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Low carbon dioxide concentrations can reverse stomatal closure during water stress

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Leaf water potentials below threshold values result in reduced stomatal conductance (g_s). Stomatal closure at low leaf water potentials may serve to protect against cavitation of xylem. Possible control of g_s by leaf water potential or hydraulic conductance was tested by drying the rooting medium in four herbaceous annual species until g_s was reduced and then lowering the $[CO_2]$ to determine whether g_s and transpiration rate could be increased and leaf water potential decreased and whether hydraulic conductance was reduced at the resulting lower leaf water potential. In all species, low $[CO_2]$ could reverse the stomatal closure because of drying despite further reductions in leaf water potential, and the resulting lower leaf water potentials did not result in reductions in hydraulic conductance. The relative sensitivity of g_s to internal $[CO_2]$ in the leaves of dry plants of each species averaged three to four times higher than in leaves of wet plants. Two species in which g_s was reputed to be insensitive to $[CO_2]$ were examined to determine whether high leaf to air water vapor pressure differences (D) resulted in increased stomatal sensitivity to $[CO_2]$. In both species, stomatal sensitivity to $[CO_2]$ was indeed negligible at low D, but increased with D, and low $[CO_2]$ partly or fully reversed closure caused by high D. In no case did low leaf water potential or low hydraulic conductance during drying of the air or the rooting medium prevent low $[CO_2]$ from increasing g_s and transpiration rate.

Introduction

Reductions in stomatal conductance of plant leaves in response to dry air and dry soil have important consequences for energy and carbon balances of many plants and ecosystems, but mechanisms controlling stomatal closure remain uncertain. Much of the literature has focused on reductions in leaf water potential as causing stomatal closure, combined with more recent concerns about loss of hydraulic conductance (c.f Bond and Kavanagh 1999, Oren et al. 1999). In an earlier paper (Bunce 2006), I reported that stomatal closure at high leaf to air vapor pressure differences (D) in four species in wet soil could be reversed by low carbon dioxide concentrations ($[CO_2]$) despite reductions in leaf water potential, and there was no loss of hydraulic conductance. Increased stomatal sensitivity to internal $[CO_2]$ (C_i) was identified as a primary cause of reduced stomatal conductance at high D in those species. Readers of the prior paper have suggested that if soil were dry, leaf water potential might more strongly control stomatal conductance, and low $[CO_2]$ might not increase stomatal conductance. In this paper, I tested this idea, using low $[CO_2]$ treatments to determine whether stomatal closure resulting from drying of the rooting medium was caused by low water potential, decreased hydraulic conductance or increased stomatal sensitivity to C_i. Additionally, two

Abbreviations – C_a, external $[CO_2]$; C_i, internal $[CO_2]$; D, vapor pressure differences; PPFD, photosynthetic photon flux density.

species reputed to have stomatal conductance insensitive to C_i were examined to determine if high D caused stomatal closure by increasing stomatal sensitivity to C_i.

The conduction of water through xylem is vulnerable to cavitation, which can be induced by excessive drying (Sperry 2000). In an evolutionary sense, the water-conducting system must be sufficient to cope with potential transpiration rates as affected by stomatal conductance and the environment (Tyree et al. 1999). It is less clear, however, whether hydraulic conductance affects responses of stomatal conductance to short-term environmental changes. Bond and Kavanagh (1999) argued that apparent stomatal responses to D actually reflect control of stomatal conductance by leaf water potential at the threshold for closure, with sensitivity affected by hydraulic conductance. Species seemed to vary as to whether leaf hydraulic conductance was affected by changes in leaf water potential near the threshold for closure. Similarly, Oren et al. (1999) have argued that stomatal responses to D are consistent with control by leaf water potential in a way that would serve to prevent loss of hydraulic conductance at high D. Brodribb and Holbrook (2004) suggested that midday reductions in stomatal conductance in a tropical tree may have been caused by reductions in leaf hydraulic conductance and leaf water potential. The data of Brodribb and Holbrook (2006) suggest that in many species, leaf hydraulic conductance may be reduced by decreasing leaf water potentials even above those causing xylem cavitation. The question addressed in this study was whether, when stomatal conductance was substantially reduced by root drying, further reductions in leaf water potential cause reductions in leaf hydraulic conductance. I focused on leaf hydraulic conductance, as did the above-cited studies, because of the difficulty in separating root from soil conductance non-destructively when the rooting medium is dry.

Materials and methods

Plants of *Glycine max* L. cv. Kent, *Gossypium hirsutum* L. cv. Stoneville 474 and *Helianthus annuus* L. cv. Mammoth and *Abutilon theophrasti* L. and *Xanthium strumarium* L. from local Beltsville, Maryland populations were grown separately in controlled environment chambers (M-8, Environmental Growth Chambers, Chagrin Falls, OH). Plants were grown in 20 cm diameter plastic pots filled with vermiculite and flushed daily with a complete nutrient solution containing 14.5 m*M* nitrogen. Chamber day/night air temperatures were 26/20°C, and the dew point temperature was 18°C. There were 14 h per day of light at a photosynthetic photon flux density (PPFD) of 1000 μmol m^{-2} s^{-1} from a mixture of high-pressure sodium and metal halide lamps (LU400 and MS400, Sylvania, Westfield, IN). The carbon dioxide concentration ($[CO_2]$) was kept between 370 and 390 μmol mol^{-1} by the injection of carbon dioxide or air scrubbed of carbon dioxide, under the control of an absolute infrared carbon dioxide analyzer (WMA-4, PP Systems, Amesbury, MA), which sampled chamber air continuously. Gas exchange experiments were conducted 3–4 weeks after seeding, when plants had total leaf areas of 450–800 cm^2.

Two-year-old seedlings of *Picea sitchensis* (Bong.) Carriere, which had been grown outdoors in pots in northern California, were transplanted into a 2:1 peat moss:sand mixture containing slow-release fertilizer and grown in a controlled environment chamber at 21/15°C day/night temperatures, under the same light and $[CO_2]$ conditions as the other species. Pots were watered four times per week with water. Gas exchange measurements were made both on foliage produced in the field, after 3 months in the controlled environment chamber, and also on 1-month-old foliage, which was expanded from buds under the chamber conditions. No differences in gas exchange occurred between these two types of tissue, and results were pooled.

Root drying experiments

Gas exchange measurements were made on plants in the growth cabinet starting a few hours after lights came on. Measurements were made on well-watered control plants, or plants that had not received nutrient solution for 2–5 days. Entire leaves of *G. hirsutum*, *A. theophrasti* and *X. strumarium*, and terminal leaflets of *G. max* were enclosed in a water-jacketed clear acrylic cuvette lined with Teflon film and containing a mixing fan. The leaf petiole was inserted through a groove in a sidewall of the cuvette, and sealed with caulk. A gas-blending system provided air with controlled concentrations of CO_2 and water vapor at a flow rate that was measured with a mass flow meter. Leaf temperature was measured using a miniature thermistor pressed against the lower leaf surface. Stomatal conductance, transpiration rate and net CO_2 assimilation rate were measured using a CIRAS-1 portable photosynthesis system (PP Systems) configured for using an external air supply and a leaf temperature probe. Leaves were first exposed to an external $[CO_2]$ (C_a) of 380 ± 10 μmol mol^{-1}, a temperature of 28 ± 2°C, a PPFD of 1500 μmol m^{-2} s^{-1} and a leaf to air water vapor pressure difference of 1.7 ± 0.3 kPa for 1.5 h, by which time gas exchange parameters had stabilized. Stable gas exchange parameters were recorded and a 6 mm diameter leaf disc was removed from the leaf in the cuvette for determination of leaf water potential using

a Wescor HR-33 dew point hygrometer (Wescor, Inc., Logan, UT) and a recently calibrated insulated leaf chamber (C-52, Wescor, Inc.). The area of leaf discs removed (0.28 cm^2 per disc) was much less than the total area of the leaves (at least 70 cm^2 in the measurement cuvette in all species), so their removal had negligible effects on subsequent leaf gas exchange, although rates were calculated on the actual leaf area in the cuvette at the time. Leaf water potential was also determined for a leaf outside the cuvette that had been covered in aluminum foil since the night before. The $[CO_2]$ of air in the cuvette was then reduced to 100 ± 10 μmol mol^{-1}. The value of 100 μmol mol^{-1} was chosen to avoid possible photoinhibition of photosynthesis, which might have occurred after long-term exposure to lower $[CO_2]$ and affected stomatal conductance. After gas exchange rates had been constant for an hour, another leaf disc was taken for determination of leaf water potential, along with a disc from a leaf that had been covered in aluminum foil since the night before. Leaf hydraulic conductance (i.e. from the stem to the leaf) was calculated from the transpiration rate and the difference between the water potential of the leaf in the cuvette and the leaf outside the cuvette, which had been covered with aluminum foil to prevent transpiration. This assumes that the leaf water potential of the non-transpiring leaf was equal to the water potential of the stem supplying water to the adjacent leaf inside the cuvette. Fiscus et al. (1973) found higher resistance to water flow between adjacent leaves of tobacco than between leaves that were phyllotactically related, implying that differences in water potential can occur across the cross section of a stem, although the magnitude of such differences was not estimated. Such possible differences in water potential would make leaf hydraulic conductance as calculated appear to decrease with increased transpiration, which did not occur.

This measurement sequence was applied to three to five control and four or five dry leaves of each species. Differences between values of all variables at the C_a of 380 and 100 μmol mol^{-1} were tested using paired *t*-tests. To better define relationships between stomatal conductance and C_i for dry plants, extra plants of each species were measured as above except that no water potentials were determined, and C_a in the cuvette was changed from 380 to 100 μmol mol^{-1} and then to less than 10 μmol mol^{-1}. With C_a less than 10 μmol mol^{-1}, C_i was less than 30 μmol mol^{-1}.

Vapor pressure difference experiments

Gas exchange measurements on *H. annuus* were made with a Ciras-2 portable photosynthesis system (PP Systems), using a ''broad-leaf'' chamber with programmable temperature, light, carbon dioxide and humidity control. Gas exchange measurements on *P. sitchensis* were made with the CIRAS-2 instrument with a ''conifer'' chamber or with the system described earlier that was used for whole-leaf measurements in the root drying experiments. In *P. sitchensis*, the gas exchange measurements were made on terminal sections of branches with one-sided needle areas of about 30 cm^2. The rest of the plant was exposed to the daytime growth conditions. The section of leaf in the cuvette was exposed to a PPFD of 1500 μmol m^{-2} s^{-1} and a leaf temperature of 28°C. This temperature was chosen so that a wide range of D values could be obtained at a constant temperature. Leaves were initially exposed to a C_a of 380 μmol mol^{-1} and a D between 0.5 and 1.5 kPa. The D was then increased to a value between 1.5 and 3.2 kPa, while keeping leaf temperature, PPFD and C_a constant. The intent was to conduct measurements over a range of low and high values of D. Steady-state values of transpiration, stomatal conductance and CO_2 assimilation rate were recorded at each D. While keeping the leaf at the higher value of D and constant PPFD and temperature, the C_a was decreased to 100 μmol mol^{-1}. The $[CO_2]$ was kept at this low level for about 1 h, by which time gas exchange rates had stabilized, and then returned to 380 μmol mol^{-1} to determine the reversibility of gas exchange rates. These measurements were made on seven different plants per species. No measurements of leaf water potential were made in this set of observations.

Stomatal responses to C_i as determined in the four species used in the root drying experiments indicated that conductance decreased exponentially with increasing C_i, based on the three C_i values per leaf. For *H. annuus* and *P. sitchensis*, preliminary measurements of stomatal conductance vs C_i also indicated exponential decreases in conductance with C_i in these species. Relative stomatal sensitivity to C_i was therefore calculated as $d(\ln g)/d(C_i)$, from the slopes of regressions of ln g on C_i in all species (Bunce 2006).

Results

Root drying

In all four species, plants in which stomatal conductance was reduced by drying of the rooting medium had stomatal conductance increased by exposure to low $[CO_2]$ (Table 1). The increased stomatal conductance resulted in increased transpiration rate and lower leaf water potential in each case. There was no reduction in leaf hydraulic conductance resulting from the prolonged

Table 1. Stomatal conductance (g, in mmol m^{-2} s^{-1}), transpiration rate (E, in mmol m^{-2} s^{-1}), leaf water potential (LWP, in MPa) and leaf hydraulic conductance (K_l, in mmol m^{-2} s^{-1} MPa^{-1}) of whole leaves of four species in wet rooting medium or in dry rooting medium measured at two values of external [CO_2] (C_a). Water potentials of non-transpiring leaves of dry plants averaged −1.24, −0.97, −0.96 and −0.96 MPa in *A. theophrasti*, *G. max*, *G. hirsutum* and *X. strumarium*, respectively. Values are means ± SE for n = 4 or 5. * indicates a significant effect of C_a for dry plants at $P = 0.05$, using paired *t*-tests.

		Treatment		
		Wet	Dry	Dry
Species	C_a (μmol mol^{-1})	380	380	100
A. theophrasti	g	551 ± 45	166 ± 22	330 ± 56*
	E	8.7 ± 1.0	2.9 ± 0.5	5.1 ± 0.9*
	LWP	−1.3 ± 10.02	−1.52 ± 0.15	−1.73 ± 0.12*
	K_l	11.5 ± 0.8	11.1 ± 1.0	11.2 ± 0.9
G. max	g	342 ± 28	164 ± 26	285 ± 51*
	E	5.8 ± 0.5	2.8 ± 0.3	4.8 ± 0.6*
	LWP	−1.18 ± 0.05	−1.35 ± 0.09	−1.63 ± 0.18*
	K_l	11.1 ± 0.5	7.4 ± 1.1	7.1 ± 0.8
G. hirsutum	g	512 ± 50	102 ± 24	161 ± 21*
	E	7.7 ± 1.1	1.7 ± 0.5	2.9 ± 0.4*
	LWP	−0.93 ± 0.04	−1.08 ± 0.03	−1.24 ± 0.06*
	K_l	13.2 ± 1.2	13.0 ± 1.5	12.6 ± 0.8
X. strumarium	g	750 ± 84	159 ± 29	272 ± 90*
	E	12.4 ± 1.2	2.6 ± 0.4	4.4 ± 0.6*
	LWP	−0.79 ± 0.04	−1.23 ± 0.05	−1.42 ± 0.09*
	K_l	20.3 ± 1.5	10.4 ± 1.2	10.7 ± 1.0

exposure to lower water potentials at low [CO_2] (Table 1), although leaf hydraulic conductance of dry plants at both [CO_2] was lower than control plants in *G. max* and *X. strumarium*. Complete reopening of stomata at near 0 [CO_2] occurred in leaves in which stomatal conductance was reduced as much as about 50% from maximal conductance at 380 μmol mol^{-1} [CO_2] in all four species (Figs 1 and 2). At lower stomatal conductances, some reopening always occurred at low [CO_2], but was not complete. This is evident in Figs 1 and 2, as all conductances were above the 1:1 line, indicating higher stomatal conductance at the lower [CO_2]. The relative sensitivity of stomatal conductance to C_i was three to four times larger in leaves of dry plants than in control plants (Table 2).

Vapor pressure difference

There was little or no response of stomatal conductance to carbon dioxide concentration at the lower range of D values in either *H. annuus* (Fig. 3) or *P. sitchensis* (Fig. 4). At higher D, stomatal conductance became increasingly sensitive to C_i. Exposure of leaves at high D to low [CO_2] resulted in increased stomatal conductance in both species. In *H. annuus*, low [CO_2] resulted in essentially complete reopening of stomata (Fig. 3). Stomatal conductances returned to the initial value when [CO_2] was returned to 380 μmol mol^{-1} in all leaves (not shown).

Discussion

The observation that even further reductions in leaf water potential at low [CO_2] in the root drying experiments did not decrease hydraulic conductance indicates that leaf water potentials did not become low enough to reduce leaf hydraulic conductance in these cases. The same result was obtained earlier in the same species in wet soil when stomatal closure resulted from high D (Bunce 2006). In the root drying experiments, stomatal conductances of drying plants were measured at D values high enough to limit stomatal conductance, so that the results are relevant to stomatal closure caused both by root drying and high D. We can conclude that in these species, initial stomatal closure with drying of the rooting medium or the air or both was not caused by decreases in leaf hydraulic conductance.

It is interesting to note that the leaf hydraulic conductances of plants under water stress reported here were the same as previously reported (Bunce 2006) for unstressed plants in the case of *A. theophrasti* and *G. hirsutum*, but were 40–50% lower than in unstressed plants in *G. max* and *X. strumarium*. The reduction in leaf hydraulic conductances in stressed *G. max* and

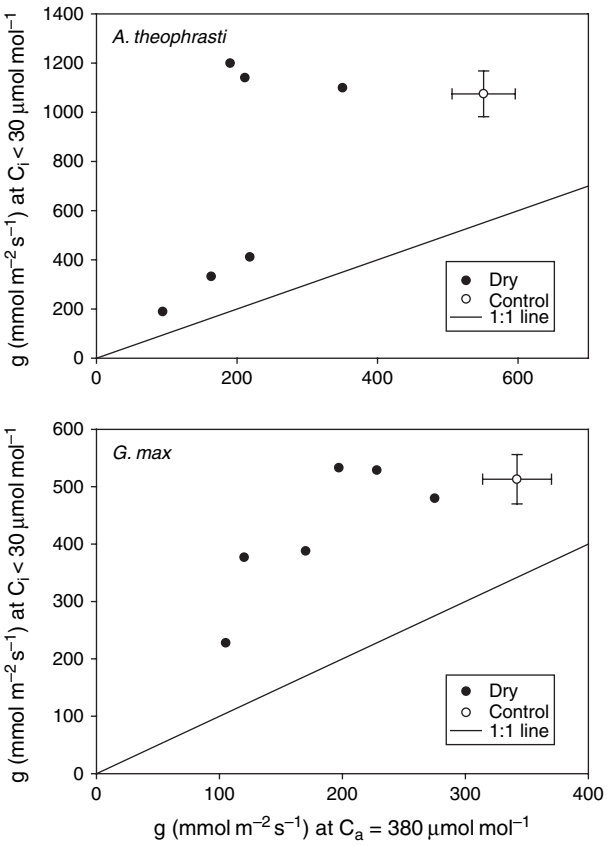

Fig. 1. Stomatal conductance (g) measured at an external ambient carbon dioxide concentration (C_a) of 380 μmol mol^{-1} and at an internal carbon dioxide concentration (C_i) of less than 30 μmol mol^{-1} in leaves of *A. theophrasti* and *G. max* plants with dry rooting medium or unstressed control plants. In dry plants, each point represents a pair of measurements on a single leaf, each leaf from a different plant. For control plants, the point represents a mean value for n = 3–5 plants, and error bars represent SE.

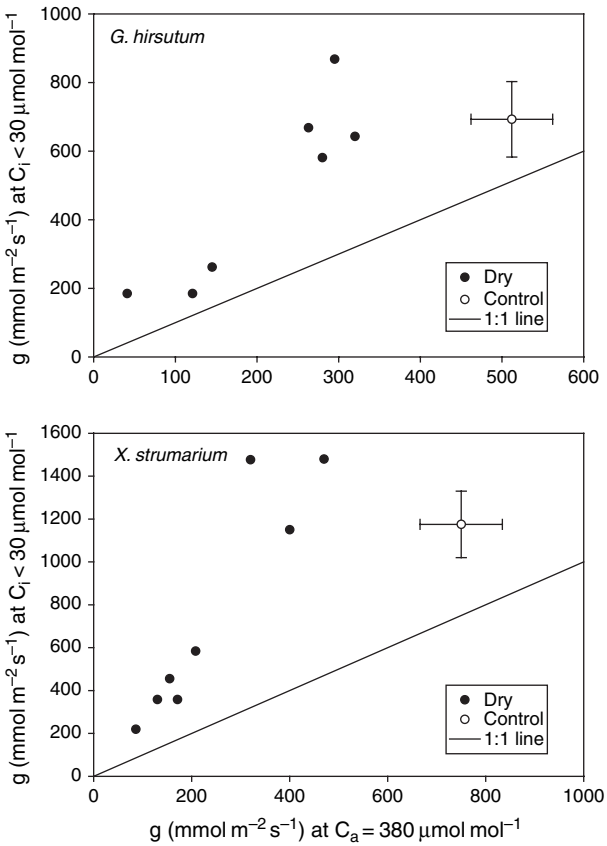

Fig. 2. Stomatal conductance (g) measured at an external ambient carbon dioxide concentration (C_a) of 380 μmol mol^{-1} and at an internal carbon dioxide concentration (C_i) of less than 30 μmol mol^{-1} in leaves of *G. hirsutum* and *X. strumarium* plants with dry rooting medium or unstressed control plants. In dry plants, each point represents a pair of measurements on a single leaf, each leaf from a different plant. For control plants, the point represents a mean value for n = 3–5 plants, and error bars represent SE.

X. strumarium plants is similar to results obtained by Brodribb and Holbrook (2006) in which leaf hydraulic conductance was reduced by water deficits too mild to cause xylem cavitation. While the cause of these reductions in hydraulic conductance is unclear, the ability of low [CO_2] to increase transpiration and reduce leaf water potential without any further change in leaf hydraulic conductance observed here indicates that they are not directly involved in causing stomatal closure during stress.

The low [CO_2] reversal of reductions in stomatal conductance caused by root drying occurred despite further decreases in leaf water potential. This indicates that low leaf water potentials did not overwhelmingly limit stomatal conductance during drying of the rooting medium, as was also the case in dry air (Bunce 2006). Numerous observations of reductions in stomatal conductance in drying soil without reductions in leaf water potential (e.g. Bates and Hall 1981, Gollan et al. 1986) led to studies that identified abscisic acid as a messenger that could be transported from drying roots to leaves and cause stomatal closure (Zhang et al. 1987). Abscisic acid can also be synthesized in leaves in response to reduced leaf water potential (Pierce and Raschke 1980, Wright and Hiron 1969), and reductions in leaf water potential may change stomatal sensitivity to abscisic acid (Tardieu and Davies 1992). A new hydromechanical model of stomatal conductance (Buckley et al. 2003) also does not envision reductions in leaf water potential causing stomatal closure directly, but by affecting the ability of guard cells to accumulate solutes, which abscisic acid does. Because abscisic acid increases stomatal sensitivity

Table 2. Relative sensitivity of stomatal conductance (g) to C_i in leaves of four species in plants rooted in wet and dry media. C_i values ranged from 65 to 285 μmol mol^{-1} for the external values of 380 and 100 μmol mol^{-1}. Relative sensitivity was calculated as d(ln g)/d(C_i), from slopes of regressions of ln g on C_i. Values are means ± SE for n = 3–5. *indicates a significant change in relative sensitivity between the wet and dry treatments at $P = 0.05$, using unpaired *t*-tests. Note: The information on the wet treatment was previously published (Bunce 2006) and is repeated here for ease of comparison

	Relative sensitivity (per μmol mol^{-1})	
Species	Wet	Dry
A. theophrasti	−0.0024 ± 0.0002	−0.0072 ± 0.0011*
G. max	−0.0015 ± 0.0001	−0.0056 ± 0.0003*
G. hirsutum	−0.0011 ± 0.0003	−0.0056 ± 0.0007*
X. strumarium	−0.0017 ± 0.0004	−0.0052 ± 0.0008*

to C_i (Dubbe et al. 1978, Leymarie et al. 1999, Raschke 1975), an abscisic acid signal causing stomatal closure could be consistent with our observations of increased relative stomatal sensitivity to C_i with drying. The

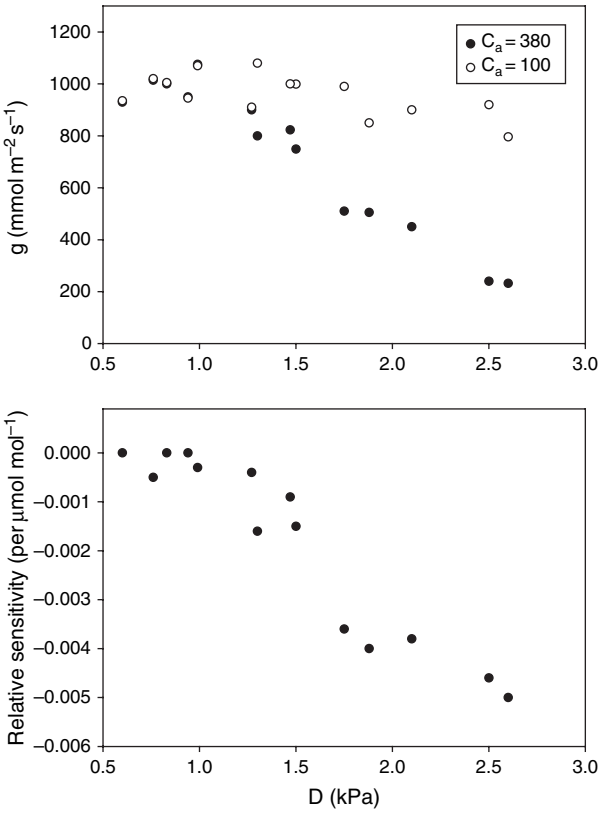

Fig. 3. Stomatal conductance (g) of *H. annuus* measured at external ambient carbon dioxide concentrations (C_a) of 380 or 100 μmol mol^{-1} at a range of values of leaf to air vapor pressure difference (D), and the relative sensitivity of stomatal conductance to internal carbon dioxide concentration (C_i), calculated as d(ln g)/d(C_i).

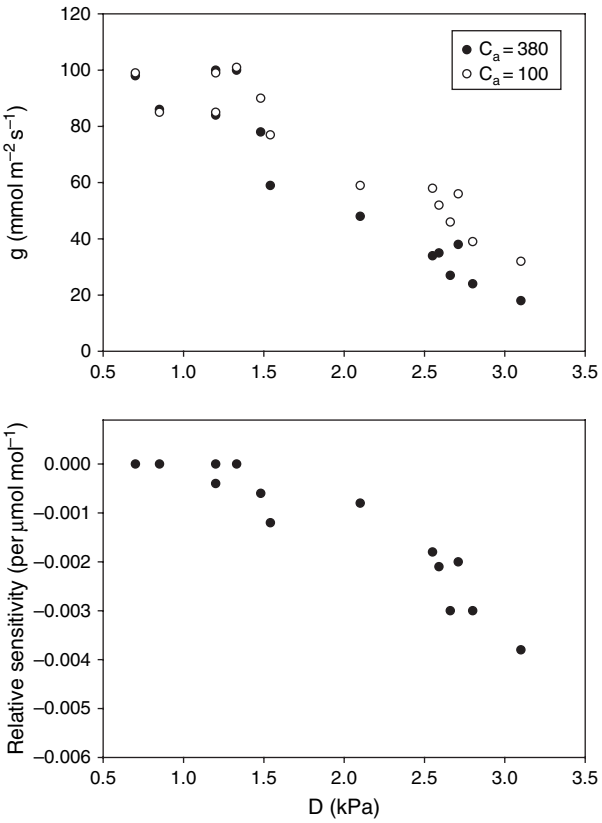

Fig. 4. Stomatal conductance (g) of *P. sitchensis* measured at external ambient carbon dioxide concentrations (C_a) of 380 or 100 μmol mol^{-1} at a range of values of leaf to air vapor pressure difference (D) and the relative sensitivity of stomatal conductance to internal carbon dioxide concentration (C_i), calculated as d(ln g)/d(C_i).

increased relative sensitivity of stomatal conductance to C_i fully accounted for the effects of drying of the rooting medium on stomatal conductance for reductions in conductance of about 50% or less and for essentially all of the closure at high D in *H. annuus*. With further drying of the rooting medium, and in the case of *P. sitchensis*, effects in addition to increased stomatal sensitivity to C_i contributed to closure. It is possible that disruption of photosynthesis by drying (Lawlor 2002) could account for the lack of full reversibility of stomatal conductance in those cases. Reopening of stomata at low [CO_2] during salinity stress also occurs and has been used to study photosynthesis without interference from changes in stomatal conductance (Centritto et al. 2003) and could also be used in that way to examine photosynthesis during mild water stress (Flexas et al. 2004).

Stomatal conductance has been reported to be insensitive to C_i in *H. annuus* (Bunce 1993, Goudriaan and van Laar 1978, Graan and Boyer 1990) and in *P. sitchensis* (Jarvis 1980). Insensitivity of stomatal conductance to C_i

was useful in demonstrating that stomatal opening in light was a direct effect of light and need not be mediated by C_i (Jarvis 1980). The stomatal sensitivity to C_i found here at high D in these species in no way challenges those observations because they were made at low D, where I also found no stomatal response to C_i in these species. Lack of response of stomatal conductance to C_i at low D has been reported for other species, which did respond at higher D (Bunce 1998, Hall and Kaufman 1975), but is not universal (Yong et al. 1997, unpublished data). Perhaps *H. annuus* and *P. sitchensis* are unusual in having stomatal conductance insensitive to C_i at higher D than many other species.

The mechanism by which stomatal conductance responds to C_i is unknown (Assmann 1999), although effects on ATP levels caused by $[CO_2]$ effects on respiration have been suggested (Shaish et al. 1989), and a kinase has been implicated in *Arabidopsis* (Hashimoto et al. 2006). The recent hydromechanical and biochemical model of stomatal conductance (Buckley et al. 2003) as currently parameterized has almost no stomatal response to C_i at high-light at low water potentials, which is not consistent with our results. The data presented here indicate that increases in stomatal sensitivity to C_i during root drying are responsible for at least the initial decreases in stomatal conductance. Increased stomatal sensitivity to C_i with drying would shift the operational C_i to lower values, as typically occurs during drying. Improved knowledge of how stomatal conductance responds to C_i and how the sensitivity of the response is controlled will be required to understand reductions in stomatal conductance in response to both high D and dry soil.

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