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The effect of doubled CO_2 on water use by alfalfa and orchard grass: simulating evapotranspiration using canopy conductance measurements

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Abstract

Alfalfa and orchard grass crops were grown at ambient and twice ambient carbon dioxide concentrations in field plots for several years in Beltsville, MD, using semi-open chambers. Canopy conductances throughout many days were determined from water vapour exchange measurements, and indicated significant reductions in canopy conductance to water vapour at elevated carbon dioxide in both species. However, recognizing that the artificial ventilation in the chambers made direct comparisons of evapotranspiration rates questionable, we used a soil–vegetation–atmosphere model to determine what field-scale evapotranspiration rates would have been with natural ventilation. Unlike the 'omega' approach, the model used allowed feedbacks between the canopy and the atmosphere, such that, for example, canopy conductance responses affected profiles of temperature and water vapour. Simulations indicated that although canopy conductances were lower at elevated carbon dioxide by as much as 20% in alfalfa and 60% in orchard grass, evapotranspiration rates never differed by more than 3% in alfalfa or 8% in orchard grass. Daily totals of evapotranspiration were only 1–2% lower at elevated carbon dioxide in alfalfa, and 2–5% lower in orchard grass. The results are partly explained by the fact that aerodynamic conductances to water vapour were generally smaller than the stomatal conductance, and also by canopy–atmosphere feedback processes which largely compensated for the lower conductance at elevated carbon dioxide by increasing the gradient for evaporation.

Keywords: alfalfa, canopy conductance, carbon dioxide, evapotranspiration, orchard grass, stomatal conductance

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Introduction

A reduction in evapotranspiration rate is often cited as one of the potentially more important responses of vegetation to the rising concentration of carbon dioxide in the atmosphere. A reduction in evapotranspiration could have an impact on the water requirements of vegetation as well as affecting climate. Lower evapotranspiration rate at elevated carbon dioxide concentrations has been observed in numerous studies of leaves and plants (Cure & Acock 1986; Eamus 1991), and results from the commonly measured partial closure of stomata as the carbon dioxide concentration inside the leaf increases. However, the evapotranspiration rate of continuous dense canopies of vegetation is less affected by changes in stomatal aperture than is the case with leaves or isolated plants (Jarvis & McNaughton 1986; McNaughton & Jarvis 1991) because of feedbacks between the vegetation and the atmosphere which increase in importance as the scale of interest increases from individual leaves to an extensive canopy.

Analysis of the effects of changes in stomatal conductance on water loss from corn and soybean canopies using a soil–vegetation–atmosphere model which accounts for canopy-atmosphere feedback processes has indicated that only minor reductions in evapotranspiration would occur for the typical changes in stomatal conductance associated with a doubling of atmospheric carbon dioxide (Carlson & Bunce 1995). However, the analysis of Carlson & Bunce

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(1995) used only fixed relative changes in conductance, and considered only midday evapotranspiration rates. Measurements made on plants grown at ambient and elevated carbon dioxide concentrations indicated that the amount of decrease in stomatal conductance at high carbon dioxide in some cases varied greatly with the water vapour pressure deficit (Bunce 1993), thus potentially complicating daily patterns of evapotranspiration, and making use of a constant relative change in conductance with carbon dioxide unrealistic. This paper extends the analysis of Carlson & Bunce (1995), by using the same soil–vegetation–atmosphere model combined with measurements of the responses of canopy conductance to the environment for alfalfa and orchard grass plots grown at ambient and twice ambient carbon dioxide concentrations. The effect of carbon dioxide doubling on evapotranspiration was simulated for six days throughout the 1992 growing season.

Materials and methods

Alfalfa, *Medicago sativa* L. cv. Arc, and orchard grass, *Dactylis glomerata* L. cv. Potomac were grown for several years in semi-open chambers in the field in Beltsville, Maryland. Plots were harvested and fertilized according to normal agronomic practice in the area. Details of plant management are given in Bunce (1995). Each chamber covered 1.25 m^2 of ground area and was constructed of clear acrylic. There were a total of eight chambers, two per species per carbon dioxide treatment. Chambers were continually flushed with ambient air (about 350 ppm CO_2 in the daytime) or with ambient air to which 350 ppm CO_2 was added. Air was blown into perforated plastic tubes lying on top of the soil and exited through the top. Flow rate through the chambers was constant at 2 m^3 min^{-1}. Mixing fans above the canopies created an air speed of 1 m s^{-1} across upper leaves. A clear acrylic lid held 1 cm above the side walls prevented the intrusion of outside air from interfering with water vapour exchange measurements. Chambers were watered to match precipitation. Daily mean air temperatures were 3 °C higher than outside air. Water content of air entering and leaving each chamber was sequentially measured using an optical-condensation dew point hygrometer and automated gas sampling system. Measurements of shaded, ventilated chamber air temperatures and rates of water vapour exchange were used to calculate canopy conductance to water vapour every 20 min. throughout whole days. Conductance was calculated by assuming that leaf temperature equalled air temperature for these small-leaved plants at high air speed. Measurements from early in the morning were excluded because of condensation on chamber walls and in the air sample lines. Conductances of pairs of ambient and elevated chambers were measured about weekly throughout the growing season. Significantly lower conductances at elevated carbon dioxide occurred in both species, and have been previously reported (Bunce 1995). However, because the chambers were artificially ventilated, and covered small ground areas, the observed evapotranspiration rates were not reliable indicators of what evapotranspiration rates of extensive canopies would have been under natural ventilation.

We used instantaneous estimates of canopy conductance and environment (photon flux density, air temperature and water vapour pressure deficit) to develop equations relating canopy conductance to environment separately for the two carbon dioxide treatments for each species. Frequent precipitation prevented soil water deficits from limiting conductance. We excluded data from days up to two weeks after harvests, so that only data for closed canopies were analysed. Data from a total of eight days for alfalfa and nine days for orchard grass were used to develop the equations. Days used were from 1991, 1992 and 1993 and ranged from early April to the middle of September. About 20 instantaneous measurements were obtained each day. A non-linear regression approach was used to fit the conductance data for each species and carbon dioxide treatment to a multiplicative model of conductance, with the forms of the photon flux density, vapour pressure deficit and temperature functions taken from Jones (1983). For both species and both carbon dioxide treatments the data seemed to be best summarized by a negative exponential function for photon flux density, a linear function for vapour pressure deficit, and no temperature dependence (Table 1). An exponential function for vapour pressure deficit gave slightly poorer fit so was not used. In spite of the wide range of temperatures represented in the data (6–39 °C), including a temperature response did not improve the fit, so none was used.

The values of the parameters of the regression equations converged quickly as data from different days were added, and thus were not greatly biased by the data for any particular day. For both species, the fitted value of maximum conductance was less at elevated carbon dioxide (Table 1), with the coefficients of the response to photon flux also differing significantly between carbon dioxide treatments in orchard grass (Table 1).

The stomatal response function for each species and carbon dioxide treatment was incorporated into the soil–vegetation–atmosphere model previously described (Lynn & Carlson 1990). The model simulates the progression of heat, momentum and water vapour exchanges within and above the plant canopy at three minute time steps from before sunrise to after sunset, using initial atmospheric sounding data and canopy characteristics. The model structure consists of a mixing layer, a surface

Table 1 Parameter values ± 95% confidence intervals resulting from fitting canopy conductance values to the equation: $G = G_{max} * (1\text{-}exp(-C * PFD)) * (1-D * VPD)$. G is canopy conductance in mol m^{-2} s^{-1}, G_{max} is the maximum conductance, PFD is photon flux density in µmol m^{-2} s^{-1}, VPD is water vapour pressure deficit in mPa Pa^{-1}, and C and D are constants. The degrees of freedom, and regression and residual mean squares are also given, along with the canopy height, leaf dimension and leaf area index used in the simulations.

Species	alfalfa		orchard grass	
CO_2	ambient	elevated	ambient	elevated
G_{max}	1.65 ± 0.24	1.40 ± 0.20	1.03 ± 0.13	0.68 ± 0.09
C	0.0018 ± 0.0005	0.0019 ± 0.0005	0.0016 ± 0.0004	0.0024 ± 0.0007
D	0.0262 ± 0.0038	0.0237 ± 0.0040	0.0203 ± 0.0020	0.0192 ± 0.0028
df	166	163	147	162
MS Regression	36.97	27.51	11.64	6.79
MS Residual	0.0494	0.0279	0.0121	0.0172
Canopy Height (m)	0.60		0.40	
Leaf Dimension (cm)	1.0		1.0	
Leaf Area Index	4.0		2.5	

Table 2 Simulated environmental conditions for the days in which evapotranspiration was simulated. The dew point is the predawn value, wind speed is the maximum value at 10 m height, temperature is that of the air within the canopy. Values are taken for the ambient alfalfa model output based on actual sounding data, but all model output values except the maximum temperature are the same for both species and both carbon dioxide treatments. The maximum temperature varied with the energy balance, hence it varied between species and treatments.

Date (1992)	Temperature (°C)		Dew point (°C)	Wind speed (m s^{-1})
	Minimum	Maximum		
April 14	3.3	20.2	1.3	3.2
May 15	12.5	25.2	12.3	9.4
June 15	16.3	31.8	16.3	2.3
July 17	21.7	33.7	21.7	5.8
August 13	18.3	33.1	11.8	1.9
September 15	11.8	27.5	11.8	1.9

layer and a surface transition layer, and a plant layer with an underlying soil surface. Leaf energy balance is calculated using standard equations. The model output has been tested against field measurements for a wide range of atmospheric conditions and plant types (Lynn & Carlson 1990; Carlson *et al*. 1991). Atmospheric sounding data from Dulles airport, about 60 km from the field site was obtained for six dates in 1992 (given in Table 2). These dates were chosen as clear days shortly before crops were harvested as part of normal agronomic practice. The days used varied greatly in temperature, wind speed and water vapour pressure simulated from the sounding data (Table 2). Based on data collected at harvest, leaf dimension, canopy height and leaf area index were set equal between carbon dioxide treatments, but different values of canopy height and leaf area index were used for alfalfa and orchard grass (Table 1). Model parameter values differed between carbon dioxide treatments only for maximum stomatal conductance and the coefficients of response to photon flux and water vapour pressure.

In order to illustrate reasons for the small responses of evapotranspiration rate to changes in canopy conductance, we have calculated from the model output the magnitude of the canopy resistance (reciprocal of conductance) relative to the sum of all the resistances to water vapour loss from the canopy (canopy resistance plus leaf boundary layer resistance summed for the canopy and aerodynamic resistances up to 2 m height and from 2 m to 50 m height), and examined the differences between treatments in canopy air temperature and leaf to air water vapour pressure deficit.

Results

Diurnal patterns are presented for 14 April and 15 July, the coolest and warmest days for which the model was run. The effect of doubled carbon dioxide concentration on evapotranspiration was also largest and smallest on those two days, respectively.

For the 14 April simulation for alfalfa, the elevated carbon dioxide treatment had as much as 1.18 times higher canopy resistance, but evapotranspiration was reduced by less than 3% (Fig. 1). Canopy resistance averaged about 30% of the total resistance in the ambient treatment (Fig. 1). The elevated carbon dioxide treatment had interleaf air temperatures up to 0.25 °C warmer than the ambient treatment, and a leaf to air vapour pressure deficit as much as 13% higher (Fig. 1). In orchard grass, the elevated carbon dioxide treatment had a canopy resistance up to 1.5 times higher than at lower carbon dioxide, but evapotranspiration was reduced by less than 8% (Fig. 2). Canopy resistance averaged about 40% of the total resistance in the ambient treatment (Fig. 1). The

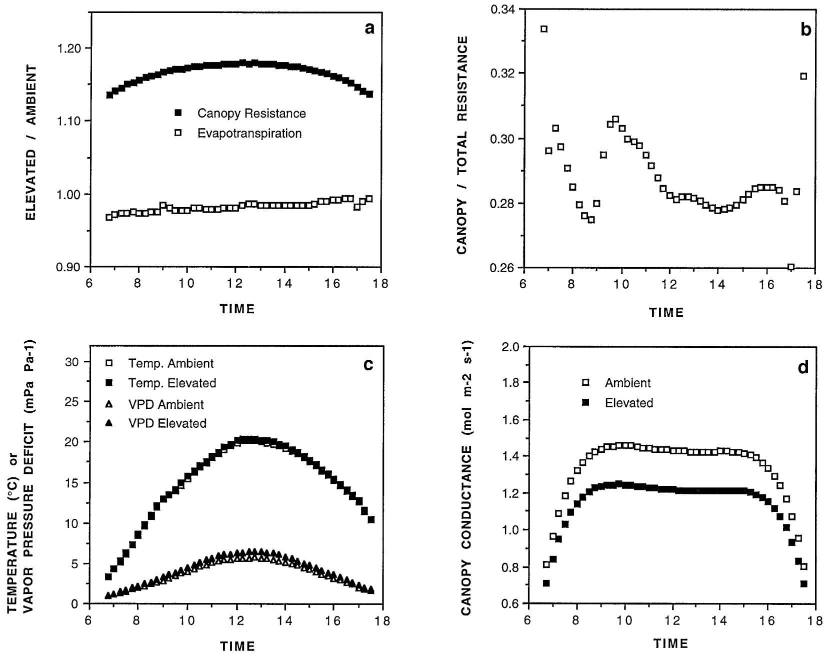

Fig. 1 Simulated diurnal patterns of water vapour exchange processes for alfalfa canopies at ambient and elevated carbon dioxide on 14 April 1992. (a) evapotranspiration and canopy resistance of elevated compared to ambient canopies. (b) Canopy resistance relative to total resistance to water vapour loss for the ambient carbon dioxide canopy. (c) Leaf temperature and the leaf to air water vapour pressure deficit of ambient and elevated canopies. (d) Canopy conductance to water vapour of ambient and elevated canopies.

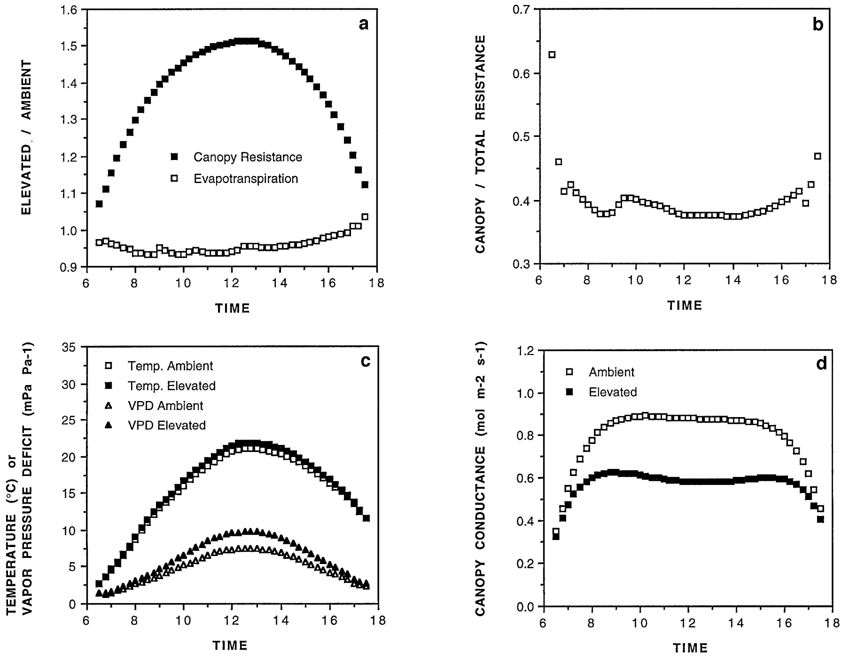

Fig. 2 Simulated diurnal patterns of water vapour exchange processes for orchard grass canopies at ambient and elevated carbon dioxide on 14 April 1992. (a) evapotranspiration and canopy resistance of elevated compared to ambient canopies. (b) Canopy resistance relative to total resistance to water vapour loss for the ambient carbon dioxide canopy. (c) Leaf temperature and the leaf to air water vapour pressure deficit of ambient and elevated canopies. (d) Canopy conductance to water vapour of ambient and elevated canopies.

elevated carbon dioxide canopy was as much as 0.8 °C warmer, and had a leaf to air vapour pressure deficit as much as 32% higher (Fig. 2). The difference in vapour pressure deficit between treatments resulted in a larger midday depression of conductance at elevated carbon dioxide. The difference between carbon dioxide treatments in temperature caused about 40–48% of the difference in leaf to air vapour pressure deficit in both species, with the remainder caused by lower water vapour pressure of air around the leaves.

In the July simulations, the midday depression of stomatal conductance by high vapour pressure deficit was larger in both species than it was in April (Fig. 3 and Fig. 4), and was larger at elevated than ambient carbon dioxide, especially in orchard grass. For alfalfa, the elevated carbon dioxide treatment had as much as 1.21 times higher canopy resistance, but evapotranspiration was reduced by less than 3% (Fig. 3). In orchard grass, the elevated carbon dioxide treatment had a canopy resistance up to 1.75 times higher than at lower carbon

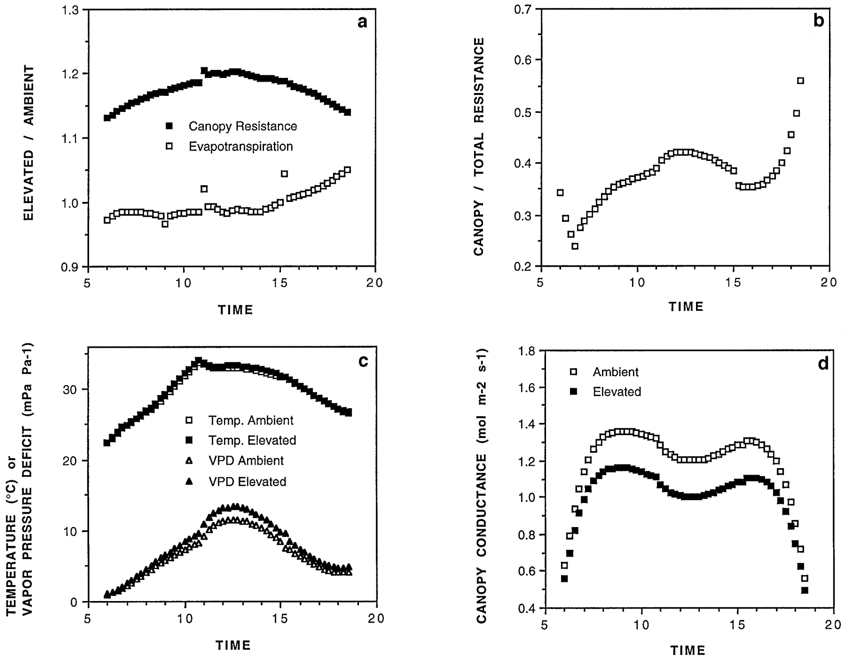

Fig. 3 Simulated diurnal patterns of water vapour exchange processes for alfalfa canopies at ambient and elevated carbon dioxide on 17 July 1992. (a) evapotranspiration and canopy resistance of elevated compared to ambient canopies. (b) Canopy resistance relative to total resistance to water vapour loss for the ambient carbon dioxide canopy. (c) Leaf temperature and the leaf to air water vapour pressure deficit of ambient and elevated canopies. (d) Canopy conductance to water vapour of ambient and elevated canopies.

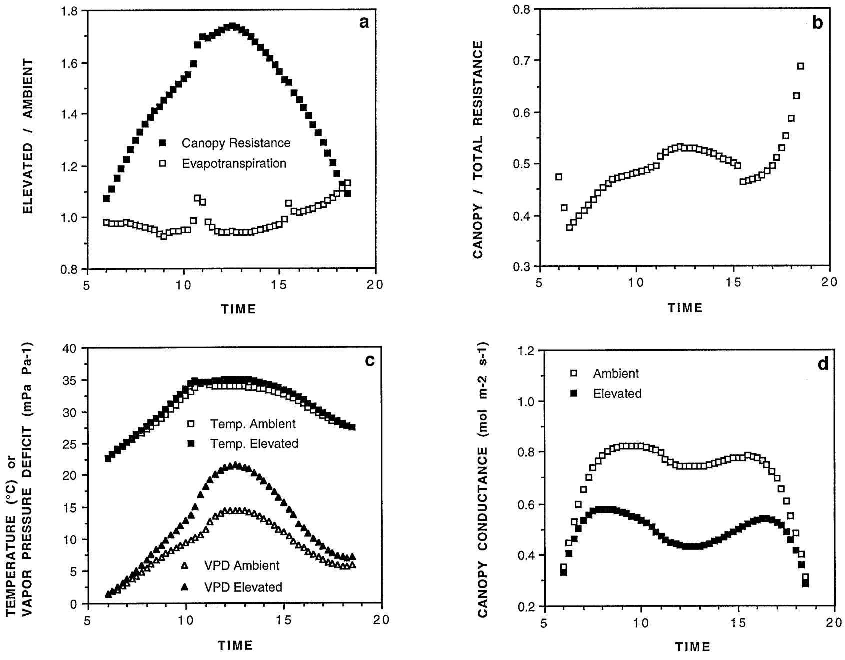

Fig. 4 Simulated diurnal patterns of water vapour exchange processes for orchard grass canopies at ambient and elevated carbon dioxide on 17 July 1992. (a) evapotranspiration and canopy resistance of elevated compared to ambient canopies. (b) Canopy resistance relative to total resistance to water vapour loss for the ambient carbon dioxide canopy. (c) Leaf temperature and the leaf to air water vapour pressure deficit of ambient and elevated canopies. (d) Canopy conductance to water vapour of ambient and elevated canopies.

dioxide, but evapotranspiration was reduced by less than 9% (Fig. 2). Canopy resistances averaged about 40% and 50% of the total resistance in the ambient alfalfa and orchard grass plots, respectively (Figs 3 and 4). The carbon dioxide treatments differed more in canopy air temperature and in leaf to air vapour pressure deficit in July than in April (Figs 3 and 4). The increased temperature at elevated carbon dioxide caused 40–60% of the increase in the leaf to air vapour pressure deficit, with the rest caused by lower water content of air around the leaves.

Daily totals of simulated evapotranspiration were less affected by carbon dioxide doubling than were the daily maxima, and did not exceed a 5% reduction at elevated carbon dioxide in orchard grass or a 2% reduction in alfalfa (Table 3). In both species, the ratio of elevated to ambient transpiration was positively correlated with maximum daily temperature (r = 0.92 and 0.93 for alfalfa

Table 3. Daily totals of simulated evapotranspiration for six days in 1992, for alfalfa and orchard plots at the ambient carbon dioxide concentration, and the ratio of simulated evapotranspiration of the elevated compared to the ambient plots for each species.

	Evapotranspiration			
Date (1992)	alfalfa ambient (mm H_2O d^{-1})	E/A	orchard grass ambient (mm H_2O d^{-1})	E/A
April 14	3.35	0.983	3.22	0.953
May 15	4.67	0.984	4.66	0.953
June 15	3.96	0.991	3.79	0.971
July 15	6.33	0.994	6.32	0.977
August 13	4.37	0.992	4.20	0.970
September 15	2.80	0.991	2.66	0.965

and orchard grass, respectively). The differences between species in evapotranspiration of the ambient carbon dioxide treatments were also no more than about 5% (Table 3), in spite of the substantial difference maximum conductance and leaf area index.

Discussion

Experimental manipulation of the carbon dioxide concentration over a large enough area of vegetation such that air even within a few metres above the canopy has equilibrated with the vegetation (hundreds of metres of fetch) has not been accomplished. Thus, there are no direct observations of the effect of increasing carbon dioxide concentrations on field-scale evapotranspiration, and we must rely on simulations to predict the response of evapotranspiration to the changes in leaf or canopy conductance observed in plants exposed to elevated carbon dioxide.

The fact that decreases in canopy conductance caused by growth at an elevated carbon dioxide concentration would result in less than proportional decreases in canopy evapotranspiration is not surprising, since canopy resistance is only one of a series of resistances affecting evapotranspiration. From the ratio of canopy resistance to the total of all resistances to evapotranspiration, we would expect evapotranspiration to change roughly from 30 to 50% as much as canopy conductance changed with carbon dioxide concentration in these crops. Actual changes in modelled evapotranspiration were much less than this estimate. This smaller change in evapotranspiration indicates the importance to evapotranspiration from extensive canopies of canopy–atmosphere feedback systems affecting the canopy environment, especially temperature and water vapour pressure deficit. The increase in canopy temperature at elevated carbon dioxide at midday consistently accounted for about 50% of the difference in leaf to air vapour pressure deficit between carbon dioxide treatments, with the remainder caused by lower water vapour pressure in the air surrounding leaves. The amount of reduction in evapotranspiration was slightly less on warm days, but there was no clear relationship with wind speed. Our results suggest that elevated carbon dioxide may have only small effects on evaportranspiration of full canopies in these species, but since we did not determine how the results might be affected by lower leaf area index, these results should not be simply extrapolated to a whole season.

The reduction in evapotranspiration rate simulated for a doubling of carbon dioxide in alfalfa and orchard grass in this study is similar to that simulated for corn and soybean canopies (Carlson & Bunce 1995). Both studies suggest fairly negligible reductions in field-scale evapotranspiration with a doubling of carbon dioxide, despite substantial measured (this study) or hypothetical (Carlson & Bunce 1995) decreases in canopy conductance. In taller canopies such as forests, a given change in leaf conductance would be expected to have more impact on evapotranspiration (Jarvis & McNaughton 1986). It is interesting to note that leaf conductance in tree species is typically much less affected by carbon dioxide concentration than in herbs (Bunce 1992; Dixon *et al.* 1995; Tesky 1995). It may be incorrect to think that rising atmospheric carbon dioxide concentrations will have a substantial effect on water use by vegetation.

Changes in temperature and vapour pressure deficit are important components of the canopy-atmosphere feedback system, and thus responses of leaf conductance to those variables are especially important in determining leaf conductance at elevated carbon dioxide. For example, in these simulations, carbon dioxide treatments often differed more in conductance than they did in maximum conductance. Since photosynthesis may be strongly affected by reductions in leaf conductance caused by high vapour pressure deficit even at elevated carbon dioxide (Bunce 1993; Eamus *et al.* 1995), it will be important to more carefully define the interactive effects of carbon dioxide, temperature and vapour pressure deficit on the gas exchange of leaves if we are to predict plant responses to the increasing concentration of carbon dioxide in the atmosphere. The simulations presented here suggest that increasing atmospheric carbon dioxide concentrations may push canopies such as alfalfa and orchard grass to higher temperatures and vapour pressure deficits, even if they do not substantially affect evapotranspiration.

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