phytocells can be found in Björkman et al. (1972). A slow-release fertilizer, 20 g m^{-2} of a 120-day release nitrogen, phosphorus, and potassium source (Osmocote (14–14–14), Horticultural Products Co., Milpitas, CA), was provided to half of the ambient and elevated CO_2 tubes in an attempt to obtain a high nutrient treatment. The rate of fertilizer amendment was chosen because it resulted in optimal growth of simulated grassland communities at Jasper Ridge in a larger companion study (Field et al. 1995). In this study, we report only on the results from the non-nutrient amended tubes. Nutrient addition more than doubled the final aboveground biomass in ambient CO_2-grown (142% stimulation) and in elevated CO_2-grown (117% stimulation) *Avena* which made 'ecosystem'-level gas exchange difficult to achieve after week three due to the excessive height and biomass of the canopy. However, even without the nutrient amendment, above-ground biomass production was ~ 5-fold greater than production in the natural ecosystem at Jasper Ridge in which *Avena* is the dominant (Field et al. 1995).

Phytocells were adjacent (~ 2 m apart) and similar in every respect. Nevertheless, phytocell designations were switched at the half-way point of the experiment by moving the CO_2 source to the opposite phytocell. In addition, tubes were re-randomized within each phytocell to control for variation in solar illumination across each phytocell. Two large (1.5 h.p.) blowers ensured adequate mixing within each phytocell. Air temperatures were maintained at 15 °C from 22:00 to 08:00 (night) and at 27 °C from 10:00 to 20:00 (day) with a 2-h linear temperature ramp at each transition. Plants received ambient light and photoperiod in the phytocells through transparent glass walls from 30 July through 15 September, 1993. The concentration of CO_2 in both phytocells was monitored with an IRGA (Li6251, LiCOR, Lincoln, NE), and controlled in the elevated CO_2 phytocell by means of a control algorithm implemented by a data logger (CR10, Campbell Scientific, Inc. Logan, UT) coupled to a mass flow controller (Datametrics 825, Dresser Ind., Wilmington, MA). *Avena fatua* seed was collected in the summer of 1991 at the Jasper Ridge Biological Preserve, Stanford, CA. Approximately 5% of the seeds collected were considerably smaller than the others (< 0.015 g) and were discarded. *Avena* was seeded at a soil depth of 4 cm. Attempts were made to achieve plant densities typical for natural sandstone communities at Jasper Ridge, approximately ~ 1600 seeds m^{-2}. Plants were watered daily for the first two weeks and thereafter every third day.

Growth analysis

Single tubes were harvested at weekly intervals starting 18 days after seeding. Three replicate tubes were harvested on a final date (September 23, 1993) when a majority of the plants had set seed. Plant material was separated into stem and leaf (dead and live), subsampled for determination of specific leaf mass, and dried at 65 °C for 5 days before weighing. We assumed that the shoot biomass had a chemical composition of CH_2O in the conversion of grams of dry matter to moles of plant carbon. Leaf areas were determined by dividing total leaf mass by average (n = 3) specific leaf mass.

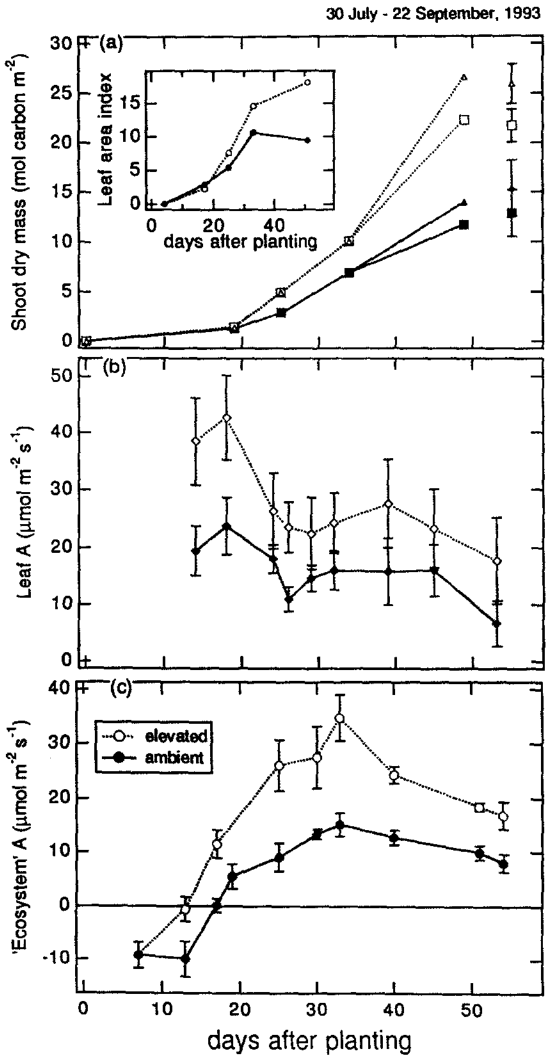

Fig. 1. (a) Shoot dry mass (mol carbon m^{-2}), (b) light-saturated leaf photosynthesis (A, μmol m^{-2} s^{-1}), (c) 'ecosystem' photosynthesis (A, μmol m^{-2} ground area s^{-1}) and (insert panel (a)) leaf area index, for *Avena fatua* monoculture grown from 30 July to 22 September, 1993 in climate controlled phytocells at either ambient CO_2 (closed symbols) or elevated CO_2 (open symbols). Shoot dry mass is presented as live shoot biomass (squares) or live + senesced shoot biomass (triangles). Means and standard deviations are shown (n = 4 to 8).

Gas exchange

Net 'ecosystem' (soil and plant contained within the pot) and leaf CO_2 exchange were measured with open gas exchange systems utilizing infra-red gas analyzers (Li6262 ('ecosystem'); Li6251 (leaf), LiCOR, Lincoln, NE) in the differential mode. Water exchange was monitored by the Li6262 for the 'ecosystem' mea-

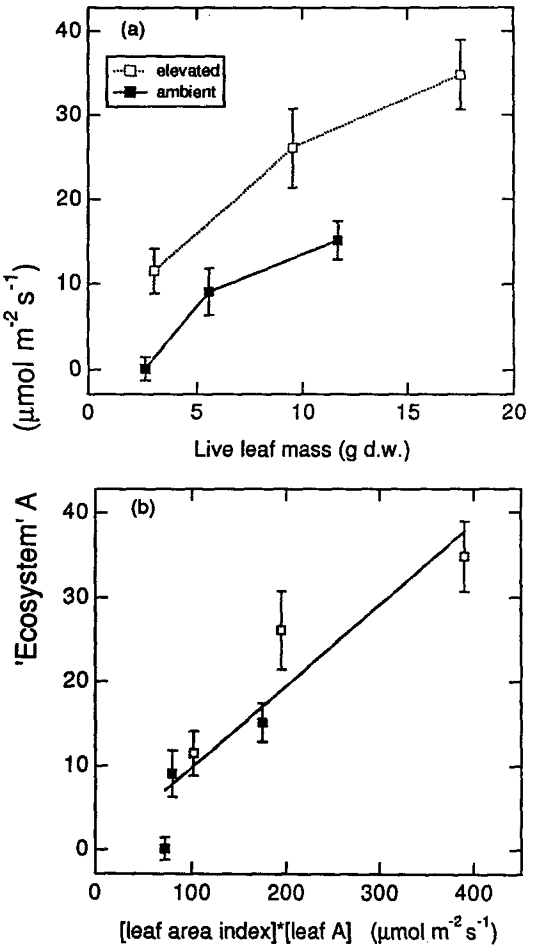

Fig. 2. (a) Live leaf mass (g d.w.), and (b) [leaf area index (LAI)] * [light-saturated leaf photosynthesis (leaf A)] versus 'ecosystem' photosynthesis (A, μmol m^{-2} ground area s^{-1}) in *Avena fatua* monoculture. In Fig. 2B, 'Ecosystem' A = (LeafA * LAI) 0.10 + 0.21 (r = 0.92).

surements and by humidity sensors in the leaf chamber (PLC-3, ADC, Co., Herts, England). All photosynthesis measurements were made within one hour of solar noon. For both leaf and 'ecosystem' measurements, air was pumped from a large-volume gas reservoir (vinyl air mattress) containing air with the desired CO_2 concentration, into (inlet pump) and out of (outlet pump) the chamber and back through the IRGA. By adjusting the speeds of the two pumps (Spectrex, Redwood City, CA) we obtained zero pressure within the 'ecosystem' chamber at all times. Return flow in the leaf chamber was governed by the inlet pump only. Typical gas-exchange measurements required 20 s for the leaf chamber and 3 min for the 'ecosystem' chamber. The latter often resulted in a slight warming (1 to 2 °C) of the chamber air. Light levels inside the chamber were reduced by 5 to 10% relative to levels within the phytocell. The chamber for 'ecosystem' measurements was made of 5 mm thick acrylic tubing (0.195 m diameter × 0.34 dm height), capped with 5 mm thick acrylic sheet, and lined with adhesive backed transparent teflon tape (S115, Saunders Engineering Corp., Los Angeles, CA) to minimize water retention. The base of the 'ecosystem' chamber was made of aluminum plate that exactly coupled with the tubes. Inlet and outlet connectors were fitted to fan housings to facilitate complete mixing within the chamber. The 'ecosystem' chamber was also equipped with a port for measuring pressure within the chamber by means of an externally located pressure transducer (PX163, Omega Engineering Inc., Stamford, CN), internally mounted thermocouples for air and canopy temperature, and a galium-arsenide sensor (PH201A, NEC Electronics, Tokyo, Japan) for light measurement (Chazdon and Field 1987).

Results

Elevated CO_2 (ambient + 35 Pa) increased shoot dry mass accumulation in *Avena fatua* by 68% after two months of growth (Fig. 1a). The increase in shoot biomass was coincident with an 81% increase in net CO_2 uptake (A) per unit of leaf area and a 65% increase in A at the 'ecosystem' level per unit of ground area, averaged over time from day 25 to seed set (Figs. 1b and 1c respectively). Elevated CO_2 also increased 'ecosystem' A per unit of live leaf mass (Fig. 2a). However, the relationship between the product of leaf area index and light-saturated leaf A versus 'ecosystem' A was similar for ambient and elevated CO_2 'ecosystems' (Fig. 2b).

Part of the net 'ecosystem' gas exchange signature for CO_2 comes from respiration of above- and below-ground plant parts and soil. We measured 'ecosystem' night respiration, including soil and plant, and found rates to be relatively similar across time and treatment. Respiration ranged from ~ −20 (at day 19) to ~ −18 (at day 40) μmol m^{-2} s^{-1} for both elevated and ambient CO_2 *Avena* 'ecosystems' (Table 1). We measured 'ecosystem' below-ground respiration in two ways. Initial 'ecosystem' CO_2 exchange (at day 7), coinciding with seedling emergence, indicated a below-ground respiration rate of -10 ± 2 μmol m^{-2} s^{-1}. Post-harvest measurements (at day 55) after removal of aboveground biomass indicated rates of

Table 1. 'Ecosystem' night respiration (μmol m^{-2} s^{-1}) and below-ground day-time respiration (μmol m^{-2} s^{-1}) for *Avena fatua* monoculture grown in phytocells at either ambient or elevated (ambient + 35 Pa) CO_2

	Days after planting	Ambient CO_2 (~ 35 Pa)[a]	Elevated CO_2 (ambient + 35 Pa)
'Ecosystem' night respiration (μmol m^{-2} s^{-1})	19	−19.2 ± 0.8 (n = 6)	−20.9 ± 0.6 (n = 6)
	40	−18.6 ± 1.8 (n = 4)	−17.6 ± 2.7 (n = 4)
Belowground respiration (μmol m^{-2} s^{-1})	55	−5.9 ± 0.8 (n = 3)	−5.1 ± 0.6 (n = 3)

[a]Means shown ± SD.

−5 to −6 μmol m^{-2} s^{-1}. No significant differences between elevated and ambient CO_2 treatments were found in either night-time or below-ground daytime 'ecosystem' respiration.

Effects of elevated CO_2 on leaf and 'ecosystem' water fluxes were qualitatively similar in that elevated CO_2 decreased water flux from day 25 until canopy maturity (~ day 50) at both spatial scales. Elevated CO_2 resulted in lower transpiration (E) (not significant, Fig. 3a) and lower evapotranspiration (ET), (significant at the $p = 0.05$ level for 5 out of 8 measurement periods, Fig. 3b) throughout most of the experiment, despite the higher biomass and associated leaf surface at elevated CO_2. Leaf and 'ecosystem' water fluxes at ambient and elevated CO_2 converged by the last sampling date. Overall, photosynthetic water use efficiencies were increased in both leaf (A/E) and 'ecosystem' (A/ET) (Figs. 3c and 3d respectively). At the leaf level, increased photosynthetic water-use efficiencies were due to significantly increased A (Fig. 1b), while at the 'ecosystem' level, it was due to significant increases in A (Fig. 1c) and decreases in ET (Fig. 3b) over much of the experiment.

Discussion

Leaf and 'ecosystem' photosynthesis

A majority of the world's species possess a photosynthetic physiology that is stimulated by elevated CO_2, and enhancements in photosynthesis are well documented for individual species from agricultural (Kimball 1983) and natural (Bazzaz 1990) communities. At the whole plant or 'ecosystem' level, stimulations of net CO_2 uptake and carbon accumulation are typically less than at the leaf level (e.g. Norby et al. 1992). More recently, this phenomenon has been observed in annual grassland in central California (Jackson et al. 1994; Fredeen et al. 1995). In an effort to better understand this discrepancy in leaf versus 'ecosystem' effects, we grew a dominant biomass species from this annual grassland (*Avena fatua*) to maturity under controlled conditions. At the leaf level, average stimulation of photosynthesis was ~ 81%, not unlike the 70% stimulation in the field for *A. barbata* (Jackson et al. 1994). In contrast, at the 'ecosystem' level, results from monoculture and field were disparate, i.e., 'ecosystem' photosynthesis was stimulated by 65% in this study compared to only 17% in the *Avena*-dominated community in the field (Fredeen et al. 1995a). Similarly, total shoot biomass was stimulated by 68% in this study, while stimulation of annual species biomass in the field ranges from none to about 20% (Field et al. 1995).

One explanation for these contrasting results in the monoculture versus the field is that the monocultures were provided with elevated resource levels relative to that occurring in the field naturally, i.e., aboveground biomass production in the phytocells was increased by at least 5-fold over that in the field (Field et al. 1995). It has long been known that resource limitations often restrict growth and leaf surface production before intrinsic rates of resource capture, e.g. leaf photosynthesis per unit area, are affected (Natr 1972, 1975). This generalization is consistent with our leaf-level photosynthesis results, i.e., stimulation of light saturated photosynthetic rates by elevated CO_2 was similar between field (Jackson et al. 1994) and phytocell (Fig 1b). These results also concur with the prediction that enhancements in productivity resulting from elevated

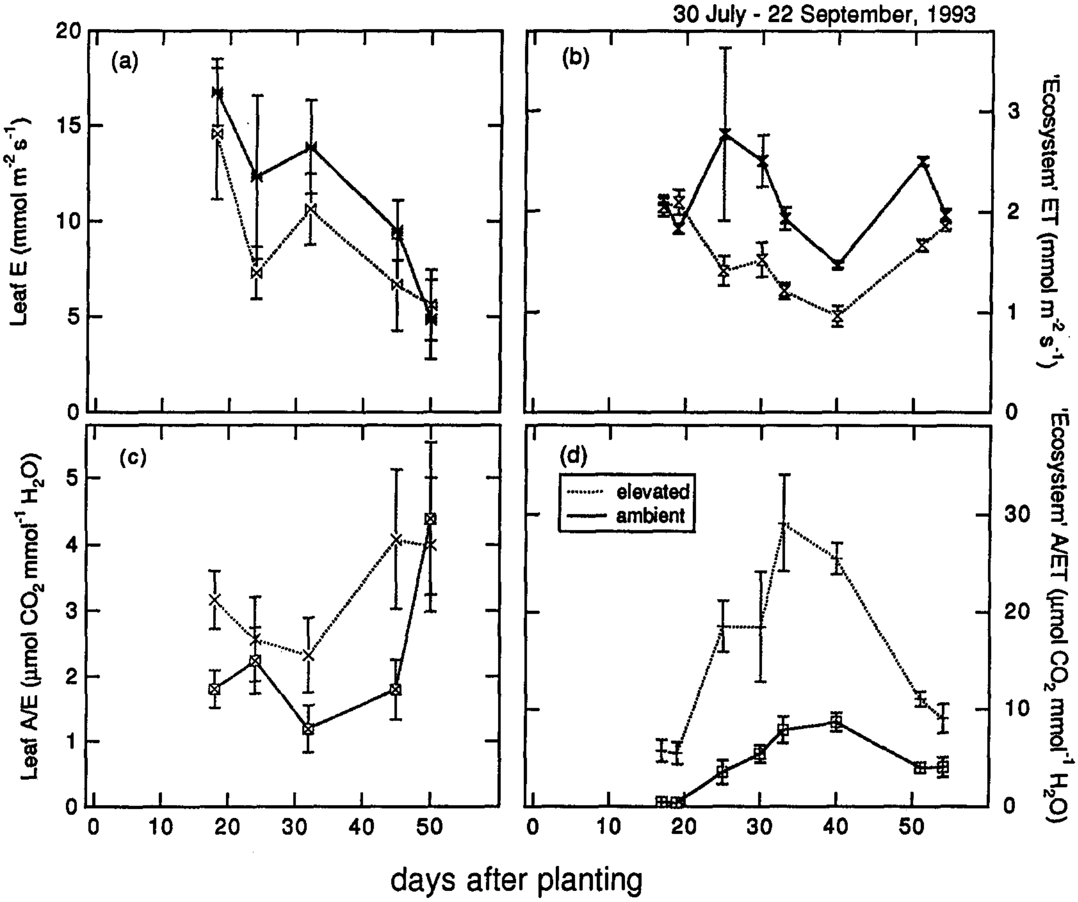

Fig. 3. (a) Light-saturated leaf transpiration (E, mmol m^{-2} s^{-1}), (b) 'ecosystem' evapotranspiration (ET, mmol m^{-2} s^{-1}, (c) light-saturated leaf photosynthetic water use efficiency (A/E, μmol CO_2 $mmol^{-1}$ H_2O), and (d) 'ecosystem' photosynthetic water use efficiency (A/ET, μmol CO_2 $mmol^{-1}$ H_2O) versus days after planting in *Avena fatua* monoculture.

CO_2 will be greatest in those 'ecosystems' with the lowest overall limitation for plant growth (Field et al. 1992).

The fact that leaf photosynthesis and its stimulation by elevated CO_2 is preserved over a wide range of resource availabilities (Bunce 1992; Silvola and Ahlholm 1992), while the corresponding stimulation of 'ecosystem' rates appears to diminish with increasing resource limitations (see Mooney et al. 1991), suggests that other processes must consume carbon, which would otherwise result in growth stimulation, when resources are limiting. A growing number of processes have been identified in 'ecosystems' or individuals exposed to elevated CO_2 that would serve to either reduce carbon income or increase carbon expenditure by the whole plant, including increased fine-root turnover (Norby et al. 1992), increased below-ground respiration (Luo et al. 1994) and increased partitioning to roots relative to shoots (see Bazzaz 1990). However, we know of no studies which clearly show that these processes are enhanced at low resource levels under elevated CO_2.

The lack of an effect of elevated CO_2 on either below-ground or whole 'ecosystem' dark respiration in the present study (Table 1), a result contrasting markedly with the large increases in below-ground respiration in the intact 'ecosystem' (Luo et al. 1995), suggests that when resources are abundant, elevated leaf photosynthesis can be partitioned into shoot production (i.e. plant photosynthetic capacity) rather than root production (below-ground heterotropic capacity). Although we did not harvest roots in the present study, this conclusion is supported by other studies on *Avena* monocultures grown at similar densities, at high and low nutrient supply and ambient or double ambient CO_2. At the low nutrient supply, neither shoot nor root biomass responded to elevated CO_2, while at high nutrient supply, elevated CO_2 nearly doubled shoot biomass but had no significant effect on root biomass (C.B. Field, unpublished results).

Light-saturated leaf photosynthetic rates multiplied by leaf area indices were ~ 10-fold higher than corresponding 'ecosystem' photosynthetic rates, irrespective of CO_2 treatment (Fig. 2b). Much of this disparity between leaf and 'ecosystem' photosynthesis probably resulted from a large fraction of the leaf surface area operating at subsaturating light intensities due to self-shading enhanced by the crowding of leaves into the cylindrical gas-exchange chamber. A second reason for this disparity is below-ground respiration occuring at the 'ecosystem' level. However, our estimate for below-ground respiration of $-10\ \mu mol\ m^{-2}\ s^{-1}$ (see next paragraph) suggests that only 12.5 to 20% of this 10-fold increase can be explained by respiration. A second point which we draw from the relationship between integrated-leaf and 'ecosystem' photosynthesis is that increased 'ecosystem' photosynthesis at elevated CO_2 resulted primarily from increased photosynthetic rates at the leaf level. This conclusion is supported by (a) a greater amount of 'ecosystem' photosynthesis resulting for a given amount of leaf biomass at elevated CO_2 (Fig. 2a), and (b) the similarity in respiration measures between ambient and elevated CO_2 'ecosystems' (Table 1).

To validate the 'ecosystem' CO_2 exchange measurements against biomass C accumulation, we calculated average 'ecosystem' A values and assumed a soil respiration rate of $-10\ \mu mol\ m^{-2}\ s^{-1}$ and night-time plant respiration of $-8\ \mu mol\ m^{-2}\ s^{-1}$ (obtained by subtracting the soil respiration ($-10\ \mu mol\ m^{-2}\ s^{-1}$) from the night-time 'ecosystem' respiration (taken as $-18\ \mu mol\ m^{-2}\ s^{-1}$). We assumed 'ecosystem' photosynthesis and dark respiration rates occurred for 8-h periods respectively and that the remaining 8-h period had a net CO_2 flux of zero. These simplifications were largely justified on the basis of our experience with 24-h flux measurements in the field. We integrated net CO_2 uptake over the entire growth period when 'ecosystem' CO_2 uptake was postive (Fig. 1c) and subtracted integrated night-time plant respiration for the same period. This crude calculation provided us with ambient and elevated net CO_2 uptake values of 12 and 27 mol of C m^{-2}, respectively. These estimates were close to the corresponding final total shoot biomass values of 15 and 26 mol of C m^{-2} that were actually observed (Fig. 1a). Since roots were not harvested, our cumulative 'ecosystem' CO_2 uptake estimates are probably lower than required. We suspect the discrepancy arises, in part, from the reduction in leaf light absorption associated with the confinement of the canopies within the 'ecosystem' gas-exchange chamber.

Transpiration and evaporation

In the field, leaf-level stomatal conductance and transpiration (E) were reduced by ~ 50% and short-term and integrative measures of photosynthetic water use efficiency were doubled in *Avena* in response to elevated CO_2 (Jackson et al. 1994). In the present study, elevated CO_2 also resulted in a 50 to 100% increase in leaf level photosynthetic water use-efficiency (A/E) and, except for the final time point, a consistent decrease (though not significant) in transpiration. Decreased leaf conductance and transpiration, and enhanced photosynthetic water-use efficiency are commonly seen in response to elevated CO_2 (e.g. Garbutt et al. 1990; Radoglou et al. 1992; and see Morison 1985; Eamus 1991).

In *Avena* dominated grassland, elevated CO_2 reduced evapotranspiration (ET) at times of peak biomass (12 to 63%) over three consecutive years (Fredeen et al. 1995b). These are comparable qualitatively and quantitatively with the reductions in ET observed over a majority of the present study, i.e. ET was reduced by 24% on average by elevated CO_2 (Fig. 3b). Although results are scarce at the 'ecosystem' level, several other recent reports concur with these findings, i.e., ET was reduced by 8 to 18% at low and high water supply, respectively, in a C4 dominated rangeland (Nie et al. 1992), while in C4 dominated tallgrass prairie, xylem water tension and estimated latent heat flux were also consistently reduced by elevated CO_2 (Owensby et al. 1993).

Light-saturated leaf transpiration rates multiplied by the various leaf area indices were 10 to 40 times higher than the corresponding 'ecosystem' rate. The explanation for this discrepancy probably involves many factors, including: (a) reduced light-energy absorption by leaves in the canopy in the gas-exchange chamber, and (b) timing of measurements, i.e., E and ET were measured on first and second days after watering, respectively. The inclusion of evaporation at the 'ecosystem' level should have enhanced water flux rates. We presume that evaporation was minimal in our study because canopy and soil surface were always dry when 'ecosystem' measurements were made.

'Ecosystem' photosynthetic water-use efficiencies (A/ET) were greatly enhanced by elevated CO_2 over the entire life-cycle of phytocell grown *Avena* (from over 1300% initially to 125% at maturity). Increased A/ET resulted from enhancements in 'ecosystem' A over the entire experiment (Fig. 1c) as well as from decreases in ET, except for those measurements made at the seedling emergence and senescing stages of growth (Fig. 3b). These increases in A/ET under well-watered conditions are greater than those observed for the intact 'ecosystem', *Avena*-dominated annual grassland, where water is commonly limiting for growth (Fredeen et al. 1995a, b). We have little ability to predict whether these effects of elevated CO_2 on A/ET in container grown plants are important at larger scales, e.g. regional. Canopy boundary layer resistances are thought to be relatively large in grassland canopies (see Eamus 1991) and vapor pressure differences could increase at the regional scale under an elevated CO_2 atmosphere if transpiration were decreased. Both of these factors would provide a negative feedback diminishing improvements in WUE observed in this study.

Acknowledgements

This research was supported by the NSF and DOE (CBF) and a grant from the A.W. Mellon Foundation to the Carnegie Institution of Washington (ALF). We also gratefully acknowledge C. Lund and C. Malmstrom for reviewing early drafts of the manuscript and technical support from H. Whitted, S. Yang, and B. Welsh.

References

Bazzaz FA (1990) The response of natural ecosystem's to the rising global CO_2 levels. Ann Rev Ecol Syst 21: 167–196

Björkman O, Berry J, Mooney HA, Nicholson F and Catanzaro B (1972) Physiological adaptation to diverse environments: Approaches and facilities to study plant responses to contrasting thermal and water regimes. CIW Yearbook 72: 393–403

Bloom AJ, Chapin FS III and Mooney HA (1985) Resource limitation in plants – an economic analogy. Ann Rev Ecol Syst 16: 363–392

Bunce JA (1992) Light, temperature and nutrients as factors in photosynhtetic adjustment to an elevated concentration of carbon dioxide. Physiol Plant 86: 173–179

Chazdon RL and Field CB (1987) Photographic estimation of photosynthetically active radiation: Evaluation of a computerized technique. Oecologia 73: 525–532

Conway TJ, Tans PP, Waterman LS, Thoning KW, Kitzis DR, Masarie KA and Zhang N (1994) Evidence for interannual variability of the carbon cycle from the National Oceanic and Atmospheric Administration/Climate Monitoring and Diagnostics Laboratory Global Air Sampling Network. J Geophys Res 99(D11): 22,831–22,855

Drake BG (1989) Effects of elevated carbon dioxide on Chesapeake Bay Wetlands. V. Ecosystem and whole plant responses. Response of Vegetation to carbon dioxide. US Dept of Energy, Washington, DC, pp 105

Eamus D (1991) The interaction of rising CO_2 and temperatures with water use efficiency. Plant Cell Environ 14: 843–852

Field CB, Chapin FS III, Matson PA and Mooney HA (1992) Responses of terrestrial ecosystem's to the changing atmosphere: A resource-based approach. Ann Rev Ecol Syst 23: 201–235

Field CB, Chapin FS III, Chiariello NK, Holland EA and Mooney HA (1995) The Jasper Ridge CO_2 experiment: Design and motivation. In H Mooney & GW Koch (eds) Ecosystem Responses to Elevated Atmospheric CO_2. Academic Press (in press)

Fredeen AL, Koch GW and Field CB (1995a) Effects of atmospheric CO_2 enrichment on 'ecosystem' CO_2 exchange in a nutrient and water limited grassland. J Biogeogr 22 (in press)

Fredeen AL, Randerson JT, Holbrook NM and Field CB (1995b) Elevated atmospheric CO_2 increases late-season water availability in a water-limited grassland 'ecosystem'. Plant Cell Environment (submitted)

Garbutt K, Williams WE and Bazzaz FA (1990) Analysis of the differential response of five annuals to elevated CO_2 during growth. Ecology 71(3): 1185–1194

Houghton JT, Jenkins GJ and Ephraums JJ (1990) Climate Change: The IPCC Scientific Assessment, p 365. Cambridge University Press, Cambridge

Idso SB and Kimball BA (1993) Tree growth in carbon dioxide enriched air and its implications for global carbon cycling and maximum levels of atmospheric CO_2. Global Biogeochem Cycles 7(3): 537–555

Jackson RB, Sala OE, Field CB and Mooney HA (1994) CO_2 alters water use, carbon gain, and yield for the dominant species in a natural grassland. Oecologia 98: 257–262

Kimball BA (1983) Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. Agron J 75: 779–788

Luo Y, Jackson RB, Field CB and Mooney HA (1995) Increased soil respiration with elevated CO_2. (submitted)

Mooney HA, Drake BG, Luxmoore RJ, Oechel WC and Pitelka LF (1991) Predicting ecosystem responses to elevated CO_2 concentrations. Bioscience 41(2): 96–104

Morison JIL (1985) Sensitivity of stomata and water use efficiency to high CO_2. Plant Cell Environ 8: 467–474

Natr L (1972) Influence of mineral nutrients on photosynthesis of higher plants. Photosynthetica 6: 80–99

Natr L (1975) Influence of mineral nutrition on photosynthesis and the use of assimilates. In: Photosynthesis and Productivity in Different Environments, Int Biol Prog, vol 3, pp 537–555. Cambridge Press, Cambridge, UK

Nie D, He H, Mo G, Kirkham MB and Kanemasu ET (1992) Canopy photosynthesis and evapotranspiration of rangeland plants under doubled carbon dioxide in closed-top chambers. Agron For Met 61: 205–217

Norby RJ, Gunderson CA, Wullschleger SD, O'Neill EG and McCracken MK (1992) Productivity and compensatory responses of yellow-poplar trees in elevated CO_2. Nature 357: 322–324

Oechel WC and Strain BR (1985) Native species responses to increased atmospheric carbon dioxide concentrations. In: Strain BR & Cure JA (eds) Direct Effects of Increasing Carbon Dioxide on Vegetation, pp 117–154. US Dept of Energy, Washington DC

Oechel WC, Cowles S, Grulke N, Hastings SJ, Lawrence B, Prudhomme T, Riechers G, Strain B, Tissue D and Vourlitis G (1994)

Transient nature of CO_2 fertilization in Arctic tundra. Nature 371: 500–503

Owensby CE, Coyne PI, Ham JM, Auen LM and Knapp AK (1993) Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO_2. Ecol Appl 3(4): 644–653

Radoglou KM, Aphalo P and Jarvis PG (1992) Response of photosynthesis, stomatal conductance and water use efficiency to elevated CO_2 and nutrient supply in acclimated seedlings of *Phaseolus vulgaris* L. Ann Bot 70: 257–264

Silvola J and Ahlholm U (1992) Photosynthesis in willows (*Salix* × *dasyclados*) grown at different CO_2 concentrations and fertilization levels. Oecologia 91: 208–213

Tans PP, Fung IY and Takahashi T (1990) Observational constraints on the global atmospheric CO_2 budget. Science 247: 1431–1438

Vitousek PM and Howarth RW (1991) Nitrogen limitation on land and in the sea: How can it occur? Biogeochem 13: 87–115