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Aust. J. Plant Physiol., 1999, **26**, 71–77

Effect of elevated carbon dioxide concentration at night on the growth and gas exchange of selected C_4 species

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Abstract. Biomass of certain C_4 species is increased when plants are grown at elevated CO_2 concentrations. Experiments using four C_4 species (*Amaranthus retroflexus* L., *Amaranthus hypochondriacus* L., *Sorghum bicolor* (L.) Moench and *Zea mays* L.) exposed both day and night from sowing to carbon dioxide concentrations of 370 (ambient) or 700 µmol mol^{-1} (elevated) or to 370 µmol mol^{-1} during the day and 700 µmol mol^{-1} at night, determined whether any biomass increase at elevated CO_2 concentrations was related to a reduction in the night-time rate of CO_2 efflux at high night-time CO_2 concentrations. Of the four species tested, only *A. retroflexus* significantly increased both CO_2 assimilation (+13%) and plant biomass (+21%) at continuous elevated relative to continuous ambient concentrations of CO_2. This increase was not associated with improvement in leaf water potential during dark or light periods. In contrast, high CO_2 only during the night significantly reduced plant biomass compared to the 24 h ambient CO_2 treatment for both *A. retroflexus* and *Z. mays*. This indicates that the observed increase in biomass at elevated CO_2 for *A. retroflexus* was not caused by a reduction of carbon loss at night (i.e. increased carbon conservation), but rather a direct stimulation of daytime CO_2 assimilation, independent of any improvement in leaf water potential.

Keywords: Climate change, carbon dioxide, C_4 plants, *Amaranthus retroflexus*, respiration.

Introduction

The increase in atmospheric CO_2 concentration, [CO_2], can stimulate net photosynthesis (and subsequent growth) in plants with the C_3 photosynthetic pathway (approximately 95% of all plant species), by increasing the [CO_2] gradient from air to the leaf interior and by decreasing the loss of CO_2 via photorespiration. However, plants with the C_4 photosynthetic pathway already have an internal biochemical 'pump' for concentrating CO_2 at the site of carboxylation which reduces photorespiratory carbon loss by inhibiting the oxygenase component of ribulosebisphosphate carboxylase/oxygenase, the primary carboxylating enzyme in plants. Because of these different pathways, C_4 photosynthesis should already be saturated at the current [CO_2], while C_3 plants should continue to respond to ongoing increases in atmospheric [CO_2] (e.g. Berry and Downton 1982).

In spite of the difference in carboxylation kinetics, increased growth in response to elevated [CO_2] has been reported for several C_4 species, e.g. *Panicum antidotale* (Ghannoum *et al.* 1997), *Bouteloua gracilis* (Read and Morgan 1996), *Echinochloa crus-galli*, *Digitaria sanguinalis*, *Eleusine indica* and *Setaria faberi* (Sionit and Patterson 1984) and *Amaranthus retroflexus* (Tremmel and Patterson 1993). These observed increases in growth are usually attributed to the indirect effects of [CO_2] on stomatal closure with a subsequent improvement in leaf water potential. However, this does not explain the positive response of C_4 plants grown at optimal water and nutrients to elevated [CO_2] (e.g. Ghannoum *et al.* 1997; Read *et al.* 1997; Ziska and Bunce 1997; LeCain and Morgan 1998).

Although the mechanism by which a C_4 plant could respond directly to increased [CO_2] is unknown, improved growth of well-watered C_4 species at elevated CO_2 suggests that some aspect of gas exchange is being directly affected. Several recent studies have shown a 10–18% increase in single leaf photosynthesis of C_4 plants at elevated relative to ambient [CO_2] (Ghannoum *et al.* 1997; Ziska and Bunce 1997; LeCain and Morgan 1998) which may be dependent on high light (Ghannoum *et al.* 1997) However, it is unclear if the stimulation can account entirely for the observed change in growth with increasing [CO_2].

Alternatively, another aspect of gas exchange which may be altered by elevated [CO_2] is inhibition of dark respiration (e.g. Bunce 1990; Amthor *et al.* 1992) which has been observed in both C_3 and C_4 species (see Amthor 1997 for review). Inhibition of dark respiration and subsequent carbon conservation have been sufficient to increase the dry mass of C_3 species such as alfalfa (Reuveni and Gale 1985) and soybean (Bunce 1995) when exposed to elevated [CO_2] only at night. However, the effect of night-time only elevated CO_2 on the growth of C_4 species is unknown.

At present, therefore, it is unclear how much of the increase in growth at elevated CO_2 in C_4 plants under well-watered conditions may be due to a stimulation of leaf photosynthesis, and/or a reduction in dark respiration and consequent carbon conservation. To distinguish between

0310-7841/99/010071

these possibilities, four C_4 species were grown at either continuous (24 h) ambient CO_2 (370 μmol mol^{-1}), elevated CO_2 (700 μmol mol^{-1}) or ambient CO_2 (day) and elevated CO_2 (night).

Materials and methods

Four C_4 species, *Amaranthus retroflexus* L. (red-root pigweed), *Amaranthus hypochondriacus* L. (grain amaranth), *Sorghum bicolor* (L.) Moench (cv. Rio) and *Zea mays* L. (cv. Pioneer 3394) were grown in one controlled environment chamber, with successive experiments at different CO_2 concentrations. This design was used to eliminate variation among different growth chambers. Temperature, humidity, light and [CO_2] were recorded every 15 min, and averaged for a given experiment. Abiotic conditions (other than [CO_2]) differed by <1% between successive runs. Two to three seeds of each species were sown in either 0.6 or 1.8 L pots filled with vermiculite and thinned to one seedling 2–3 days after emergence. For each treatment 26–29 pots of a given species were used. Pots were arranged to avoid shading from other plants. All pots were watered to the drip point daily with complete nutrient solution containing 13.5 mmol m^{-3} nitrogen (Robinson 1984). *A. retroflexus* seed was obtained locally and *A. hypochondriacus* seed was from Mexico.

In all experiments the air temperature was 28°C day, and 22°C night, the dew point temperature was 18°C (VPD of 0.6–1.7 kPa for night and day temperatures, respectively). There were 14 h d^{-1} of light at 1000 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD*) at the tops of the plants from a mixture of high pressure sodium and metal halide lamps. The CO_2 concentration of the chamber air was controlled by continuous flushing with CO_2-free air, then re-injection with CO_2 to maintain the desired CO_2 concentration. Injection of CO_2 was controlled by an absolute infra-red gas analyser (WMA-2, PP Systems, Haverhill, MA, USA) which activated a solenoid valve to control the injection of pure CO_2. Experiments were performed with the following CO_2 treatments: (*a*) 370±35 μmol mol^{-1} day and night, (*b*) 700±28 μmol mol^{-1} day and night, and (*c*) 370 during the day and 700 μmol mol^{-1} during the night. When elevated CO_2 was applied only at night, the injection of CO_2 ended about 45 min before the end of the dark period to ensure that the CO_2 concentration would be within the daytime control range when the lights came on.

Plants were grown for 19–23 days after sowing (DAS) depending on the growth rate of the species. Harvests of eight plants were made every 3–5 days with plants from the smaller volume pots (i.e. 0.6 L) harvested first to avoid root-binding and possible complications due to feedback inhibition (see Thomas and Strain 1991). No visual signs of root-binding were observed during the study. At each harvest, leaf area was determined photometrically with a leaf area meter (Li-Cor Corp., Li-3000, Lincoln, NE, USA). Dry mass was measured separately for leaves, stems and roots after drying 55°C for a minimum of 72 h (or until dry mass was constant). Relative growth rates (RGR) were calculated from the harvest data (Jones 1983).

On each sampling date, respiration was determined at the end of the dark period (0700–0800 h) on the uppermost most recently expanded whole leaf for six plants of a given species. Respiration, measured as net CO_2 efflux, was determined using a differential infra-red carbon dioxide analyser (model 6252, Li-Cor Corp.) in an open system attached to a single leaf cuvette. Temperature, humidity and CO_2 concentration were set to approximate those of the larger growth chamber. On the afternoon of the same day, photosynthesis was determined on the same individual leaves measured for respiration. Photosynthesis (measured as *A*, the net rate of CO_2 assimilation) was determined in the afternoon (1300–1400 h) using a portable, open-gas exchange system, incorporating infra-red CO_2 and water vapor analysers for determining net photosynthetic CO_2 uptake rate and stomatal conductance (CIRAS-1, PP Systems). Illumination was supplied by a separate light unit which produced a constant PPFD of 1600 μmol m^{-2} s^{-1} for all measurements. For *A. retroflexus*, additional measurements of single leaf photosynthesis were made for each CO_2 treatment 21 DAS, but at 1000 μmol m^{-2} s^{-1} (i.e. the growth PPFD). For all measurements, the water vapor pressure surrounding the leaf was approximately 1.7 kPa, and did not vary between CO_2 treatments or species. Leaf temperature was maintained between 28°C and 29°C during the measurement.

For afternoon measurements of photosynthesis at the higher PPFD in *A. retroflexus*, leaves grown in ambient [CO_2] were exposed to short-term (5–10 min) increases in the CO_2 concentration to 700 μmol mol^{-1}. Comparisons between the short-term response of assimilation rate of ambient leaves to elevated CO_2 with rates of leaves grown and measured at the higher CO_2 concentration were used to determine the extent of photosynthetic acclimation in this species. In addition, in order to determine if the observed increase in growth for *A. retroflexus* at elevated CO_2 resulted in improved water relations, leaf water potential was measured in the dewpoint mode using a HR-33 microvoltmeter and six insulated C-51 sample chambers (Wescor Inc., Logan, UT, USA). Water potential was measured in the dark following the respiration measurement (0700–0800 h), and again following the CO_2 assimilation measurement in the afternoon (1300–1400 h) for six *A. retroflexus* plants at a given [CO_2] treatment.

Because of the limited number of chambers, each CO_2 treatment was run twice, and pooled data from the two runs are presented (e.g. 16 plants per sampling period). The effect of the CO_2 treatment on gas exchange parameters, and water potential was analysed by species, using a Student's unpaired *t*-test. Leaf area and dry mass were analysed for each species using a one-way analysis of variance (ANOVA) with means separated by a least squares means table. Unless otherwise stated, differences were determined as significant at the $P<0.05$ level.

Results

Of the four C_4 species examined, only *A. retroflexus* showed a significant stimulation of total plant biomass (+21%) at continuous elevated [CO_2] (Table 1; Fig. 1). The stimulation of plant biomass by continuous elevated [CO_2] was due to increased leaf and root dry mass as well as leaf area (Table 1). For *A. retroflexus*, RGR was not increased by continuous elevated [CO_2] relative to ambient [CO_2], but was reduced at the high-night time [CO_2] treatment (Table 2). Relative to the continuous ambient [CO_2] treatment, net assimilation rate (NAR) was significantly increased at continuous elevated [CO_2] and decreased at high night-time [CO_2] in *A. retroflexus* (Table 2). In contrast to the stimulation of total biomass with continuous elevated CO_2, high night-time [CO_2] reduced total biomass for two species, *A. retroflexus* (–30%) and *Z. mays* (–25%) relative to the continuous ambient CO_2 condition (Table 1). Similar reductions in leaf area also occurred for *A. retroflexus* and *Z. mays* (–17 and –33%, respectively).

Because growth of *A. retroflexus* was significantly stimulated by continuous elevated [CO_2] treatment, measurements of leaf water potential were made during the second run. The leaf water potentials for both the early morning dark period and afternoon light period are consistent with the well-watered condition of the plants (Table 3). However, elevated CO_2 concentration (either night-time or continuous), did not result in an increased water potential for this species.

Stimulation of leaf assimilation rate was observed at the continuous elevated CO_2 treatment at 15 and 23 DAS for *A. retroflexus* and at 23 DAS for *S. bicolor* (Fig. 2). A comparison of different assimilation rates with short-term exposure

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*Abbreviations used: *A*, leaf assimilation rate; DAS, days after sowing; LAR, leaf area ratio; NAR, net assimilation rate; PPFD, photosynthetic photon flux density; RGR, relative growth rate.

Table 1. Leaf area and dry mass at the final harvest of selected C_4 species exposed to 370/370, 370/700, 700/700 µmol mol^{-1} day/night CO_2 concentrations

Different letters within a column for a given species indicate significant differences (least square means). For simplicity, letters are shown only if significant treatment differences were observed, n=16

Species	CO_2	DAS	Leaf area (cm^2)	Leaf (g)	Stem (g)	Root (g)	Total (g)
A. retroflexus	370/370	23	1245 b	7.34 b	1.79 a	2.93 b	12.07 b
	370/700	23	1028 c	4.99 c	1.06 b	2.38 b	8.43 c
	700/700	23	1603 a	8.42 a	2.22 a	4.02 a	14.65 a
A. hypochondriacus	370/370	20	1614 a	10.83 a	2.51	4.14 b	17.48
	370/700	20	1547 a	10.10 a	2.16	5.41 a	17.67
	700/700	20	1491 b	8.72 b	2.19	5.41 a	16.32
S. bicolor	370/370	23	1430	5.52	3.83 b	6.13	15.48
	370/700	23	1495	5.95	3.41 b	6.75	16.11
	700/700	23	1454	6.09	4.53 a	6.62	17.24
Z. mays	370/370	19	1156 a	4.97 a	4.73 a	3.96 a	13.67 a
	370/700	19	776 b	3.42 b	3.69 b	3.08 b	10.19 b
	700/700	19	1052 a	4.95 a	4.33 a	4.10 a	13.39 a

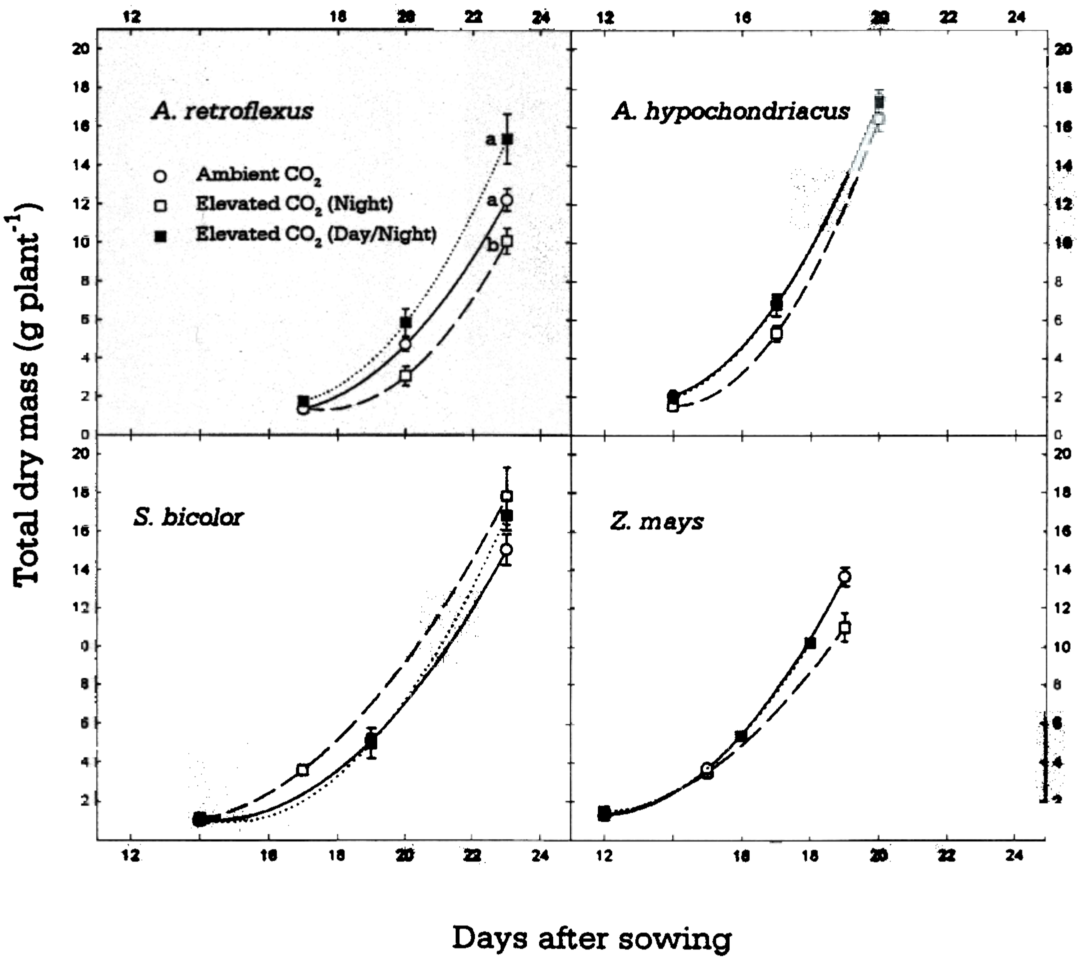

Fig. 1. Total plant dry mass (g plant^{-1}) as a function of days after sowing (DAS) for selected C_4 species exposed to 370/370 (○), 370/700 (□), 700/700 (■) µmol mol^{-1} day/night CO_2 concentrations. Different letters for *A. retroflexus* indicate significant differences (least square means) in RGR. RGR was determined as the slope of the ln of dry weight to time for the last two harvests. n=16.

Table 2. Relative growth rate (RGR), leaf area ratio (LAR), and net assimilation rate (NAR) for *A. retroflexus* exposed to 370/370, 370/700, 700/700 µmol mol^{-1} day/night CO$_2$ concentrations

Different letters within a column indicate significant differences (least square means). For simplicity letters are shown only if significant treatment differences were observed, *n*=16

CO$_2$ treatment (µmol mol^{-1})(day/night)	RGR (g g^{-1} day^{-1})	LAR (m^2 g^{-1})	NAR (g m^{-2} day^{-1})
370/370	0.366 a	0.0126 a	29.0 b
370/700	0.329 b	0.0134 a	24.6 c
700/700	0.362 a	0.0106 b	34.2 a

Table 3. Average predawn and afternoon leaf water potentials (±SE) for *A. retroflexus* exposed to 370/370, 370/700, 700/700 µmol mol^{-1} day/night CO$_2$ concentrations, *n*=6

No differences were observed as a function of CO$_2$ treatment. Predawn values were obtained from 0700–0800 h, afternoon values were obtained from 1300–1400 h

CO$_2$ treatment (µmol mol^{-1})(day/night)	Predawn	Afternoon
	MPa	
370/370	−0.63±0.06	−1.04±0.05
370/700	−0.68±0.03	−1.17±0.12
700/700	−0.60±0.04	−1.03±0.09

(minutes) to a different CO$_2$ concentration can be used to determine photosynthetic acclimation. For *A. retroflexus*, single leaf assimilation increased at the continuous elevated relative to the continuous ambient [CO$_2$] at both PPFD levels (Table 4). No difference in *A* between PPFD was observed, indicating that assimilation rates were near light saturation at 1000 µmol m^{-2} s^{-1}. No difference was observed in *A* between plants grown at 370/370 µmol mol^{-1} and 700/700 µmol mol^{-1} when measured at a common [CO$_2$] of 700 µmol mol^{-1} indicating no photosynthetic acclimation to elevated [CO$_2$] (Table 4). However, the high-night time CO$_2$ treatment showed a slight, but significant reduction relative to continuous ambient [CO$_2$] at the 370 µmol mol^{-1} measurement concentration, indicating photosynthetic acclimation to ambient [CO$_2$] for this treatment (Table 4).

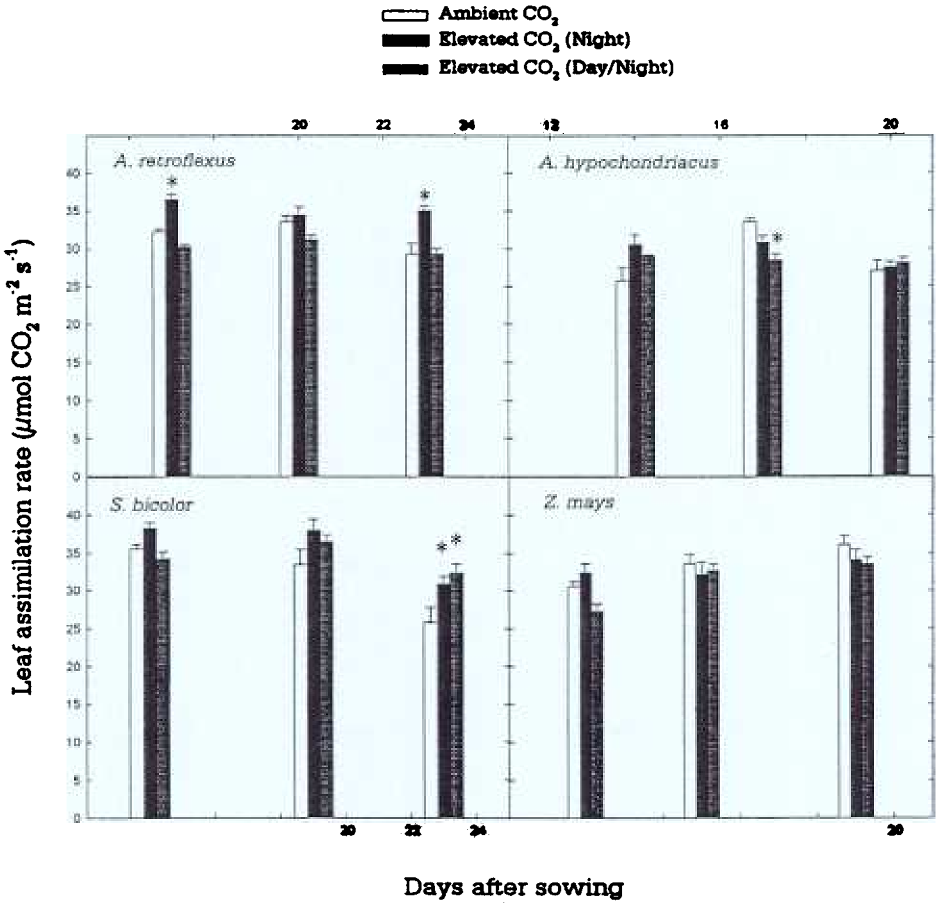

Fig. 2. Photosynthesis determined as leaf assimilation rate (µmol CO$_2$ m^{-2} s^{-1}) ±SE for selected C$_4$ species grown at 370/370 (open bars), 370/700 (grey bars), 700/700 (dark bars) µmol mol^{-1} day/night CO$_2$ concentrations. * indicates a significant difference relative to the 370/370 µmol mol^{-1} control for a given sampling period ($P<0.05$, Student's unpaired *t*-test, *n*=12).

Table 4. **Average rates of CO_2 assimilation (±SE, n=12–16) for single leaves of *A. retroflexus* grown at 370/370, 370/700, 700/700 µmol mol^{-1} day/night CO_2 concentrations and measured at ambient (370 µmol mol^{-1}) and elevated CO_2 (700 µmol mol^{-1})**

*indicates a significant difference in photosynthesis between the 700/700 CO_2 treatment and the 370/370 control. Different letters shown for a given measured CO_2 concentration (i.e. within a column) indicate photosynthetic acclimation for the 1600 µmol m^{-2} s^{-1} PPFD. N/A, not available

CO_2 treatment (µmol mol^{-1})(day/night)	CO_2 assimilation (µmol mol^{-2} s^{-1}) at [CO_2] of: 370 (µmol m^{-1})	700
1000 µmol m^{-2} s^{-1}		
370/370	34.3±0.5	N/A
700/700	N/A	37.0+0.7*
1600 µmol m^{-2} s^{-1}		
370/370	31.0±0.8 a	36.2±1.5 a
370/700	29.4±0.5 b	34.5±1.4 a
700/700	N/A	34.9±0.4* a

High night-time [CO_2] significantly reduced CO_2 efflux 19 and 15 DAS for *S. bicolor* and *Z. mays*, respectively (Fig. 3). Although reductions in the rate of CO_2 efflux at the high night-time CO_2 treatment were not significant for *A. retroflexus* for any given sampling time, pooled data for all sampling periods indicated a significant reduction in leaf respiration at the high night-time relative to the continuous ambient CO_2 treatment (1.34 *vs* 1.75 µmol CO_2 m^{-2} s^{-1})

Discussion

Because the C_4 photosynthetic pathway has the ability to concentrate CO_2 at the site of carboxylation with a subsequent reduction in CO_2 lost via photorespiration, increasing ambient CO_2 concentration is expected to have little or no effect on the photosynthetic and growth response of C_4 plants (assuming water stress is not a factor). This is consistent with the observations many researchers for a wide range of C_4 species (cf. Pearcy 1977; Lin and Ehleringer 1983; Harley and Ehleringer 1987; Greer *et al.* 1995). This hypothesis is also consistent for the photosynthetic and growth response of *A. hypochondriacus*, *S. bicolor* and *Z. mays* reported in our study at continuous elevated [CO_2].

In contrast, a significant increase in biomass was observed for *A. retroflexus* at continuous elevated (relative to ambient) [CO_2]. The observed increase was not associated with differ-

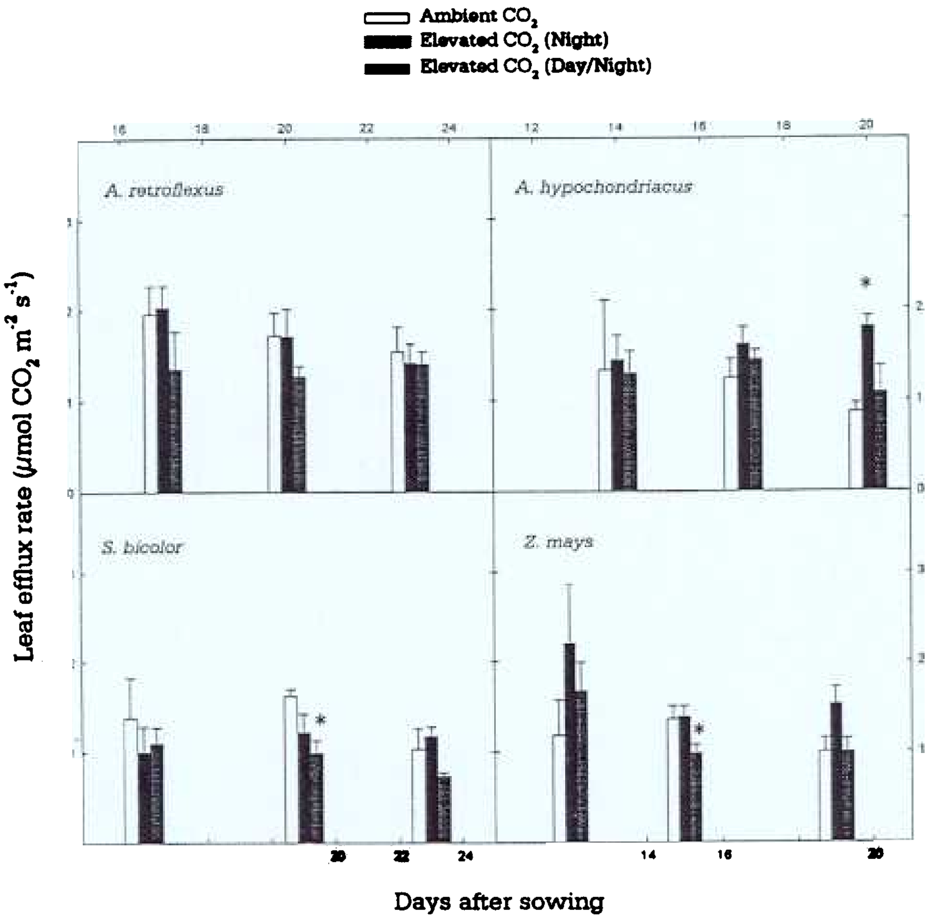

Fig. 3. Same as for Fig. 2, but for dark respiration, determined as leaf efflux rate (µmol CO_2 m^{-2} s^{-1}).

ences in plant morphology, senescence or improved water potentials (either predawn or afternoon) between CO_2 treatments. There was a significant decrease in LAR for *A. retroflexus* at continuous elevated compared to ambient concentrations of CO_2. The observed increase in biomass for *A. retroflexus* at elevated [CO_2] is consistent with other reports for this species (Black 1986; Coleman and Bazzaz 1992; Tremmel and Patterson 1993; Ziska and Bunce 1997). However, the basis for the observed increase in *A. retroflexus* at elevated CO_2 is not known.

Can the observed increase in biomass for *A. retroflexus* be due to an inhibition of dark respiration and subsequent carbon conservation? High night-time CO_2 only has been shown to increase the dry mass of alfalfa and initial dry weights of soybean (Reuveni and Gale 1985; Bunce 1995, respectively), and inhibition of dark respiration at elevated CO_2 has been observed in both C_3 and C_4 species (Poorter *et al.* 1992; Amthor 1997). The effects of high night-time [CO_2] *per se* are applicable not only to future atmospheric CO_2 conditions but to current conditions where high night-time CO_2 concentrations occur in agricultural fields (cf. Verma and Rosenberg 1976).

However, none of the species in our study increased dry mass when elevated [CO_2] was given only at night. Although specific rates of leaf respiration were reduced for some species at high night-time CO_2, this did not translate into conservation of carbon and increased biomass. Rather, for *A. retroflexus*, both RGR and biomass at the end of the experimental period were significantly reduced relative to the continuous ambient CO_2 control. A similar reduction in biomass at the high night-time only CO_2 concentration was also observed for *Z. mays*. The reduction in growth for these two species suggests a decrease in some functionally important component of respiration overcoming carbon conservation.

In addition to inhibition of respiration, high night-time CO_2 also resulted in slight, but significantly lower leaf photosynthetic rate and NAR compared to the ambient control. These lower rates may have also contributed to the reduction in RGR for this treatment. Although initial growth in soybean was stimulated by high [CO_2] at night, after 14 days leaf area and RGR were reduced (Bunce 1995). Reductions in growth with high night-time only [CO_2] have also been observed for *Xanthium strumarium*, depending on salinity (Reuveni *et al.* 1997). Reduced photosynthesis following high night-time CO_2 concentrations also occurs in soybean (Bunce 1992).

The increase in biomass of *A. retroflexus* at continuous elevated [CO_2] was consistent with the observed stimulation of photosynthetic rate (measured as CO_2 assimilation) and NAR for *A. retroflexus* leaves at continuous elevated relative to the ambient control in this and the previous study (Ziska and Bunce 1997). This stimulation was observed for both measurement and growth CO_2 concentrations with no evidence of photosynthetic acclimation. This reinforces earlier observations (e.g. Ziska and Bunce 1997), that *A. retroflexus* and other C_4 species can respond both photosynthetically and with respect to growth as atmospheric [CO_2] increases. If the photosynthetic rate and the growth response of certain C_4 species (e.g. *A. retroflexus*) are not, in fact, saturated at current [CO_2], this may have important implications with respect to variability among C_4 plants and potential competition with C_3 species as atmospheric [CO_2] continues to increase.

Acknowledgments

The authors thank Drs Jack Morgan and Dave Patterson for their editorial advice and Fran Caulfield, Sam Benson and Jennifer O'Brien for invaluable technical assistance.

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Manuscript received 22 September 1998, accepted 24 November 1998