

Disproportional increases in photosynthesis and plant biomass in a Californian grassland exposed to elevated CO₂: a simulation analysis

Y. LUO,* J.-L. CHEN,† J.F. REYNOLDS,† C.B. FIELD,‡ and H.A. MOONEY§

*Biological Sciences Center, Desert Research Institute, Reno, NV 89512, †Department of Botany, Duke University, Durham, NC 27708, ‡Department of Plant Biology, Carnegie Institution of Washington, 280 Panama Street, Stanford, CA 94305 and §Department of Biological Sciences, Stanford University, Stanford, CA 94305, USA

Summary

1. Elevated CO₂ concentrations often lead to increased photosynthetic carbon uptake in plants, but this does not necessarily result in a proportional increase in plant biomass. We examined this paradox for grasslands in northern California that have been exposed to elevated CO₂ since 1992. We evaluated the effects of physiological adjustments on plant growth and carbon balance of the dominant species, *Avena barbata*, using a plant growth model.

2. Without physiological adjustments, an observed 70% increase in leaf photosynthesis in elevated CO₂ was predicted to increase plant biomass by 97% whereas experimental measurements suggested 5 and 13% decreases in 1992 and 1993, respectively, and a 40% increase in 1994.

3. Simulations with an increase in carbon allocation to roots by 29%, or leaf death rate by 80%, or non-structural carbohydrate storage by 60%, or leaf mass per unit area by 25% each predicted an approximately 40% increase in plant biomass in 1994 under elevated CO₂. It follows that greater suppression of the biomass responses to elevated CO₂ in 1992 and 1993 resulted from variable combinations of these physiological adjustments.

4. This modelling study concludes that (a) an increase in carbon loss or (b) a decrease in carbon-use efficiency or (c) an increase in carbon allocation to root growth will result in an increase in biomass growth that is less than that in leaf photosynthesis under elevated CO₂. Alternatively, if carbon loss is reduced (e.g. depressed respiration) and/or carbon allocation to leaf growth is increased, biomass growth may be stimulated more than leaf photosynthesis by atmospheric CO₂ concentration. Moreover, this modelling exercise suggests that physiological adjustments may have substantial effects on ecosystem carbon processes by varying ecosystem carbon influx, litterfall and litter quality.

Key-words: *Avena barbata*, carbon allocation, Jasper Ridge, model, physiological adjustments

Functional Ecology (1997) **11**, 696–704

Introduction

Climatic factors and elevated levels of atmospheric carbon dioxide (CO₂) affect plants and ecosystems in a number of direct and indirect ways, from cellular processes to plant–herbivore interactions (Bazzaz 1990). Numerous on-going field and laboratory studies are aimed at elucidating some of these complex interactions and synthesizing them into predictive models (Koch & Mooney 1996). One example is the Jasper Ridge CO₂ Project in annual grasslands of northern California, initiated in 1992. The goal of

this project is to quantify the relative importance of resource availabilities, species characteristics and community composition in controlling the response of this ecosystem to elevated atmospheric CO₂ (Field *et al.* 1996). Modelling is an important component of this study and is based on a variety of existing models, including the generic plant simulator (GePSi) (Reynolds, Hilbert & Kemp 1993; Chen & Reynolds 1996).

In this paper we present a case study in the Jasper Ridge grassland where we used a plant simulator, GePSi, to address an observed paradox: elevated CO₂

may lead to increased photosynthetic carbon uptake, but this does not necessarily lead to a proportional increase in plant biomass. For example, photosynthetic rates under elevated CO₂ (compared with ambient conditions) increased approximately 70% for *Avena barbata*, the dominant species, in both 1993 and 1994 (Jackson *et al.* 1994, 1995). Yet the plant biomass at elevated CO₂ was decreased by 5 and 13%, respectively, in 1992 and 1993 (Field *et al.* 1996) and increased by 40% in 1994 in comparison to that at ambient CO₂ (C. B. Field *et al.*, unpublished data). The phenomenon of disproportional increases in plant biomass and photosynthesis in elevated CO₂ has also been observed in most of other ecosystem studies (see a review by Körner 1996). Young Yellow Poplar (*Liriodendron tulipifera*) trees maintained a large photosynthetic response to high CO₂ but showed no above-ground growth response (Norby *et al.* 1992). In the Chesapeake Bay, Drake & Leadley (1991) found that elevated CO₂ increased the photosynthesis rate of *Spartina* by 80%, which was accompanied by only a 40% increase in biomass.

A number of physiological processes could potentially explain these disproportional increases in growth and photosynthesis (Körner 1991, 1996), including adjustments in carbon allocation (Hirose *et al.* 1989; Poorter 1993; Luo, Field & Mooney 1994; Lambers *et al.* 1995), leaf senescence, root turnover rates (Rogers, Runion & Krupa 1994), root exudation (Norby *et al.* 1987), respiration (Amthor 1991), leaf mass per unit area (Lambers & Poorter 1992), and non-structural carbon storage (Chapin, Schulze & Mooney 1990). Above-ground litterfall, for example, increased by 100% in a Mediterranean grassland in France under elevated CO₂ concentration (Navas *et al.* 1995), indicating a large increase in leaf senescence rate. Increased leaf mass per unit area and non-structural carbon storage reduce growth efficiency per unit photosynthetically fixed carbon (Chapin *et al.* 1990), leading to less biomass growth. A small difference in carbon allocation between leaves and other parts can have an enormous influence on plant growth over time because of the compounding effect of carbon investment (Monsi & Murata 1970).

Experimental studies to identify physiological mechanisms underlying the disproportional increases in plant biomass and photosynthesis are not easy. Photosynthetically fixed carbon can be dissipated through several pathways including respiration, root exudation, root and leaf death. Monitoring these processes over time is a daunting task. In addition, measurements of root exudation and root turnover are technically quite difficult (Whipps 1990). Other complications also exist, e.g. carbon allocation, acclimation, etc. Modelling offers a way to address such complexity. The use of physiologically based simulation models have the potential to provide insights into the regulating mechanisms and to identify key processes on which experimental studies may be focused.

Indeed, growth models have been used to study relationships between leaf photosynthesis and plant biomass growth in response to different levels of nitrogen supply (Hirose 1988; Hilbert & Reynolds 1991), SO₂ stress (Mooney *et al.* 1988) and light availability (Sims, Gebauer & Pearcy 1994). Although Körner (1996) has proposed numerous possible mechanisms responsible for the CO₂-induced disproportional increases in leaf photosynthesis and biomass growth, we have not quantitatively evaluated the relative importance of these processes in regulating whole-plant and ecosystem carbon balance.

Our objective in this paper was to use GePSi to evaluate the effects of physiological adjustments on plant growth and carbon balance and thus to examine the paradox of disproportional changes in photosynthesis and biomass observed at elevated CO₂. We modified GePSi by changing some of the model structure and reparameterization based on experimental measurements on *Avena barbata* in the sandstone grassland of Jasper Ridge, northern California. We validated the model against experimental data in ambient CO₂ treatment in 1993. Instead of directly fitting model predictions with experimental data at elevated CO₂, we used the model to evaluate effects of physiological adjustments in carbon allocation between roots and shoots, non-structural carbohydrate storage, leaf death rate and leaf mass per unit area on plant growth and carbon balance. A comparison of model predictions with experimental data provides some insight into possible physiological mechanisms underlying this paradox. In addition, we examine possible effects of the physiological adjustments on ecosystem carbon processes.

Overview of model and parameterization

The generic plant simulator, GePSi, described by Chen & Reynolds (1996), evolved from the *Larrea/Pinus* model of Reynolds *et al.* (1980) and Reynolds & Cunningham (1981). GePSi combines inputs from modules for canopy, root environment, water relations and potential growth to generate whole-plant carbon and nitrogen balance (Table 1). To date, GePSi has been parameterized for chaparral shrubs (Reynolds, Acock & Whitney 1993), desert shrubs (Reynolds, Virginia & Schlesinger 1996) and Loblolly Pine (J.-L. Chen & J. Reynolds, unpublished data).

The abiotic part of GePSi includes both above- and below-ground components. In the above-ground aerial environment, the weather conditions above a canopy and the vertical profiles of micro-meteorological variables in a canopy are both used in the simulations. The below-ground soil environment is characterized by the vertical profiles of physical and chemical variables in a soil column. At Jasper Ridge, we recorded radiation, daily temperature (including minimum, maximum and mean temperature), precipitation and wind speed in a weather station near the experimental site (Table 1). These data were used to drive both

Table 1. Model structure of GePSi and sources of data from the Jasper Ridge CO₂ project for parameterization

Class	Model (GePSi)	Experimental measurement
Microclimate	Radiation, precipitation, temperature, humidity, CO ₂ , wind	Recorded from a weather station near the experimental site
Soil environment	Temperature, water, and nitrogen	Water content measured by TDR (Fredeen, Koch & Field 1995); N mineralization (Hungate <i>et al.</i> , 1996)
Canopy	Stratified canopy structure based on stem height, leaf area	Light penetration at the bottom of canopy
Photosynthesis	Farquhar & von Caemmerer (1982) model; parameters V_{cmax} , J_{max} , etc.	A/C_a curves of <i>Avena barbata</i> in field, <i>A. sativa</i> in laboratory (Jackson <i>et al.</i> 1995)
Respiration	Maintenance, growth respiration, as function of temperature	No measurement
Partitioning	Partitioning coefficients varying with phenology	Root/shoot ratio, leaf/root ratio (G. Joel, unpublished data)
Growth	Increment of biomass based on available photosynthate	Biomass data twice a year in field (Field <i>et al.</i> 1996)
Phenology	Degree-days	Chiariello (1989); recorded flowering time as affected by CO ₂

physical and biological processes in the model. The canopy structure in the sandstone grassland of the Jasper Ridge is not well developed because of the small stature of the plants and short growing seasons. Leaf area index may reach 2–3 at the peak growth period. We measured light at the bottom of the canopy

but did not characterize canopy profiles of light and temperature. Thus, we approximated the grassland canopy as a big leaf (Table 1).

Photosynthesis in GePSi is based on the leaf photosynthesis model of Farquhar & von Caemmerer (1982) as modified by Harley *et al.* (1992) and the canopy microclimate model of Caldwell *et al.* (1986) as modified by Reynolds *et al.* (1992). These components of GePSi were well suited for the Jasper Ridge grassland (Table 1). GePSi simulates both maintenance and growth respiration. The former is a function of temperature and also varies with tissue types. A lack of a mechanistic understanding of carbon allocation remains a major limitation in plant growth modelling. GePSi is no exception. Although we have developed a number of allocation models (e.g. Hilbert & Reynolds 1991; Luo *et al.* 1994) and are exploring new algorithms based on coordination theory (e.g. Reynolds & Chen 1996), we did not attempt to include these approaches in GePSi for the Jasper Ridge application. Rather, we defined carbon allocation to different plant parts following phenological patterns as observed in field experiments (Chiariello 1989; Table 1). In our simulation study, we varied the carbon allocation coefficients to explore their influences on plant growth. Phenology is controlled by degree days as observed by Chiariello (1989).

Parameter values used for whole-plant carbon balance are shown in Table 2. For comparison, the values used in GePSi for Loblolly Pine (*Pinus taeda*) are also shown. Photosynthesis is based on both field measurements of A/C_a (assimilation/ambient CO₂ concentration) response for species *A. barbata* and laboratory

Table 2. Parameterization of GePSi for the Jasper Ridge CO₂ project based on carbon processes in classes. Values used for simulation of *Pinus taeda* shown for comparison

Process/parameter	Jasper Ridge (<i>Avena barbata</i>)	Loblolly pine (<i>Pinus taeda</i>)
Photosynthesis		
V_{cmax} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	45	18
J_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	100	38.5
R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.16	0.16
Respiration		
R_G (g g^{-1})	0.33	0.33
Leaf R_m (g d^{-1})	0.02	0.02
Root R_m (g d^{-1})	0.04	0.04*
Stem R_m (g d^{-1})	0.01	0.01
Partitioning between root and shoot		
0–30 days after germination (%)	0.35	
30–90 days after germination (%)	0.23	
90–180 days after germination (%)	0.15	
Carbon storage (%)		
Root exudation rate ($\text{g g}^{-1} \text{day}^{-1}$)	0.02	N/A
Leaf senescence rate (day^{-1})	0.025	0.001
Specific leaf area ($\text{m}^2 \text{g}^{-1}$)	0.025	0.037
Root death (g g^{-1})	0.04	0.01

*, Loblolly Pine has course roots with $R_m = 0.01 \text{ g day}^{-1}$.

measurements of A/C_i (assimilation/intercellular CO₂ concentration) responses of *Avena sativa* (Jackson *et al.* 1995). Maintenance respiration for *Avena* varies with tissue types: higher for roots, low for stems. Growth respiration is the same for *Avena* and Loblolly Pine. The partitioning coefficient between shoot and roots, content of non-structural carbohydrate and specific leaf area were based on measured data, respectively, by G. Joel (unpublished data), Chu, Field & Mooney (1996) and Jackson *et al.* (1995). They vary with phenology: higher in the early growing season and lower in the late growing season (Chiariello 1989). Leaf senescence rate was chosen so that average leaf live span is 40 days for *Avena* in the grassland. Root death rate of 0.04 g g⁻¹ is equivalent to root turnover rate of 25 days.

Model behaviour

GePSi was parameterized and validated using data obtained at ambient (35 Pa) CO₂ conditions in 1993. We then use this parameterization and the validated model to predict whole-plant carbon balance at elevated (70 Pa) CO₂ conditions for the 1993–1994 growing season. Time intervals of the model simulation vary with physical and biological processes from minutes for soil heat and water transfers to 1 day for carbon partitioning. The model output is presented on a daily basis during 1994 and summarized to compare to measured values. Because the sandstone grassland is a multi-species ecosystem, measurements of plant biomass, ecosystem photosynthesis and evapotranspiration in field represent the community values. Leaf-level measurements of photosynthesis, stomatal conductance and transpiration are available only for the dominant species *A. barbata* and not for other species because these measurements are difficult with small plants. Model behaviour based on the dominant species is assumed to be representative for the grassland community.

AMBIENT CONDITIONS, MODEL VALIDATION

Predicted leaf photosynthetic rates were consistent with observed values (Fig. 1a). Photosynthetic rates were high in the early spring of 1993 and declined in the late growing season because of both declining soil water availability through the season and plant senescence (Jackson *et al.* 1994). Predicted leaf transpiration rate is consistently lower than measurements (Fig. 1b); consequently, predicted leaf water-use efficiency is higher than observed (Table 3). Predictions of leaf stomatal conductance were lower than observed values when the conductance is high and higher when the conductance is low (Fig. 1c), indicating that the model underestimates stomatal conductance in the spring and overestimates it in the late growing season.

Predicted ecosystem photosynthesis was generally consistent with observed data (Table 3). Ecosystem

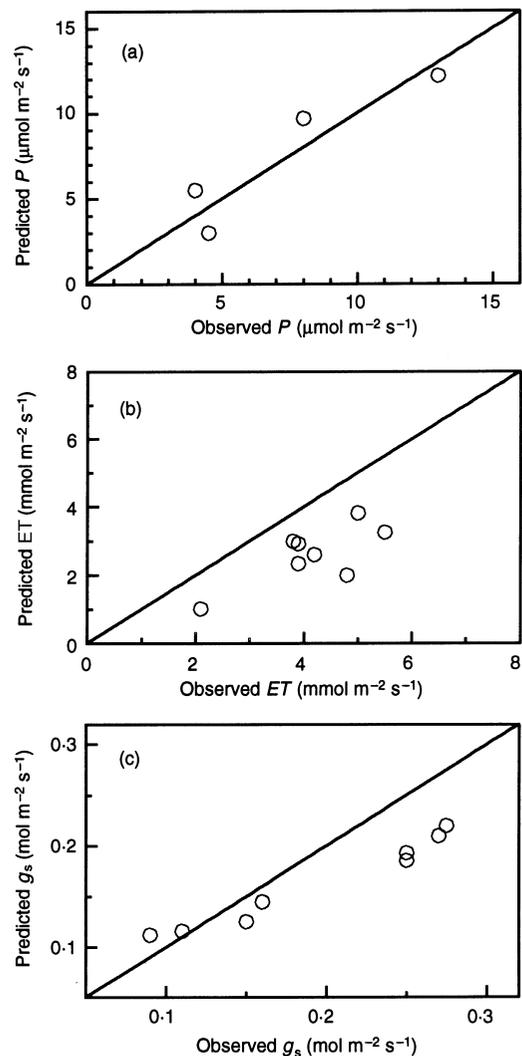


Fig. 1. Comparison of predictions and measurements of (a) midday leaf photosynthetic rate (P), (b) leaf transpiration rate (ET) and (c) stomatal conductance (g_s) from the middle of March to the middle of June 1993. Values of all the three parameters were generally higher in the early than late growing season. Experimental data were from Jackson *et al.* (1994).

photosynthesis measured in late April was 11 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Field *et al.* 1996) whereas predicted values ranged from 7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the middle of March to about 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in May. Similarly, predicted ranges of ecosystem evapotranspiration and water-use efficiency from the middle of March to May covered values of point measurements in later April (Table 3). Measured standing biomass on 5 May, 1993, the harvest date, was about 5% higher than predicted. Model predictions of litterfall was similar to field observations (Table 3).

The predicted amount of carbon that ultimately enters the soil was similar to that estimated from seasonal measurements of below-ground respiration in the grassland. The seasonal total of photosynthetically fixed carbon was estimated to be 516 g C m⁻²; shoot respiration released 25% of the fixed carbon; about 42% of the carbon was used for root respiration and

root growth; leaf and stem growth utilized 33% of the fixed carbon. Assuming shoot biomass ultimately becomes litter as carbon input to the soil, the fixed carbon entering the soil totalled $385 \text{ g C m}^{-2} \text{ year}^{-1}$ for the season. Estimated annual carbon efflux from the soil based on seasonal measurements of below-ground respiration was $325 \text{ g C m}^{-2} \text{ year}^{-1}$ on the ambient CO_2 plots and $485 \text{ g C m}^{-2} \text{ year}^{-1}$ in the natural sandstone grassland outside of the CO_2 experimental sites (Luo *et al.* 1996). Although there is a time lag between litterfall and respiration associated with microbial decomposition of the litter, the general consistency between model predictions of carbon influx into soils and measured carbon efflux out of the soils indicates the model did a reasonable job of simulating carbon dynamics in this grassland.

ELEVATED CONDITIONS, MODEL PREDICTIONS

We ran five simulations (S1–S5) to examine alternative adjustments in physiological processes in regulating plant biomass growth and whole-plant carbon balance. S1 is a standard run where leaf photosynthetic rate was set to be 70% higher in elevated CO_2 than in ambient CO_2 according to experimental measurements (Jackson

et al. 1995). All other parameters had the same value as in the ambient simulation (Table 2). In S2–S5, a single parameter value was changed: (S2) increased carbon allocation to roots from 35 to 45% of the daily fixed carbon; (S3) increased leaf death rate from 0.025 to 0.045 day^{-1} , equivalent to a reduction in live span from 40 to 22 days; (S4) increased leaf non-structural carbohydrate storage from 0.20 to 0.32; (S5) increased leaf mass per unit of area from 40 to 50 g m^{-2} without a change in leaf photosynthetic rate. The magnitude of changes in S2–S5 was selected to yield a biomass prediction on 5 May 1994 that is close to the observed one. The changes in allocation, nonstructural carbohydrate and leaf mass per unit area are also within observed ranges (Long & Drake 1992; Luo *et al.* 1994; Rogers *et al.* 1994). The large change in leaf death rate may be supported by an observation in a Mediterranean grassland in France that aboveground litterfall was increased by 100% under elevated CO_2 (Navas *et al.* 1995). In these simulation studies, we examined effects of the physiological adjustments on (1) plant biomass and gas exchanges, (2) plant seasonal carbon balance, (3) and dynamics of plant growth and carbon balance.

Plant biomass and gas exchange

Without physiological adjustment (S1), predicted plant biomass under elevated CO_2 was 441 g m^{-2} , which is 40% higher than the observed 314 g m^{-2} in the elevated CO_2 treatment (Table 4) and 97% higher than the observed 224 g m^{-2} in the ambient CO_2 treatment on 5 May 1994 (C. B. Field, unpublished data). Increasing carbon allocation to roots by 29%, leaf death rate by 80%, non-structural carbohydrate storage by 60% or leaf mass per unit area by 25% each reduced biomass production to approximately 320 g m^{-2} , close to the measured biomass in the elevated CO_2 treatment on 5 May 1994. Above-ground litter production is lowest when additional carbohydrate

Table 3. Model validation by comparing simulation results with experimental data at ambient CO_2 in 1993. Experimental data of leaf water-use efficiency (WUE) were from Jackson *et al.* 1994; midday ecosystem photosynthetic rate, evapotranspiration (ET) and WUE from Fredeen *et al.* 1995; standing biomass and above-ground litterfall on 6 May 1993 from Field *et al.* 1996

Parameter	Measurement	Simulation
Leaf WUE (g g^{-1})	1.7	5.4–10.1
Ecosystem P_n ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	11	6.8–20
Ecosystem ET ($\text{mmol m}^{-2} \text{ s}^{-1}$)	1.8	0.9–3.2
Ecosystem WUE (g g^{-1})	8.8	5.2–9.8
Biomass (g)	279	263
Litter (g)	285	250

Table 4. Predicted standing biomass on 5 May 1994, seasonal total of above-ground litterfall, midday leaf and ecosystem photosynthetic rate (P_n), stomatal conductance (g_s), leaf transpiration (Tr) and ecosystem evapotranspiration (ET), leaf and ecosystem water-use efficiency (WUE) from mid-March to mid-May 1994 at 70 CO_2 concentration. Simulation 1 (S1) is a standard simulation in which leaf photosynthetic rate was set according to experimental measurements (Jackson *et al.* 1995) and all the other parameter values were the same as in ambient CO_2 . In each of simulations S2–S5, only one parameter value was changed. In simulation 2 (S2), carbon allocation to root increased from 0.35 to 0.45% of the daily carbon assimilation. In simulation 3 (S3), leaf death rate changed from 0.025 to 0.045 per day. In simulation 4 (S4), leaf non-structural carbohydrate changed from 0.20 to 0.32. In simulation 5, leaf weight per unit of area changed from 40 to 50 g m^{-1} . Measured biomass was on 5 May 1994. Other measurements were in mid-April in 1993 for reference

Parameter	S1	S2	S3	S4	S5	Measurement
Biomass (g)	441	327	316	322	313	314
Litter (g)	341	219	290	182	172	
Leaf P_n ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	5.1–16.2	1.8–15.5	6.0–17.2	7.9–17.8	10.6–17.6	18.0
Leaf g_s ($\text{mol m}^{-2} \text{ s}^{-1}$)	0.03–0.11	0.04–0.12	0.04–0.12	0.06–0.12	0.06–0.12	0.12
Leaf Tr ($\text{mmol m}^{-2} \text{ s}^{-1}$)	0.2–1.14	0.4–1.2	0.5–1.3	0.6–1.5	0.6–1.5	2.4
Leaf WUE (g g^{-1})	12.2–22.8	13.0–22.0	13.0–20.1	10.8–20.1	10.9–20.0	7.5
Ecosystem P_n ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	5.7–31.9	2.7–25.5	3.0–26.4	3.1–20.3	3.0–23.7	12.8
Ecosystem ET ($\text{mmol m}^{-2} \text{ s}^{-1}$)	0.3–2.3	0.4–1.9	0.1–1.8	0.1–1.4	0.1–1.4	1.5
Ecosystem WUE (g g^{-1})	12.1–22.3	12.0–18.9	10.6–19.2	10.4–19.2	10.4–19.3	11.5

fixed under elevated CO₂ is stored as non-structural carbohydrate (S4) or used for increased leaf thickness without an increase in photosynthetic rate (S5). Litter production is high in the standard simulation (S1) or when leaf death rate is increased (S3).

Predicted leaf and ecosystem gas exchanges including photosynthesis, stomatal conductance, evapotranspiration (ET) and water-use efficiency (WUE) during a period from the middle of March to the middle of May 1994 are presented in Table 4. Because no experimental data are available in 1994, we listed the corresponding experimental data measured in the mid-April 1993 (Field *et al.* 1996) in Table 4 for reference. Model predictions do not vary much across these simulations in leaf-level photosynthesis, stomatal conductance, ET and WUE, but do differ in ecosystem photosynthesis and ET. Ecosystem photosynthesis and ET are highest in the standard simulation (S1) and lowest when non-structural carbohydrate is increased by 60% in S4. Ecosystem WUE is also higher in S1 than the other four simulations (S2–S4). It follows that physiological adjustments in carbon allocation, leaf death rate, non-structural carbohydrate storage and leaf mass per unit area do not change leaf gas-exchange properties but alter ecosystem gas exchanges through changes in leaf area development. In comparison to the mid-April 1993 measurements, the model over-predicts leaf WUE and under-predicts leaf ET in 1994. Model predictions in leaf photosynthesis, leaf stomatal conductance, ecosystem photosynthesis, ET and WUE in 1994 generally consistent with the experimental data in 1993 (Table 4).

Plant seasonal carbon balance

Predicted seasonal carbohydrate fixation was 2378 g biomass m⁻² under elevated CO₂ in the standard simulation (S1) (Table 5), 107% higher than 1147 g m⁻²

under ambient CO₂. An increase in either carbon allocation to roots, leaf death rate, non-structural carbohydrate storage or leaf mass per unit area in simulation experiments S2–S5 substantially reduced photosynthetic carbon fixation. Total seasonal carbon fixation was 1939, 1789, 1522 and 1500 g m⁻² (Table 5), respectively for simulations S2 through S5, 69%, 56%, 33% and 31% higher than that in ambient CO₂.

Both elevated CO₂ and physiological adjustments considerably alter carbon utilization (Table 5). In ambient CO₂ 56.5% of photosynthetically fixed carbon is utilized for leaf, stem and root growth and 43.5% for plant growth and maintenance respiration. When plants grow in elevated CO₂ without physiological adjustments (S1), portions of carbon utilized for stem and root growth are increased whereas portions for leaf growth and maintenance respiration are reduced. Increasing carbon allocation to roots in simulation experiment S2 results in decreased leaf and stem growth and increased root growth. An increase in leaf death rate, non-structural carbohydrate storage and leaf mass per unit area lead to an increased percentage of carbon used for leaf growth but a decreased percentage of carbon for maintenance respiration.

Dynamics of plant growth and carbon balance

Substantial changes in photosynthetic carbon influx and carbon utilization shown in Table 5 result from dynamic changes in plant growth and carbon investments. In comparison with plants grown at ambient CO₂, elevated CO₂ increases leaf photosynthetic rate by 70%, plant biomass growth by 97% and seasonal carbon fixation by 107% (S1), resulting from compounding effects of investing additional carbohydrate for leaf growth. As a result, leaf area index on the basis of unit ground area increases up to 5 in May 1994, nearly 70% higher than that at ambient CO₂ (Fig. 2a). Increased leaf area index (LAI) yields more canopy assimilation rate (Fig. 2b), shoot and root biomass (Fig. 2c, d). Increased carbon allocation to root growth in S2 leads to reduced carbon investment in leaf growth. As a consequence, LAI and canopy assimilation are substantially reduced in comparison to that in S1 (Fig. 2). Although the absolute root growth was 4% less in S2 than in S1, the root/shoot ratio was substantially increased and leaf and stem growth was reduced (Table 6). Increased leaf death rate in S3 substantially reduced standing leaf biomass as well as total carbon investment for leaf growth during the whole growth season. The root/shoot ratio was also reduced by increased leaf death rate (Table 6). Increased carbon storage and leaf mass per unit area in S4 and S5 proportionally reduced biomass growth in leaf, stem and root. Peak leaf area index was approximately 40% lower than that in S1 (data not presented). Thus, the seasonal total of photosynthetically fixed carbon was 36% lower than that in S1.

Table 5. Predictions of whole-plant carbon balance at ambient CO₂ and five scenarios (see descriptions in Table 4) at elevated CO₂. Components of carbon balance include seasonal totals of photosynthetic carbon influx, carbon effluxes through maintenance and growth respiration and carbon utilization for leaf, stem and root growth

	Ambient CO ₂	Elevated CO ₂				
		S1	S2	S3	S4	S5
<i>Influx (g biomass m⁻²)</i>						
Photosynthesis	1147	2378	1939	1789	1522	1500
<i>Efflux (% of the photosynthetic carbon influx)</i>						
Growth						
Leaf	23.5	22.0	19.8	24.3	24.0	24.0
Stem	9.6	10.7	8.6	10.6	10.2	9.9
Root	23.4	25.4	31.1	25.4	25.9	25.7
Total	56.5	58.2	58.5	60.3	60.1	59.7
Respiration						
Maintenance	24.7	22.6	22.2	19.7	19.9	20.5
Growth	18.7	19.3	19.3	20.0	20.0	19.8
Total	43.5	41.8	41.5	39.7	39.9	40.3

Discussion

This modelling study evaluates the consequences of differing physiological adjustments and then examines the paradox of disproportional changes in photosynthesis and biomass at elevated CO₂. The disproportionalities are a widely observed phenomenon in CO₂ research. Körner (1996) compiled data from field

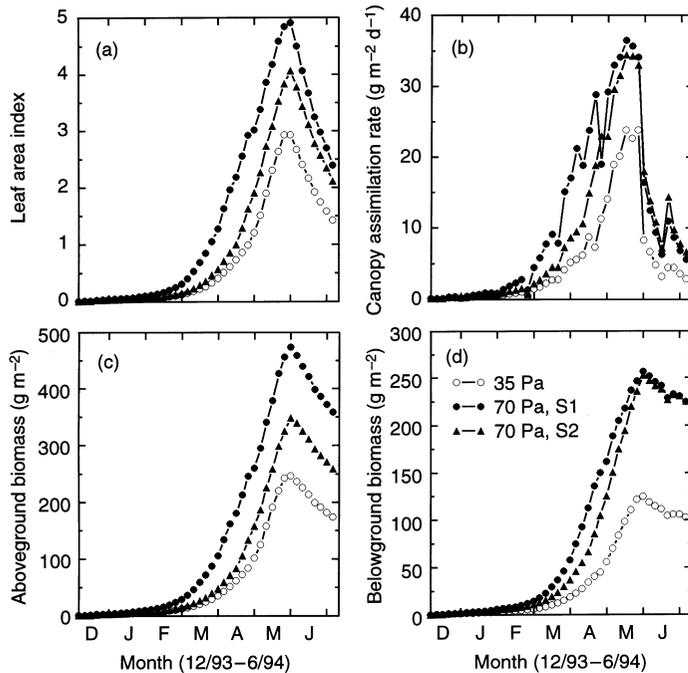


Fig. 2. Predictions of (a) leaf area index, (b) daily canopy assimilation rate, (c) above-ground biomass and (d) below-ground biomass for plants grown in ambient CO₂ (open circles), in elevated CO₂ without any physiological adjustments (S1, solid circles), in elevated CO₂ with an increase in carbon allocation to roots from 0.35 to 0.45 of daily carbon assimilation (S2, solid triangles).

Table 6. Predictions of seasonal totals of growth and death and end-seasonal standing biomass (ESSB) of leaf, stem and roots (all in g biomass m⁻²), root/shoot ratio and leaf/plant ratio calculated from seasonal totals of growth and end-seasonal standing biomass (ESSB) at ambient CO₂ and five scenarios (see descriptions in Table 4) at elevated CO₂

Organ	Components	Ambient CO ₂	Elevated CO ₂				
			S1	S2	S3	S4	S5
Leaf	Growth	269	524	384	435	365	360
	Death	206	415	290	373	252	247
	ESSB	63	109	94	62	113	113
Stem	Growth	110	255	166	189	156	149
	Death	0	0	0	0	0	0
	ESSB	110	255	166	189	156	149
Root	Growth	266	595	572	451	391	383
	Death	164	370	347	263	219	213
	ESSB	102	225	225	188	172	170
Root/shoot ratio							
	Total growth	0.70	0.76	1.04	0.72	0.75	0.75
	ESSB	0.59	0.62	0.87	0.75	0.64	0.65
Leaf/plant ratio							
	Total growth	0.42	0.38	0.34	0.40	0.40	0.40
	ESSB	0.23	0.19	0.19	0.14	0.26	0.26

experiments and found that the disproportional increases occurred in 13 out of 14 experiments, with the exception of one in the Alaskan Tundra. Understanding the disproportionalities is not only important in plant physiological studies but also crucial in balancing local ecosystem carbon balance as atmospheric CO₂ concentration increases (Canadell, Pitelka & Ingram 1996).

Using the plant growth model GePSi, our simulations conclude that without any physiological adjustments, a 70% increase in photosynthesis of *A. barbata* in the Jasper Ridge annual grassland, resulting from an increase of CO₂ concentration from 35 to 70 Pa, would lead to a 107% increase in total carbon fixation and a 97% increase in biomass. The observed decreases in 1992 and 1993 and a small increase in 1994 in plant biomass at elevated CO₂ (Field *et al.* 1996) are the result of physiological adjustments that increase carbon loss from plants (e.g. increased leaf death rate in S3) or reduce carbon allocation to leaf growth (e.g. S2) or reduce carbon-use efficiency (e.g. increased carbon storage in S4 and leaf mass per unit area in S5). Physiological processes other than the four examined in this paper that also have a potential to alter whole-plant carbon balance include root exudation (Norby *et al.* 1987), root turnover rates (Rogers *et al.* 1994) and plant respiration (Amthor, Koch & Bloom 1992). For example, the larger the root exudation and turnover rates are, the more carbon is lost from a plant, leading to less plant biomass growth. Alternatively, if plant respiration is suppressed or more carbon is allocated to leaf growth under elevated CO₂, plant biomass growth may be stimulated more than leaf photosynthesis by CO₂.

In this modelling exercise we changed each of the physiological processes (carbon allocation to root, leaf death rate, non-structural carbohydrate storage and leaf mass per unit area) to match predicted standing biomass on 5 May 1994 to the observed biomass. In reality, a plant grown in elevated CO₂ adjusts a suite of physiological and morphological processes. Any combinations of these adjustments would cause greater suppression in biomass responses to elevated CO₂, and their variation would result in yearly variation in CO₂-induced biomass changes. It is apparent that observed decreases of plant biomass in elevated CO₂ by 5% and 13% in 1992 and 1993, respectively, in the Jasper Ridge CO₂ experiments result from variable combinations of numerous physiological and morphological adjustments.

Physiological and morphological responses to elevated CO₂ are usually variable, varying with species and environmental conditions (Bazzaz 1990; Field *et al.* 1992). This study suggests that despite the variable responses, whole-plant and ecosystem carbon balance at elevated CO₂ is largely determined by leaf area development. Reduction in leaf area development at a given photosynthesis is a result of either increased carbon loss from plants through leaf death rate, root turnover and root exudation, or reduced carbon alloca-

tion to leaf growth, or decreased carbon-use efficiency by increased carbon storage, leaf and root mass per unit area, or any combinations. These changes are generally species and/or environment specific (Schäppi & Körner 1996). Experimental studies that help identify mechanisms of CO₂-induced changes in these carbon processes of an individual plant and plant community in an ecosystem will improve the understanding of whole-plant and ecosystem carbon balance in elevated CO₂.

This exercise also demonstrates that physiological adjustments differentially affect plant biomass growth and ecosystem carbon processes. An increase in either carbon allocation to roots by 29%, or leaf death rate by 80%, or non-structural carbohydrate storage by 60%, or leaf mass per unit area by 25% each leads to an approximately 40% increase in plant biomass in elevated CO₂ in 1994. These changes, however, result in differing changes in annual ecosystem carbon influx, litterfall, and possibly litter quality. For example, increased carbon allocation to roots results in a largest annual ecosystem carbon influx among the four physiological adjustments (Table 5). Increased leaf death rate (S3) leads to the largest litterfall whereas increased non-structural carbohydrate storage (S4) and leaf mass per unit area (S5) result in the smallest annual ecosystem carbon influx (Table 5) and litterfall (Table 4). In addition, litter quality may vary with these physiological adjustments. Increased leaf death rate is accompanied with the largest stem growth (Table 6) and then stem litter to the ecosystem which has the highest C/N ratio and lignin content (Chu *et al.* 1996). Such potential effects of plant physiology on terrestrial ecosystem carbon sinks have not been carefully examined at either local, regional or global scales.

In conclusion, the observed CO₂-stimulation in plant biomass growth that is much less than that in leaf photosynthesis in the Jasper Ridge as well as in many other ecosystems are caused by physiological adjustments. These adjustments result in either (1) an increase in carbon loss from a plant through leaf and root turnover and root exudation, (2) a reduction in carbon allocation to leaf growth, or (3) an decrease in carbon-use efficiency via storage of non-structural carbohydrate and increased leaf and root mass per unit surface area. Alternatively, if physiological adjustments lead to reduced carbon loss from a plant (e.g. depressed respiration) and increase carbon allocation to leaf growth, CO₂-stimulated biomass growth may be more than leaf photosynthesis. In addition, this modelling exercise indicates that these physiological adjustments may have substantial impacts on ecosystem carbon processes by varying ecosystem carbon influx, litterfall and litter quality.

Acknowledgements

We thank Nona Chiariello for providing weather data at the Jasper Ridge and Professor Christian Körner for

helpful suggestions. Y.L. acknowledges financial support by USDA NRICGP 94-37100-0345; J.-L. C. and J.F.R. by DOE grants DE-FG05-92ER61493 and DE-FG05-95ER62083 and NSF grant DEB-9524058; C.B.F. by NSF grant DEB-9020134; H.A.M. by NSF grant DEB-9020347. CIWDPB publication no. 1311.

References

- Amthor, J.S. (1991) Respiration in a future, higher CO₂ world. *Plant, Cell and Environment* **14**, 13–20.
- Amthor, J.S., Koch, G.W., & Bloom, A.F. (1992) CO₂ inhibits respiration in leaves of *Rumex crispus* L. *Plant Physiology* **98**, 757–760.
- Bazzaz, F.A. (1990) The response of natural ecosystems to the rising global CO₂ levels. *Annual Review of Ecology and Systematics* **21**, 167–196.
- Caldwell, M.M., Meister, H.P., Tenhunen, J.D. & Lange, O.L. (1986) Canopy structure, light microclimate and leaf gas exchange of *Quercus coccifera* L. in a Portuguese macchia: measurements in different canopy layers and simulations with a canopy model. *Trees* **1**, 25–41.
- Canadell, J.G., Pitelka, L.F. & Ingram, J.S.I. (1996) The effects of elevated CO₂ on plant-soil carbon below ground: a synthesis. *Plant and Soil* **187**, 391–400.
- Chapin, F.S., III, Schulze, E.-D. & Mooney, H.A. (1990) The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* **21**, 423–448.
- Chen, J.-L. & Reynolds, J.F. (1997) GePs: a generic plant simulator based on objected-oriented principles. *Ecological Modelling* **94**, 53–66.
- Chiariello, N.R. (1989) Phenology of California grasslands. *Grassland Structure and Function: California Annual Grassland* (eds L. F. Huenneke, H.A. Mooney), pp 47–58, Kluwer Academic Publishers, Dordrecht, Netherlands.
- Chu, C.C., Field, C.B. & Mooney, H.A. (1996) Effects of CO₂ and nutrient enrichment on tissue quality of two California annuals. *Oecologia* **107**, 433–440.
- Drake, B.G. & Leadley, P.W. (1991) Canopy photosynthesis of crops and native plants exposed to long-term elevated CO₂: commissioned review. *Plant, Cell and Environment* **14**, 853–860.
- Farquhar, G.D. & von Caemmerer, S. (1982) Modelling of photosynthetic response to environmental conditions. *Encyclopedia of Plant Physiology: Physiological Plant Ecology II, Water Relations and Carbon Assimilation* (eds O. L. Lange, P. S. Nobel, C. B. Osmond & H. Ziegler), pp. 549–587. Springer, Berlin, Heidelberg, New York.
- Field, C., Chapin, F.S., III, Matson, P.A. & Mooney, H.A. (1992) Responses of terrestrial ecosystems to the changing atmosphere: A resource-based approach. *Annual Review of Ecology and Systematics* **23**, 201–235.
- Field, C.B., Chapin, F.S., III, Chiariello, N.R., Holland, E.A. & Mooney, H.A. (1996) The Jasper Ridge CO₂ experiment: design and motivation. *Carbon Dioxide and Terrestrial Ecosystems* (eds G. W. Koch & H. A. Mooney), pp. 121–145. Academic Press, San Diego.
- Fredeen, A.L., Koch, G.W. & Field, C.B. (1995) Effects of atmospheric CO₂ enrichment on ecosystem CO₂ exchange in a nutrient and water limited grassland. *Journal of Biogeography* **22**, 215–220.
- Harley, P.C. Thomas, R. Reynolds, J.F. & Strain, B.R. (1992) Modeling photosynthesis of cotton grown in elevated CO₂. *Plant, Cell, and Environment* **15**, 271–282.
- Hilbert, D.W. & Reynolds, J.F. (1991) A model allocating growth among leaf proteins, shoot structure, and root biomass to produce balanced activity. *Annals of Botany* **68**, 417–425.

- Hirose, T. (1988) Modeling the relative growth rate as a function of plant nitrogen concentration. *Physiologia Plantarum* **72**, 185–189.
- Hirose, T., Lambers, H., Konings, H. & Van der Werf, A. (1989) Modeling of respiration: effect of variation in respiration on plant growth in two *Carex* species. *Functional Ecology* **3**, 655–665.
- Hungate, B.-A., Canadell, J. & Chapin, F.S., III (1996) Plant species mediate changes in soil microbial N in response to elevated CO₂. *Ecology* **77**, 2505–2515.
- Jackson, R.B., Sala, O.E., Field, C.B. & Mooney, H.A. (1994) CO₂ alters water use, carbon gain, and yield for the dominant species in a natural grassland. *Oecologia* **98**, 257–262.
- Jackson, R.B., Luo, Y., Cardon, Z.G., Sala, O.E., Field, C.B. & Mooney, H.A. (1995) Photosynthesis, growth, and density for the dominant species in a CO₂-enriched grassland. *Journal of Biogeography* **22**, 221–225.
- Koch, G. & Mooney, H.A. (eds) (1996) *Carbon Dioxide and Terrestrial Ecosystems*. Academic Press, San Diego.
- Körner, Ch. (1991) Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. *Functional Ecology* **5**, 162–173.
- Körner, Ch. (1996) The response of complex multispecies systems to elevated CO₂. *Global Changes and Terrestrial Ecosystems* (eds B. H. Walker & W. L. Steffen), pp. 20–42. Cambridge University Press, Cambridge.
- Lambers, H. & Poorter, H. (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* **23**, 187–261.
- Lambers, H., Van den Boogaard, R., Veneklaas, E.J. & Villar, R. (1995) Effects of global environmental change on carbon partitioning in vegetative plants of *Triticum aestivum* and closely related *Aegilops* species. *Global Change Biology* **1**, 397–406.
- Long, S.P. & Drake, B.G. (1992) Photosynthetic CO₂ assimilation and rising atmospheric CO₂ concentration. *Crop Photosynthesis: Spatial and Temporal Determinants* (eds N. R. Baker & H. Thomas), pp. 69–95. Elsevier Science Publishers, Amsterdam.
- Luo, Y., Field, C.B. & Mooney, H.A. (1994) Predicting responses of photosynthesis and root fraction to elevated [CO₂](a): interactions among carbon, nitrogen, and growth: theoretical paper. *Plant Cell and Environment* **17**, 1195–1204.
- Luo, Y., Jackson, R.B., Field, C.B. & Mooney, H.A. (1996) Elevated CO₂ increases belowground respiration in California grasslands. *Oecologia* **108**, 130–137.
- Monsi, M. & Murata, Y. (1970) Development of photosynthetic systems as influenced by distribution of matter. *Prediction and Measurement of Photosynthetic Productivity*. (ed I. Setlik), pp. 115–129. Pudoc, Wageningen, The Netherlands.
- Mooney, H.A., Küppers, M., Koch, G.W., Gorham, J., Chu, C.C. & Winner, W.E. (1988) Compensating effects to growth of carbon partitioning changes in response to SO₂-induced photosynthetic reduction in radish. *Oecologia* **75**, 502–506.
- Navas, M.-L., Guillermin, J.-L., Fabreguettes, J. & Roy, J. (1995) The influence of elevated CO₂ on community structure, biomass and carbon balance of mediterranean old-field microcosms. *Global Change Biology* **1**, 325–335.
- Norby, R.J., Gunderson, C.A., Wullschlegel, S.D., O'Neill, E.G. & McCracken, M.K. (1992) Productivity and compensatory response of yellow-poplar trees in elevated CO₂. *Nature* **357**, 322–324.
- Norby, R.J., O'Neill, E.G., Hood, W.G. & Luxmoore, R.J. (1987) Carbon allocation, root exudation and mycorrhizal colonization of *Pinus echinata* seedlings grown under CO₂ enrichment. *Tree Physiology* **3**, 203–210.
- Poorter, H. (1993) Interspecific variation in the growth response of plants to an elevated ambient CO₂ concentration. *Vegatatio* **104/105**, 77–97.
- Reynolds, J.F. & Chen, J.-L. (1996) Modeling shoot:root ratio in relation to carbon and nitrogen supply: coordination versus optimization. *Plant and Soil* **65–74**.
- Reynolds, J.F. & Cunningham, G.L. (1981) Validation of a primary production model of the desert shrub *Larrea tridentata* using soil-moisture augmentation experiments. *Oecologia* **51**, 357–363.
- Reynolds, J.F., Strain, B.R., Cunningham, G.L. & Knoerr, K.R. (1980) Predicting primary productivity for forest and desert ecosystem models. *Predicting Photosynthesis for Ecosystem Models*, vol. II (eds J. D. Hesketh & J. W. Jones), pp. 169–207. CRC Press, Boca Raton, FL.
- Reynolds, J.F., Chen, J.-L., Harley, P., Hilbert, D.W. & Tenhunen, J.D. (1992) Modeling the effects of elevated carbon dioxide on plants: extrapolating leaf response to a canopy. *Agriculture & Forest Meteorology* **61**, 69–94.
- Reynolds, J.F., Acock, B. & Whitney, R. (1993) Linking CO₂ experiments and modeling. *Design and Execution of Experiments on CO₂ Enrichment*, Report No. 6. (eds E.-D. Schulze & H. A. Mooney), pp. 93–106. Ecosystems Research Series of Environmental Research Programme, Commission of the European Communities, Brussels.
- Reynolds, J.F., Hilbert, D.W. & Kemp, P.R. (1993) Scaling ecophysiology from the plant to the ecosystem: a conceptual framework. *Scaling Processes Between Leaf and the Globe* (eds J. Ehleringer & C. Field), pp. 127–140. Academic Press, New York.
- Reynolds, J.F., Virginia, R.A. & Schlesinger, W.H. (1996) Defining functional types for models of desertification. *Functional Types* (eds H. H. S. T. M. Smith & F. I. Woodward), pp. 194–214. Cambridge University Press, Cambridge, UK.
- Rogers, H.H., Runion, G.B. & Krupa, S.V. (1994) Plant responses to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. *Environmental Pollution* **83**, 155–189.
- Schäppi, B. & Körner, Ch. (1996) Growth responses of an alpine grassland to elevated CO₂. *Oecologia* **105**, 43–52.
- Sims, D.A., Gebauer, R.L.E. & Percy, R.W. (1994) Scaling sun and shade photosynthetic acclimation of *Alocasia macrorrhiza* to whole-plant performance. II. Simulation of carbon balance and growth at different photon flux densities. *Plant, Cell and Environment* **17**, 889–900.
- Whipps, J.M. (1990) Carbon economy. *The Rhizosphere*. (ed J. M. Lynch), pp. 59–98. John Wiley & Sons, Chichester, NY.

Received 25 June 1996; revised 22 October 1996; accepted 6 November 1996