CONCEPTS, REVIEWS, AND SYNTHESES

James A. Bunce

Carbon dioxide effects on stomatal responses to the environment and water use by crops under field conditions

Abstract Reductions in leaf stomatal conductance with rising atmospheric carbon dioxide concentration ($[CO_2]$) could reduce water use by vegetation and potentially alter climate. Crop plants have among the largest reductions in stomatal conductance at elevated $[CO_2]$. The relative reduction in stomatal conductance caused by a given increase in $[CO_2]$ is often not constant within a day nor between days, but may vary considerably with light, temperature and humidity. Species also differ in response, with a doubling of $[CO_2]$ reducing mean midday conductances by <15% in some crop species to >50% in others. Elevated $[CO_2]$ increases leaf area index throughout the growing season in some species. Simulations, and measurements in free air carbon dioxide enrichment systems both indicate that the relatively large reductions in stomatal conductance in crops would translate into reductions of <10% in evapotranspiration, partly because of increases in temperature and decreases in humidity in the air around crop leaves. The reduction in evapotranspiration in crops is similar to that in other types of vegetation which have smaller relative reductions in stomatal conductance, because of the poorer aerodynamic coupling of the canopy to the atmosphere in crops. The small decreases in evapotranspiration at elevated $[CO_2]$ may themselves be important to crop production in dry environments, but changes in climate and microclimate caused by reduced stomatal conductance could also be important to crop production.

J. A. Bunce (✉)
ACSL Plant Science Institute B-001, ARS-USDA, Beltsville Agricultural Research Center,
10300 Baltimore Avenue,
Beltsville, MD 20705-2350, USA
e-mail: buncej@ba.ars.usda.gov
Tel.: +1-301-5047629
Fax: +1-301-5045823

Introduction

The rising concentration of carbon dioxide ($[CO_2]$) in the atmosphere may affect climate not only by reducing the transfer of radiant energy from earth to space (the usual "greenhouse effect"), but also by changing the partitioning of energy between latent and sensible heat at the earth's surface (Bounoua et al. 1999). The latter may occur because leaf stomatal conductance to water vapor often decreases with increasing $[CO_2]$, potentially reducing the energy used in evaporating water from plant leaves (Bounoua et al. 1999). Recent information suggests that the relative reduction in stomatal conductance may vary substantially with vegetation type, for example between crops and forests or shrub lands (Curtis and Wang 1998; Pataki et al. 2000). In addition, the structure and seasonality of vegetation affects the partitioning of energy at the vegetation-atmosphere interface, so that any global assessment of effects of rising atmospheric $[CO_2]$ on the water cycle requires a differentiation among vegetation types.

On the global scale, crop plants are a vegetation type that needs to be considered in such an analysis, for several reasons. Crop plants cover roughly 11% of the total land surface [FAO (http://apps.fao.org/page/collections?subset=agriculture)], but cover much larger fractions of the landscape over extensive agricultural areas. Crops are major consumers of fresh water resources, so that any changes in crop water use with rising atmospheric $[CO_2]$ would have important environmental and economic impacts. Crops also have among the largest reductions in stomatal conductance at elevated $[CO_2]$ of any vegetation type (e.g., Bryant et al. 1998; Curtis and Wang 1998; Pataki et al. 2000).

Since the review by Jarvis and McNaughton (1986), it has been widely recognized that the sensitivity of transpiration or evapotranspiration to changes in stomatal aperture progressively decreases as the scale of interest increases from an individual stoma, to leaves, whole plants, canopies and extensive vegetated surfaces. Poorer aerodynamic coupling of vegetation to the atmospheric

surface layer for crops than for other types of vegetation would largely offset the effect of the larger decrease in stomatal conductance in crops, and make the reduction in canopy transpiration with $[CO_2]$ doubling similar across vegetation types (Fig. 1). This analysis makes the simplifying assumption that aerodynamic coupling is the only factor affecting how changes in stomatal conductance translate into changes in transpiration. In fact, how stomatal conductance reacts to the changes in canopy micro climate caused by poor aerodynamic coupling in crops modifies how transpiration responds to elevated $[CO_2]$ (Wilson et al. 1999), and other processes also affect the outcome (c.f. Wilson et al. 1999).

Because plants in growth cabinets, glasshouses and open-top chambers have unnatural ventilation and coupling to the atmosphere, the responses of transpiration to elevated $[CO_2]$ in these environments will not accurately reflect $[CO_2]$ effects on transpiration of naturally ventilated vegetation (e.g., McNaughton and Jarvis 1991). Even the largest experimental systems for exposing crops to elevated $[CO_2]$ are only 25 m in diameter (e.g., Pinter et al. 1996), and thus do not include all of the vegetation-atmosphere feedback processes that affect responses of evapotranspiration to changes in stomatal conductance (McNaughton and Jarvis 1991; Jacobs and De Bruin 1997; Wilson et al. 1999; Grant et al. 2001). Extrapolation to larger scales can be accomplished using soil-vegetation-atmosphere models (e.g., Bunce et al. 1997; Wilson et al. 1999) or general circulation models (e.g., Gottschalk and Gilles 2001), but realistic use of such models requires
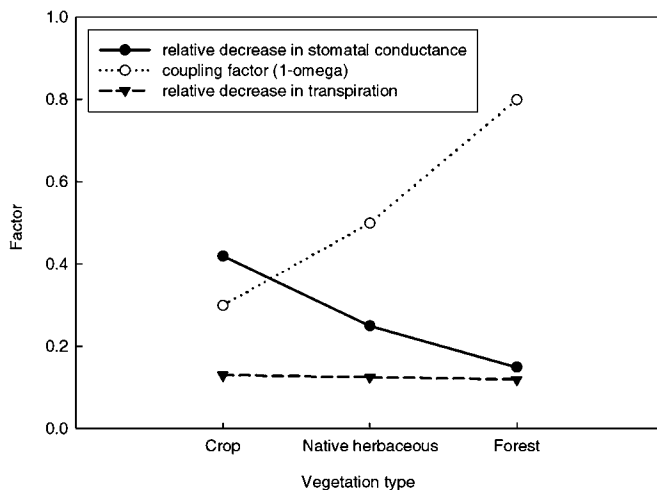

Fig. 1 Reductions in leaf stomatal conductance with a doubling of the current atmospheric carbon dioxide concentration ($[CO_2]$) for three vegetation types differing in the aerodynamic coupling between the canopy and the atmosphere, and the resulting hypothetical reductions in canopy transpiration. Reductions in leaf stomatal conductance are: (1) for crops, the area-weighted mean value from Table 1, (2) for native herbaceous vegetation, a mean value from Bryant et al. (1998), Lauber and Korner (1997) and Lee et al. (2001); and (3) for forests, a mean value from the reviews of Curtis and Wang (1998) and Medlyn et al. (2001). Average coupling factors for the vegetation types were obtained from Jarvis and McNaughton (1986). The reduction in conductance for native herbaceous vegetation is least certain, since most of the data are for less than a doubling of $[CO_2]$

information on how stomatal conductance responds to environmental factors such as light, temperature, humidity and soil moisture, as well as information on leaf area index (LAI). Considerable field-based information on this aspect of responses to elevated $[CO_2]$ now exists for most major crops, and the primary purpose of this review is to summarize that information. Results of utilizing this type of information in models of evapotranspiration will also be discussed and compared with data on responses of evapotranspiration to $[CO_2]$ in free air carbon dioxide enrichment studies.

Stomatal responses to the aerial environment at elevated $[CO_2]$

Crop species for which I found enough information to estimate a mean midday value for the ratio of conductance at approximately twice the current ambient $[CO_2]$ to that at the current ambient $[CO_2]$ are presented in Table 1. Most of the data summarized here were obtained by measuring leaf conductances under close to the ambient conditions of $[CO_2]$, light, temperature and water vapor pressure for plants which had been exposed to the $[CO_2]$ treatments since emergence. The data are restricted to amply watered and fertilized situations. The crop species in Table 1 are listed in descending order of land area covered. The most notable species absent from Table 1 because of lack of field-based information on conductance at elevated $[CO_2]$ are rice, with 1.5×10^{12} m^2 land area, and millet, with 0.4×10^{12} m^2 [FAO (http://apps.fao.org/page/collections?subset=agriculture)]. There are several other species covering about 0.2×10^{12} m^2 for which little or no information on conductance at elevated $[CO_2]$ under field conditions was found.

Two notable features of the information in Table 1 are the large differences in mean values among species, and the large day to day variation in midday values of the ratio of conductances within the same study. It is unlikely that the large variation in midday values of the ratio primarily represents measurement errors, as it is present in most such data sets. For example, Garcia et al. (1998) summarized their data for wheat as having a 36% lower midday stomatal conductances at 550 μmol mol^{-1} $[CO_2]$, but actual midday reductions varied from 10 to 55% on different days, and in sorghum Wall et al. (2001) reported a mean reduction of 37% in midday conductances at 550 μmol mol^{-1} $[CO_2]$ in the wet soil treatment, but reductions varied from 0 to 60% on different days. It seems that differences in other factors of the aerial environment may greatly influence the magnitude of the relative reduction in stomatal conductance at elevated $[CO_2]$. This important aspect is discussed later. Differences in response among groups of species are suggested by the data, but with only ten total species, they are not conclusive. Using arcsin transformation of the ratio of stomatal conductances, the monocots (wheat, barley, maize, orchard grass and sorghum) averaged larger reductions (42%) than the dicots (28%), with $P = 0.073$.

Table 1 Land area for major crops, and the mean, maximum (*Max.*) and minimum (*Min.*) ratios of midday stomatal conductance (*g*) at approximately twice the current ambient carbon dioxide concentration ([CO$_2$]) (700 µmol mol^{-1}; *g 700*) to *g* at the current ambient [CO$_2$] under field conditions (350 µmol mol^{-1}; *g 350*). The Max. and Min. values for the ratio of *g* represent day to day variation in midday values within the same study. *A* Diurnal patterns of environmental conditions, *B* day to day variation of environmental conditions, *C* short-term manipulation of environmental conditions

Species	Land area (×10^{12} m^2)	*g* 700/ *g* 350			Method	Reference
		Mean	Max.	Min.		
Wheat	2.1	0.56	0.87	0.36	B, C	Bunce (2000), Tuba et al. (1994)
Maize	1.4	0.43	–	–	C	Wilson et al. (1999)
Soybean	0.8	0.58	0.75	0.40	B, C	Wilson et al. (1999), Bunce (unpublished data)
Barley	0.5	0.66	0.86	0.42	B, C	Bunce (2000)
Sorghum	0.4	0.58	0.75	0.44	B, C	Bunce (2001a)
Cotton	0.3	0.86	1.0	0.72	B	Radin et al. (1987)
Potato	0.2	0.68	1.2	0.49	B, C	Bunce (2001a)
Beans	0.2	0.62	0.78	0.35	B	Bunce (unpublished data)
Alfalfa	0.15	0.85	–	–	A[b]	Bunce et al. (1997)
Orchard grass	0.15 [a]	0.66	–	–	A[b]	Bunce et al. (1997)

[a]Total area for all grass hay crops

[b]Canopy conductance rather than *g*

The three perennial species (alfalfa, orchard grass and cotton) averaged smaller reductions (24%) than the annuals (40%), with *P* =0.045. Cotton is a perennial species grown commercially as an annual.

There are only two crop species for which reductions in stomatal conductance at elevated [CO$_2$] can be compared between experiments conducted at different locations. They are wheat measured in Hungary, Arizona and Maryland, and sorghum measured in Arizona and Maryland. The mean reduction in midday stomatal conductance in wheat in Hungary at twice the current ambient [CO$_2$] was 39% (Tuba et al. 1994), compared with 44% in Maryland (Bunce 2000). At about 1.5 times the current ambient [CO$_2$], the mean midday reduction in stomatal conductance in Arizona was 36% (Garcia et al. 1998) and 34% in Maryland (Bunce 2000). In sorghum reductions in midday stomatal conductance at about 1.5 times the current atmospheric [CO$_2$] averaged 37% in Arizona (Wall et al. 2001) and 40% in Maryland (Bunce 2001a). Given the large day to day variation in reductions in stomatal conductance at elevated [CO$_2$] within each study, and the limited number of sampling days, these mean values are remarkably close.

For some simulations of climate change, the shape of the response of stomatal conductance to elevated [CO$_2$] may be required. Stomatal conductances of plants grown at 1.0, 1.5 and 2.0 times the current ambient [CO$_2$] have been measured in six species, wheat and barley (Bunce 2000), maize and soybean (Wilson et al. 1999), and potato and sorghum (J. A. Bunce, unpublished data). The relative reduction in stomatal conductance at 1.5 times the current ambient [CO$_2$] ranged between 50% of that at twice ambient [CO$_2$] in potato, indicating a linear response of conductance to [CO$_2$], to 95% of that at twice ambient [CO$_2$] in sorghum, indicating a nearly saturated response of conductance at 1.5 times the current [CO$_2$]. Averaged across all six species, plants at 1.5 times the current ambient [CO$_2$] had relative reductions in stomatal conductance 75% as large as the reductions at 2.0 times the current ambient [CO$_2$].

Temperature, photosynthetic photon flux density (PPFD), and leaf to air water vapor pressure difference, in addition to [CO$_2$], are known to affect stomatal conductance in many species. Additionally, there is often a correlation between photosynthetic capacity and stomatal conductance which tends to keep the ratio of internal to external [CO$_2$] constant (Wong et al. 1979). This correlation has led to the hypothesis that the relative reduction in stomatal conductance would depend on the occurrence of down regulation of photosynthesis at elevated [CO$_2$] (Bounoua et al. 1999). It is of particular interest to know how the relative reduction in stomatal conductance at elevated [CO$_2$] for a given species varies with temperature, PPFD and water vapor pressure difference. A constant relative reduction would obviously simplify the utilization of this information, but the day to day variation in the data summarized in (Table 1) suggests that a constant relative reduction is unrealistic. Another hypothesis which would provide almost as easy a simplification of the stomatal response is the Ball-Berry model of stomatal conductance: $g = b + m \times A \times H / C_a$, where *g* is stomatal conductance, *A* is CO$_2$ assimilation rate, *H* is the fractional humidity, C_a is the external [CO$_2$], and *m* and *b* are constants (Ball et al. 1987). While mechanistically incorrect, this model adequately summarizes much experimental data, and if it worked adequately for plants grown at elevated [CO$_2$], predicting stomatal conductance as a function of the aerial environment would become "merely" a problem of predicting assimilation rate. Of course, photosynthetic characteristics often change seasonally (e.g., Hikosaka et al. 1999; Medlyn et al. 2002), and constants of the Ball-

Berry model may also vary seasonally (e.g., Valentini et al. 1995).

Data to test for a constant relative reduction in stomatal conductance at elevated $[CO_2]$ or for conformity to the Ball-Berry model come from observations of diurnal or day to day variation in leaf gas exchange or from responses to short-term manipulations of environmental factors, for plants grown at different $[CO_2]$ levels. Statistical tests for variation in the relative reduction in stomatal conductance at elevated $[CO_2]$ with PPFD, temperature and water vapor pressure difference have been conducted in several studies. Effects of PPFD on the relative reduction in stomatal conductance have been examined in four species, wheat and barley (Bunce 2000), and maize and soybean (Wilson et al. 1999). A significant interaction was found in all species, with a larger relative reduction in conductance at elevated $[CO_2]$ at low PPFD (a mean reduction of 60% at 100 μmol m^{-2} s^{-1} PPFD) than at high PPFD (a mean reduction of 40% at 1,500 μmol m^{-2} s^{-1}). Additionally, canopy conductance at elevated $[CO_2]$ was reduced relatively more at low PPFD than at high PPFD in orchard grass, but not in alfalfa (Bunce et al. 1997).

An effect of temperature on the relative reduction in midday stomatal conductance at elevated $[CO_2]$ has been examined in eight species, wheat and barley (Bunce 2000), soybean and maize (Wilson et al. 1999), rice (Homma et al. 1999), cotton (Radin et al. 1987), and potato and sorghum (J. A. Bunce, unpublished data). No significant effects were found in the C_4 species maize or sorghum. In three cool climate species, wheat, barley and potato, the relative reduction in stomatal conductance at elevated $[CO_2]$ became larger at warmer temperatures, with the average reduction for these species increasing from 25% to 42% for a 10°C increase in temperature. In three warm climate species, cotton, rice and soybean, the relative reduction became much smaller at warmer temperatures, with the average reduction for these species decreasing from 49% to 10% for a 10°C increase in temperature.

An effect of vapor pressure difference on the relative reduction in stomatal conductance at elevated $[CO_2]$ has been examined in seven crop species under field conditions, wheat and barley (Bunce 2000), maize and soybeans (Wilson et al. 1999), potato and sorghum (Bunce 2003) and beans (J. A. Bunce, unpublished data). In four of these species, wheat, barley, maize, and soybeans, the relative reduction in stomatal conductance at elevated $[CO_2]$ was less at higher values of water vapor pressure difference, at least for some temperatures (Wilson and Bunce 1997; Bunce 2000). In other words, stomatal conductance was relatively less sensitive to water vapor pressure difference at elevated than at ambient $[CO_2]$. This response has also been reported in some tree species (Gunderson et al. 2002; Heath 1998). In the four crop species, the relative sensitivity of conductance to water pressure difference averaged 28% less at 700 than at 350 μmol mol^{-1} $[CO_2]$. No significant interaction occurred in the other three crop species examined. Canopy conductance was less sensitive to water vapor pressure

difference at elevated than at ambient $[CO_2]$ in orchard grass on some measurement days (Bunce 1993), although in a larger sample the reduction in sensitivity was not significant overall in either orchard grass or alfalfa (Bunce et al. 1997). In wheat, barley and soybeans, the reduction in the relative sensitivity to water vapor pressure difference at elevated $[CO_2]$ only occurred for a restricted range of lower temperatures (Wilson and Bunce 1997; Bunce 2000).

Some of these observed effects of environment on the relative reduction in stomatal conductance at elevated $[CO_2]$ are predicted by the Ball-Berry model of stomatal conductance, but many are not. Because the relative stimulation of C_3 photosynthesis by elevated $[CO_2]$ decreases slightly from light-saturated to light-limited regions (Long 1991), a larger relative reduction in stomatal conductance at elevated $[CO_2]$ at low PPFD would fit the Ball-Berry model. However, this trend did not occur in all of the C_3 species, but did occur in maize, which has C_4 metabolism. Elevated $[CO_2]$ increases the optimum temperature for photosynthesis in C_3 species (Long 1991). Therefore a decrease in the relative reduction in stomatal conductance at elevated $[CO_2]$ with increasing temperature, as observed in three warm climate C_3 species, would fit the Ball-Berry model. However, the opposite response occurred in three cool climate C_3 species. One might expect that photosynthesis would be less sensitive to reduced stomatal conductance at high water vapor pressure difference at elevated than at ambient $[CO_2]$ in C_3 species because of a smaller stomatal limitation to photosynthesis at elevated $[CO_2]$. This could explain a smaller relative reduction in stomatal conductance by high water vapor pressure difference at elevated $[CO_2]$, according to the Ball-Berry model. However, this explanation does not fit the data for soybean (Wilson and Bunce 1997), nor does it apply to maize. The interaction between temperature and $[CO_2]$ in effects of water vapor pressure difference on stomatal conductance, which has been found in wheat, barley and soybean, also does not fit the Ball-Berry model (Wilson and Bunce 1997; Bunce 2000).

The occurrence of acclimation of stomatal conductance to elevated $[CO_2]$ and its hypothesized relationship to down-regulation of photosynthesis (Bounoua et al. 1999) has been examined in four species under field conditions, wheat, barley, potato and sorghum (Bunce 2001a). Acclimation of stomatal conductance was consistently evident in wheat, potato and sorghum. Acclimation of stomatal conductance in wheat grown at twice the current ambient $[CO_2]$ was also found by Tuba et al. (1994). In wheat and potato the acclimation of stomatal conductance was tightly correlated with down-regulation of photosynthesis, such that C_i/C_a was constant (Bunce 2001a) where C_i is the internal $[CO_2]$. However, in barley, down-regulation of photosynthesis occurred without any acclimation of stomatal conductance, and in sorghum there was acclimation of stomatal conductance without any down-regulation of photosynthesis (Bunce 2001a). In the three species in which acclimation of stomatal conductance to elevated $[CO_2]$ occurred, the reduction in stomatal conductance due

to acclimation exceeded the reduction caused by direct, short-term responses to increased [CO_2].

Equations that summarize environmental responses of conductances of crop plants grown at ambient and elevated [CO_2] under field conditions have been published for seven species, alfalfa and orchard grass (Bunce et al. 1997), perennial rye grass (Nijs et al. 1997), wheat and barley (Bunce 2000), and maize and soybean (Wilson et al. 1999). For alfalfa and orchard grass, diurnal patterns of canopy conductance were used to develop Jarvis-type multiplicative functions (Jarvis 1976) for responses to PPFD, temperature and water vapor pressure difference (Bunce et al. 1997). Similarly, for maize and soybean, short-term responses of stomatal conductance to variation in PPFD, temperature and water vapor pressure difference were represented as multiplicative models (Wilson et al. 1999). For wheat and barley, midday values of stomatal conductance at high PPFD were presented as functions of temperature, water vapor pressure difference and CO_2 assimilation rate, using multiplicative, Ball-Berry, and multiple linear regression formulations (Bunce 2000). In perennial rye grass, diurnal patterns of stomatal conductance were fitted to three variations of the basic Ball-Berry

model (Nijs et al. 1997). Previously unpublished parameters of Ball-Berry models and multiple linear regression equations relating midday values of stomatal conductance to variation in temperature, water vapor pressure difference and measured assimilation rates are presented in Table 2 for potato, soybean, sorghum, and bean crops grown at the current ambient [CO_2] and at twice the current ambient [CO_2] in the field. For uniformity across species and [CO_2] treatments, coefficients are presented for the same parameters for all species in Table 2, regardless of whether they are statistically significant in a particular case (the significance is indicated in the table). Usually, equations using measured assimilation rates, either in multiple linear regressions or in the Ball-Berry model have larger R^2 values than multiplicative formulations or multiple linear regressions not using assimilation rate (Bunce 2000; Table 2). Among the six species in which both the Ball-Berry model and multiple linear regressions including assimilation rate were fit to midday values of stomatal conductance (those shown in Table 2 plus wheat and barley), the multiple linear regressions had larger R^2 values than the Ball-Berry models at both [CO_2]

Table 2 Three models relating midday (high photosynthetic photon flux density) values of g to temperature (T), leaf to air water vapor pressure difference (D) and CO_2 assimilation rate (A) for four crop species grown and measured at the current ambient [CO_2] (350 μmol mol^{-1}) or at twice the current concentration (700 μmol mol^{-1}) under field conditions

Ball-Berry model

	Intercept		Slope		r^2	
CO_2	350	700	350	700	350	700
Soybean	0.01	0.08	11.0*	5.6*	0.77	0.78
Potato	−0.36*	−0.18*	25.3*	20.8*	0.85	0.77
Bean	0.57	0.26	13.1	15.5*	0.11	0.32
Sorghum	−0.33*	−0.21*	10.9*	11.6*	0.93	0.84

Multiple linear regression including A

	Intercept		T coefficient		D coefficient		A coefficient		R^2	
CO_2	350	700	350	700	350	700	350	700	350	700
Soybean	−0.18	0.06	0.38*	0.010	−0.29*	−0.08*	0.004	0.002	0.89	0.83
Potato	−1.42*	−0.28	0.059*	0.015	−0.39*	−0.18*	0.041*	0.018*	0.81	0.71
Bean	−6.05	0.41	−0.067	0.033	0.97	−0.38*	0.34*	−0.001	0.52	0.45
Sorghum	−1.09*	−0.04	0.029	−0.019	−0.23*	−0.01	0.026*	0.019*	0.94	0.91

Multiple linear regression without A

	Intercept		T coefficient		D coefficient		R^2	
CO_2 (μmol mol^{-1})	350	700	350	700	350	700	350	700
Soybean	0.04	0.24	0.037*	0.007	−0.32*	−0.092*	0.87	0.66
Potato	−0.19	0.27	0.063*	0.023	−0.67*	−0.33*	0.67	0.56
Bean	1.33	0.43	−0.005	0.026	−0.26	−0.35*	0.08	0.44
Sorghum	−0.065	0.54	0.054*	0.013	−0.60*	−0.35*	0.82	0.72

Ranges of T, D, A and g

CO_2 (μmol mol^{-1})	350				700	
Species	T	D	A	g	A	g
Soybean	32–37	0.6–3.7	13–31	0.2–2.6	23–49	0.15–1.6
Potato	24–37	0.8–3.3	11–25	0.2–1.6	17–42	0.15–1.2
Bean	24–32	0.6–2.4	19–26	0.4–2.0	17–36	0.25–1.3
Sorghum	29–35	1.1–2.5	35–59	0.3–1.1	40–66	0.15–0.7

*P =0.05 (term significantly different from 0)

levels in all species except potato, where the Ball-Berry models had slightly higher R^2 values.

Stomatal responses to soil water deficits at elevated [CO_2]

Leaf stomatal conductances decrease as soils dry, either in response to drying of roots or leaves, or both (c.f. Bunce 1999). Numerous studies in controlled environments have shown that elevated [CO_2] can delay soil drying and stomatal closure. However, in predicting effects of rising atmospheric [CO_2] on evapotranspiration under field conditions, it is important to determine whether the relative reduction in stomatal conductance by elevated [CO_2] depends on soil water deficits. This is technically difficult to accomplish under field conditions, because different rates of soil drying among [CO_2] treatments imply that stomatal conductances measured at the same soil water content are measured on different days, with potentially different aerial environmental conditions. Under more controlled conditions it is possible to standardize rates of soil drying across [CO_2] treatments, but stomatal responses to water deficits are notoriously sensitive to prior conditions, making this approach some-

what less desirable. Partly because of the technical problems, there is less information on [CO_2] effects on crop stomatal conductance responses to water deficits than on most other aspects of stomatal responses to environment.

Experiments in growth chambers, where uniform rates of soil drying were imposed at ambient and elevated [CO_2], indicated that [CO_2] did not affect the relative reduction of transpiration rate by soil water deficits in wheat (Mitchell et al. 2001). Similar results were obtained for soybeans in glasshouses (Seffaj et al. 1999), but in this experiment plants were exposed to elevated carbon dioxide for only 2 days before the soil water depletion treatments began. For both wheat and soybean, transpiration began to decline when about 60% of the available soil water was depleted. In experiments with maize and soybeans (Wilson et al. 1999), plants that were grown in pots filled with soil in open-top chambers in the field were moved into controlled-environment chambers to impose soil water deficits. The results (Fig. 2) indicated that stomatal conductance decreased with leaf water potential to the same relative extent at 350 and at 700 μmol mol^{-1} [CO_2] in both species. Thus, based on very limited information, it appears that water deficits may not alter the relative response of stomatal conductance to elevated
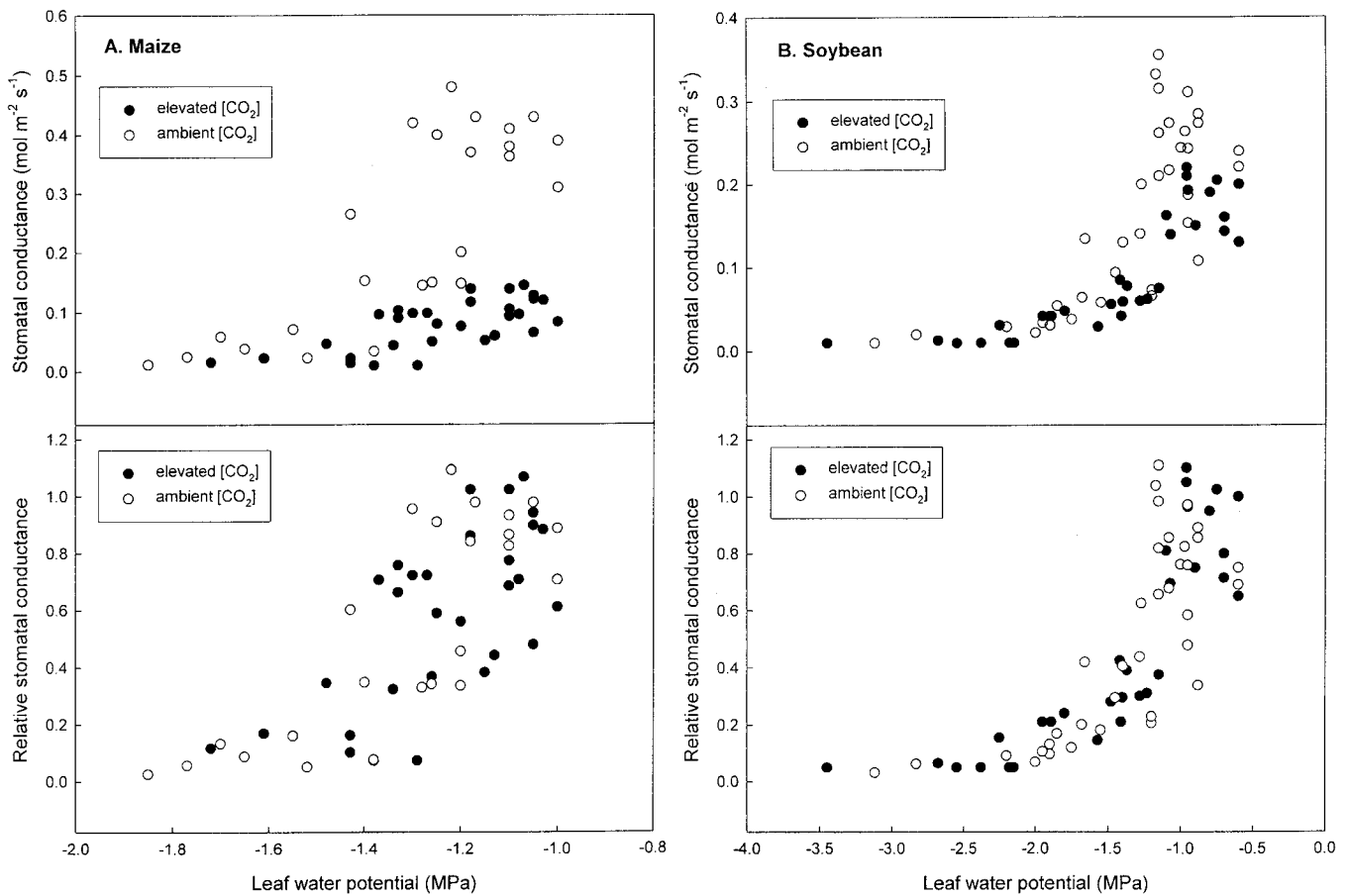

Fig. 2 Responses of stomatal conductance to leaf water potential for maize (**A**) and soybean (**B**) grown and measured at the current ambient [CO_2] or at twice the current ambient [CO_2] under field conditions. See text for details. For each species both absolute values of conductance and conductances relative to the mean values of well-watered plants are given

[CO_2]. However, another equally valid way of interpreting the data in Fig. 2 is that the difference between [CO_2] treatments in the absolute values of stomatal conductance becomes very small under dry conditions.

Responses of LAI to elevated [CO_2]

The rate of transpiration of a plant increases with the leaf area of the plant. The increase in the area of fully illuminated leaves is of primary importance, but shaded leaves also transpire. Growth at elevated [CO_2] often increases the leaf area of plants, and increased area tends to offset effects of reduced stomatal conductance on transpiration. Some studies with isolated plants have shown that increased leaf area can more than compensate for reductions in stomatal conductance and actually increase water use per plant at elevated [CO_2] (e.g., Samarkoon and Gifford 1995). In artificially ventilated sunlit chambers, an approximate doubling of leaf area at elevated [CO_2] in soybeans completely offset lower stomatal conductance (Jones et al. 1985), resulting in no change in canopy transpiration. In stands of crops, interception of radiation is generally nearly complete at a LAI of about 3, and evapotranspiration increases asymptotically with LAI, changing little above a LAI of 3 or 4 (e.g., Kelliher et al. 1995). In naturally ventilated plant canopies additional shaded leaf area contributes little to evapotranspiration partly because low light reduces stomatal conductance but also because humidification of the air reduces the leaf to air water vapor pressure difference and low wind speed inside the canopy increases leaf boundary layer resistance. Therefore impacts of leaf area on evapotranspiration in artificially ventilated systems or for isolated plants cannot be simply extrapolated to the field.

Many annual crops spend a substantial fraction of the growing season with a LAI of <3. Therefore stimulation of leaf growth by elevated [CO_2] has the potential to offset reductions in stomatal conductance in determining evapotranspiration. However, the stimulation of leaf area growth by elevated [CO_2] may be less under field conditions than anticipated from responses observed in artificial environments, and simulation of evapotranspiration using a soil-vegetation-atmosphere model suggests that even when increased leaf area occurs at elevated [CO_2], it may have only a small effect on seasonal evapotranspiration at the field scale.

Of the annual crop species listed in Table 1, neither the C_3 or C_4 grasses had substantially increased leaf area at elevated [CO_2] under field conditions. For example, in rice grown at 600 μmol mol^{-1} [CO_2], Weerakoon et al. (2000) found only very small increases in LAI for any of three nitrogen treatments, and only very early in the season. This is consistent with other observations on rice (Baker et al. 1990; Ziska et al. 1997). No significant increase in LAI occurred at elevated [CO_2] in winter wheat or winter barley in the study described in Bunce (2000) at any time during the season (Fig. 3). Spring wheat in the free air

carbon dioxide enrichment studies at 550 μmol mol^{-1} [CO_2] had less than a 10% increase in LAI in well-watered treatments (Pinter et al.1996). LAI increased by <10% in maize grown at twice the current concentration (Wilson et al. 1999) and did not increase significantly in well-watered sorghum grown in the free air carbon dioxide enrichment studies at 550 μmol mol^{-1} (Ottman et al. 2001), or at 700 μmol mol^{-1} in open-top chambers (J. A. Bunce, unpublished data).

Three of the four dicot species listed in Table 1 also had little or no increase in LAI at elevated [CO_2]. For example, cotton grown at 550 μmol mol^{-1} [CO_2] in free air carbon dioxide enrichment studies had no consistent increase in LAI in the wet treatments (Pinter et al. 1996). In the potato and bean experiments listed in Table 1, in which stomatal responses to [CO_2] doubling were obtained, LAI was not increased by elevated [CO_2] (J. A. Bunce, unpublished data).

However, soybean has consistently shown higher LAI at elevated [CO_2]. Wilson et al. (1999) reported that growing soybeans at twice the current ambient [CO_2] increased LAI about 27% throughout the season, in agreement with more recent measurements (Bunce 2001b). Simulations of
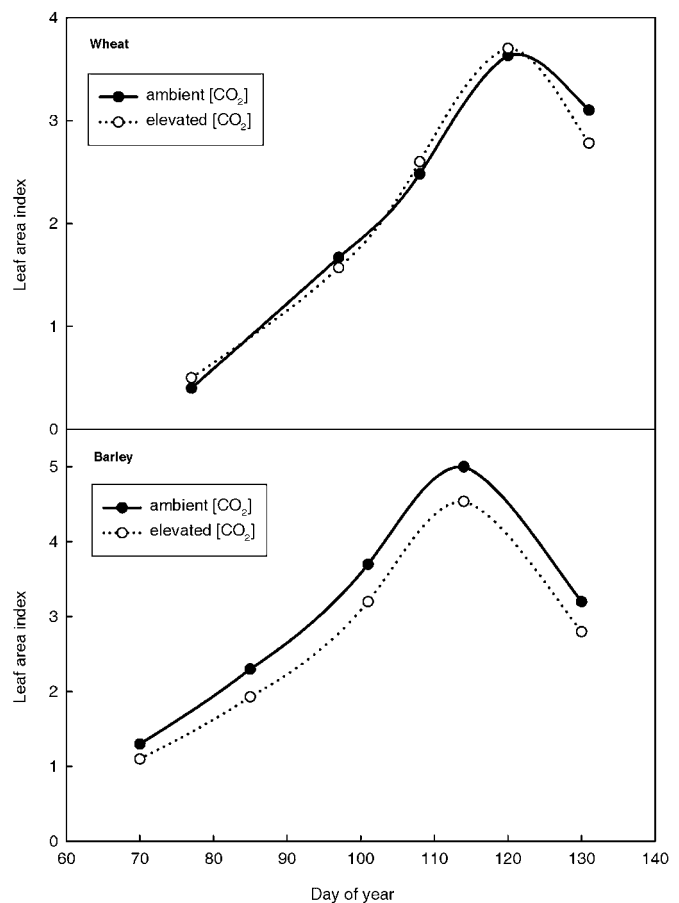

Fig. 3 Seasonal patterns of leaf area index of winter wheat and winter barley crops grown under field conditions (described in Bunce 2000) at the current ambient [CO_2] or at twice the current ambient [CO_2]. Only data for the spring regrowth period are presented. *Each point* represents a mean value for 3 years. No [CO_2] treatments effects were significant at P =0.05

evapotranspiration for soybean using a soil-vegetation-atmosphere model (Wilson et al. 1999) indicated that the greater LAI would result in higher values of evapotranspiration at elevated $[CO_2]$ than at ambient $[CO_2]$ for a few days early in the season, when high temperatures minimized the reduction in stomatal conductance by elevated $[CO_2]$ and LAI was still low enough to be limiting to evapotranspiration. However, these simulations for soybeans indicated that the reduction in evapotranspiration at elevated $[CO_2]$ over the season was only slightly affected by the increase in LAI at elevated $[CO_2]$ (Wilson et al. 1999). This was partly because soil evaporation was greater in the ambient $[CO_2]$ treatment with the lower LAI, and also because more solar radiation reached the soil surface. Increased evaporation from soil largely offset reduced water loss from leaves.

The lack of response of LAI to elevated $[CO_2]$ in most crop species under field conditions is somewhat surprising and suggests that leaf area growth often is not carbon limited under field conditions.

Simulations and measurements of crop water loss at elevated $[CO_2]$

Three studies using one-dimensional soil-vegetation-atmosphere models, and two studies using atmospheric general circulation models to simulate effects of increased atmospheric $[CO_2]$ on evapotranspiration have included information on how other environmental factors affect the reduction in conductance by elevated $[CO_2]$, rather than the more usual simulations using a constant relative reduction in conductance. In alfalfa and orchard grass, reductions in maximum canopy conductances at twice the current atmospheric $[CO_2]$ of 15 and 34%, respectively, led to simulated reductions in midday conductances of up to 20% and 60% for the two species, respectively, using a one-dimensional soil-vegetation-atmosphere model (Bunce et al. 1997). Simulated daily values of evapotranspiration were reduced by only 1–2% in alfalfa and 2–5% in orchard grass, for 5 days of simulations, during which LAI was high and not different between $[CO_2]$ treatments. Similarly, in soybean and maize, reductions of 25 and 58% in maximum stomatal conductances at twice the current ambient $[CO_2]$ resulted in reductions in mean conductances of 58 and 50%, and reductions in simulated seasonal totals of evapotranspiration of about 5 and 9%, for the two species, respectively (Wilson et al. 1999). This latter paper systematically quantified the contributions of various types of feedback, including surface layer and mixed layer atmospheric processes, soil evaporation, leaf physiology, and LAI, in altering the impact of lower stomatal conductance at elevated $[CO_2]$ on evapotranspiration. Gottschalck and Gilles (2001) compared responses of maize evapotranspiration to doubled $[CO_2]$ for two different one-dimensional soil-vegetation-atmosphere models, using reductions in stomatal conductance at elevated $[CO_2]$ which varied with light, temperature, humidity, and soil moisture according to responses

presented by Wilson et al. (1999). More importantly, Gottschalck and Gilles (2001) also incorporated these stomatal responses to the environment for maize grown at ambient and twice ambient $[CO_2]$ into an atmospheric general circulation model. They found few significant changes in evapotranspiration in the maize-growing regions in North America, with areas of both decreased and increased evapotranspiration. Bounoua et al. (1999) used the Ball-Berry model of stomatal conductance in a different atmospheric general circulation model to simulate global climate changes resulting from stomatal responses to doubled atmospheric $[CO_2]$. They found that reductions of 25 and 50% in maximum stomatal conductance for all vegetation reduced evapotranspiration averaged over all land surfaces by 2.3 and 3.5%, respectively. These studies suggest that doubling atmospheric $[CO_2]$ from its present value would probably reduce evapotranspiration by a few percent, but probably by <10%. Although the small simulated reductions in evapotranspiration at elevated $[CO_2]$ compared with the reductions in stomatal conductance may give the impression that it is not too important how much stomatal closure occurs, the various simulations reported by Wilson et al. (1999) clearly indicate that the reduction in evapotranspiration depends strongly on the amount of reduction in maximum stomatal conductance and also on the response of conductance to the consequent changes in the leaf temperature and humidity.

Large diameter free air carbon dioxide enrichment studies provide the closest experimental approximations currently available indicating how field-scale evapotranspiration may respond to rising atmospheric $[CO_2]$. Because feedback processes operating only at larger spatial scales are not represented, free air carbon dioxide enrichment systems probably provide an upper limit for reductions in evapotranspiration to be expected with rising atmospheric $[CO_2]$. There are three crop species in which reductions in evapotranspiration at about 1.5 times the current ambient concentration have been reported for the Arizona free air carbon dioxide enrichment system, cotton, wheat and sorghum. In cotton, no reduction in evapotranspiration could be detected by any of three methods (Reddy et al. 2000), at least partly because reductions in stomatal conductance were small. In wheat, a reduction in evapotranspiration of about 4% (Hunsaker et al. 2000) was found, while midday stomatal conductances were reduced by about 36% (Garcia et al. 1998). The reduction in evapotranspiration by elevated $[CO_2]$ was less in a low nitrogen treatment. A similar reduction in midday stomatal conductance in sorghum (Wall et al. 2001) resulted in about a 10% reduction in evapotranspiration in the "wet" treatment (Conley et al. 2001). Elevated $[CO_2]$ caused a smaller reduction in evapotranspiration under water stress. The results for these three species are generally consistent with expectations from the simulations of evapotranspiration at elevated $[CO_2]$ discussed earlier.

Even reductions of a few percent in evapotranspiration from crops as atmospheric $[CO_2]$ rises could be important to crop yield and to the economics of crop production,

particularly in water-limited situations. The smaller reduction in evapotranspiration than in stomatal conductance at elevated [CO_2] results partly from increases in the temperature and decreases in the humidity in the air around crops, which may themselves have important impacts on crop yields. The results of simulations of climate at doubled [CO_2] using atmospheric general circulation models (Buonoma et al. 1999; Gottschalck and Gilles 2001) suggest that reduced stomatal conductance at elevated [CO_2] may have important effects on temperature and precipitation which may vary regionally. A significant limitation of the climate simulations reported to date is lack of differentiation among vegetation types in the relative reduction in stomatal conductance at elevated [CO_2]. Crops probably represent the vegetation type for which stomatal and leaf area responses to elevated [CO_2] have best been characterized. Incorporation of more realistic plant responses into climate models can only improve their accuracy.

References

Baker JY, Allen LH Jr, Boote KJ (1990) Growth and yield responses of rice to carbon dioxide concentration. J Agric Sci 115:313–320

Ball JT, Woodrow IE, Berry JA (1987) A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggens I (ed) Progress in photosynthesis research. Nijhoff, The Netherlands, pp 221–224

Bounoua L, Collatz GJ, Sellers PJ, Randall DA, Dazlich DA, Los SO, Berry JA, Fung I, Tucker CJ, Field CB, Jensen TG (1999) Interaction between vegetation and climate: radiative and physiological effects of doubled atmospheric CO_2. J Climate 12:309–324

Bryant J, Taylor G, Frehner M (1998) Photosynthetic acclimation to elevated CO_2 is modified by source:sink balance in three component species of a chalk grassland sward grown in a free air carbon dioxide enrichment (FACE) study. Plant Cell Environ 21:159–168.

Bunce JA (1993) Effects of doubled atmospheric carbon dioxide concentration on the responses of assimilation and conductance to humidity. Plant Cell Environ 16:189–197

Bunce JA (1999) Leaf and root control of stomatal closure during drying in soybean. Physiol Plant 106:190–195

Bunce JA (2000) Responses of stomatal conductance to light, humidity and temperature in winter wheat and barley grown at three concentrations of carbon dioxide in the field. Global Change Biol 6:371–382

Bunce JA (2001a) Direct and acclimatory responses of stomatal conductance to elevated carbon dioxide in four herbaceous crop species in the field. Global Change Biol 7:323–331

Bunce JA (2001b) The response of soybean seedling growth to carbon dioxide concentration at night in different thermal regimes. Biotronics 30:15–26

Bunce JA (2003) Effects of water vapor pressure difference on leaf gas exchange in potato and sorghum at ambient and elevated carbon dioxide under field conditions. Field Crops Res 82:37–47

Bunce JA, Wilson KB, Carlson TN (1997) The effect of doubled CO_2 on water use by alfalfa and orchard grass: simulating evapotranspiration using canopy conductance measurements. Global Change Biol 3:81–87

Conley MM, Kimball BA, Brooks TJ, Pinter PA, Hunsaker DJ, Wall GW, Adam NR, LaMorte RL, Matthias AD, Thompson TL, Leavitt SW, Ottman MH, Cousins AB, Triggs JM (2001) CO_2 enrichment increases water-use efficiency in sorghum. New Phytol 151:407–412

Curtis PS, Wang XZ (1998) A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. Oecol 113:299–313

Garcia RL, Long SP, Wall GW, Osborne CP, Kimball BA, Nie GY, Pinter PH Jr, LaMorte RL, Wechsung F (1998) Photosynthesis and conductance of spring-wheat leaves: field response to continuous free-air atmospheric CO_2 enrichment. Plant Cell Environ 21:659–66

Gottschalck JC, Gilles RR (2001) Implications of feedback processes in plant water usage and resulting climate change. J Am Water Res Assoc 37:305–314

Grant RF, Kimball BA, Brooks TJ, Wall GW, Pinter PJ, Hunsaker DJ, Adamsen FJ, Leavitt SW, Thonpson TL, Matthias AD (2001) Modeling interactions among carbon dioxide, nitrogen, and climate on energy exchange of wheat in a free air carbon dioxide experiment. Agron J 93:638–649

Gunderson CA, Sholtis JD, Wullschleger SD, Tissue DT, Hanson PJ, Norby RJ (2002) Environmental and stomatal control of photosynthetic enhancement in the canopy of a sweetgum (*Liquidambar styraciflua* L.) plantation during 3 years of CO_2 enrichment. Plant Cell Environ 25:379–393

Heath J (1998) Stomata of trees growing in CO_2-enriched air show reduced sensitivity to vapour pressure deficit and drought. Plant Cell Environ 21:1077–1088

Hikosaka K, Murakami A, Hirose T (1999) Balancing carboxylation and regeneration of ribulose-1,5-bisphosphate in leaf photosynthesis: temperature acclimation of an evergreen tree, *Quercus myrsinaefolia*. Plant Cell Environ 22:841–849

Homma K, Nakagawa H, Horie H, Ohnishi H, Kim HY, Ohnishi M (1999) Energy budget and transpiration characteristics of rice growth under elevated CO_2 and high temperature conditions as determined by remotely sensed canopy temperatures. Jpn J Crop Sci 68:137–145

Hunsaker DJ, Kimball BA, Pinter PJ, Wall GW, LaMorte RL, Adamsen FJ, Leavitt SW, Thompson TL, Matthias AD, Brooks TJ (2000) CO_2 enrichment and soil nitrogen effects on wheat evapotranspiration and water use efficiency. Agric For Meteorol 104:85–105

Jacobs CMJ, DeBriun HAR (1997) Predicting regional transpiration at elevated atmospheric CO_2: influence of the PBL-vegetation interactions. J Appl Meteorol 36:1663–1675.

Jarvis PG (1976) The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. Phil Trans R Soc Lond 273:593–610

Jarvis PG, McNaughton KG (1986) Stomatal control of transpiration: scaling up from leaf to region. Adv Ecol Res 15:1–49

Jones P, Allen LH Jr, Jones JW, Valle R (1985) Photosynthesis and transpiration responses of soybean canopies to short- and long-term CO_2 treatments. Agron J 77:119–126

Kelliher FM, Leuning R, Raupach MR, Schulze E-D (1995) Maximum conductances for evaporation from global vegetation types. Agric For Meteorol 73:1–16

Lauber W, Korner C (1997) In situ stomatal responses to long-term CO_2 enrichment in calcareous grassland species. Acta Oecol 18:221–229

Lee TD, Tjoelker MG, Ellsworth DS, Reich PB (2001) Leaf gas exchange responses of 13 prairie greassland species to elevated CO_2 and increased nitrogen supply. New Phytol 150:405–418.

Long SP (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: has its importance been underestimated? Plant Cell Environ 14:729–739

McNaughton KG, Jarvis PG (1991) Effects of spatial scale on stomatal control of transpiration. Agric For Meteorol 54:279–302

Medlyn BE, et al. (2001) Stomatal conductance of forest species after long-term exposure to elevated CO2 concentration: a synthesis. New Phytol 14:247–267.

Medlyn BE, Loustau D, Delzon S (2002) Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (*Pinus pinaster* Ait.) Plant Cell Environ 25:1155-1165.

Mitchell RAC, Mitchell VJ, Lawlor DW (2001) Response of wheat canopy CO_2 and water gas-exchange to soil water content under ambient and elevated CO_2. Global Change Biol 7:599–611

Nijs I, Ferris R, Blum H, Hendrey G, Impens I (1997) Stomatal regulation in a changing climate: a field study using free air temperature increase (FATI) and free air CO_2 enrichment (FACE). Plant Cell Environ 20:1041–1050

Ottman MJ, Kimball BA, Pinter PJ, Wall GW, Vanderlig RL, Leavitt SW, LaMorte RL, Matthias AD, Brooks TJ (2001) Elevated CO_2 increases sorghum biomass under drought conditions. New Phytol 150:261–273

Pataki DE, Huxman TE, Jordan DN, Zitzer SF, Coleman JS, Smith SD, Nowak RS, Seemann JR (2000) Water use by two Mojave Desert shrubs under elevated CO_2. Global Change Biol 6:889–897

Pinter PJ Jr, Kimball BA, Garcia RL, Wall GA, Hunsaker DJ, LaMorte RL (1996) Free-air CO_2 enrichment: responses of cotton and wheat crops. In: Koch GW, Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, Calif., pp 215–249

Radin JW, Kimball BA, Hendrix DL, Mauney JR (1987) Photosynthesis of cotton plants exposed to elevated levels of carbon dioxide in the field. Photosynth Res 12:191–203

Reddy KR, Hodeges HF, Kimball BA (2000) Crop ecosystem response to climatic change: cotton. In: Reddy KR, Hodges HF (eds) Climate change and global crop productivity. CABI, New York, pp 161–187

Samarakoon AB, Gifford RM (1995) Soil water content under plants at high CO_2 concentration and interactions with direct CO_2 effects: a species comparison. J Biogeogr 22:193–202

Seffaj R, Allen LH Jr, Sinclair TR (1999) Soybean leaf growth and gas exchange responses to drought under carbon dioxide enrichment. Global Change Biol 5:283–291

Tuba Z, Szente K, Kock J (1994) Responses of photosynthesis, stomatal conductance, water use efficiency and production to long-term elevated CO_2 in winter wheat. J Plant Physiol 144:661–668

Valentini R, Gamon JA, Field CG (1995) Ecosystem gas exchange in a California grassland: seasonal patterns and implication for scaling. Ecology 76:1940–1952.

Wall GW, Brooks TJ, Adam NR, Cousins AB, Kimball BA, Pinter PJ Jr, LaMorte RL, Triggs J, Ottman MH, Leavitt SW, Matthias AD, Willimas DG, Webber AN (2001) Elevated atmospheric CO_2 improved *Sorghum* plant water status by ameliorating the adverse effects of drought. New Phytol 152:231–248

Weerakoon WMW, Ingram KT, Moss DN (2000) Atmospheric carbon dioxide and fertilizer nitrogen effects on radiation interception by rice. Plant Soil 220:99–106

Wilson KB, Bunce JA (1997) Effects of carbon dioxide concentration on the interactive effects of temperature and water vapour on stomatal conductance in soybean. Plant Cell Environ 20:230–238

Wilson KB, Carlson TN, Bunce JA (1999) Feedback significantly influences the simulated effect of CO_2 on seasonal evapotranspiration from two agricultural species. Global Change Biol 5:903–917

Wong SC, Cowan IF, Farquhar GD (1979) Stomatal conductance correlates with photosynthetic capacity. Nature 282:424–426

Ziska LH, Namuco O, Moya T, Quilang J (1997) Growth and yield response of field-grown tropical rice to increasing carbon dioxide and air temperature. Agron J 89:45–53