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Effects of water vapor pressure difference on leaf gas exchange in potato and sorghum at ambient and elevated carbon dioxide under field conditions

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Abstract

High leaf to air water vapor pressure differences often substantially reduce rates of assimilation of carbon dioxide, especially in C_3 species. Rising concentrations of carbon dioxide [CO_2] in the atmosphere could reduce the sensitivity of assimilation rate to partial stomatal closure caused by high vapor pressure difference by a variety of mechanisms. However, field data addressing this question are scarce. In this study, we examined day-to-day variation in midday gas exchange rates of upper canopy leaves of potato and sorghum grown at the current ambient [CO_2] and ambient + 350 $\mu\text{mol mol}^{-1}$ [CO_2] in field plots. Stomatal conductance and assimilation rate were negatively correlated with vapor pressure difference across days. Assimilation rate was not less sensitive to vapor pressure difference at elevated than at ambient [CO_2] in either species. For both potato and sorghum short-term increases in vapor pressure difference for individual leaves produced significantly smaller responses of leaf gas exchange than did the day-to-day variation in vapor pressure difference, again with no reduced sensitivity at elevated [CO_2]. The smaller response of gas exchange to short-term manipulations of vapor pressure difference than to day-to-day variation may indicate that much of the response to high vapor pressure difference apparent in the day-to-day variation resulted from leaf water deficits caused by exposure of the whole canopy to high vapor pressure difference, rather than from direct effects of high water vapor pressure difference. The lack of a [CO_2] effect on the sensitivity of assimilation rate to vapor pressure difference, and the substantial sensitivity of assimilation rate to vapor pressure difference in the C_4 species both resulted from reductions in assimilation at a given internal [CO_2] at high vapor pressure difference. An implication of these results is that high leaf to air water vapor pressure difference may continue to be a major limitation to assimilation rates in C_3 and C_4 crop species even at twice the current concentration of carbon dioxide in the atmosphere.

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1. Introduction

Based on several diverse lines of evidence, it appears that high leaf to air differences in water vapor

pressure limit carbon dioxide assimilation rates in many species under field conditions. For most species, increasing the leaf to air water vapor pressure difference at constant temperature results in a reduction in stomatal conductance to water vapor (Schulze and Hall, 1982; El-Sharkawy et al., 1984). When carbon dioxide concentration ($[CO_2]$) limits assimilation

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rates, lower conductance at high vapor pressure differences reduces assimilation by reducing internal $[\text{CO}_2]$. This has been demonstrated innumerable times under laboratory conditions, where water vapor pressure can be manipulated around single leaves while temperature is kept constant, and reductions in assimilation rate at high vapor pressure difference can be overcome with increased $[\text{CO}_2]$. Under field conditions, diurnal changes in assimilation rate at high light are often attributed to changes in vapor pressure difference, but temperature and vapor pressure difference are usually highly correlated in this type of data. However, manipulations of water vapor pressure at constant temperature in the field have also shown that high vapor pressure difference reduces the assimilation rate of single leaves when assimilation is limited by $[\text{CO}_2]$. For example, increasing the water vapor pressure around individual leaves strongly increased daily assimilation in soybean (Bunce, 1982a), wheat (Xu et al., 1984) and rice (Ishihara and Saitoh, 1986; Kuroda and Kumura, 1990). Smaller or no responses of assimilation rate to manipulations of water vapor pressure around individual leaves were found in C_4 species (Bunce, 1982b, 1983), because assimilation was at or near saturation for $[\text{CO}_2]$. High water vapor pressure difference also seems to affect assimilation rates at the whole canopy scale. For example, variation in average vapor pressure difference between locations correlated with canopy radiation use efficiency, high vapor pressure difference reducing efficiency (Stockle and Kiniry, 1990; Kiniry et al., 1998; Kiniry, 1999). Canopy assimilation rates were also negatively correlated with water vapor pressure difference in eddy covariance measurements (e.g. Grace et al., 1998). Altering the microenvironment to increase water vapor pressure at the whole canopy level increased plant growth in cassava (Cock et al., 1985). Thus responses of assimilation rate to water vapor pressure difference at the single leaf level seem to translate into sensitivity of assimilation and growth to vapor pressure difference at the stand level.

However, responses of assimilation rate to water vapor pressure difference at the larger spatial scales may not be mediated by direct responses of stomatal conductance to vapor pressure difference, but by leaf water deficits caused by exposure of whole canopies to high vapor pressure difference, as demonstrated in maize (Bunce, 1990). Strong responses of assimilation

to water vapor pressure difference at the canopy level in C_4 species (e.g. Grace et al., 1998; Kiniry et al., 1998) would not be expected solely from direct responses of stomatal conductance to water vapor pressure, since in C_4 species assimilation is usually nearly saturated for CO_2 (e.g. Kawamitsu et al., 1987). The distinction between direct responses of gas exchange to water vapor pressure difference and responses mediated through plant water status is of importance in predicting how rising atmospheric $[\text{CO}_2]$ may affect assimilation rates at high vapor pressure differences.

Under the scenario where high water vapor pressure difference reduces assimilation rates by direct effects on stomatal conductance, the rising $[\text{CO}_2]$ in the atmosphere might reduce the sensitivity of assimilation rate to vapor pressure difference in C_3 species, but have little effect on the sensitivity in most C_4 species. In both C_3 and C_4 species, carbon dioxide assimilation rates increase with $[\text{CO}_2]$ with a slope which decreases with increasing $[\text{CO}_2]$. In C_3 species the current atmospheric $[\text{CO}_2]$ is still quite limiting to assimilation rates except at very cool temperatures (Sage and Sharkey, 1987). Therefore, elevated $[\text{CO}_2]$ would usually make assimilation rate of C_3 species less sensitive to reductions in carbon dioxide supply caused by lower stomatal conductance at high water vapor pressure difference. Of course, the sensitivity of assimilation rate to vapor pressure difference depends on the magnitude of the response of stomatal conductance to vapor pressure difference, which could also vary with $[\text{CO}_2]$. In most C_4 species the assimilation rate is at or near saturation for $[\text{CO}_2]$ at the current atmospheric concentration, and assimilation is less sensitive to vapor pressure difference at the leaf level than in C_3 species. However, there are some C_4 species in which the current atmospheric $[\text{CO}_2]$ limits assimilation (e.g. Ziska and Bunce, 1997; Anderson et al., 2001; Morgan et al., 2001), and in these species rising atmospheric $[\text{CO}_2]$ would also be expected to reduce the sensitivity of assimilation rate to high vapor pressure difference to some extent.

In cases where high water vapor pressure difference reduces assimilation rate by causing leaf water deficits, then rising atmospheric $[\text{CO}_2]$ could reduce the sensitivity of assimilation rate to vapor pressure difference for both C_3 and C_4 species. Elevated $[\text{CO}_2]$

reduces stomatal conductance and transpiration in both C₃ and C₄ species, and would be expected to reduce midday leaf water deficits caused by high vapor pressure difference. Furthermore, because water deficits often increase the sensitivity of stomatal conductance to vapor pressure difference (e.g. Maier and Tesky, 1992; Thomas and Eamus, 1999), elevated [CO₂] could decrease the sensitivity of leaf gas exchange to water vapor pressure difference by reducing water deficits.

The way in which high leaf to air water vapor pressure difference reduces stomatal conductance and assimilation rate is also important to how rising atmospheric [CO₂] may affect the sensitivity of assimilation rate to high vapor pressure difference. If lower conductance at high vapor pressure difference occurs as complete closure of stomata in “patches” (Beyschlag et al., 1992), then high vapor pressure difference effectively prevents patches of leaves from exchanging CO₂, and assimilation would decrease at high vapor pressure difference for either C₃ or C₄ species. In this situation, elevated [CO₂] might not reduce the sensitivity of assimilation to vapor pressure difference. There is evidence that stomatal closure, whether caused by directly by high vapor pressure difference or by leaf water deficits may sometimes occur by “patchy” closure (Downton et al., 1988; Beyschlag et al., 1992).

These experiments were designed to test whether carbon dioxide assimilation rate was less sensitive to high leaf to air water vapor pressure difference at elevated [CO₂] than at the current ambient [CO₂] in a C₃ and a C₄ crop species grown under field conditions, and examine reasons for any differences in response between species or [CO₂] treatments. Comparisons were made between responses to day-to-day variation in vapor pressure difference and responses to short-term manipulations of vapor pressure difference, in order to separate direct responses of leaf gas exchange to vapor pressure difference from responses mediated by leaf water deficits.

2. Materials and methods

Potato (*Solanum tuberosum* L. cv. Atlantic) and grain sorghum (*Sorghum bicolor* L. Moench cv. ATx399xRTx430) were grown in field plots at the

South Farm of the Beltsville Agricultural Research Center. Carbon dioxide treatments were imposed in open top chambers maintained at either the current ambient concentration of carbon dioxide or ambient+350 ± 50 μmol mol⁻¹ [CO₂], as previously described (Bunce, 2001a). There were two chambers per [CO₂] treatment in potato and three in sorghum. Stand densities and fertilizer treatments followed standard agronomic practice in the area (Sicher and Bunce, 1999; Bunce, 2001a). Plots received normal precipitation, and were not irrigated.

Gas exchange rates of mature fully illuminated upper canopy leaves were measured near midday on clear days over 2 years (1996–1997) in sorghum and 3 years (1996–1998) in potato. Measurements were confined to the period between canopy closure and crop senescence. Photosynthetic photon flux density (PPFD) was at least 1500 μmol m⁻² s⁻¹. Carbon dioxide assimilation rate and stomatal conductance were measured using a CIRAS-1 portable photosynthesis system (PP Systems, Haverhill, MA), with automatic [CO₂] control and a broad leaf cuvette. Leaf gas exchange rates at the growth [CO₂] condition were obtained within 30 s of placing a leaf in the cuvette. During measurements of responses of assimilation rate and stomatal conductance to imposed changes in water vapor pressure difference (see later), leaf gas exchange took >1 min to respond to changes in vapor pressure difference. For these <30 s measurement periods, it was therefore assumed that leaves were adjusted to the vapor pressure difference conditions outside the cuvette, rather than to the altered conditions within the cuvette. The leaf to air water vapor pressure difference of leaves outside the cuvette was calculated from measurements of leaf temperatures made by pressing a 0.75 mm diameter thermocouple against the underside of leaves before placing them in the cuvette, and the water vapor pressure of the air in the [CO₂] treatment chambers, taken from the reference air stream of the photosynthesis system. On each day mean values of gas exchange of six leaves per species were determined for each [CO₂] treatment, with samples evenly split among the two or three chambers per [CO₂] treatment. Leaf gas exchange data from 1 day when dry soil limited gas exchange rates in potato were excluded (Bunce, 2001a). Data were analyzed for 16 measurement days for potato and 11 for sorghum.

On several other days, responses of leaf carbon dioxide assimilation rate and stomatal conductance to imposed increases in leaf to air water vapor pressure difference were determined. These measurements were also made near midday on clear days, using the CIRAS-1 system with real-time graphical display of data, with the $[\text{CO}_2]$ set to match the growth $[\text{CO}_2]$. Leaves were placed in the cuvette without drying of the air stream before entering the cuvette, and left for several minutes to equilibrate to the cuvette conditions. After steady-state values of leaf gas exchange and environment were recorded, the air stream entering the cuvette was dried and gas exchange was monitored until new steady-state values occurred. Responses of assimilation rate and stomatal conductance to vapor pressure difference were obtained for three leaves from each $[\text{CO}_2]$ treatment on each measurement day. These measurements were conducted on a total of 6 days for each species over the 2 or 3 years, but both species were measured on the same date only twice.

Responses of carbon dioxide assimilation rate to internal $[\text{CO}_2]$ caused by varying external $[\text{CO}_2]$ at constant water vapor pressure difference were measured on a few leaves of both species grown at ambient $[\text{CO}_2]$. This allowed judgment of whether relationships between assimilation rate and internal $[\text{CO}_2]$ from varying water vapor pressure difference followed typical relationships for the species, and also whether the assimilation rate of the ambient grown sorghum plants was saturated for CO_2 under ambient $[\text{CO}_2]$ conditions. The automatic $[\text{CO}_2]$ control system was used to provide external $[\text{CO}_2]$ of 100, 200, 350, 500 and $700 \mu\text{mol mol}^{-1}$. These measurements were made in full sunlight, with PPF $> 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, a leaf temperature of about 30°C , and a water vapor pressure difference of about 2.0 kPa.

Analysis of covariance (ANCOVA) of regressions relating assimilation rate and stomatal conductance to the leaf to air water vapor pressure difference was used to test for $[\text{CO}_2]$ treatment effects on the slope of the response to water vapor pressure difference. Either assimilation rate, stomatal conductance or the natural log of those variables was regressed against water vapor pressure difference. Other simple transformations of the variables did not increase the r^2 values. ANCOVA was conducted using the regressions which produced the largest r^2 values for each variable and species.

3. Results

Midday values of leaf to air water vapor pressure difference varied from about 1 to about 3 kPa on the days when gas exchange was measured. Variation in vapor pressure difference among days was mostly related to the water content of the air masses rather than to air temperature. The result was that in sorghum, there was no significant correlation between vapor pressure difference and air temperature across days, and only a weak correlation in the data for potato (Fig. 1). Several types of regressions relating assimilation rate and stomatal conductance to temperature with or without vapor pressure difference as an independent variable failed to indicate a significant effect of temperature on leaf gas exchange rate for either species in these data sets (not shown). Thus the day-to-day variation of assimilation rate and stomatal conductance primarily represents responses to water vapor pressure difference, because measurements were made at high PPF and soil water was not limiting.

In both species, growth at elevated $[\text{CO}_2]$ increased assimilation rate and decreased stomatal conductance at a given value of water vapor pressure difference (Fig. 2). Linear regressions indicated that high vapor pressure difference reduced assimilation rate in both species (Fig. 2), and that the slopes were similar at elevated and ambient $[\text{CO}_2]$ (Table 1). In both species the natural log of conductance produced a better linear regression with day-to-day variation in vapor pressure difference than did conductance (Fig. 2). In neither species did the slope of the response of the natural log of conductance to vapor pressure difference differ significantly between the $[\text{CO}_2]$ treatments (Table 1), using ANCOVA. Variation in assimilation rate and stomatal conductance among the six leaves measured on each date was not large compared with the variation in mean values among days. The standard deviation averaged 20% of the mean for conductance in sorghum and 12% for assimilation rate, with no differences between $[\text{CO}_2]$ treatments. The standard deviation averaged 22% of the mean for conductance in potato and 16% for assimilation rate, with no differences between $[\text{CO}_2]$ treatments.

Decreasing assimilation rate at high vapor pressure difference was associated with lower internal $[\text{CO}_2]$ in sorghum for both $[\text{CO}_2]$ treatments (Fig. 3), but

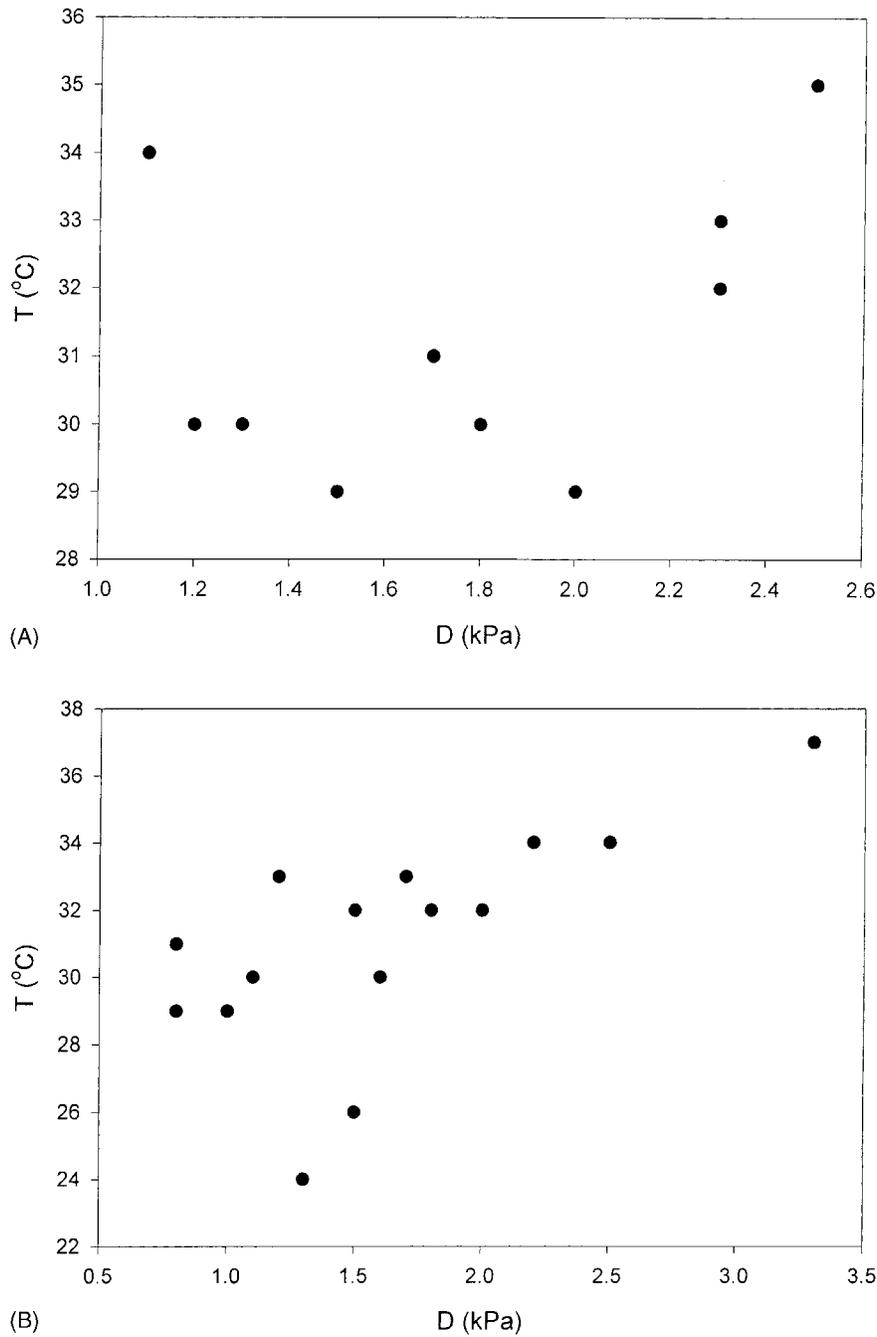


Fig. 1. Leaf temperature (T_l) and leaf to air water vapor pressure difference (D) on days when midday leaf gas exchange measurements were conducted to determine the effect of day-to-day variation in environment on gas exchange for (A) sorghum, and (B) potato. The r^2 between T_l and D was 0.17 in sorghum and 0.47 in potato.

internal $[CO_2]$ changed little in potato in the low $[CO_2]$ treatment. In all cases variation in water vapor pressure difference caused a larger change in assimilation rate for a given change in internal $[CO_2]$ than occurred

when external $[CO_2]$ was varied at constant water vapor pressure difference (Fig. 3).

Changing the leaf to air water vapor pressure difference around portions of individual leaves changed

steady-state leaf temperatures by less than 1 °C. Leaf gas exchange was much less responsive to short-term manipulation of vapor pressure difference around portions of individual leaves than to day-to-day variation in vapor pressure difference. The slopes of the

responses of the natural log of stomatal conductance to short-term manipulations of vapor pressure difference were significantly different from zero in all cases (Table 2), but were only 15–34% as large as the responses to day-to-day variation in vapor pressure

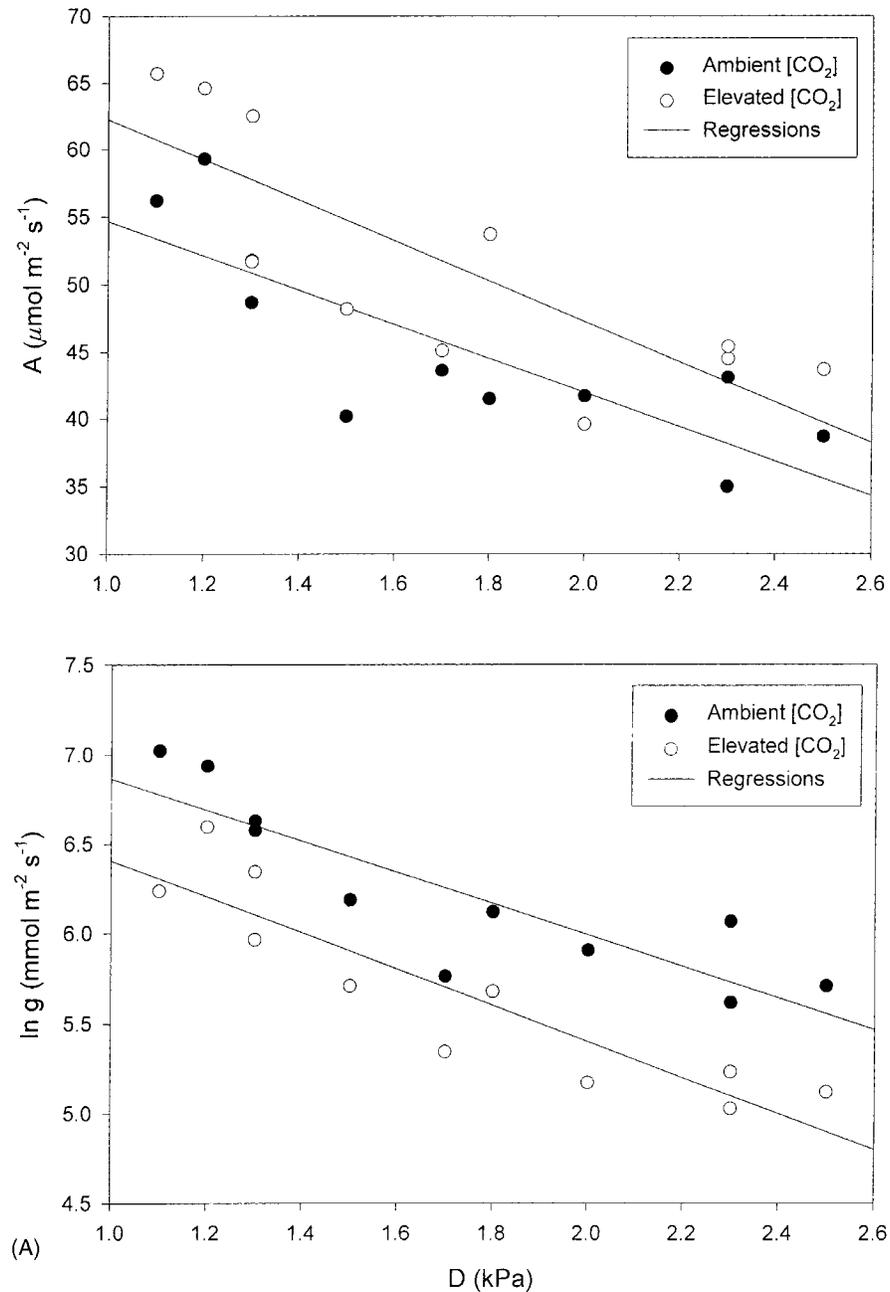


Fig. 2. Day-to-day variation in midday assimilation rate (A) and stomatal conductance (g) as functions of leaf to air water vapor pressure difference (D) for (A) sorghum and (B) potato grown at the current ambient $[\text{CO}_2]$ or at ambient + $350 \mu\text{mol mol}^{-1} [\text{CO}_2]$. Equations for the linear regressions are given in Table 1.

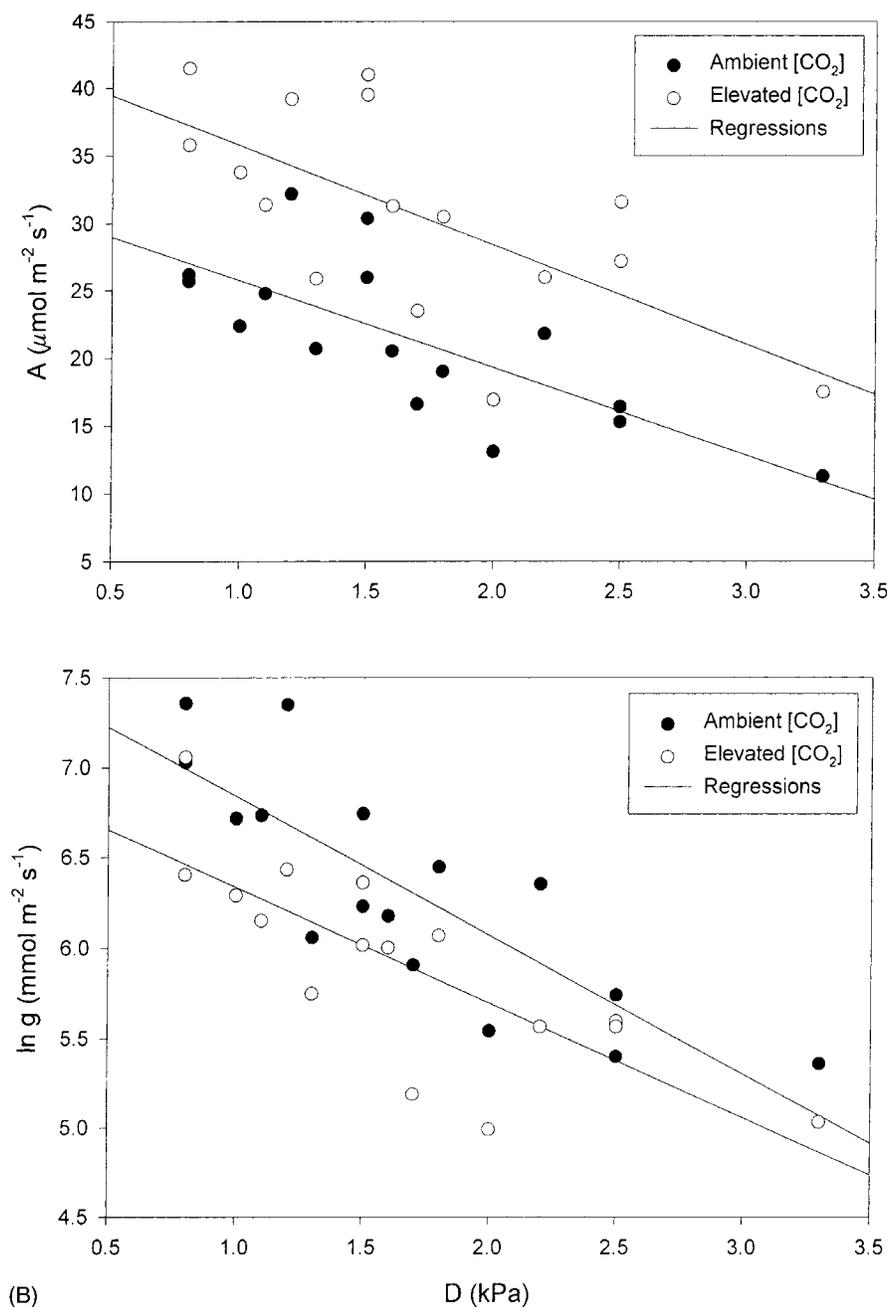


Fig. 2. (Continued).

difference (Table 1). In neither species did the slope of the response differ between [CO₂] treatments. The slopes of the responses of assimilation rates to short-term manipulations of vapor pressure difference (Table 2) were only 18–41% as large as for day-to-day variation in vapor pressure difference (Table 1). In neither species did the elevated [CO₂] treatment

decrease the slope of the response of assimilation rate to vapor pressure difference.

The short-term increase in vapor pressure difference reduced internal [CO₂] in sorghum, but there was no decrease in the internal [CO₂] in potato at the lower [CO₂] treatment (Fig. 3). For both the [CO₂] treatments and species, the response of assimilation rate to

Table 1

Linear regression equations relating mean values of midday assimilation rate (A) and the natural log of stomatal conductance (g) to the leaf to air water vapor pressure difference (D) on different days, for potato and sorghum grown at the current ambient and elevated (ambient + 350 $\mu\text{mol mol}^{-1}$) [CO_2]^a

Species	[CO_2]	Variable	Intercept \pm S.E.	Slope \pm S.E.	r^2
Potato	Ambient	A	32.2 ± 2.8	-6.5 ± 1.5	0.558
Potato	Elevated	A	43.2 ± 4.0	-7.4 ± 2.2	0.441
Sorghum	Ambient	A	67.4 ± 5.3	-12.7 ± 2.9	0.675
Sorghum	Elevated	A	77.2 ± 6.6	-15.0 ± 3.7	0.648
Potato	Ambient	$\ln(g)$	7.61 ± 0.25	-0.77 ± 0.14	0.690
Potato	Elevated	$\ln(g)$	6.98 ± 0.25	-0.64 ± 0.14	0.612
Sorghum	Ambient	$\ln(g)$	7.74 ± 0.29	-0.87 ± 0.16	0.760
Sorghum	Elevated	$\ln(g)$	7.41 ± 0.28	-1.00 ± 0.16	0.821

^a A is in $\mu\text{mol m}^{-2} \text{s}^{-1}$, g is in $\text{mmol m}^{-2} \text{s}^{-1}$, and D is in kPa. Mean values for each date were based on measurements of six leaves per [CO_2] treatment. Measurements were made on 16 days over 3 years for potato and on 11 days over 2 years for sorghum. Slopes did not differ between [CO_2] treatments at $P = 0.05$ for either variable for either species, using ANCOVA.

Table 2

Slopes of responses of assimilation rate (A) or the natural log of stomatal conductance (g) to short-term manipulation of leaf to air water vapor pressure difference (D), for potato and sorghum plants grown at the current ambient and elevated (ambient + 350 $\mu\text{mol mol}^{-1}$) [CO_2]^a

Species	[CO_2]	Variable	Slope \pm S.E.
Potato	Ambient	A	-1.7 ± 0.3
Potato	Elevated	A	-3.0 ± 0.8
Sorghum	Ambient	A	-2.5 ± 0.8
Sorghum	Elevated	A	-2.7 ± 0.6
Potato	Ambient	$\ln(g)$	-0.22 ± 0.04
Potato	Elevated	$\ln(g)$	-0.22 ± 0.03
Sorghum	Ambient	$\ln(g)$	-0.16 ± 0.03
Sorghum	Elevated	$\ln(g)$	-0.15 ± 0.04

^a A is in $\mu\text{mol m}^{-2} \text{s}^{-1}$, g is in $\text{mmol m}^{-2} \text{s}^{-1}$, and D is in kPa. S.E. are based on mean values for six measurement dates for each species. On each date three leaves per [CO_2] treatment were measured. Measurements were made on 6 days for each species, over 2 years in sorghum and 3 years in potato. Slopes did not differ between [CO_2] treatments at $P = 0.05$ for either variable for either species, using paired t -tests.

internal [CO_2] for the short-term manipulations of water vapor pressure difference was steeper than the response of assimilation rate to internal [CO_2] caused by varying external [CO_2] at constant water vapor pressure difference (Fig. 3).

4. Discussion

The two sources of variation in leaf to air water vapor pressure difference, day-to-day variation in

midday values caused primarily by the differing water contents of air masses, and short-term manipulations of vapor pressure difference caused by drying of the air stream entering the leaf cuvette, produced contrasting magnitudes of responses of leaf gas exchange to vapor pressure difference. The contrasting responses provide information on how the environment limits assimilation rate and stomatal conductance, but for neither source of variation in vapor pressure difference was assimilation less sensitive to vapor pressure difference at elevated [CO_2] in either species. This was not the result of increased sensitivity of stomatal conductance to vapor pressure at elevated [CO_2], but resulted from the steeper than expected response of assimilation rate to the changes in internal [CO_2] caused by lower stomatal conductance at high vapor pressure differences.

For both species and both sources of variation in water vapor pressure difference, the response of assimilation rate to changes in internal [CO_2] caused by stomatal closure at high vapor pressure difference was steeper than responses of assimilation to internal [CO_2] caused by changing external [CO_2]. Steeper than expected apparent responses of assimilation rate to internal [CO_2] caused by stresses have variously been attributed to non-stomatal inhibition of photosynthesis (e.g. Guehl and Aussenac, 1987; Bunce, 1988; Nicoldi et al., 1988; Demmig-Adams et al., 1989; Beyschlag and Pfanz, 1990; Gimenez et al., 1992) or to “patchy” stomatal closure (e.g. Downton et al., 1988; Beyschlag et al., 1992; Lal et al., 1996). Our data cannot distinguish between these possibili-

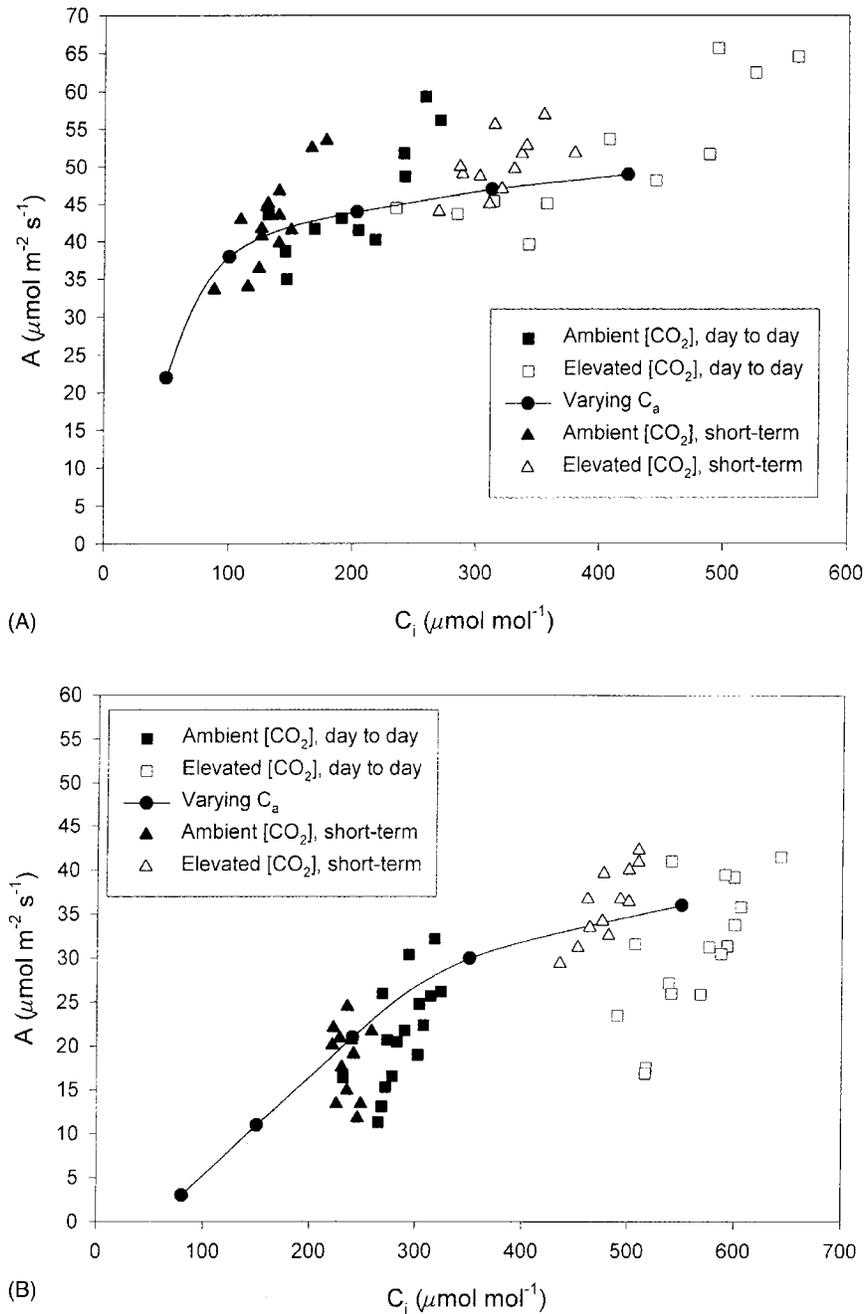


Fig. 3. Assimilation rate (A) and internal $[\text{CO}_2]$ (C_i) for (A) sorghum and (B) potato grown at the current ambient $[\text{CO}_2]$ and at ambient + $350 \mu\text{mol mol}^{-1}$ $[\text{CO}_2]$. Variation in A was induced by day-to-day variation in leaf to air water vapor pressure difference, or short-term increases in leaf to air water vapor pressure difference, or by varying external $[\text{CO}_2]$ (C_a) at constant D . When changes in D caused the variation in A , A was negatively correlated with D .

ties, except that observed reductions in internal $[\text{CO}_2]$ at high vapor pressure difference, especially in sorghum, indicate that reductions in stomatal conductance did not only result from complete closure of

stomata in patches, but that some partial closure also occurred. The lack of reduced sensitivity of assimilation rate to vapor pressure difference at elevated $[\text{CO}_2]$ in this study is similar to field data for tree species

(Goodfellow et al., 1997; Singaas et al., 2000), and potted soybean plants grown outdoors (Bunce, 1993).

For both species and both [CO₂] treatments, smaller changes in assimilation rate and stomatal conductance occurred for a given change in water vapor pressure difference in the short-term manipulation of vapor pressure difference than for the day-to-day variation in vapor pressure difference. In contrast to potato and sorghum, in wheat and barley the responses of stomatal conductance to day-to-day variation in vapor pressure difference and short-term manipulation of vapor pressure difference were indistinguishable (Bunce, 2001b). The difference between the day-to-day variation in vapor pressure difference and short-term manipulation of vapor pressure difference is the vapor pressure difference to which the rest of the shoot is exposed. Although a leaf to air water vapor pressure difference for a whole shoot is difficult to define because of varying leaf temperatures and probably humidities through the canopy, it remained at the lower value during the short-term increase in vapor pressure difference for the measured leaf section in the cuvette, but increased with the vapor pressure difference of the measured leaf section in the day-to-day variation. The implication of the much larger changes in leaf gas exchange for the day-to-day variation in vapor pressure difference is that high vapor pressure difference for the canopy strongly reduced gas exchange for leaf sections measured at a given value of vapor pressure difference. The most likely explanation of this is that high vapor pressure difference for the canopy increased leaf water deficits, and that leaf water deficits reduced *g* and *A*. High vapor pressure difference for a canopy reducing leaf gas exchange by increasing leaf water deficits has been observed in other species, for example, in tomato (Bunce, 1988) and maize (Bunce, 1990). Thus it appears that even when leaf water deficits are involved in reductions in assimilation rate and stomatal conductance at high vapor pressure difference, elevated [CO₂] will not necessarily decrease the sensitivity of assimilation rate or stomatal conductance to high vapor pressure difference.

Day-to-day variation in leaf to air water vapor pressure difference in sorghum at the current ambient [CO₂] resulted in changes in midday carbon dioxide assimilation rates which were very similar to the changes in canopy radiation use efficiency reported by Kiniry (1999) for this species grown in environ-

ments differing in vapor pressure difference. The relative sensitivity, calculated as the slope divided by the intercept of the linear regressions, had a value of -0.20 for the data summarized by Kiniry (1999), compared with values of -0.19 for the data presented here for both ambient and elevated [CO₂]. Our values for potato were -0.20 and -0.17 at the current ambient and elevated [CO₂], respectively. The expectation from responses of assimilation rate to internal [CO₂] of smaller sensitivity of assimilation to high vapor pressure difference in C₄ than in C₃ species may not apply when whole canopies are exposed to the higher vapor pressure difference.

The hypothesis that elevated [CO₂] would reduce the sensitivity of assimilation rate to high water vapor pressure difference was not supported by the data, and high vapor pressure difference may continue to be a significant limitation to assimilation rate in both C₃ and C₄ species as atmospheric [CO₂] continues to rise. This limitation could become even larger if global warming and/or microclimatic feedback effects of an overall reduction in conductance (Wilson et al., 1999) increase the water vapor pressure difference to which plants are exposed.

References

- Anderson, L.J., Maherali, H., Johnson, H.B., Polley, H.W., Jackson, R.B., 2001. Gas exchange and photosynthetic acclimation over subambient to elevated CO₂ in a C₃–C₄ grassland. *Global Change Biol.* 7, 693–707.
- Beyschlag, W., Pfanz, H.P., 1990. A fast method to detect the occurrence of nonhomogeneous distribution of stomatal aperture in heterobaric plant leaves. Experiments with *Arbutus unedo* L. during the diurnal course. *Oecologia* 82, 52–55.
- Beyschlag, W., Pfanz, H., Ryel, R.J., 1992. Stomatal patchiness in Mediterranean evergreen species. Phenomenology and consequences for the interpretation of the midday depression of photosynthesis and transpiration. *Planta* 187, 546–553.
- Bunce, J.A., 1982a. Photosynthesis at ambient and elevated humidity over a growing season in soybean. *Photosynth. Res.* 3, 307–311.
- Bunce, J.A., 1982b. Low humidity effects on photosynthesis in single leaves of C₄ plants. *Oecologia* 54, 233–235.
- Bunce, J.A., 1983. Differential sensitivity to humidity of daily photosynthesis in the field in C₃ and C₄ species. *Oecologia* 57, 262–265.
- Bunce, J.A., 1988. Nonstomatal inhibition of photosynthesis by water stress. Reduction in photosynthesis at high transpiration rate without stomatal closure in field-grown tomato. *Photosynth. Res.* 18, 357–362.

- Bunce, J.A., 1990. Afternoon inhibition of photosynthesis in maize. 2. Environmental causes and physiological symptoms. *Field Crops Res.* 24, 261–271.
- Bunce, J.A., 1993. Effects of doubled atmospheric carbon dioxide concentration on the responses of assimilation and conductance to humidity. *Plant Cell Environ.* 16, 189–197.
- Bunce, J.A., 2001a. Direct and acclamatory responses of stomatal conductance to elevated carbon dioxide in four herbaceous crop species in the field. *Global Change Biol.* 7, 323–331.
- Bunce, J.A., 2001b. 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.
- Cock, J.H., Porto, M.C.M., El-Sharkawy, M.A., 1985. Water use efficiency of cassava. III. Influence of air humidity and water stress on gas exchange field grown cassava. *Crop Sci.* 25, 265–272.
- Demmig-Adams, B., Adams III, W.W., Winter, K., Meyer, A., Schreiber, U., Pereira, J.S., Kruger, A., Czygan, F.-C., Lange, O.L., 1989. Photochemical efficiency of photosystem II, photon yield of O₂ evolution, photosynthetic capacity, and carotenoid composition during the midday depression of net CO₂ uptake in *Arbutus unedo* growing in Portugal. *Planta* 177, 377–387.
- Downton, W.J.S., Loveys, B.R., Grant, W.J.R., 1988. Non-uniform stomatal closure induced by water stress causes putative non-stomatal inhibition of photosynthesis. *New Phytol.* 110, 503–510.
- El-Sharkawy, M.A., Cock, J.H., Held, K.A.A., 1984. Water use efficiency of cassava. II. Differing sensitivity of stomata to air humidity in cassava and other warm-climate species. *Crop Sci.* 24, 503–507.
- Gimenez, C., Mitchell, V.J., Lawlor, D.W., 1992. Regulation of photosynthetic rate of two sunflower hybrids under water stress. *Plant Physiol.* 98, 516–524.
- Goodfellow, J., Eamus, D., Duff, G., 1997. Diurnal and seasonal changes in the impact of CO₂ enrichment on assimilation, stomatal conductance and growth in a long-term study of *Mangifera indica* in the wet-dry tropics of Australia. *Tree Physiol.* 17, 291–299.
- Grace, J., Lloyd, J., Miranda, A.C., Miranda, H., Gash, J.H.C., 1998. Fluxes of carbon dioxide and water vapour over a C₄ pasture in south-western Amazonia (Brazil). *Aust. J. Plant Physiol.* 25, 519–530.
- Guehl, J.-M., Aussenac, G., 1987. Photosynthesis decrease and stomatal control of gas exchange in *Abies alba* Mill. in response to vapor pressure difference. *Plant Physiol.* 83, 316–322.
- Ishihara, K., Saitoh, K., 1986. Diurnal courses of photosynthesis, transpiration and diffusive conductance in the single-leaf of rice plants grown in the paddy field under submerged condition. *Jpn. J. Crop Sci.* 56, 8–17.
- Kawamitsu, Y., Agata, W., Miura, S., 1987. Effects of vapour pressure difference on CO₂ assimilation rate, leaf conductance and water use efficiency in grass species. *J. Fac. Agric. Kyushu Univ.* 31, 1–10.
- Kiniry, J.R., 1999. Response to questions raised by Sinclair and Muchow. *Field Crops Res.* 62, 245–247.
- Kiniry, J.R., Landivar, J.A., Witt, M., Gerik, T.J., Caverio, J., Wade, L.J., 1998. Radiation-use efficiency response to vapor pressure deficit for maize and sorghum. *Field Crops Res.* 56, 265–270.
- Kuroda, E., Kumura, A., 1990. Single leaf photosynthesis of rice plants under field conditions. VI. The degree of depression in leaf photosynthesis induced by water shortage estimate by an ambient air humidifying treatment. *Jpn. J. Crop Sci.* 59, 120–124.
- Lal, A., Ku, M.S.B., Edwards, G.E., 1996. Analysis of inhibition of photosynthesis due to water stress in the C₃ species *Hordeum vulgare* and *Vicia faba*: electron transport, CO₂ fixation and carboxylation capacity. *Photosynth. Res.* 49, 57–69.
- Maier, C.A., Tesky, R.O., 1992. Internal and external control of net photosynthesis and stomatal conductance of mature eastern white pine (*Pinus strobus*). *Can. J. For. Res.* 22, 1387–1394.
- Morgan, J.A., Lecain, D.R., Mosier, A., Michunas, D.G., 2001. Elevated carbon dioxide enhances water relations and productivity and affects gas exchange in C₃ and C₄ grasses of the Colorado shortgrass steppe. *Global Change Biol.* 7, 451–466.
- Nicolodi, C., Massacci, A., Di Marco, G., 1988. Water status effects on net photosynthesis in field-grown alfalfa. *Crop Sci.* 28, 944–948.
- Sage, R.F., Sharkey, T.D., 1987. The effect of temperature on the occurrence of O₂ and CO₂ insensitive photosynthesis in field grown plants. *Plant Physiol.* 84, 658–664.
- Schulze, E.-D., Hall, A.E., 1982. Stomatal responses, water loss and CO₂ assimilation rates of plants in contrasting environments. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Zeiger, H. (Eds.), *Physiological Plant Ecology. II. Water Relations and Carbon Assimilation*. Springer, Berlin, pp. 181–230.
- Sicher, R.C., Bunce, J.A., 1999. Photosynthetic enhancement and conductance to water vapor of field-grown *Solanum tuberosum* (L.) in response to CO₂ enrichment. *Photosynth. Res.* 62, 155–163.
- Singsaas, E.L., Ort, D.R., DeLucia, E.H., 2000. Diurnal regulation of photosynthesis in understorey saplings. *New Phytol.* 145, 39–49.
- Stockle, C.O., Kiniry, J.R., 1990. Variability in crop radiation use efficiency associated with vapor pressure deficit. *Field Crops Res.* 25, 171–182.
- Thomas, D.S., Eamus, D., 1999. The influence of predawn leaf water potential on stomatal responses to atmospheric water content at constant C_i and on stem hydraulic conductance and foliar ABA concentrations. *J. Exp. Bot.* 50, 243–251.
- Wilson, K.B., Carlson, T.N., Bunce, J.A., 1999. Feedback significantly influences the simulated effect of CO₂ on seasonal evapotranspiration from two agricultural species. *Global Change Biol.* 5, 903–917.
- Xu, D., Li, D., Shen, Y., Liang, G., 1984. On midday depression of photosynthesis of wheat leaf under field conditions. *Acta Phytophysiol. Sin.* 10, 269–276.
- Ziska, L.H., Bunce, J.A., 1997. Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C₄ crops and weeds. *Photosynth. Res.* 54, 199–208.