Oecologia (1998) 113:537–546

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Ecosystem water fluxes for two grasslands in elevated CO_2: a modeling analysis

Received: 11 March 1997 / Accepted: 23 September 1997

Abstract The need to combine data from CO_2 field experiments with climate data remains urgent, particularly because each CO_2 experiment cannot run for decades to centuries. Furthermore, predictions for a given biome need to take into account differences in productivity and leaf area index (LAI) independent of CO_2-derived changes. In this study, we use long-term weather records and field data from the Jasper Ridge CO_2 experiment in Palo Alto, California, to model the effects of CO_2 and climate variability on ecosystem water fluxes. The sandstone and serpentine grasslands at Jasper Ridge provide a range of primary productivity and LAI, with the sandstone as the more productive system. Modeled soil water availability agreed well with published observations of time-domain reflectometry in the CO_2 experiment. Simulated water fluxes based on 10-year weather data (January 1985–December 1994) showed that the sandstone grassland had a much greater proportion of water movement through plants than did the serpentine; transpiration accounted for approximately 30% of annual fluxes in the sandstone and only 10% in the serpentine. Although simulated physiological and biomass changes were similar in both grasslands, the consequences of elevated CO_2 were greater for the sandstone water budget. Elevated CO_2 increased soil drainage by 20% in the sandstone, despite an approximately one-fifth increase in plant biomass; in the serpentine, drainage increased by $<10\%$ and soil evaporation was unchanged for the same simulated biomass change. Phenological changes, simulated by a 15-day lengthening of the growing season, had minimal impacts on the water budget. Annual variation in the timing and amount of rainfall was important for water fluxes in both grasslands. Elevated CO_2 increased sandstone drainage >50 mm in seven of ten years, but the relative increase in drainage varied from 10% to 300% depending on the year. Early-season transpiration in the sandstone decreased between 26% and 41%, with elevated CO_2 resulting in a simulated water savings of 54–76 mm. Even in years when precipitation was similar (e.g., 505 and 479 mm in years 3 and 4), the effect of CO_2 varied dramatically. The response of grassland water budgets to CO_2 depends on the productivity and structure of the grassland, the amount and timing of rainfall, and CO_2-induced changes in physiology. In systems with low LAI, large physiological changes may not necessarily alter total ecosystem water budgets dramatically.

Key words Drainage · Ecosystem water budget · Leaf area index · Soil evaporation · Plant transpiration

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Introduction

The increase in atmospheric CO_2 over the last two centuries provides a clear and continuing example of global environmental change. How ecosystems will respond to this change remains an important challenge as CO_2 concentrations continue to rise (Mooney et al. 1991; Oechel et al. 1993; Pitelka 1994). For arid and semi-arid systems, it is becoming increasingly clear that changes in water dynamics with increased CO_2 can be as important as the direct effects of CO_2 on photosynthesis (Kirkham et al. 1991; Owensby et al. 1993; Field et al. 1995). Increased atmospheric CO_2 on average significantly reduces leaf-level stomatal conductance and transpiration (Morison and Gifford 1984; Polley et al. 1992; Nie et al. 1992), though tree species may not respond as dramatically as herbaceous ones (Field et al.

1995; Curtis 1996). For plants grown in the field, conductance decreased between 20 and 60% for a dominant C_4 grass in tallgrass prairie (Knapp et al. 1993), 45% for a dominant C_3 grass in California (Jackson et al. 1994), and 10–45% for cotton in Arizona (Hileman et al. 1994). Although the effect of decreased transpiration and conductance on ecosystem water fluxes depends, in part, on feedbacks from the atmosphere and on potential changes in leaf area index (LAI; e.g., Jarvis and McNaughton 1986; Allen 1990; Chaudhuri et al. 1990; Sellers et al. 1996), increased soil moisture in elevated CO_2 has now been seen in a number of grassland communities (Kirkham et al. 1991; Fredeen et al. 1997; Field et al. 1997).

Grasslands cover more of North America than any other potential vegetation type (Barbour et al. 1987), and are limited by both nitrogen and water availability (Risser 1985). The proportion of annual net primary production (NPP) allocated belowground in grasslands ranges from 50–85% (e.g., Kucera et al. 1967; Sims and Singh 1978; Jackson et al. 1996). Consequently, predicting water and carbon fluxes in grasslands must include both above- and belowground responses to CO_2. These include direct responses, such as changes in root production, and indirect ones, such as changes in plant water use and resulting effects on soil water availability and fluxes to groundwater and the atmosphere.

Several models have been used to examine the effects of CO_2 on hydrology (Aston 1984; Idso and Brazel 1984; Hatton et al. 1992). Aston (1984) and Idso and Brazel (1984) simulated elevated CO_2 by reducing leaf stomatal conductance (g_l) for watersheds in Australia and Arizona, respectively. Their studies focused primarily on changes in run-off, which generally increased in elevated CO_2 (particularly when LAI was high). Neither of those important early simulations included ecosystem feedbacks in their analysis, such as increased plant production and LAI or changes in plant species composition. To date, Hatton et al. (1992) published the most detailed analysis of the effects of increased CO_2 on hydrology. They focused on a simulated *Eucalyptus* forest at the catchment scale, with a spatially explicit landscape model of water, carbon, and energy balances. Their model indicated a slight increase in water yield, but reductions in leaf stomatal conductance were partially offset by increased leaf area. None of the previous studies was based on data from local CO_2 experiments to parameterize and validate the simulations.

We used the water model of Paruelo and Sala (1995) to compare the effects of elevated CO_2 on the water balance of two grassland communities. We were interested in a number of questions. How will elevated CO_2 change the fluxes of soil water to the atmosphere and groundwater? Under what conditions of climate and productivity will CO_2 increase soil moisture? How do these conditions change as LAI changes? We first parameterized the model based on the soils, climate, physiology, and phenology of the sandstone and serpentine grasslands at Stanford University's Jasper Ridge Biological Preserve. This parameterization, which involved no tuning of the model to soil moisture data, was then used to compare modeled soil moisture to actual time domain reflectrometry data from the field in ambient and elevated CO_2 at Jasper Ridge. We then used 10-year climate records at Jasper Ridge to simulate water dynamics for the two ecosystem types and to address the potential effects of CO_2 for grassland ecosystems. Outputs for the model included soil water availability, transpiration, soil evaporation, and drainage. The two grassland types provide a range of productivity, LAI, and water-holding capacity for comparing the role of biotic and abiotic factors.

Materials and methods

Site description

The California annual grasslands are located at the Jasper Ridge Biological Preserve in Palo Alto, California (37°24′N 122°13′W). The Mediterranean climate is characterized by cool, wet winters and warm, dry summers (Mooney et al. 1986). Average annual precipitation from 1975 to 1990 was approximately 580 mm, with a minimum of 200 mm (1975–1976) and a maximum of 1200 mm (1982–1983). CO_2 manipulations (ambient and ambient + 360 ppm CO_2) have been in place for more than 4 years on adjacent sandstone and serpentine grassland ecosystems. Species composition of the sandstone grassland is typical for cismontane California, consisting almost entirely of C_3 Eurasian annuals, including *Avena*, *Bromus*, and *Lolium* spp. (Gulmon 1979). The serpentine grassland is dominated by native C_3 annuals, including *Lasthenia*, *Plantago*, and *Vulpia* spp. Both communities have at least one prominent late-season C_3 annual, *Hemizonia congesta* ssp. *luzulifolia* and *Calycadenia multiglandulosa*, for the sandstone and serpentine, respectively. These late-season species show strong density-dependent mortality in response to water availability and could benefit the most from increased soil water availability (Chiariello 1981).

The field CO_2 manipulations were carried out in cylindrical open-top chambers, 0.65 m wide and 1 m tall (taller than all plants in the system). Three treatments with ten replicates per treatment were established in both grassland systems: no-chamber controls, chambers with ambient CO_2, and chambers with ambient + 360 ppm CO_2 (a seasonal average of 723 μmol mol^{-1} CO_2). Approximately 4500 l min^{-1} of ambient air were forced through each chamber by blowers, supplemented by 350 μmol mol^{-1} CO_2 in elevated CO_2. No fertilizer or water was added to any of the treatments. A description of the sandstone and serpentine soils can be found in Luo et al. (1996) and Jackson and Reynolds (1996). The primary description of the CO_2 experiment is in Field et al. (1996).

The model

We used the water balance model of Paruelo and Sala (1995) to examine the relationship between elevated CO_2 and climate variability (Tables 1 and 2). The model calculates on a daily basis the amount of water evaporated from the soil and transpired by the canopy. Calculations of soil evaporation are based on Ritchie (1972) which distinguishes two separate phases. During the wetter phase I, water loss is limited primarily by energy availability. The length of phase I depends on potential evaporation and soil hydraulic conductivity. Potential evapotranspiration is calculated using the equations of Priestley and Taylor (1972). During the drier phase II, evaporation is an inverse function of time and hydraulic conductivity (Ritchie 1972). Evaporation is assumed to take place only from the upper soil layer.

Table 1 Parameters for the soil water model for a given date (i), soil layer (j), and plant functional group (k)

Parameter	Value	Description
$DBEG_k$	303	Day of year corresponding to the start of the growing season for functional type k
$DEND_k$	150^4 250^5	Day of year corresponding to the end of the growing season for functional type k
$DMAX_k$	$106^{1,4}$ $76^{2,4}$ 213^5	Day of year corresponding to maximum biomass for functional type k
$ROOTS_{jk}$	$0.35\text{-}0.25\text{-}0.2\text{-}0.1\text{-}0.05\text{-}0.05^3$	Relative root density for layer j and functional type k
$THICK_j$	7.5-7.5-15-20-20-30	Soil thickness (cm) for layer j
FC_j	$30\%^1/20\%^2$	Water content at field capacity for layer j
WIP_j	6%	Water content at wilting point for layer j
SUN	70% (0% for rainy days)	Relative sunshine (a function of solar radiation)
$TPOTmax_k$	65	Maximum transpiration rate for functional type k
$LIMAW_k$	20	Threshold below which $TREAL$ decreases with EAW for functional type k

[1] Sandstone
[2] Serpentine
[3] Values for the different layers of the soil profile
[4] Early season species
[5] Late season species

Table 2 Variables for the soil water model for a given date (i), soil layer (j), and plant functional group (k)

Variable	Description
AW_{ij}	Available water for layer j on date i
PET_i	Potential evapotranspiration on date i
$TREAL_{ijk}$	Transpiration from layer j for functional type k on date i
$TPOT_{ik}$	Potential transpiration for functional type k on date i
EAW_{ik}	Available water for functional type k on date i

Transpiration is a function of potential transpiration ($TPOT_{ik}$) and water availability for each functional type. Potential transpiration (g H_2O g^{-1} green biomass day^{-1}) is calculated as:

$$TPOT_{ik} = TPOTmax_k \times (PET_i/PETtest)$$

where $TPOTmax_k$ is the maximum value of transpiration experimentally recorded during the growing season, $PETtest$ is the evapotranspiration corresponding to the day when $TPOTmax_k$ was recorded and PET_i is the potential evapotranspiration of day i.

Actual transpiration $TREAL_{ijk}$ (g H_2O g^{-1} green biomass day^{-1}) is reduced from potential transpiration as a function of soil water availability as soil water falls below a defined threshold ($LIMAW_k$) (Sala et al. 1981). The model calculates the effective available water (EAW_{ik}) by weighting the soil water content of each layer by the relative root biomass:

$$EAW_{ik} = \sum^{j} ROOTS_{jk}\ (AW_{ij}/THICK_j)$$

where $THICK_j$ is the thickness of layer j, AW_{ij} is the available H_2O in layer j (mm), $ROOTS_{jk}$ is the relative root density of functional type k in layer j, and EAW_{ik} is the effective available H_2O at time i for functional type k. Actual transpiration $TREAL_{ijk}$ is reduced compared to potential transpiration based on a linear function of EAW_{ik} when it falls below a threshold ($LIMAW_k$):

$$\begin{aligned}&\text{if } EAW_{ik} > LIMAW_k,\\ &\quad TREAL_{ijk} = TPOT_{ik}\\ &\text{if } EAW_{ik} \leq LIMAW_k,\\ &\quad TREAL_{ijk} = TPOT_{ik} - [SLOP_k\ (LIMAW_k - EAW_{ik})]\end{aligned}$$

where $SLOP_k$ is the slope of the relationship between actual transpiration and available water. $TREAL_{ijk}$ (g H_2O g^{-1} green biomass day^{-1}) is transformed to mm H_2O day^{-1} by multiplying it by the green biomass of each functional type on day i.

Water in precipitation penetrates to a soil depth that depends on precipitation amount, the water holding capacity of the soil, and the current soil water content. Only saturated (downward) water flow is considered in the model, and deep percolation corresponds to downward flow from the bottom soil layer. The model iterates the water content of each soil layer after calculating evaporation, transpiration, and downward saturated flow. Run-on and run-off are not currently included in the model, nor is macropore flow. See Paruelo and Sala (1995) for further details and additional equations.

Inputs to the model include soil parameters, plant variables, and daily weather inputs; modeled water outputs include evaporation, transpiration, soil water content, and deep percolation or drainage of soil water. The number of soil layers and plant functional types are adjustable as appropriate for a particular site. For this study we modeled two dominant functional groups, early- and late-season annuals, and divided the soil into seven layers: 0–7.5 cm, 7.5–15 cm, 15–30 cm, 30–50 cm, 50–70 cm, 70–100 cm, and >100 cm (Table 1).

The climate inputs to the model are daily measurements of maximum and minimum temperature, precipitation, and solar radiation. A 10-year dataset from a micrometeorological station at Jasper Ridge provided the inputs. There was a small amount of missing data for the ten-year period due to mechanical failure or equipment maintenance; these were filled with data from other weather stations near Jasper Ridge. The complete data set begins on 1 January 1985 and ends on 31 December 1994, so year 1 corresponds to 1985 and year 10 to 1994. Annual precipitation was 377, 556, 505, 479, 439, 804, 475, 773, 778, and 607 mm for the 10 years. Weekly precipitation was as high as 200 mm, with maxima in December or January in most years (Fig. 1).

The soil inputs to the model include soil horizon thickness, texture, the proportion of stones in each layer, bulk density, and the soil's hydraulic conductance at field capacity. The root profiles and soil bulk densities came from 5-cm-diameter soil cores taken at the time of peak biomass (R.B. Jackson, unpublished work). Modeled soil water content at field capacity and wilting point were calculated from particle size distributions using the approach of Cosby et al. (1984). Actual soil water data are from Fredeen et al. (1997) using TDR (time domain reflectometry; Tektronix Inc.). Plant parameters include the phenology of plant growth, the proportion of roots in each soil layer, maximum transpiration for each plant functional type, and ranges of biomass for each functional type. Maximum transpiration values were taken from Jackson et al. (1994) as 67 g g^{-1} day^{-1} in ambient CO_2 and 33.5 g g^{-1} day^{-1} in elevated CO_2, a maximum reduction of 50%. Average specific leaf area for the two communities was taken from Schulze et al. (1994) as 245 cm^2 g^{-1}, similar to the value obtained for the dominant species in the sandstone grassland (Jackson et al. 1995); LAI for the sandstone grassland was 2.4, twice that in the serpentine (Gamon et al. 1995). We simulated three primary treatments: ambient CO_2 (A), elevated CO_2 (E) as modeled solely through reduced transpiration, and elevated CO_2 as modeled by the same reduction in transpiration as well as an increase in plant biomass (E+B). Peak biomass for the sandstone A and E treatments was 98 g m^{-2} for

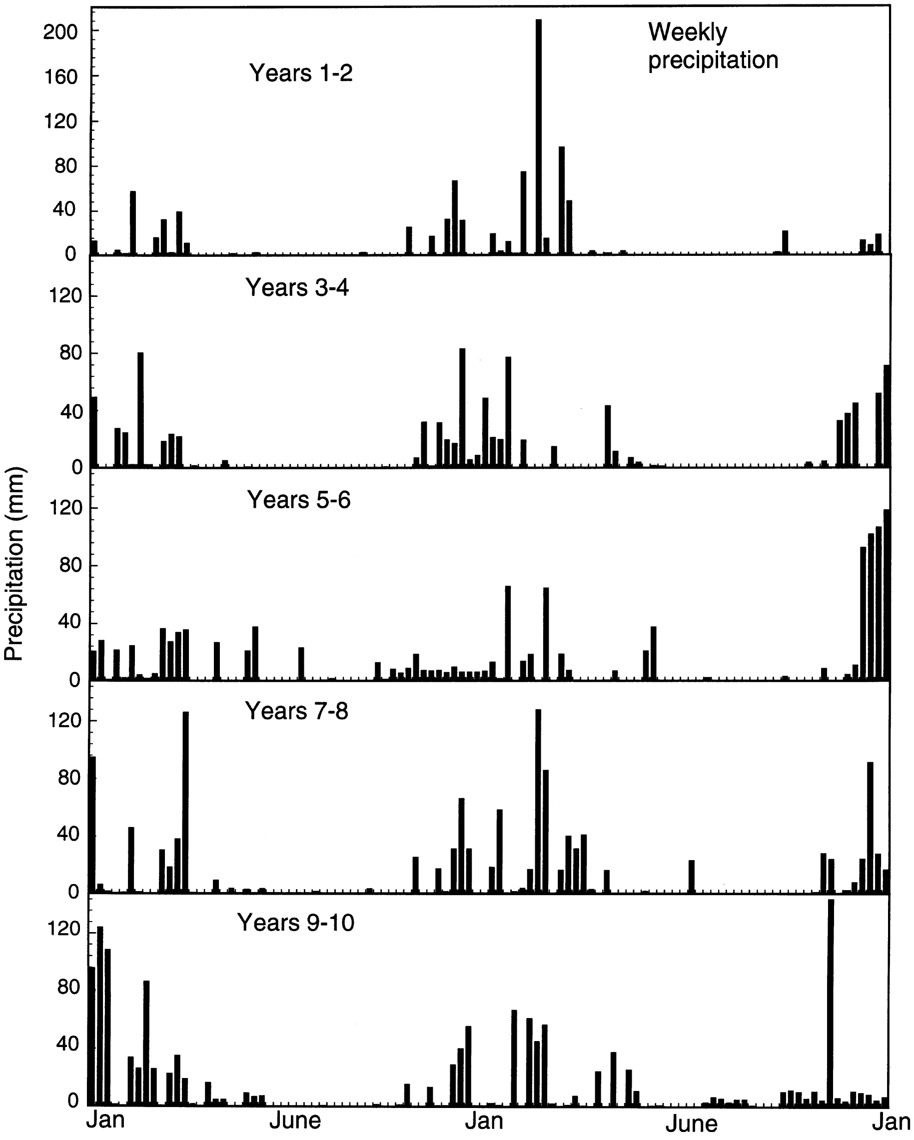

Fig. 1 Ten years of weekly precipitation for the Jasper Ridge ecosystem. The data set begins on 1 January 1985 and ends on 31 December 1994, so year 1 corresponds to 1985 and year 10 to 1994. Annual precipitation was 377, 556, 505, 479, 439, 804, 475, 773, 778, and 607 mm for years 1–10

early-season annuals and 3 g m^{-2} for late-season annuals; for the E + B treatment the simulated biomass was 118 g m^{-2} for early-season annuals (a 20% increase) and 7 g m^{-2} for late-season annuals (a three-fold increase) (Hungate et al. 1997; Field et al. 1996). Serpentine biomass values were 49 g m^{-2} and 4.5 g m^{-2} for early- and late-season annuals in the A and E treatments; for the E + B treatment the biomass was 59 g m^{-2} for early annuals (a 20% increase) and 13 g m^{-2} for late annuals (a three-fold increase). The start of the growing season was set at day-of-year 303. Peak biomass on the sandstone was assumed to occur on day-of-year 116, 1 month later than in the serpentine ecosystem. Table 1 summarizes the parameters of the model for the present analysis and the values used. Table 2 lists the outputs of the model. A copy of the model can be obtained through anonymous FTP on the internet (http://www.ifeva.edu.ar/daq/).

Paruelo and Sala (1995) performed a sensitivity analysis with four output variables (annual evaporation, annual transpiration of two plant functional types, and drainage) and nine parameters of the model using a fractional factorial design (Box et al. 1978). They increased and decreased the value of each parameter by 30% and evaluated the effect on each output variable. Evaporation was the variable least affected, and annual transpiration was sensitive mainly to changes in maximum transpiration rate and the threshold below which *TREAL* decreases with effective available water. Drainage was affected by the value of relative sunshine, mainly through the effect of this parameter on transpiration losses.

The model was evaluated by comparing simulated soil moisture with TDR data from the CO_2 experiment at Jasper Ridge (Field et al. 1995; Fredeen et al. 1997). The seasonal trajectory of simulated and observed soil moisture measurements were similar (Fig. 2). The correlation between the observed and simulated data of water content was 0.90 (n = 10, F = 32, $P < 0.01$) and 0.91 (n = 10, F = 37, $P < 0.01$) for the ambient and elevated CO_2 treatments, respectively. For both treatments the slopes and the Y-intercepts of the lines fitted to the estimated and observed data did not differ significantly from 1 or 0, respectively. The data used to test the model were not used in its calibration.

Results

Ten-year averages of simulated annual water fluxes showed large differences between the sandstone and serpentine grasslands, due primarily to differences in LAI (Fig. 3). The higher-LAI sandstone grassland had greater simulated transpiration than did the serpentine

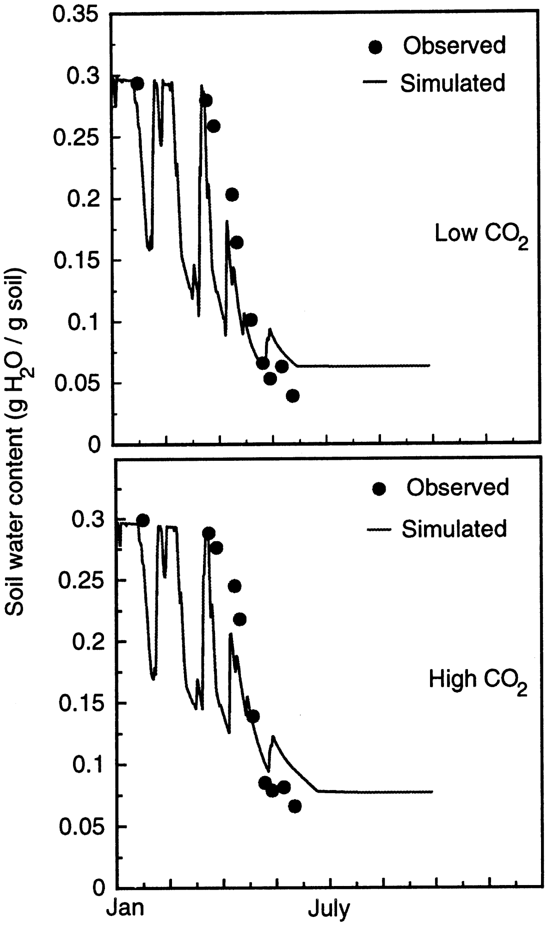

Fig. 2 Simulated and observed soil moisture in 1993 for the sandstone grassland in ambient and elevated CO_2. Observed moisture values are for the upper 15 cm of soil taken with a time-domain reflectometry system

grassland, approximately 30% of the total budget for the sandstone and 10% for the serpentine (Fig. 3; early- plus late-season transpiration). The abiotic component (soil evaporation plus drainage) showed the opposite pattern (70% vs. 90% of the annual budget for the sandstone and serpentine, respectively). The largest differences were in early-season transpiration and soil drainage. Early-season transpiration was three-fold higher in the sandstone, while drainage was approximately two-thirds that in the serpentine (Fig. 3).

Despite the similar proportional biomass and physiological changes simulated in both grasslands, the consequences of elevated CO_2 were greater in the water budgets of the sandstone than in the serpentine (Figs. 3, 4). Soil drainage from the sandstone increased 29% and 20% in E and E+B treatments compared to controls (representing 11% and 8% of the total water budget, respectively), and soil evaporation increased 3.5% and 2% for the same treatments (Figs. 3A, 4A). In the serpentine grassland, soil drainage varied <10% across treatments and soil evaporation increased by only 1% (Fig. 4B). Transpiration (early+late transpiration) decreased 44% and 22% for E and E+B in the serpentine, and 38% and 26% in the sandstone. The different patterns arose from the higher LAI in the sandstone, the greater proportion of water that move through plants in that system, and earlier plant senescence in the serpentine.

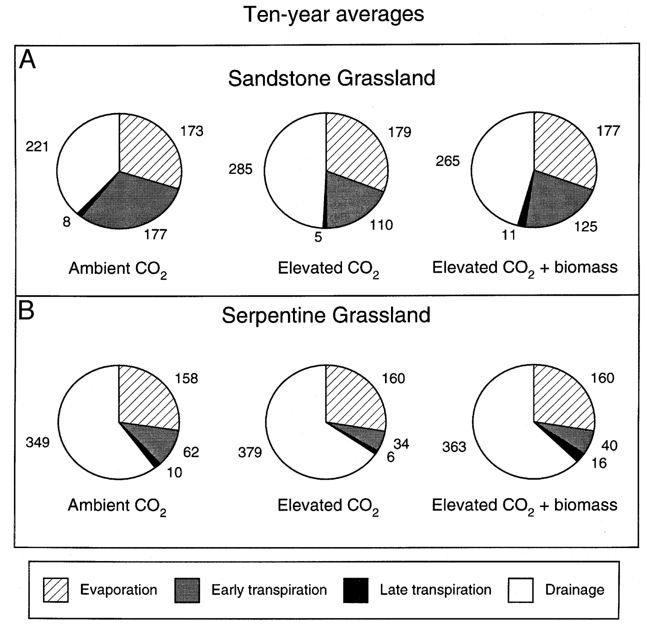

Fig. 3 Ten-year averages of simulated water fluxes (mm H_2O yr^{-1}) for the **A** sandstone and **B** serpentine grasslands. The three treatments are ambient CO_2 (*A*), elevated CO_2 (*E*) as simulated by reduced transpiration, and elevated CO_2 + biomass (20% more early-season annuals and a 3-fold increase in late-season annuals)

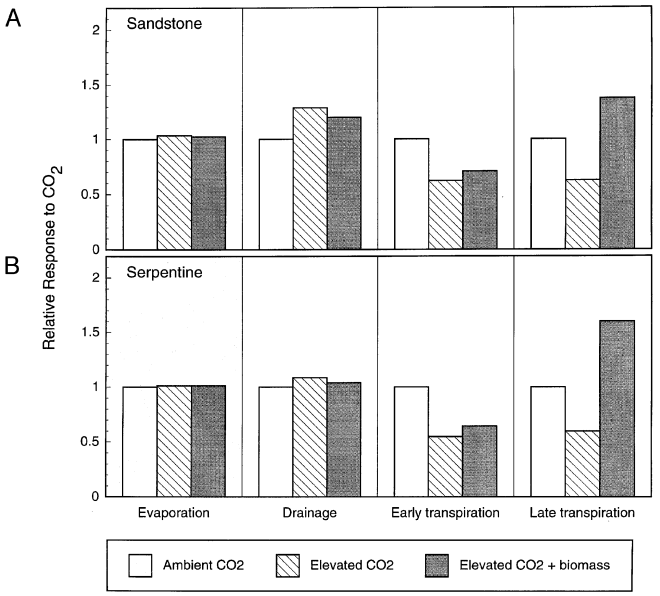

Fig. 4 Relative changes from ambient CO_2 in soil evaporation, soil drainage, early-season transpiration, and late-season transpiration in elevated CO_2 (E) and elevated CO_2 + biomass (E+B) for the **A** sandstone and **B** serpentine grasslands. Values are based on the 10-year averages from Fig. 3; the eight *ambient CO_2 bars* all equal one

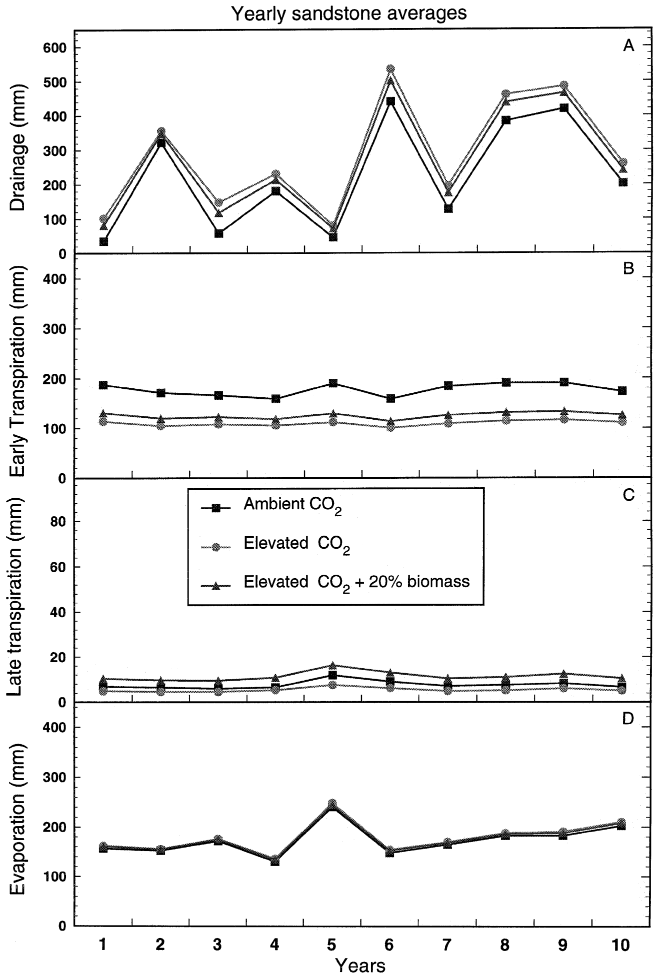

Fig. 5 Yearly values (mm H_2O) for **A** soil drainage, **B** early-season transpiration, **C** late-season transpiration, and soil evaporation in the sandstone grassland at ambient CO_2, elevated CO_2 (E) and elevated CO_2 + biomass (E + B)

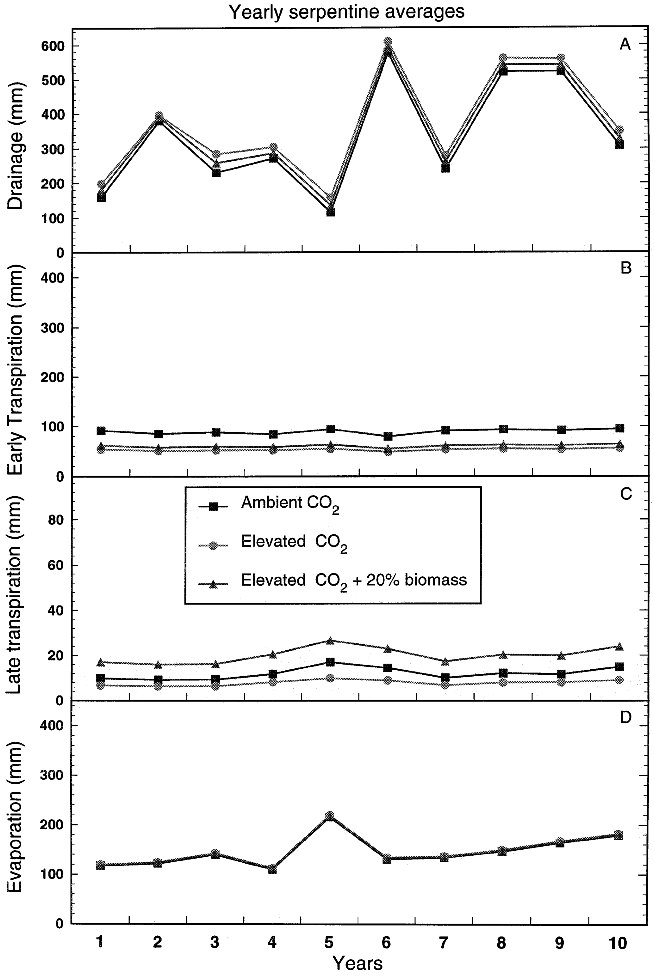

Fig. 6 Yearly values (mm H_2O) for **A** soil drainage, **B** early-season transpiration, **C** late-season transpiration, and **D** soil evaporation in the serpentine grassland at ambient CO_2, elevated CO_2 (E) and elevated CO_2 + biomass (E + B)

Yearly treatment differences showed large changes dependent on the timing and amount of rainfall (Figs. 5, 6). Compared to ambient CO_2, elevated CO_2 increased sandstone drainage by 34 mm to 94 mm depending on the year, with increases of at least 50 mm in 7 of 10 years (Fig. 5A). The relative change due to CO_2 was much greater in dry years, with drainage increasing 2.5–3-fold in years 1 and 3; the smallest relative increase was 10% in year 2. With a 20% increase in biomass (E + B), drainage in the sandstone increased > 50 mm in 3 of 10 years. Elevated CO_2 increased drainage in the serpentine between 4% and 37%, and never more than 54 mm (Fig. 6A). Early-season transpiration in the sandstone decreased between 34% and 41% for the E treatment and 26% and 32% for E + B (Fig. 5B). The related water savings were 54–76 mm and 44–61 mm for E and E + B, respectively, depending on year. The water savings by early or late transpiration were never more than 40 mm in the serpentine for any treatment (Fig. 5B, C).

Although the patterns for each ecosystem were consistent across years, the data from individual years demonstrate how the ecosystem effects of CO_2 can vary depending on the pattern of rainfall. Years 2 and 3 had similar annual precipitation (556 and 502), but rainfall in year two was concentrated in a few large rain events (Fig. 1). Those large rain events resulted in similar drainage independent of CO_2 treatment (only 33 mm more drainage at high CO_2 in year 2, a relative increase of 10%). In year 3, rainfall was more equally distributed throughout the year and simulated physiological changes due to CO_2 played a much larger role; drainage increased 91 mm at high CO_2, a 2.5-fold increase. Consequently, the same simulated biomass and physiological response to CO_2 resulted in different ecosystem consequences depending on the timing of rainfall. A comparison of years 3 and 4 is equally illuminating. Precipitation in those years was 505 mm and 479 mm respectively (Fig. 1). Despite lower precipitation in year 4, annual drainage was considerably higher for that year in all sandstone treatments (from 82 to 123 mm higher, depending on treatment). Both the amount and the timing of rainfall are critical for predicting the ecosystem consequences of elevated CO_2.

Discussion

There are strong indications that water plays an important, possibly the preeminent, role in understanding ecosystem changes in response to elevated CO_2 at Jasper Ridge. Increased soil moisture with CO_2, as has been observed in the sandstone grassland (Fredeen et al. 1997; Field et al. 1995, 1997), can affect nitrogen mineralization, rates of decomposition, and the abundance of late-season annuals dramatically at Jasper Ridge (e.g., Field et al. 1996). If grassland ecosystems are to act as net carbon sinks, long-term carbon storage (on a scale of decades to centuries) can only occur in the soil. The potential for such storage through modest increases in primary production may be offset by increased decomposition if soil moisture increases (Wildung et al. 1977). To date, while there is some evidence for modest increases in primary production at Jasper Ridge in elevated CO_2, there is no evidence of increased soil organic matter (Hungate et al. 1996).

Elevated CO_2 has the potential to alter the phenology of plant growth in this and other systems. There was some evidence for an extension of physiological activity in the data of Jackson et al. (1994) and Field et al. (1997), as plants in elevated CO_2 maintained photosynthetic activity for an additional 10–15 days. Although we have not focused on such phenological changes in this study, we did simulate the effect of a 15-day lengthening of the growing season and of the timing of peak biomass in both grasslands. Overall, the simulated changes were small. Drainage decreased slightly with the extended growing season, though never more than 7 mm per year or 4% of annual drainage in either grassland. The largest changes were in transpiration of early-season plants, which increased between 4 and 10 mm annually in both grasslands depending on treatment (3–9% of early-season transpiration). Changes in soil evaporation and late-season transpiration were negligible. While phenological changes have the potential to be quite important for a host of community and ecosystem processes, the small phenological changes observed in the field appear to have minimal consequences for the ecosystem water budget in either grassland.

Both grassland ecosystems at Jasper Ridge have relatively low productivity and green LAI (<2.5). In contrast, the range of productivity for grasslands worldwide is much greater than observed at Jasper Ridge (Coupland 1993). One might predict that as LAI increases, accompanied by an increase in the ratio of transpiration to evaporation, the biological consequences of CO_2 would become increasingly important for ecosystem water budgets. To test this idea we simulated a productive grassland with LAI = 7 and the same physiological responses and phenology as the sandstone ecosystem at Jasper Ridge (Fig. 7). For this simulated grassland, transpiration increased to approximately 50% of the annual water budget, compared to 30% for the sandstone and 10% for the serpentine ecosystems at Jasper Ridge. In addition, simulated changes due to elevated CO_2 were more important than for the Jasper Ridge ecosystems. Soil drainage increased 60% and 37% on average for E and E + B treatments in the hypothetical grassland, but the annual variation was larger than for the Jasper Ridge grasslands. Elevated CO_2 increased drainage between 3 mm and 127 mm depending on the amount and the timing of rainfall in any particular year (Fig. 7). Although it is likely that the relative effects of CO_2 on ecosystem water budgets will increase as ecosystem productivity increases, the amount and timing of rainfall also become increasingly important for predicting ecosystem water budgets with elevated CO_2.

If there is an increase in deep soil moisture in elevated CO_2 as predicted here, these results have important implications for the balance of grasses and woody plants in this and other systems. It is possible that over time the composition of the grassland would change with an increase in woody species (Polley et al. 1997). Shrubs in particular tend to be more deeply rooted than grasses (Jackson et al. 1996) and better able to extract deep soil moisture. At least one shrub, *Baccharis pilularis*, has already been identified as a grassland invader at Jasper Ridge (Williams et al. 1987; Williams and Hobbs 1989). In most years its seedlings fail to become established because the soil surface layers are relatively dry and its roots are unable to reach depths of permanently moist soil (Williams and Hobbs 1989). While other factors such as fire and land-use change will obviously play a role, the observed changes in soil moisture and the increase in deep soil moisture predicted here are exactly the kinds of conditions we expect for Jasper Ridge as atmospheric CO_2 increases. Woody plant abundance may increase in this and other systems.

Our current model has several limitations. It does not incorporate effects from leaf energy balance or the possibility of altered boundary layer depth (e.g., Jones 1983; Leuning et al. 1995; Baldocchi and Harley 1995). As an example, reduced transpiration in elevated CO_2 could increase leaf temperatures and, depending on canopy coupling to the atmosphere, result in greater transpiration than predicted based on data from single leaves. The model also does not integrate landscape processes or account for the effects of standing dead material on evaporation and transpiration. Model predictions were validated with soil moisture measurements, but the simulated partitioning between evaporation, transpiration, and drainage remains only an estimate. There may also be evolutionary changes in these annual grasses over multiple generations that we are unable to take into account, including phenological shifts in the length of the growing season (though our current analysis suggests a short lengthening of the season would likely have small effects) and ecological

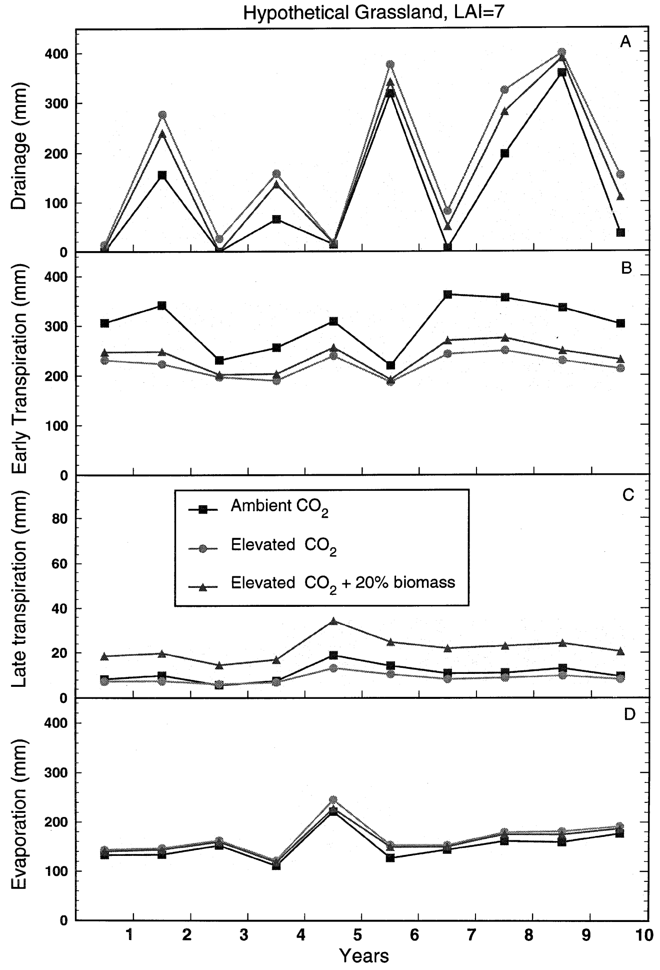

Fig. 7 Yearly values (mm H_2O) for **A** soil drainage, **B** early-season transpiration, **C** late-season transpiration and **D** soil evaporation in a hypothetical grassland with LAI = 7 at ambient CO_2, elevated CO_2 (E) and elevated CO_2 + biomass (E + B)

changes such as an increased abundance of deeply-rooted woody species. For predicting changes over evolutionary time, no CO_2 project has run sufficiently long to predict such changes accurately, and there is a great need for integrating short-term data with longer-term simulations (e.g., Bolker et al. 1995).

The data from the Jasper Ridge CO_2 experiment (e.g., Field et al. 1996; Jackson et al. 1994; Hungate et al. 1997) and this modeling analysis indicate that even if grasslands increase in biomass by the amount simulated here (and field data from several years at Jasper Ridge show no increase in biomass at all), decreases in leaf-level transpiration with CO_2 will likely outweigh small increases in LAI. This result has important consequences for recirculation of water to the atmosphere and to groundwater. In the sandstone, the simulated effect of CO_2 with no change in biomass was to shift 70 mm of water (12% of the ecosystem budget) from atmospheric circulation into relatively deep soil pools. With a simulated increase in biomass there was a similar shift of 49 mm (8% of the total budget). While the changes for the serpentine were smaller (32 and 16 mm), they were not inconsequential. Changes in the water budget, such as those simulated here, can have important effects not only for ecosystems but also for regional hydrology and continental temperatures (e.g., Pollard and Thompson 1995; Henderson-Sellers et al. 1995; Houghton et al. 1990; Sellers et al. 1996).

From the first studies that showed the antitranspirant effect of CO_2 (e.g., van Bavel 1974), reduced leaf-level conductance and transpiration for herbaceous vegetation have been a fair consistent outcome of CO_2 experiments (Bazzaz 1990). This is true whether plants were grown from sub-ambient to ambient CO_2 or ambient to elevated CO_2 (e.g., Polley et al. 1992; Rogers et al. 1983), and appears to hold for both C_3 and C_4 plants (Morison and Gifford 1984). In addition, instantaneous water-use efficiency often doubles with a doubling of CO_2 (e.g., Morison 1993; Jackson et al. 1994). Despite such dramatic responses at the leaf level, ecosystem changes tend to be buffered compared to the physiological responses observed in plants (e.g., Fredeen and Field 1995; Schäppi and Körner 1996). As demonstrated here, grassland responses to elevated CO_2 and climate variability depend not just on plant physiological changes, but on a host of larger-scale phenomena, both biotic and abiotic. These factors include the productivity of the grassland, the amount and timing of rainfall, and interactions among multiple limiting resources (Field et al. 1992). Only by combining these phenomena in large-scale field experiments and through modeling can we hope to understand and predict the ecosystem consequences of elevated atmospheric CO_2.

Acknowledgements Support for this study comes from NIGEC/DOE (TUL-038-95/98 to RBJ) and the National Science Foundation (DEB 90-20347 to H.A.M.). We thank Nona Chiariello for supplying micrometeorological data, Jon Ganz for helping format and supplement the data, and Lisa Moore and Sharron Rush for technical assistance. C.B. Field, D. Hollinger, and M.B. Kirkham provided helpful comments on the manuscript.

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