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Adaptation to high CO_2 concentration in an optimal environment: radiation capture, canopy quantum yield and carbon use efficiency

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ABSTRACT

The effect of elevated [CO_2] on wheat *(Triticum aestivum* L. Veery 10) productivity was examined by analysing radiation capture, canopy quantum yield, canopy carbon use efficiency, harvest index and daily C gain. Canopies were grown at either 330 or 1200 μmol mol^{-1} [CO_2] in controlled environments, where root and shoot C fluxes were monitored continuously from emergence to harvest. A rapidly circulating hydroponic solution supplied nutrients, water and root zone oxygen. At harvest, dry mass predicted from gas exchange data was 102·8 ± 4·7% of the observed dry mass in six trials. Neither radiation capture efficiency nor carbon use efficiency were affected by elevated [CO_2], but yield increased by 13% due to a sustained increase in canopy quantum yield. CO_2 enrichment increased root mass, tiller number and seed mass. Harvest index and chlorophyll concentration were unchanged, but CO_2 enrichment increased average life cycle net photosynthesis (13%, *P* < 0·05) and root respiration (24%, *P* < 0·05). These data indicate that plant communities adapt to CO_2 enrichment through changes in C allocation. Elevated [CO_2] increases sink strength in optimal environments, resulting in sustained increases in photosynthetic capacity, canopy quantum yield and daily C gain throughout the life cycle.

Key-words: canopy quantum yield; carbon use efficiency; crop productivity; C partitioning; elevated [CO_2]; radiation capture; wheat.

INTRODUCTION

Crop responses to increased [CO_2] include increased biomass accumulation, increased yield and improved water use efficiency (Kramer 1981; Kimball 1983; Cure & Acock 1986). Most studies have examined short-term effects and much less is known about long-term effects. Long-term studies of crop productivity typically involve determining final yields and making periodic harvests to estimate growth analysis parameters. However, this adds little to our understanding of the mechanisms through which elevated [CO_2] affects productivity. Crop productivity and daily C gain (DCG) can also be described by three components: radiation capture, canopy quantum yield (CQY) and carbon use efficiency (CUE) (Monteith 1981; Charles-Edwards 1982; Bugbee & Monje 1992), but little is known about the effect of CO_2 enrichment on these physiological yield determinants.

Radiation capture, or the fraction of radiation absorbed, is usually the most important of these three components (Monteith 1981). Elevated [CO_2] increased radiation capture by 15–20% during the first half of the life cycle in field-grown cotton and wheat (Pinter *et al*. 1994, 1996). In contrast, radiation capture in hydroponically-grown wheat canopies did not change in elevated [CO_2] in spite of a 30% increase in leaf area index (Smart, Chatterton & Bugbee 1994).

CQY is related to the quantum yield of single leaves, but is determined from the ratio of canopy gross photosynthesis to the absorbed radiation. CQY measures the photochemical conversion efficiency of absorbed radiation into fixed C. In C_3 plants, elevated [CO_2] increases the quantum yield of photosynthesis by reducing photorespiration caused by the oxygenase activity of Rubisco. Maximum, single-leaf quantum yield was increased from 0·065 to 0·080 (Long & Drake 1991) in CO_2-enriched, estuarine marsh plant communities. Drake & Leadley (1991) suggested that a higher quantum yield should not only increase canopy photosynthetic rates, but also extend the duration of positive DCG.

CUE (or growth efficiency) measures the conversion efficiency of fixed C into dry matter and relates respiratory costs to crop growth (McCree 1988). Elevated [CO_2] may decrease dark respiration per unit biomass (Reuveni, Mayer & Gale 1995), which combined with higher photosynthetic rates would substantially increase CUE. In rice, CO_2 enrichment increased canopy respiration per unit ground area, but decreased specific respiration (per unit biomass), probably due to a reduction in maintenance respiration (Baker *et al*. 1992). Elevated [CO_2] typically reduces protein nitrogen (N) concentration in leaves, which could reduce protein turnover, maintenance respiration, and the construction cost of biomass (Wullschleger, Ziska & Bunce 1994). CUE might increase during grain fill as more photosynthate is allocated to seeds, which

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have high growth conversion efficiencies and reduced maintenance respiration (Amthor 1989).

Changes in C partitioning caused by elevated [CO_2] are also important to crop productivity because they can significantly alter source–sink relationships (Farrar & Williams 1991). Short-term CO_2 enrichment studies often overestimate long-term effects because growth rates can decline after an initial increase (Bowes 1991). Temporary increases in growth rates may not be sustained because carbohydrate accumulation can result in feedback inhibition of photosynthesis (Thomas & Strain 1991). Feedback inhibition occurs in CO_2-enriched pot-grown plants, but typically not in field studies, where unrestricted root growth may help prevent sink limitation (Arp 1991).

Long-term studies are critical for understanding whole plant C partitioning and respiration in elevated [CO_2] because stimulation of plant growth by elevated [CO_2] is time dependent and varies with ontogeny (Farrar & Williams 1991). Discerning whether responses to CO_2 enrichment are due to increased photosynthetic rates, increased sink strength, or both, is difficult because few studies have estimated simultaneous changes in community photosynthesis, respiration and dry weight accumulation. The purpose of this study was to quantify the effect of CO_2 enrichment on community radiation capture, CQY, CUE and DCG through continuous measurement of canopy carbon fluxes from emergence to physiological maturity.

MATERIALS AND METHODS

Cultural and environmental conditions

Wheat (*Triticum aestivum* L. cv. Veery-10) canopies were grown in two sealed, water cooled, controlled environment chambers (model EGC-13, Environmental Growth Chambers, Chagrin Falls, OH, USA). Seeds were planted in a 10-mm-deep layer of diatomaceous earth (Isolite, size CG-2, Sumitomo Corp., Denver, CO, USA) at a density of 700 plants m^{-2}. The environmental conditions were: vapour pressure deficit: 0·7 kPa (75% RH); wind speed above the canopy: 1·5 m s^{-1}; total air pressure: 86 kPa (85% of sea level, 1·4 km elevation); and a 20 h photoperiod. Air temperature was 23·0 °C (day/night) with day to day variability of ± 0·1 °C. Six canopies were grown for this study: three at 1200 μmol mol^{-1} and three at 330 μmol mol^{-1}. The CO_2 treatments were randomized between two identical chambers.

Lighting was provided by four 1000 W high pressure sodium lamps, which were adjusted to achieve ± 5% photosynthetic photon flux (PPF) uniformity over the crop surface. Longwave radiation from the lamps was reduced by a 10-cm-deep, recirculating, chilled water filter (Bubenheim, Bugbee & Salisbury 1988). Incident PPF was measured at the top of the canopy with a quantum sensor (model LI-190SB, LI-COR, Lincoln, NE, USA), and was maintained constant throughout the life cycle by lowering the canopy platform as the plants grew taller. PPF was maintained at 300 μmol m^{-2} s^{-1} from seedling emergence (0·0 d) to 1·5 d; 800 μmol m^{-2} s^{-1} from 1·5 to 8 d; and 1400 μmol m^{-2} s^{-1} (101 mol m^{-2} d^{-1}) from 8 d until harvest (63 d). PPF was kept low early in the life cycle to avoid photobleaching of the seedlings.

The root zone was a recirculating hydroponic system controlled at 23 ± 0·2 °C and pH 4·2 throughout the life cycle. Solution pH was kept low to facilitate the measurement of root respiration via [CO_2] in the head space above the solution (Bugbee 1992). Previous studies indicated no significant difference in root growth or nutrient uptake between a solution pH of 4 and 5·5. Rapid circulation of nutrient solution maximized oxygen and nutrient transport to the roots. The oxygen concentrations in the bulk root zone solution exceeded 90% of saturation, regardless of root metabolic activity. The solution was replenished daily to provide ample nutrients over the life cycle.

Canopy gas exchange measurements

Gas exchange in each chamber was measured every 8 min for the duration of the life cycle. Shoot net photosynthesis, P_{net}, and dark respiration rates, R_{dark}, were calculated from the difference between pre- and postchamber [CO_2] (ΔCO_2), multiplied by the mass flow rate of air through the chamber. Prechamber [CO_2] was measured by an infra-red gas analyser (IRGA; model LI-6251, LI-COR), configured in absolute mode. ΔCO_2 was measured by a differential IRGA (model LI-6251), and air flow into the chamber was measured with a mass flow meter (model 730, Sierra Instruments, Monterey, CA, USA). Root ΔCO_2 (the difference between postchamber and root zone head space air) was measured using a second differential IRGA. Root respiration rate, R_{root}, was calculated from the product of root ΔCO_2 and the air mass flow rate into the nutrient solution tank.

[CO_2] in prechamber, postchamber and root zone head space air was measured after the air streams were brought to a 1·0 °C dewpoint using polyethylene glycol condensers. The condensers eliminated band broadening and dilution effects due to water vapour. IRGA output was corrected for fluctuating temperature and pressure. The data acquisition system included a datalogger (model CR-10, Campbell Scientific, Logan, UT, USA) with an input multiplexer and an analogue control module. Design and additional details of the system have been described previously (Bugbee 1992).

System calibration and carbon recovery tests

System accuracy and response times were determined using both empty chamber and C recovery tests because several sources of error cannot be determined from empty chamber tests alone. The empty chamber test detected leaks and quantified temperature-induced adsorption and desorption of CO_2 from chamber materials. C recovery was quantified by reacting dilute acid with a freshly prepared solution of $NaHCO_3$ in the chamber and comparing the integrated CO_2 efflux with the molar quantity of C in the bicarbonate. Carbon recovery from the shoot environment was 104 ± 2·7% (mean ± SD, $n = 10$), and ranged from 99 to 107%.

Because the [CO_2] in the root zone was typically 200 μmol mol^{-1} higher than in the shoot environment, CO_2 diffusion through the porous planting substrate (Isolite) was significant and was determined with a C recovery test. For the tests, a mature canopy was kept in the dark until its respiration rate was constant (80 h), thereby effectively simulating the canopy boundary layer. $NaHCO_3$ solutions were then added to the root zone, and the CO_2 fraction recovered in the root and shoot environments was determined. These tests indicated that 11 ± 2·5% of the [CO_2] from root zone respiration diffused into the shoot environment. This diffusion rate was assumed to remain constant and was used to correct the raw root and shoot gas exchange rates.

Chemical analyses

The dry mass fractions (ratio of organ mass to total mass) of stems, leaves, roots, seeds and heads for one entire canopy from each treatment were determined at harvest after 63 d. Each 1 m^2 canopy was subdivided into four replicate plots, separated into fractions, heated in a microwave oven for 5 min, oven dried at 80 °C to a constant mass, and weighed. Tissues were heated in a microwave oven to avoid C loss via respiration during subsequent oven drying, especially in CO_2-enriched plants, which have higher total non-structural carbohydrate levels (TNC)(Smart *et al*. 1994). The percentage of C in finely ground samples (< 200 mg) from each organ fraction was determined using a CHN analyser (model CHN-1000, LECO, St. Joseph, MI, USA). Two samples were taken from each organ fraction in each replicate tub for a total of eight samples per organ fraction. Samples were combusted at 1050 °C. The canopy C fraction (CF; mg C g dry mass^{-1}) was determined using organ dry mass fractions (m_i) and C fraction analysis (C_i) from CF = $\Sigma(C_i\ m_i)$. The canopy N fraction was determined similarly.

Calculating DCG and dry mass

DCG (mol C m^{-2} d^{-1}; Eqn 1) was calculated from daily net photosynthesis (DP_{net}; P_{net} 20 h pd) minus the daily night-time shoot respiration (DR_{dark}; R_{dark} 4 h pd) and daily root respiration (DR_{root}; R_{root} 24 h pd), where pd is 3600×10^{-6} s h^{-1}

$$\mathrm{DCG} = DP_{net} - (DR_{dark} + DR_{root}). \qquad (1)$$

The daily crop growth rate (CGR; g m^{-2} d^{-1}) was (DCG×12 g C mol C^{-1})/CF and the cumulative dry mass, W, was the integral of CGR over time. Total daily respiration, R_T (mol m^{-2} d^{-1}) = $DR_{light} + DR_{dark} + DR_{root}$, where DR_{light} is the daily shoot respiration in the light (R_{dark} 20 h pd). Specific respiration was calculated for comparing respiration between the treatments because the amount of dry mass per unit ground area was increased. Daily specific respiration (mmol kg^{-1} d^{-1}) was determined from R_T/W.

Measuring physiological components

Radiation capture was determined from the ratio of absorbed (PPF_{abs}; μmol m^{-2} s^{-1}) to incident PPF (PPF_O). PPF_{abs} was calculated from $PPF_{abs} = PPF_O - PPF_{RO} - PPF_T + PPF_{RT}$ (Gallo & Daughtry 1986), where PPF_{RO} is the reflected incident PPF, PPF_T is the transmitted PPF, and PPF_{RT} is the transmitted PPF reflected by the media. These components were measured daily with a gallium arsenide photodiode (model G1118, Hamamatsu, San Jose, CA, USA), which was calibrated under HPS lamps against a LI-COR quantum sensor. This photodiode has similar spectral and cosine responses to the quantum sensor and its smaller size (10 mm^2) reduces self-shading and canopy disturbance. Each component was the average of six, 10 s integrated PPF measurements because transmitted, reflected, and incident PPF were not distributed homogeneously.

CQY was calculated from daily averages of gross photosynthesis, P_{gross}, and PPF_{abs} from CQY = P_{gross}/PPF_{abs}. P_{gross} was calculated from the daily average of P_{net} plus the daily average of R_{dark}, ($P_{gross} = P_{net} + R_{dark}$) assuming that respiration in the dark occurs at the same rate as in the light at the same temperature. Photorespiratory C losses are not included in P_{gross}, when it is calculated from P_{net} measured in the light, but reduced photorespiration directly increases P_{net} and P_{gross} (McCree 1986). CUE (dimensionless), the ratio DCG to DP_{gross} (P_{gross} 20 h pd) measures the proportion of C retained in biomass to total C fixed. CUE is a measure of growth efficiency that includes the carbon use for maintenance processes (Amthor 1989).

Seed yield

Seed yield was expressed as g seed m^{-2} ground area. Harvest index was the seed mass fraction at harvest after a 63 d life cycle. The harvest index was also calculated from CGR assuming that the daily increments of biomass from anthesis (33 d) until harvest were allocated entirely to seeds.

Chlorophyll concentration

The chlorophyll concentration (mg m^{-2}) in the centre of 20 randomly selected leaves in the top of the canopy was measured daily using a hand-held chlorophyll meter (SPAD 502, Minolta Corp., Ramsey, NJ, USA), calibrated as described by Monje & Bugbee (1992).

Statistical analysis

Mean values of P_{net}, R_{dark}, R_{root}, P_{gross}, CGR, radiation capture, CQY and CUE for the two CO_2 treatments were compared over the life cycle using a randomized block design with repeated measures. Differences between treatment means were also compared for four periods: days 0–8, 9–15, 16–33, and the entire life cycle by an ANOVA. A split-plot design was used to compare CO_2 treatment means during the same time periods. Standard error of the means, weighted for the average of whole and subunit errors, and least squares differences values were calculated at the $P < 0{\cdot}05$ level of significance. Statistical significance could not be tested during the postanthesis stage (days 34–63), due to a lack of degrees of freedom resulting from unbalanced data sets and missing data. All statistical tests were performed using Minitab 9·1 (Minitab Inc., State College, PA, USA).

RESULTS

Carbon and nitrogen concentrations

The harvest C and N concentrations in five plant organs are shown in Table 1. Elevated [CO_2] decreased N concentration by 28% in leaves and by 10% in seeds, but increased leaf C concentration by 4%. The effect of elevated [CO_2] on C and N concentrations in other plant organs was remarkably small. Canopy C and N fractions were calculated from data in Tables 1 and 2. In elevated [CO_2], the harvest canopy N fraction was reduced by 14% (from 2·43 to 2·12%), but the canopy CF was not changed (43·6% versus 43·8%). This resulted in a 16% increase in canopy C:N ratio (from 17·9 to 20·7) in elevated [CO_2].

Predicted versus measured biomass

The dry mass at harvest was predicted by integrating daily crop growth rates over time. Differences between the observed and predicted dry masses were small (103 ± 4·7%; mean ± SD), and may have resulted from errors in flow meter calibration, IRGA calibration, calibration standards, or measurement of C concentration. For the dry mass calculations, canopy CF was assumed constant (43·7%) throughout each study.

Table 1. Carbon and nitrogen contents in five plant organs from ambient and CO_2-enriched canopies at harvest. The heads fraction includes the stem tip, glumes and awns. Values are averages ± SD of eight measurements

Organ	[CO_2] (μmol mol^{-1})	C fraction (%)	N fraction (%)
Stem	330	42·7 ± 1·2	1·5 ± 0·3
	1200	43·2 ± 0·6	1·3 ± 0·3
Leaf	330	37·8 ± 1·2	3·2 ± 0·4
	1200	39·4 ± 0·5*	2·5 ± 0·2*
Root	330	44·3 ± 1·5	2·1 ± 0·4
	1200	44·5 ± 1·5	2·1 ± 0·4
Seed	330	45·5 ± 0·7	3·2 ± 0·1
	1200	45·2 ± 0·2	2·9 ± 0·1*
Heads	330	44·9 ± 1·1	1·3 ± 0·1
	1200	44·6 ± 0·5	1·2 ± 0·1

*Significantly different from control at the $P < 0{\cdot}05$ level.

Table 2. A comparison of organ mass fraction from ambient and CO_2-enriched plants, expressed as percentage of total biomass. The seed mass fraction is the harvest index (edible biomass/total biomass). Values are averages ± SD of four measurements

Organ	330 μmol mol^{-1} (%)	1200 μmol mol^{-1} (%)	Ratio (1200/330)
Stem	18·5 ± 0·81	18·7 ± 0·77	101·1
Leaf	15·5 ± 1·07	13·3 ± 1·03	85·8*
Root	5·5 ± 0·38	6·6 ± 0·29	120·0*
Seed	39·6 ± 0·85	39·4 ± 2·49	99·5
Heads	21·0 ± 1·14	21·9 ± 1·46	104·3

*****Significant differences at the $P < 0{\cdot}05$ level.

Canopy carbon fluxes and ontogeny

The largest increases in P_{net} (23%), R_{dark} (36%), P_{gross} (26%), and CGR (22%) by elevated [CO_2] took place during seedling development (Table 3). In contrast, R_{root} was not affected in high [CO_2] during the seedling stage (Fig. 1b). During early vegetative growth, only P_{net} increased in the shoots, but R_{root} increased rapidly and peaked 11–13 d after emergence (DAE). The peak in R_{root} occurred before canopy photosynthetic rates peaked, indicating that the roots developed well before maximum growth occurred. Elevated [CO_2] continued to alter metabolic rates during the late vegetative and postanthesis stages, but the greatest effect was on R_{root}, which was dramatically increased (62%) in elevated [CO_2] (Fig. 1b). These results suggest that elevated [CO_2] has a much larger effect on shoots during early development than during grain fill and senescence, but this trend may be reversed in the root zone (Table 3).

Although there were significant changes in metabolic rates in response to elevated [CO_2] (Table 3), there was only a moderate increase in CGR (11%) during the life cycle (Fig. 2). This occurs because CGR integrates the photosynthetic and respiratory changes that determine biomass accumulation over the entire life cycle.

R_{dark} was not significantly different from the controls for the duration of the life cycle (Table 3), except during the seedling stage. The ratio of specific respiration rates between elevated and ambient [CO_2] decreased by 16% ($P < 0{\cdot}05$) during the seedling stage (Fig. 3). Elevated [CO_2] reduced average specific respiration by only 3% (ns) from 9 to 52 DAE, and was 14% (ns) higher during the last 10 d of the life cycle.

Physiological components

Radiation capture increased to about 90% by 15 d as the canopy closed, and remained above 95% until the onset of senescence (40 d; Fig. 4a). Canopy reflectance increased and absorbed radiation declined as the canopy senesced. Averaged over the life cycle, radiation capture was not significantly different in elevated [CO_2]

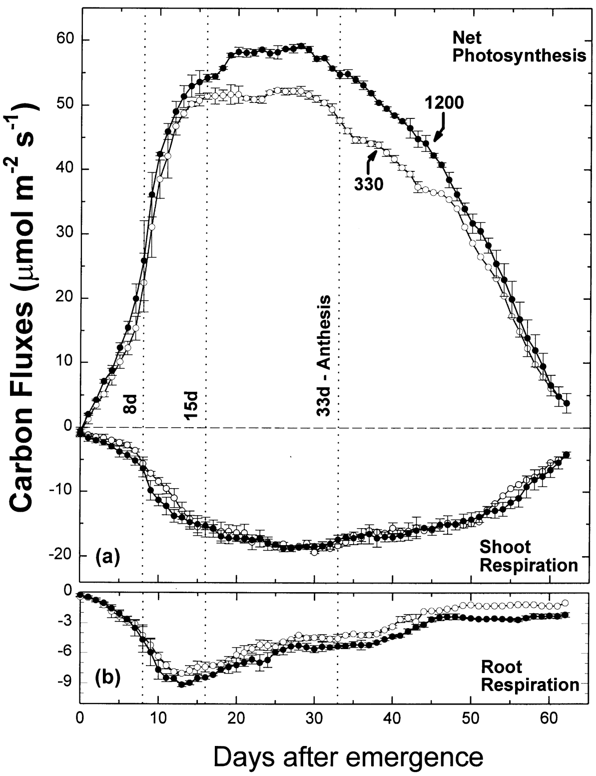

Figure 1. (a) Average daily canopy net photosynthesis and shoot respiration of three ambient trials and three CO_2-enriched trials. (b) Average daily root respiration. Data are expressed per m^2 of ground area. The vertical lines divide the life cycle into four stages: seedling, early vegetative, late vegetative, and postanthesis. The error bars represent the standard error of the mean.

(Table 3). The greatest increase in CQY (30%) by elevated $[CO_2]$ was during the seedling stage, although CQY was increased over the entire life cycle (Table 3). CQY began to decrease at both $[CO_2]$ levels after anthesis and decreased rapidly in the final 10 d of the life cycle (Fig. 4b). CUE in elevated $[CO_2]$ was not significantly different from the ambient control (Table 3). CUE remained fairly constant until the final week of the life cycle, when it decreased rapidly due to senescence (Fig. 4c).

Crop productivity

The effect of elevated $[CO_2]$ on crop productivity is shown in Tables 2 and 4. Harvest index was not significantly affected by elevated $[CO_2]$ (39·6% versus 39·4%; Table 2). The calculated harvest index from gas exchange data in Fig. 2 was nearly identical to the measured harvest index. Elevated $[CO_2]$ significantly increased seed yield (g seed m^{-2}), the number of heads m^{-2}, and the average mass per seed, but decreased the number of seeds per head (– 12%, $P < 0{\cdot}08$) (Table 4).

Chlorophyll concentration during ontogeny

Chlorophyll concentration, measured in the uppermost leaves of the canopy, increased rapidly during the first 10 d, remained constant until ≈ 45 d, and decreased rapidly prior to harvest in both CO_2 concentrations (Fig. 5). Elevated $[CO_2]$ had no significant effect on the chlorophyll content over the life cycle.

Table 3. Average gas exchange parameters (P_{net}, R_{dark}, R_{root}, and P_{gross}), yield determinants [radiation capture (Q), canopy quantum yield (CQY) and carbon use efficiency (CUE)] at intervals during the life cycle, and the ratios between them (elevated/ambient). The life cycle was divided into four stages: seedling [0–8 d after emergence (DAE)], early vegetative (9–15 DAE), late vegetative (16–33 DAE) and postanthesis (34–62 DAE)

$[CO_2]$ (μmol mol^{-1})	DAE (d)	P_{net} (μmol m^{-2} s^{-1})	R_{dark}	R_{root}	P_{gross}	CGR (g m^{-2} d^{-1})	Q (PPF_{abs}/PPF_O)	CQY (mol mol^{-1})	CUE
330	0–8	8·6	–2·4	–1·9	11·0	11·7	0·30	0·047	0·53
	9–15	44·0	–11·3	–7·1	32·7	67·3	0·73	0·053	0·60
	16–33	51·4	–17·3	–5·6	34·1	81·1	0·93	0·052	0·61
	34–63	28·8	–13·0	–2·1	41·8	46·9	0·91	0·033	0·52
	Life cycle	34·6	–12·8	–3·7	47·4	54·9	0·81	0·042	0·56
1200	0–8	10·6	–3·3	–1·9	13·8	14·3	0·28	0·061	0·56
	9–15	47·4	–13·0	–8·2	34·3	69·6	0·70	0·062	0·58
	16–33	57·3	–17·7	–6·4	39·7	90·9	0·93	0·057	0·61
	34–63	33·2	–13·7	–3·4	46·7	52·6	0·91	0·036	0·53
	Life cycle	39·1	–13·3	–4·6	52·4	61·0	0·79	0·048	0·56
Ratio 1200/330	0–8	1·23*	1·36*	1·00	1·26*	1·22*	0·93	1·30*	1·06
	9–15	1·08*	1·15	1·15	1·05	1·03	0·96	1·17*	0·96
	16–33	1·11*	1·02	1·14	1·16*	1·12	1·00	1·10*	1·00
	34–63†	1·15	1·05	1·62	1·12	1·12	1·00	1·09	1·02
	Life cycle	1·13*	1·04	1·24*	1·12*	1·11*	0·98	1·14*	1·00

*****Significant differences at the $P < 0{\cdot}05$ level**.** †Statistical significance tests were not possible.

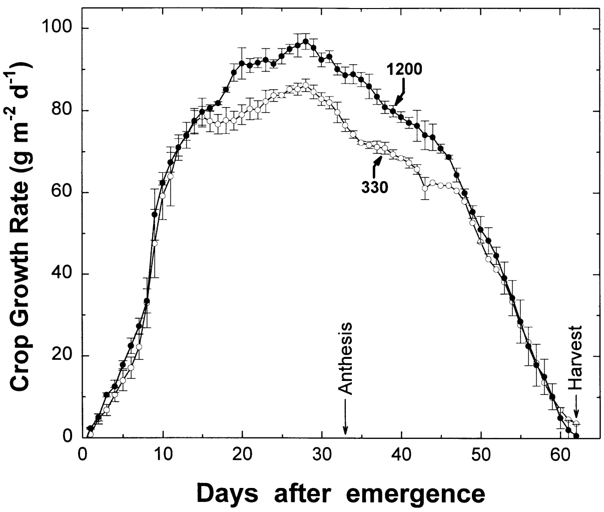

Figure 2. Daily crop growth rates (CGR) of wheat grown at 330 μmol mol^{-1} and 1200 μmol mol^{-1} [CO_2] for the duration of the life cycle. CGR was calculated from daily C gain (DCG) measurements assuming that the C fraction of the biomass at harvest was constant over the life cycle (see text). Anthesis occurred after 33 d. Physiological maturity was reached when DCG was zero (63 d). The error bars represent the standard error of the mean.

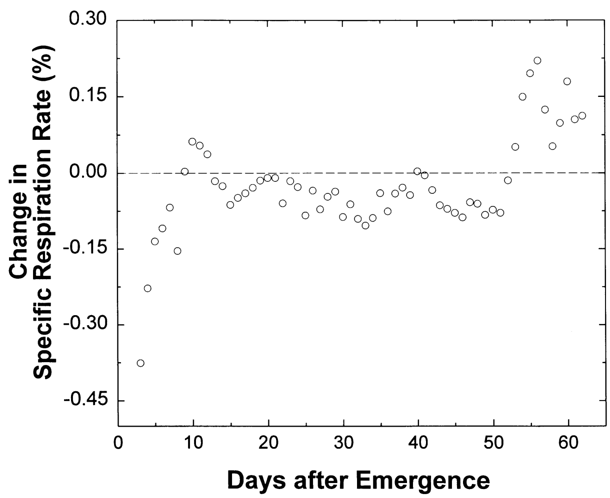

Figure 3. The effect of elevated [CO_2] on canopy specific respiration rate (daily total CO_2 efflux per kg biomass; mmol kg^{-1} d^{-1}) as a function of the life cycle. Data points indicate the percentage change relative to the value at 330 μmol mol^{-1}. Average specific respiration was significantly (16%; $P < 0{\cdot}05$) lower during early vegetative growth in elevated [CO_2]. Differences in specific respiration rates were not significantly different for the remainder of the life cycle.

DISCUSSION

Sustained effects of elevated [CO_2]

Continuous exposure to elevated [CO_2] resulted in sustained increases in net photosynthetic rates (Fig. 1), CGR (Fig. 2), and photosynthetic capacity or CQY throughout the life cycle (Fig. 4). A sustained increase in photosynthetic capacity, coupled with an increased head number and increased root mass, indicates that CO_2-enriched plants can develop stronger sinks, thus preventing feedback inhibition (Ziska, Drake & Chamberlain 1990). Smart *et al*. (1994) measured increased TNC accumulation in CO_2-enriched wheat canopies grown under conditions identical to ours, but our results indicate that these increases did not result in sufficient feedback inhibition to limit photosynthetic rates compared with the controls.

Our observations suggest that photosynthetic and growth rates may continue to respond to CO_2 enrichment when sink capacity can be increased. Increased sink capacity associated with more heads and root mass in the CO_2-enriched canopies probably reduced excessive carbohydrate accumulation, resulting in higher photosynthetic and crop growth rates throughout the life cycle (Stitt 1991; Farrar & Williams 1991). The capacity to increase sink strength in response to elevated [CO_2] may be dynamic. Changes in sink strength may explain why the leaf growth rates of continuously defoliated clover plants continued to respond to elevated [CO_2], whereas growth rates of control plants increased only temporarily (Ryle & Powell 1992). However, not all plants may be able to maintain these sustained increases in growth rates in elevated [CO_2]. In non-crop plants growing continuously exposed to elevated [CO_2], the concentration of TNC was up to 47% greater than in ambient controls. The increased TNC may reflect a sink limitation to growth that was not ameliorated by CO_2 enrichment, because these plants may lack the genetic capacity for rapid growth (Körner & Miglietta 1994).

CO_2 enrichment effects on respiration

The effect of elevated [CO_2] on respiration was not constant throughout the life cycle, and it differentially affected respiration rates of shoots and roots (Table 3). CO_2 enrichment increased shoot respiration (per m^2 ground area) during early vegetative growth when high rates of leaf expansion and large increases in photosynthesis were taking place. Higher respiration during early growth may be associated with greater numbers of mitochondria per unit cell and increased carbohydrate utilization in young, CO_2-enriched wheat leaves (Robertson & Leech 1995). Although shoot respiration per m^2 of ground area was increased, specific respiration rate was lower in elevated [CO_2], but only during early growth (Fig. 3). This decrease in specific respiration may reflect a reduction in the growth respiration coefficient in elevated [CO_2], caused by a decrease in protein N and an increase in TNC accumulation in leaves (Poorter *et al*. 1997). After canopy closure, shoot respiration was only marginally higher than the ambient controls (Table 3). The effects of CO_2 enrichment on shoot respiration declined as the canopy matured, probably due to increased C partitioning to roots, and reduced maintenance respiration. The 4% increase in shoot respiration in

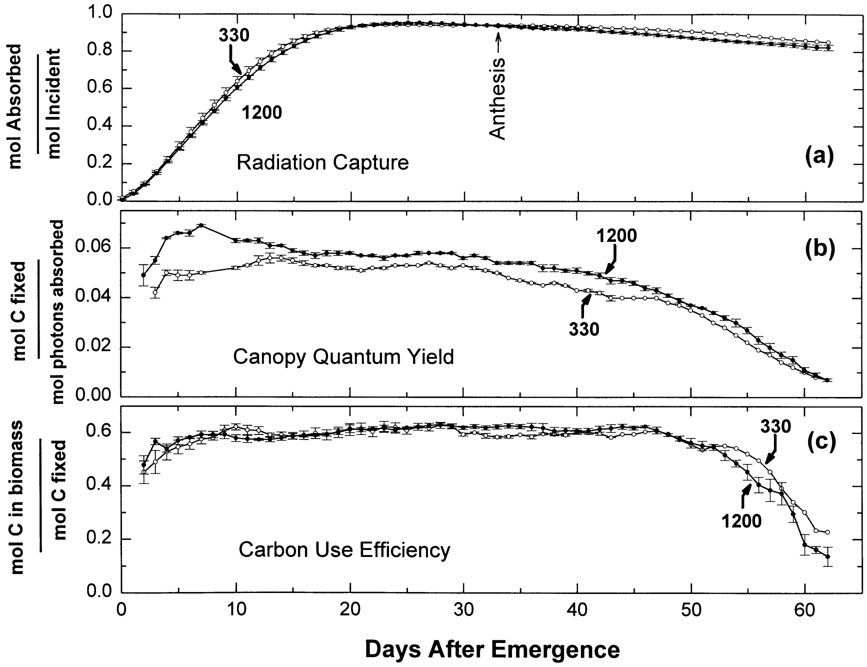

Figure 4. The effect of CO_2 enrichment on the three determinants of biomass yield: (a) radiation capture; (b) canopy quantum yield (CQY); and (c) carbon use efficiency (CUE). Differences in these determinants during the first and last 10 d of the life cycle have a small effect on final average values because growth rates are small compared with the middle of the life cycle. The error bars represent the standard error of the mean.

Table 4. A comparison of yield components computed from the harvested material. Seed yield is expressed in g seed m^{-2}. Values are averages ± SD of four measurements

[CO_2] treatment	Heads m^{-2}	Seeds per head	Mass per seed (mg)	Seed yield (g m^{-2})
330	2316 ± 81	20·8 ± 1·3	29·0 ± 1·9	1397 ± 72
1200	2534 ± 55	18·2 ± 2·1	34·3 ± 0·9	1583 ± 37
Ratio (1200/330)	1·09*	0·88	1·18*	1·13*

*****Significant differences at the $P < 0{\cdot}05$ level.

elevated [CO_2], averaged over the life cycle, was much smaller than that observed in rice (Baker *et al.* 1992).

Root respiration per m^2 of ground area dramatically increased throughout the life cycle in elevated [CO_2] (Table 3). Elevated [CO_2] increased root respiration during grain fill by 62%, and led to a significant increase in root mass (20%; Table 2). These large changes in C allocation suggest that roots are strong sinks for excess carbohydrates in CO_2-enriched plants. Similarly, Körner & Arnone (1992) found greater production of fine root biomass, as well as a doubling of CO_2 efflux from soils in elevated [CO_2].

CO_2 enrichment effects on radiation capture

In spite of a 30% increase in DCG, elevated [CO_2] *decreased* radiation capture by 5% in the first 15 d. It is unlikely that this apparent anomaly is caused by a reduced leaf area in elevated [CO_2] because tiller number increased. Furthermore, in a similar study, Smart *et al.* (1994) measured a 30% increase in leaf area index in elevated [CO_2]. However, they also found that elevated [CO_2] increased radiation penetration in wheat canopies. Their measurements indicated a 17% reduction in the Beer's law extinction coefficient in elevated [CO_2]. This reduction means that a 20% increase in leaf area is necessary to absorb the same amount of radiation. Thus, the CO_2-induced increase in leaf area index may have been offset by a reduction in the extinction coefficient in these studies.

Elevated [CO_2] did not significantly alter PPF absorption after canopy closure. Overall, we observed only small changes in radiation capture during the life cycle as a result of CO_2 enrichment (Table 3). These results contrast radiation absorption measurements made in FACE studies, where elevated [CO_2] increased PPF absorption by roughly 15% in field-grown cotton and wheat canopies during the first half of the life cycle (Pinter *et al.* 1996). This disparity could be explained by soil water potential limitations dur-

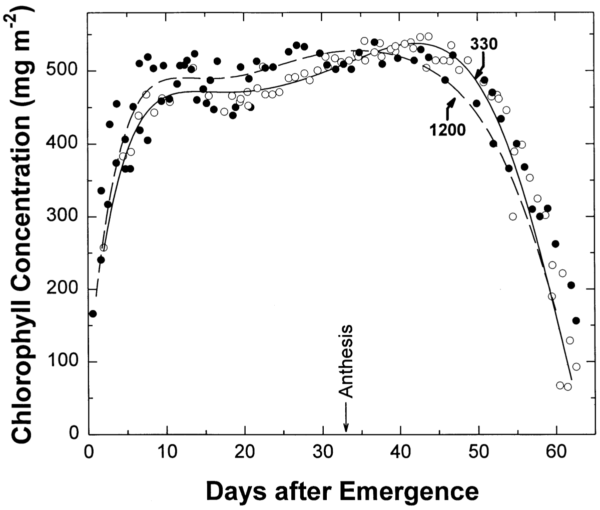

Figure 5. The effect of [CO_2] on chlorophyll concentration. The lines are regression lines through the data points. Each data point represents the average of 20 non-destructive chlorophyll measurements. Chlorophyll measurements were made at half leaf length from leaves at the top of the canopy. The error bars represent the standard error of the mean.

ing early growth, leading to differences in cell enlargement and leaf size between their CO_2 treatments. Stomatal closure in high [CO_2] should improve leaf water potential even at the same soil water potential. In this study, differences in leaf water potential between the CO_2 treatments were probably insignificant because of the low vapour pressure deficit, low net radiation, and the hydroponic root zone.

CO_2 enrichment effects on CQY and CUE

CQY is lower than the maximal leaf photosynthetic efficiency because it is measured at higher PPF levels. However, it is a more appropriate measure of the conversion efficiency of PPF into fixed C in plant communities because it accounts for whole plant respiration. Leaf quantum yields are measured as the initial slope of a P_{net} versus PPF_{abs} response curve, while CQY represents the slope of a P_{gross} versus PPF_{abs} response curve. Elevated [CO_2] increased the average life cycle CQY (14%; Table 3), which is lower than the increases observed in single leaves by Long & Drake (1991), but consistent with the results of Warren Wilson, Hand & Hannah (1992).

CUE remained remarkably constant over roughly the first 45 d of the life cycle (Fig. 4c), in spite of significant ontological changes in C partitioning as C moves from leaves to stems, and then into seeds. Although wheat seeds have a higher growth conversion efficiency than leaf tissue, we did not observe an increase in CUE after anthesis (Amthor 1989). The constant CUE means that a constant fraction of the daily fixed C is respired each day, indicating the possibility of a regulatory link between C gain and respiration that is not affected by CO_2 enrichment.

CQY and CUE were calculated assuming that R_{dark} occurs at the same rate as in the light. However, this assumption has not yet been rigorously confirmed. Current evidence suggests that the rate of *leaf* dark respiration in the light may be less than the rate in the dark. Villar, Held & Merino (1994) present data suggesting that dark respiration in the light is 55% of R_{dark} in leaves. In the light, TCA cycle activity may be lower, and energy produced in photophosphorylation could be used to offset both nitrate reduction and maintenance costs in chloroplasts. However, leaf respiration accounts for only 30–50% of total plant respiration because other organs, such as meristematic tissue, also make significant contributions. In fact, meristematic respiration (e.g. roots) increases during the light period (data not shown). If leaf dark respiration was reduced in the light, CQY would decrease due to lower P_{gross}, CUE would increase correspondingly, and DCG would remain unaffected. However, large changes in leaf respiration in the light have only a small effect on CQY and CUE. We estimate that CQY and CUE would change by only 11% if there was a 50% decrease in shoot dark respiration during the light period.

Elevated [CO_2] effects on seed yield

Elevated [CO_2] increased seed yield by 13% (Table 4), which is lower than the average yield increase (35%) often observed in CO_2 enrichment studies (Cure & Acock 1986). The response to CO_2 enrichment in crop plants is typically greater when water or nutrients limit the growth of ambient [CO_2] controls. In field studies, elevated [CO_2] may increase root growth of crop plants, thus alleviating moisture and nutrient stresses and increasing yield (Chaudhuri, Kirkham & Kanemasu 1990). In FACE studies, wheat grown in water-limited conditions showed a 23% increase in seed yield in response to CO_2 enrichment (550 μmol mol^{-1}), whereas well-watered wheat showed only a 10% increase in yield (Pinter *et al*. 1996). In this study, ample water and nutrients minimized root zone limitations to yield at both CO_2 concentrations, thus we expect smaller increases in yield due to elevated [CO_2] than in field-grown plants. The yield increase in this study is similar to the 17% yield increase reported in field-grown wheat exposed to 1200 μmol mol^{-1} (Havelka, Wittenbach & Boyle 1984b).

Elevated [CO_2] increases sink strength by increasing the development of secondary branches in soybeans (Havelka *et al*. 1984a), and by increasing tillering in wheat (Havelka *et al*. 1984b). Our results are consistent with Havelka *et al*. (1984b), who observed higher seed yield resulting from a greater number of heads m^{-2} (number of sinks) in elevated [CO_2].

CO_2 enrichment effects on chlorophyll concentration

Chlorophyll concentration (averaged over the life cycle) was not significantly higher in elevated [CO_2] (Fig. 5). Foliar chlorophyll concentration often decreases if leaf N is deficient. Leaf N per unit mass was decreased by elevated $[CO_2]$, but it did not significantly alter chlorophyll in this study. These results agree with the findings of Sage, Sharkey & Seemann (1989), who observed no effect of elevated $[CO_2]$ on chlorophyll content coupled with a decrease in leaf N per unit mass. In natural systems, large decreases (10–30%) in N content per unit mass by elevated $[CO_2]$ often disappear when the data are corrected for increased TNC (Körner & Miglietta 1994). Our results support the hypothesis that decreased leaf N in elevated $[CO_2]$ is associated with the loss of N from substances other than chlorophyll, such as protein (Bowes 1991; Robertson & Leech 1995; Poorter *et al*. 1997).

CONCLUSIONS

CO_2 enrichment increased crop productivity in wheat because of a sustained increase in CQY, but did not increase yield as a result of changes in radiation capture, CUE, or harvest index. Increased $[CO_2]$ altered whole plant C partitioning in this study, as evidenced by increased tillering, increased root biomass, and increased root respiration. Our results indicate that, in optimal environments, elevated $[CO_2]$ increases sink strength, which results in increased photosynthetic capacity and DCG throughout the life cycle. This supports the hypothesis that elevated rates of photosynthesis and crop growth rates are maintained in CO_2-enriched plants when sink capacity can become sufficiently large to prevent feedback inhibition.

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