

# Decreased hydraulic conductance in plants at elevated carbon dioxide

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## ABSTRACT

Previous work indicated that long-term exposure to elevated carbon dioxide levels can reduce hydraulic conductance in some species, but the basis of the response was not determined. In this study, hydraulic conductance was measured at concentrations of both 350 and 700 cm<sup>3</sup> nT<sup>3</sup> carbon dioxide for plants grown at both concentrations, to determine the reversibility of the response. In *Zea mays* and *Amaranthus hypochondriacus*, exposure to the higher carbon dioxide concentration for several hours reduced whole-plant transpiration rate by 22–40%, without any consistent change in leaf water potential, indicating reversible reductions in hydraulic conductance at elevated carbon dioxide levels. Hydraulic conductance in these species grown at both carbon dioxide concentrations responded similarly to measurement concentration of carbon dioxide, indicating that the response was reversible. In *Glycine max*, which in earlier work had shown a long-term decrease in hydraulic conductance at elevated carbon dioxide levels, and in *Abutilon theophrasti*, no short-term changes in hydraulic conductance with measurement concentration of carbon dioxide were found, despite lower transpiration rates at elevated carbon dioxide. In *G. max* and *Medicago sativa*, growth at high dew-point temperature reduced transpiration rate and decreased hydraulic conductance. The results indicate that both reversible and irreversible decreases in hydraulic conductance can occur at elevated carbon dioxide concentrations, and that both could be responses to reduced transpiration rate, rather than to carbon dioxide concentration itself.

**Key-words:** carbon dioxide; hydraulic conductance; stomatal conductance; transpiration; water potential.

## INTRODUCTION

Because elevated carbon dioxide concentrations frequently reduce stomatal conductance, improved plant water status is often expected to be an important consequence of increasing concentrations of carbon dioxide in the atmosphere. Indeed, in experiments where stomatal conductance strongly affects soil water depletion, elevated carbon dioxide may stimulate growth partly by conserving soil

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water (e.g. Sionit *et al.* 1980; Gifford & Morison 1985; Owensby *et al.* 1993; Policy *et al.* 1994).

However, when soil water is not limiting to growth, increased leaf water potentials at elevated carbon dioxide concentrations have not always been observed, even when stomatal conductance or transpiration was reduced. For example, leaf water potential was lower at elevated carbon dioxide in alfalfa (Bunce 1995) and was not higher at elevated carbon dioxide in soybean in wet soil (Patterson & Flint 1982; Rogers *et al.* 1984; Prior *et al.* 1991; Bunce 1996). Similarly, no increase in leaf water potential at elevated carbon dioxide in wet soil was found in sweet potato (Bhattacharya *et al.* 1990), in paspalum (Gifford & Morison 1985), in four chalk grassland herbs (Ferns & Taylor 1994), in three salt marsh species under low salinity and aerobic conditions (Rozema *et al.* 1991), or in two herbaceous weed species (Patterson & Flint 1982). Tree seedlings may also not always have improved water status at elevated carbon dioxide. For example, no increase in leaf water potential was found in five tropical tree species (Reekie & Bazzaz 1989), two other tropical tree species (Eamus *et al.* 1995), or in two temperate tree species (Tolley & Strain 1985) in wet soil, despite lower conductance or transpiration rate. The expected higher leaf water potential at elevated carbon dioxide for plants with wet soil (e.g. Sasek & Strain 1989; Clifford *et al.* 1993; Jackson *et al.* 1994; Bunce 1995) seems to be either less common, or less commonly reported.

A reduction in transpiration rate at elevated carbon dioxide with no increase in leaf water potential in wet soil implies a decrease in hydraulic conductance. However, hydraulic conductances have seldom been explicitly reported in studies comparing carbon dioxide concentrations. Very large decreases in hydraulic conductance (3–5-fold) were reported for two tropical tree species (Eamus *et al.* 1995) grown at elevated carbon dioxide. We previously reported (Bunce 1996) that growth at elevated carbon dioxide concentration reduced hydraulic conductance in alfalfa and soybean. In these studies hydraulic conductance was calculated from transpiration rates and water potentials measured under the growth conditions. These decreases could have a structural basis. However, because apparent hydraulic conductance can sometimes vary with transpiration rate and measurement environment (e.g. Koide 1985; Passioura & Tanner 1985; Fiscus 1986; Else *et al.* 1995; cf. Weatherley 1982), we examined the

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reversibility of changes in conductance with carbon dioxide concentration. In addition, we tested the hypothesis (Bunce 1996) that lower hydraulic conductance in plants grown at elevated carbon dioxide represents a homeostatic response to lower transpiration rate during growth, rather than a direct response to carbon dioxide concentration.

## MATERIALS AND METHODS

*Zea mays* (L.) cv. SS885, *Amaranthus hypochondriacus* (L.) and *Abutilon theophrasti* (Medikus) were grown in two air-conditioned glasshouses at Beltsville, MD, from August to October 1996. Each glasshouse was controlled at day/night temperatures of 28/19 °C, each  $\pm 2$  °C. The lower temperature was maintained for 12 h beginning 8 h after solar noon. Shaded, ventilated air temperatures were recorded every 15 min. Twenty-four-hour mean temperatures did not differ between the glasshouses by more than 0.5 °C on any day, and long-term mean temperatures were indistinguishable. Dew-point temperatures were determined periodically near midday, and closely approximated those of outside air (e.g. 18–23 °C). Dew-point temperatures did not differ between glasshouses. Carbon dioxide was injected as needed to maintain minimum values of either 350 or 700 cm<sup>3</sup> m<sup>-3</sup>. Carbon dioxide injection was controlled by absolute infrared analysers which sampled the air continuously. Carbon dioxide treatments were switched between glasshouses once during these experiments. Blowers constantly circulated air in the glasshouses and provided an air speed of about 0.5 m s<sup>-1</sup> over leaves. Plants were grown in 20-cm-diameter plastic pots with ver-miculite as the rooting medium. Pots were flushed daily with a complete nutrient solution. Plants of *Glycine max* L. Merr. cv. Clark were grown in the same-sized pots in ver-miculite in a controlled-environment chamber at a carbon dioxide concentration of 350  $\pm$  20 cm<sup>3</sup> m<sup>-3</sup>. The chamber air temperature was 25 °C, and the dew-point temperature was 18 °C. There was 14 h d<sup>-1</sup> of light from high-pressure sodium and metal halide lamps at a photosynthetic photon flux density (PPFD) of 1.0 mmol m<sup>-2</sup> s<sup>-1</sup>. These plants were grown in the same-sized pots as plants in the glasshouse, and flushed daily with nutrient solution.

Measurements of hydraulic conductance were made in a controlled-environment chamber so that steady-state conditions could be achieved. The conditions in the chamber were 25  $\pm$  0.3 °C air temperature, 18  $\pm$  1 °C dew-point temperature, 1.0 mmol m<sup>-2</sup> s<sup>-1</sup> PPFD, and either 350 or 700  $\pm$  20 cm<sup>3</sup> m<sup>-3</sup> carbon dioxide concentration. Carbon dioxide concentration was controlled by the injection of either carbon dioxide or carbon dioxide-free air. Therefore opening the chamber doors to sample plants disrupted the carbon dioxide control for only a few minutes. Five or six plants grown at each carbon dioxide concentration were watered with the nutrient solution and placed in the measurement chamber early in the morning at the higher carbon dioxide concentration. After a 90–120 min equilibration period, a 3-cm-thick layer of dry vermiculite was placed over the soil surface to minimize

evaporation from the surface, and the initial mass of the whole pot determined. The change in mass was determined after about 60 min and again after 120 min. Midway through both of these 60 min periods, discs were excised from fully illuminated mature upper leaves for determination of leaf water potential. Water potential was measured using six recently calibrated, insulated C-52 sample chambers and a dew-point hygrometer (Wescor HR-33T). Water potentials were determined after a 60 min equilibration period. Tests indicated that water-potential readings did not differ between 60 and 90 min. At each sampling, three samples were taken from plants grown at each carbon dioxide concentration. The carbon dioxide concentration in the measurement chamber was then switched to 350 cm<sup>3</sup> m<sup>-3</sup>, and, after another 90–120 min equilibration period, changes in pot mass and leaf water potentials were again determined for two 60 min periods. Total plant leaf area was then determined using a photoelectric area meter (LI 3100, LiCor, Lincoln, NB), and leaf, stem and root dry masses were measured. The different species were measured on different days.

Because plants of *Z. mays*, *A. hypochondriacus* and *A. theophrasti* were measured both at the carbon dioxide concentration at which they were grown and at the alternative concentration, reversibility of any change in conductance with carbon dioxide concentration could be assessed. In addition, half the plants were first measured at the carbon dioxide concentration at which they were grown, and half were first measured at the alternative concentration. The higher carbon dioxide concentration was used for the first measurements of conductance so that any possible reduction in conductance caused by depletion of soil water in later measurements at lower carbon dioxide would bias the data toward lower conductance at the lower carbon dioxide concentration. Thus, an increased conductance at the lower carbon dioxide concentration would be robust against this source of error. The pots held about 2 kg of water. Over the whole measurement period the pots lost no more than 100 g of water, so that any reduction in soil water potential would have been minor. To exclude the possibility that the time of day at which measurements were made influenced the comparison of water potentials at different measurement concentrations of carbon dioxides, simultaneous measurements of water potential were also made at both carbon dioxide concentrations in the glasshouses for *Z. mays* and *A. hypochondriacus*. Leaves were sampled at 0900–1000 h and again at 1300–1500 h on clear days shortly before hydraulic conductance was measured in the controlled-environment chamber.

Hydraulic conductance was calculated for individual plants by dividing the transpiration rate expressed per unit of leaf area by the difference between the measured leaf water potential and the osmotic potential of the nutrient solution (-0.03 MPa). These are 'apparent' hydraulic conductances, because no correction was made for any osmotically driven water flux. Osmotically driven water flux is usually small relative to that driven by tension at transpiration rates as high as those which occurred in these experiments. Growth-induced reductions in water potential were also not assessed.

For each plant there were two determinations of transpiration rate, and one leaf water potential measurement for each measurement concentration of carbon dioxide. Hydraulic conductance was based on the transpiration rate during the period in which the leaf water potential of that plant was determined. Results were analysed using two-way ANOVA to test for effects of growth and measurement concentrations of carbon dioxide and their interaction on transpiration rate, leaf water potential, and hydraulic conductance. For *G. max* grown in the controlled-environment chamber, hydraulic conductance was measured in the same way, except that there was only one growth carbon dioxide treatment.

Additional hydraulic conductance measurements were made on *Glycine max* L. Merr. cv. Clark and *Medicago sativa* (L.) cv. Arc plants grown in a controlled-environment chamber at two different dew-point temperatures. The carbon dioxide concentration was  $350 \pm 20 \text{ cm}^3 \text{ m}^{-3}$ , the chamber air temperature was 25 °C and the dew-point temperature was either 10 or 19 °C,  $\pm 1$  °C. A PPFD of  $1.0 \text{ mmol m}^{-2} \text{ s}^{-1}$  was provided for 14 h d<sup>-1</sup>. Whole-plant transpiration rates and water potentials were determined on plants in the daytime growth conditions. Transpiration rates were measured as described previously, beginning 4 h after the lights came on. After the final weighing, the stem was severed at the base, the shoot enclosed in a plastic bag, and the xylem pressure potential determined immediately using a pressure chamber. Hydraulic conductances were calculated based on both leaf water potentials and xylem pressure potentials. One-way ANOVA was used to compare treatments for leaf water potential, transpiration rate and hydraulic conductance. Total plant leaf areas at the time of

Measurement of hydraulic conductance averaged 360 cm<sup>2</sup> in *G. max*, and 55 cm<sup>2</sup> in *M. sativa*.

## RESULTS

There was no significant change in transpiration rate or water potential between the first and second measurement periods at a given carbon dioxide concentration for any species (not shown). This indicates that steady-state conditions of transpiration rate and water potential occurred during the measurements of hydraulic conductance.

In *A. hypochondriacus* there was no significant effect of growth concentration of carbon dioxide on transpiration rate, leaf water potential or hydraulic conductance measured at the same carbon dioxide concentration (Tables 1 & 2). There was also no significant difference in leaf area between carbon dioxide treatments (Table 1). The higher carbon dioxide concentration during the measurement reduced transpiration rate in this species, with no significant change in leaf water potential. This reflected an 18% reduction in hydraulic conductance at the higher measurement concentration of carbon dioxide (Table 1). This reduction in hydraulic conductance at high measurement concentration of carbon dioxide occurred for both growth carbon dioxide treatments. Reductions in transpiration rate and hydraulic conductance (37% lower) at the higher measurement-carbon dioxide condition also occurred in *Z. mays*, but there was no effect of growth concentration of carbon dioxide and no interaction between growth concentration and measurement concentration (Tables 1 & 2). Leaf water potential in *Z. mays* increased slightly at the

Table 1. Transpiration rate ( $E$ ), leaf water potential ( $LWP$ ) and hydraulic conductance ( $Lp$ ), each  $\pm$  SE, measured at two carbon dioxide concentrations for plants of *Amaranthus hypochondriacus*, *Zea mays* and *Abutilon theophrasti* grown in glasshouses at two carbon dioxide concentrations, and for *Glycine max* grown in a controlled-environment chamber. See Table 2 for statistical tests

CO <sub>2</sub> (cm <sup>3</sup> m <sup>-3</sup> )		$E$ (gm <sup>-2</sup> min <sup>-1</sup> )	$LWP$ (MPa)	$Lp$ (gn <sup>-1</sup> m <sup>2</sup> MPa <sup>-1</sup> )	Leaf area (cm <sup>2</sup> )
Measurement	Growth				
<b>A.</b>					
<i>hypochondriacus</i>					
350	350	4.7 $\pm$ 0.5	-0.70 $\pm$ 0.02	7.1 $\pm$ 0.8	579 $\pm$ 90
700	350	3.7 $\pm$ 0.3	-0.70 $\pm$ 0.03	5.7 $\pm$ 0.4	
350	700	4.3 $\pm$ 0.2	-0.72 $\pm$ 0.03	6.3 $\pm$ 0.5	607 $\pm$ 40
700	700	3.3 $\pm$ 0.1	-0.65 $\pm$ 0.02	5.4 $\pm$ 0.3	
<b>Z. mays</b>					
350	350	3.5 $\pm$ 0.2	-0.62 $\pm$ 0.04	6.1 $\pm$ 0.5	404 $\pm$ 12
700	350	2.4 $\pm$ 0.2	-0.75 $\pm$ 0.05	3.3 $\pm$ 0.2	
350	700	3.8 $\pm$ 0.4	-0.84 $\pm$ 0.04	4.8 $\pm$ 0.6	391 $\pm$ 38
700	700	2.3 $\pm$ 0.2	-0.74 $\pm$ 0.05	3.6 $\pm$ 0.1	
<b>A. theophrasti</b>					
350	350	5.4 $\pm$ 0.1	-1.33 $\pm$ 0.11	4.3 $\pm$ 0.3	329 $\pm$ 27
700	350	4.0 $\pm$ 0.1	-1.21 $\pm$ 0.07	3.5 $\pm$ 0.3	
350	700	4.9 $\pm$ 0.1	-1.39 $\pm$ 0.11	3.7 $\pm$ 0.3	465 $\pm$ 37
700	700	3.7 $\pm$ 0.1	-1.08 $\pm$ 0.11	3.6 $\pm$ 0.3	
<b>G. max</b>					
350	350	3.8 $\pm$ 0.1	-1.24 $\pm$ 0.02	3.1 $\pm$ 0.1	947 $\pm$ 78
700	350	2.7 $\pm$ 0.1	-0.98 $\pm$ 0.06	2.9 $\pm$ 0.2	

Species	Variable	Probability of a greater F-value for:		
		Measurement	Growth	Interaction
<i>A. hypochondriacus</i> 6 >	<i>E</i>	0-007	0-176	0-982
	<i>LWP</i>	0-260	0-661	0-260
	<i>Lp</i>	0-040	0-324	0-667
<i>Z. mays</i>	6 <i>E</i>	0-000	0-629	0-425
	<i>LWP</i>	0-759	0-031	0-017
	<i>Lp</i>	0-000	0-252	0-071
<i>A. theophrasti</i> -	<i>E</i>	0-000	0-000	0-287
	<i>LWP</i>	0-046	0-763	0-382
	<i>Lp</i>	0-159	0-471	0-267
<i>G. max</i>	6 <i>E</i>	0-000	—	—
	<i>LWP</i>	0-002	—	—
	<i>Lp</i>	0-325	—	—

Table 2. Statistical analysis of the effect of growth and measurement concentration of carbon dioxide on transpiration rate (*E*), leaf water potential (*LWP*) and hydraulic conductance (*Lp*) for plants of *Amaranthus hypochondriacus*, *Zea mays* and *Abutilon theophrasti* grown in glasshouses at two carbon dioxide concentrations, and for *Glycine max* grown in a controlled-environment chamber at one concentration. Means

higher measurement concentration of carbon dioxide for plants grown at the higher concentration, but decreased slightly for plants grown at the lower concentration (Table 1).

Measurements of leaf water potential in the glasshouses indicated no differences between carbon dioxide concentrations for either time of measurement. Mean values were -0.91 and -0.88 MPa for *Z. mays* at the lower and higher carbon dioxide concentrations, respectively, and -0.89 and -0.96 for *A. hypochondriacus* at the lower and higher carbon dioxide concentrations, respectively.

In *A. theophrasti*, plants grown at both carbon dioxide concentrations had lower transpiration rates and higher leaf water potentials when measured at the higher carbon dioxide concentration (Tables 1 & 2). There was no significant effect of carbon dioxide concentration during measurement on hydraulic conductance in this species (Tables 1 & 2). Plants grown at the lower carbon dioxide concentration had smaller leaf areas, and higher transpiration rates per unit of area, with lower water potentials and similar hydraulic conductances (Table 1). Similarly, transpiration rate was decreased, and leaf water potential was increased by high measurement concentration of carbon dioxide in *G. max*, with no change in hydraulic conductance (Tables 1 & 2).

Growth at the higher dew-point temperature reduced transpiration rate in both *G. max* and *M. saliva*, but did not increase leaf water potential (Table 3). Hydraulic conductances calculated from either leaf water potential or stem xylem pressure potential were significantly lower in plants grown at the higher dew-point temperature (Table 3). From the difference between leaf and stem water potentials, the conductance from the base of the stem to the measured leaf can be calculated to be 11 and 7 g rrT<sup>2</sup> min<sup>-1</sup> MPa<sup>-1</sup> for plants at the lower and higher dew points, respectively, in *G. max*, and 284 and 111 g m<sup>-2</sup> min<sup>-1</sup> MPa<sup>-1</sup> in *M. saliva*. These estimates of stem conductance assume that xylem solute potentials are zero, and that the pressure chamber and hygrometric methods are equivalent. In neither species did the ratio of leaf area to root dry mass or the fractions of total dry mass in leaves, stems and roots differ between growth dew-point conditions (not shown).

## DISCUSSION

In both *Z. mays* and *A. hypochondriacus*, hydraulic conductance increased when the measurement concentration of carbon dioxide was decreased from 700 to 350 cm<sup>3</sup> trT<sup>3</sup>. Any reduction in conductance due to drying of soil during the measurements would have lowered conductance at the

Table 3. Transpiration rates (*E*), leaf water potentials (*LWP*), stem xylem pressure potentials (*XPP*) and hydraulic conductances (*Lp*) calculated from either *LWP* or *XPP*. Plants of *Glycine max* and *Medicago saliva* were grown in controlled-environment chambers at two dew-point temperatures and measured under the growth conditions. Standard errors of the mean are given, for *n* = 6. \* indicates a significant effect of dew-point temperature within a species, at *P* = 0-05

Species	(°C)	<i>E</i> (g m <sup>-2</sup> min <sup>-1</sup> )	<i>LWP</i> (MPa)	<i>AII</i> (MPa)	<i>Lp</i> (g m <sup>-2</sup> min <sup>-1</sup> MPa <sup>-1</sup> )	
					<i>LWP</i>	<i>XPP</i>
<i>G. max</i>	10	4.4* ± 0.3	-1.12 ± 0.03	-0.72* ± 0.01	3.9* ± 0.3	6.1* ± 0.4
<i>G. max</i>	19	3.3 ± 0.2	-1.13 ± 0.01	-0.67 ± 0.01	3.0 ± 0.1	5.0 ± 0.3
<i>M. saliva</i>	10	14.2* ± 0.9	-0.92 ± 0.07	-0.87 ± 0.04	15.8* ± 1.5	16.5* ± 1.5
<i>M. saliva</i>	19	7.8 ± 0.8	-1.03 ± 0.06	-0.96 ± 0.04	7.8 ± 1.1	8.2 ± 0.9

lower carbon dioxide concentration. The fact that higher conductance at low carbon dioxide levels occurred in plants raised at both ambient and elevated carbon dioxide levels indicates that the response was reversible. Furthermore, the same pattern of response of conductance was obtained whether the plants were first measured at the carbon dioxide concentration at which they were grown, or at the alternative concentration. The constancy of leaf water potential and transpiration over the exposure times at each carbon dioxide concentration, and the lack of difference in simultaneous measurements of leaf water potentials in the glasshouses, indicate that diurnal changes in conductance did not confound these results.

An increase in leaf water potential in response to reduced transpiration rate during growth at an elevated carbon dioxide concentration did not occur in two of the three species examined in this study. The same result, which leads to a lower calculated hydraulic conductance at elevated carbon dioxide, has been reported for soybean and alfalfa (Bunce 1996), and for two rain forest tree species (Eamus *et al.* 1995). Lower hydraulic conductance at elevated carbon dioxide may be quite common, based on the scarcity of reports indicating increased leaf water potential and the frequency of reports of decreased transpiration rate at elevated carbon dioxide (cf. Cure & Acock 1986; Eamus 1991).

Lower hydraulic conductance in plants growing at an elevated carbon dioxide concentration could represent a response to the growth or to the measurement concentration of carbon dioxide. The results of this study indicate that both effects can occur, depending on the species.

The results obtained with *G. max* and *A. theophrasti*, which had no change in hydraulic conductance with measurement concentration of carbon dioxide, indicate that hydraulic conductance does not always respond to elevated carbon dioxide during measurement, and that the method for determining hydraulic conductance used here did not introduce an artefact. Because plants of *A. theophrasti* grown at the two carbon dioxide concentrations differed in size, and hydraulic conductance could change with size, it is less certain that growth at elevated carbon dioxide did not change conductance in this species. In *G. max*, no effect of measurement concentration of carbon dioxide was found, indicating that the previously reported lower hydraulic conductance in plants at elevated carbon dioxide in this species (Bunce 1996) was caused by growth at elevated carbon dioxide, presumably through anatomical changes. Other work has also shown that hydraulic conductance in soybean is not dependent on the evaporative conditions during measurement (Bunce 1978; Moreshet *et al.* 1990), when steady-state conditions occur.

The data presented here for *G. max* and *M. saliva* grown at two dew-point temperatures indicate that hydraulic conductance can change in response to a change just in the evaporative conditions during development, with higher hydraulic conductance in plants developed under more strongly evaporative conditions. It seems likely that irreversible decreases in hydraulic conductance in plants

grown at elevated carbon dioxide may be a response to lower transpiration rate during development, rather than a direct effect of carbon dioxide. We did not investigate the basis of the change in conductance with evaporative conditions during growth, but it could be caused, for example, by changes in xylem cross-sectional area or the radius of xylem vessels (e.g. Schultz & Matthews 1993).

A response of hydraulic conductance to evaporative conditions could also be involved in reversible decreases in conductance at elevated carbon dioxide, such as occurred in *A. hypochondriacus* and *Z. mays* in this study. Constant leaf water potential, despite an imposed change in transpiration rate, is a common experimental result for many species (cf. Weatherley 1982), although the cause has not been clear. A change in the proportion of water flowing through a high-resistance symplastic pathway to that flowing through a lower-resistance apoplastic pathway in response to increased transpiration rate has been proposed as a possible mechanism for changes in apparent hydraulic conductance with transpiration rate (Boyer 1974; Fiscus *et al.* 1983). The fact that the permeability of membranes to water seems to be influenced by aquaporins, which respond to various aspects of the environment (Steudle & Henzler 1995), may provide an explanation of how hydraulic conductance may respond to transpiration rate. One could envision, for example, that an increase in transpiration would temporarily decrease the water potential of root cells involved in the symplastic transport of water in the transpiration stream, and this could trigger aquaporins to increase the conductance of the plasma membrane in these cells. There are no data to indicate that the reversible response of hydraulic conductance to carbon dioxide concentration found in this study is different from the response to other factors affecting transpiration rate.

It is now clear that, because of changes in hydraulic conductance in response to either growth or measurement concentration of carbon dioxide, leaf water potential of C<sub>3</sub> and C<sub>4</sub> plants is not necessarily increased by long-term exposure of plants to elevated carbon dioxide even when the transpiration rate is reduced. Lack of an increase in leaf water potential at elevated carbon dioxide could reduce the beneficial effects of elevated carbon dioxide on plant growth.

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