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Responses of shoot and root gas exchange, leaf blade expansion and biomass production to pulses of elevated CO_2 in hydroponic wheat

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Abstract

Short-term effects of elevated CO_2 during the early life phase of plants may have long lasting consequences for growth and biomass in later periods. We exposed hydroponically grown wheat seedlings to 5 d pulses of elevated CO_2 while leaf expansion growth as well as shoot and root gas exchange were measured simultaneously and continuously. Shoot photosynthesis, night-time shoot respiration and below-ground respiration (largely by roots) roughly doubled when atmospheric CO_2 concentration was doubled. An interruption of CO_2 enrichment caused CO_2 assimilation and respiration to return to control levels. However, while the response of photosynthesis was immediate, that of respiration showed a hysteresis of about 3 d. Since shoot biomass increased at elevated CO_2 (with no change in allocation pattern) equal fluxes per shoot or root system after a return to control CO_2 concentrations indicate substantial downward adjustment of the capacity for CO_2 fixation and release in high-CO_2 grown plants. Leaf expansion growth was completely unaffected by CO_2 enrichment, whereas tiller initiation was significantly increased (doubled in 18 d). We conclude that leaf growth in these wheat plants was already carbon-saturated at ambient CO_2 concentration at optimum mineral nutrient supply. The stimulation of growth of whole plants was exclusively due to enhanced tillering during this very early part of the life of these wheat plants.

Key words: Allocation, atmospheric carbon dioxide enrichment, growth, photosynthesis, respiration, tillering, *Triticum aestivum*.

Introduction

A large number of papers on vegetative plant responses to elevated CO_2 describe phenomena such as photosynthesis, biomass production, shoot growth or, in some instances, respiration of certain plant parts. However, these components are rarely all assessed simultaneously and with high temporal resolution. Thus, it usually remains unclear precisely at what time the key events which led to a stimulation of biomass production took place. Poorter *et al.* (1988) and Norby *et al.* (1996) have demonstrated that the first few days or weeks under contrasting levels of CO_2 may determine the results obtained much later, with little explanatory alterations in key growth determinants observed after this initial phase. Hence, much of what is considered to be a 'long-term' CO_2 response, may turn out to be a carry-over effect of a rather short-term response, that has been hidden in most experimental protocols. A number of studies with wheat cultivars support the view that such initial vegetative responses may be the key to understanding the comparatively moderate stimulation of yield by elevated CO_2 in this important crop (Havelka *et al.*, 1984; Mitchell *et al.*, 1993; Weigel *et al.*, 1994). The study of Weigel *et al.* (1994) clearly documented that CO_2 enrichment effects on grain yield were entirely due to increased tillering, i.e. a process taking place very early in the life of a wheat plant.

The understanding of the interaction of various growth determinants during CO_2 enrichment in this early life phase is, therefore, of great importance for the understanding of differences observed much later. Since growth is the result of photosynthetic CO_2 uptake, respiratory and other carbon losses, and dry matter investment into various plant organs, a whole plant study is the only

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feasible approach to this problem. However, a major problem in a whole plant approach is that neither carbon losses nor investments can be measured accurately in below-ground plant parts when these are in a natural soil environment. Fully aware of the fact that root systems may exhibit quite different responses in a hydroponic system, we have still used this method for the sake of being able continuously to monitor the gas exchange of below- and above-ground plant parts at the same time. Here we utilize young wheat plants, growing under unlimited nutrient supply in gas exchange chambers in which root and shoot systems could be analysed separately. Linear variable displacement transducers were installed which monitored leaf expansion growth continuously over several days before and after providing additional CO_2 and also after returning to control CO_2 concentrations. Although this experimental system lacks natural rhizosphere feedbacks and does not account for nutritional constraints, it allows us to demonstrate the significance of simultaneous carbon losses by the root system, above-ground respiration and the dynamics of leaf growth during this initial phase of CO_2 enrichment.

Since experimental CO_2 enrichment, of necessity, will always be several orders of magnitude faster than the rate of CO_2 accumulation which takes place in our atmosphere, we are dealing with step responses, even if gradual elevations of CO_2 were attempted in the laboratory. Our experimental design permits the analysis of the immediate effect of such step increases of CO_2, as well as a possible reversal of such effects when CO_2 is returned to ambient levels.

Materials and methods

Plant material

Wheat (*Triticum aestivum* L. cv. Probus) was germinated and grown for 7–10 d on Zeolite ($NaAlSiO_2O_6.H_2O$ granules, Vermica AG, Bözen, Switzerland) in a greenhouse (25 °C, natural light) and then transferred to hydroponic culture. The nutrient solution consisted of 4 mM KNO_3 and $Ca(NO_3)_2$, 1.5 mM $MgSO_4.7H_2O$, 1.3 mM $NaH_2PO_4.2H_2O$ per litre plus micro-nutrients with Fe as Fe-EDDHA. When the tip of the third leaf appeared, plants were sealed above the root into rubber gaskets fitted into the air-tight lid of a 2.5 l PVC container which was filled with 2 l of the above nutrient solution. Thereby the root compartment could be flushed with an air-flow separate from the shoot compartment. Five plants were placed in one container. This hydroponic system has been used for many years, and has been proven to allow good growth and development of this wheat cultivar (Christ, 1978). At harvest, plants were separated into roots and shoots and dried at 80 °C.

Cuvette system and CO_2 treatment

Four ventilated glass chambers of 40 l volume, each accommodating one of the above PVC containers, were flushed with 300 l air per hour by means of a high pressure fan supplied with fresh ambient air from outside the greenhouse (350–410 (mostly around 375) $\mu l\ l^{-1}$ CO_2). One PVC container was placed into each of the 40 l glass chambers. The nutrient solution was aerated, i.e. separate air inlets and outlets were fitted to these containers (flow rate 90 l of air per hour). Two 40 l polyethylene containers were used as buffers before manifolds distributed the air stream (via flowmeters/flow controllers) to the eight aerated compartments (four root and four shoot compartments). The CO_2 concentration in one of the entry buffers was periodically elevated to roughly twice ambient levels. Each chamber contained a thermistor, both in the shoot and root compartments, and one chamber was supplied with a quantum sensor. The gas exchange chambers were set up in a temperature-controlled greenhouse and were supplied with additional illumination by one 1000 W lamp per chamber (Power Star, HQI, Osram, Germany), providing a minimum quantum flux density of 250 $\mu mol\ m^{-2}\ s^{-1}$ for 12 h (during normal sunshine up to 450 $\mu mol\ m^{-2}\ s^{-1}$). The heating of the chambers by the lamps caused the temperature to rise to mid-summer conditions (25–35 °C), depending on additional sunlight. In other words, radiant heating varied in the chambers (as documented in the results), depending on sunshine, but with no significant difference between chambers. Owing to transpirational water loss of the plants, chamber humidity was high and increased with increasing plant mass from approximately 60% relative humidity at the beginning of the experiment to >90% at the end. Chambers were ventilated by an internal fan producing a wind speed of about 0.5 $m\ s^{-1}$ at plant level.

Gas exchange measurements

Gas exchange chambers were part of an open differential gas exchange system, with rates calculated from inlet flow rates and differences in CO_2 concentration between inlet and mixed interior air. Magnetic valves automatically switched sampling lines via a cool trap every 2 min to an infra-red gas analyser (LICOR 6000, Lincoln, Nebraska, USA). These air samples were taken with a separate small sampling pump (300 $ml\ min^{-1}$) between the chambers and the IRGA. The flow in the sampling line was an order of magnitude smaller than the chamber air supply flow, the surplus of which was blown off via open end tubes, thus assuring that the chambers were always under slight overpressure. This guarantees a constant, leak-independent flow of sampling gas to the IRGA. With the given flow rate of 300 $l\ h^{-1}$, photosynthesizing plants were allowed to deplete mixed chamber CO_2 levels by about 100 $\mu l\ l^{-1}$ under low-CO_2 conditions, and about 200 $\mu l\ l^{-1}$ under elevated CO_2, yielding mixed air setpoints of CO_2 concentration within the chambers of around 275 $\mu l\ l^{-1}$ in the low-CO_2, and around 500 $\mu l\ l^{-1}$ in the high-CO_2 treatment. These values represent pre-industrial and expected CO_2 concentrations during the middle of the next century. The IRGA was used in the absolute mode only. Actual CO_2 concentration differences were calculated during data processing. Two dummy shoot and root cuvette systems (one for each CO_2 level) with identical dimensions and throughflows, but containing no plants, were used as physical controls. The system worked automatically, and all gas exchange and climate data as well as LVDT readings (see below) were stored on diskettes.

Measurement of leaf expansion rate

Inductive displacement transducers (model CXI-100-2C, LN-Industries, Gaillard, France) with a 200 mm displacement range were used (Christ, 1978). Four plants in each chamber were connected to four transducers by clamping the leaf tip to a metal string with a very small temperature coefficient. To keep the leaf and the string straight, a counter-weight of

approximately 6 g was applied. Since each leaf grows only for 5–7 d, the transducers had to be changed from one leaf to the next, starting with the third leaf tip up to the 5th or 6th leaf. The leaf growing at the fastest rate was selected by beginning with leaves of approximately 2 cm visible blade length. From previous experience (Christ, 1978), it was known that the rate of expansion growth of leaves does not significantly change before the leaf length exceeds approximately 15 cm.

Experimental procedure

After transfer of seedlings into the gas exchange growth chamber, plants were allowed to grow for 2 d at ambient CO_2 while all gas exchange and growth parameters were already recorded. By day 5 to 10 (depending on the experiment) we doubled the CO_2 concentration in two of the four chambers and continued data monitoring until or beyond the time when the high CO_2 concentrations were returned to ambient levels. In some instances, this cycle was repeated once or twice. Since the new CO_2 concentration was established within less than 30 min it was possible to study immediate and longer-term (several days) responses of plants. Due to unavoidable small leaks, readings of root compartment CO_2 levels became too noisy when shoot compartments were CO_2-depleted, compared to root compartments, during the day. Therefore, root respiration data for the dark period only, during which CO_2 gradients between shoot and root compartments were very small, are presented. In total, the experiments were repeated five times with new sets of plants and with different treatment durations over the period of one year (see synthesis in Figs 2 and 3). Since the results were virtually identical, the data set from October 1993 was selected in which CO_2 reversal experiments had also been conducted.

Results

Exposing the wheat seedlings to roughly twice the pre-industrial ambient CO_2 concentration caused the rate of whole shoot photosynthesis to double with no significant downward regulation within the first 5 d of continuous exposure (Fig. 1). The response is fully reversible: i.e. plants exposed to high CO_2 and thereafter treated with control CO_2 concentrations exhibited rates of photosynthesis identical to the controls. In the course of the experiment, per shoot rates of photosynthesis under elevated CO_2 were more than twice as high as in the controls due to enhanced leaf production. After the second 5 d CO_2 enrichment cycle shown in Fig. 1 (in this case the third cycle in total), some downward adjustment of photosynthesis had occurred in the high-CO_2-grown shoots, i.e. the rates of photosynthesis measured at pre-industrial CO_2 levels were identical to the controls, despite an approximately 52% greater shoot dry mass measured soon after the end of the experiment (see below).

Within the 5 d period of exposure to elevated CO_2, shoot respiration during the night increased, but when CO_2 concentrations were switched back to ambient levels, rates started to decline immediately and merged with controls in only 3 d. The effect was repeated in the second high and low CO_2 cycle shown in Fig. 1. The increase in night-time respiration in shoots was largely due to CO_2-induced growth stimulation and hence, enhanced growth respiration, while maintenance respiration on a dry matter basis may even have been reduced. This is supported by the fact that equal rates of respiration were found in plants which had previously received elevated CO_2 and those grown under ambient CO_2, despite larger shoot mass in the high CO_2-treated ones at the end of the experiment.

Whole root system respiration during the night (including that of any microbial life supported by roots in the hydroponic solution) was also strongly stimulated by elevated CO_2, but the time-course showed a characteristic hysteresis compared to the shoot alone. There is a clear trend for increasing rates of respiration during the first 5 d of exposure to elevated CO_2, possibly reflecting an almost immediate and persistent stimulation of root growth. When CO_2 is switched back to the lower level the trend is immediately reversed, and after 3 d the difference between formerly CO_2-treated and control plants disappeared. Since high-CO_2-grown plants possibly had a greater root mass at this stage, the rate of respiration per unit root dry mass is possibly even lower in formerly CO_2-treated plants compared to controls. During the second CO_2 enrichment cycle the picture observed during the first one was repeated, but the second reversal to low CO_2 levels did not bring rates down as fast as in the first cycle. This may be because the increased mass of roots accumulated under high CO_2 already included a larger fraction of older roots, the response of which masks trends which may have occurred in the youngest roots alone, as indicated by the still moderate reduction of total respiration compared to controls after switching back to low CO_2. Given the fact that total root mass at the end of the experiment was 83% higher in high-CO_2 plants compared to low-CO_2 plants, and total root respiration measured under elevated CO_2 was 108% higher than in controls, the rates of respiration under elevated CO_2 per unit dry mass of roots also appear to have been higher in the high-CO_2 group at the end of the experiment.

Figure 1 also illustrates the light regime during this experiment and the temperatures in the shoot and root compartments. Since there were no differences between temperatures in high- and low-CO_2 chambers, means for all chambers are presented only.

The rates of leaf extension did not show any relation to the CO_2 supply (Fig. 2). In no case was a difference between treatments found within the first 2 d, and later differences between high- and low-CO_2-treated leaves were still very small. The extension growth of leaves appears to be maximum under ambient CO_2 levels and does not seem to be carbon-limited, even under the high mineral nutrient supply provided in this experiment.

Above- and below-ground biomass accumulation was stimulated by elevated CO_2 even during such short periods

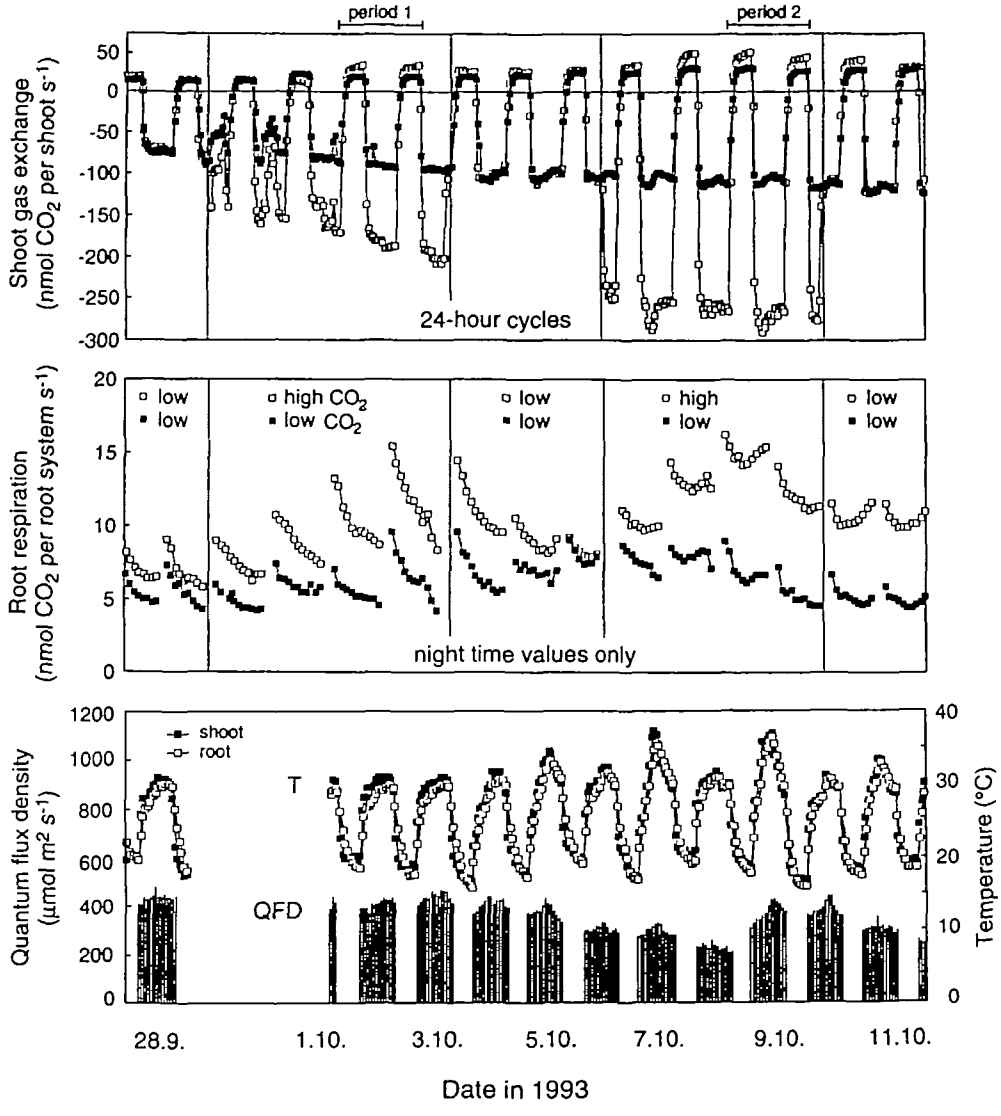

Fig. 1. Continuous recordings of CO_2 gas exchange of shoots and roots of wheat seedlings grown under low (closed symbols) and high CO_2 concentrations (open symbols). Note that 'high-CO_2 plants' were periodically switched to low CO_2 concentrations. The last two of a total of three high-CO_2 cycles are shown. Climate data in the lower diagram relate to hourly means of shoot and root temperatures and quantum flux density within the gas exchange chamber. Since there were no differences between high- and low-CO_2-grown plants, means for all chambers are presented here.

of exposure, but the differences became significant only after at least 12 d of CO_2 fertilization. Environmental influences were also indicated with less stimulation in experimental series conducted in winter or under overcast conditions (Fig. 3). The final degree of CO_2 stimulation of biomass accumulation was also influenced by the number of days seedlings had developed under ambient conditions before they were big enough to be installed in the gas exchange chamber and exposed to the step increase of CO_2.

There was a slight trend for CO_2-fertilized plants to have a greater fraction of biomass in the root compartment. However, the differences were not significant (numbers in the lower part of Fig. 3), which is in accordance with earlier findings in cereals (Farrar and Williams, 1991). When CO_2 enrichment lasted long enough to result in significant biomass differences, the number of tillers was also significantly increased. Plants which were exposed to elevated CO_2 for 18 d produced almost twice as many tillers as controls (Fig. 3).

The CO_2 balance of plants growing under elevated CO_2 was doubled at the end of the first CO_2 enrichment cycle and almost tripled at the end of the second cycle (Table 1). This is the combined result of increased rates of photosynthesis per unit leaf area and the stimulation of leaf area production (tillering) with periods of exposure possibly too short to affect biomass allocation and specific leaf area significantly.

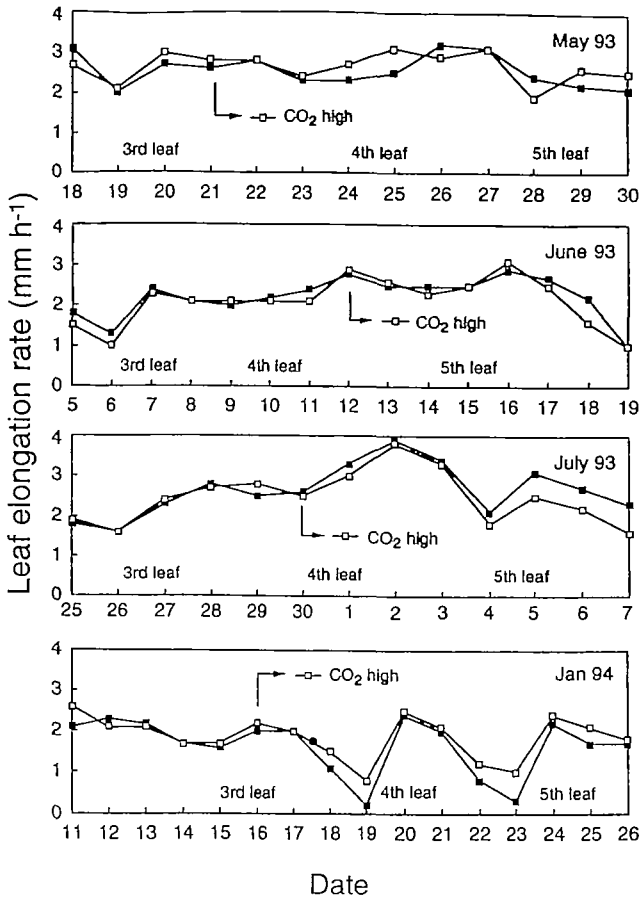

Fig. 2. Continuous recordings of leaf expansion growth measured by inductive displacement transducers in four cohorts of wheat seedlings. Arrows indicate when CO_2 level was switched from low to high CO_2 concentration. Plants periodically receiving elevated CO_2 are labelled with open symbols throughout the experimental period presented here.

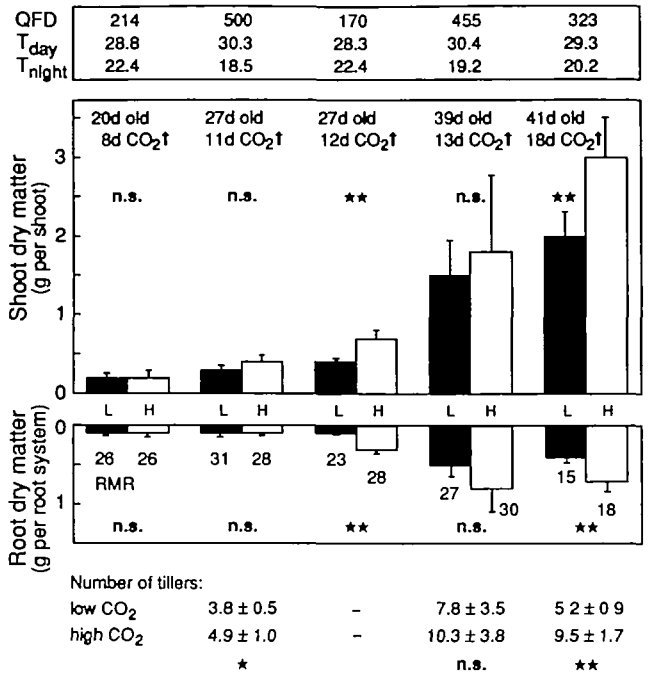

Fig. 3. Biomass responses of wheat seedlings exposed to various periods of CO_2 enrichment (independent replication of experiments between May 1993 and January 1994; age of plants at harvest in days). Climate data (top): QFD, mean quantum flux density (400–700 nm) between 08:00 and 18:00 h for all treatment days (μmol m^{-2} s^{-1}); T_{day} and T_{night}, mean air temperature in chambers between 08:00 and 18:00 h, and 21:00 and 06:00 h, respectively (°C). Note that humidity was much lower in the 11 d CO_2 treatment compared to all other experiments, because three times larger flow rates (no continuous readings) were used. RMR indicates the root mass ratio, i.e. the percentage of root biomass compared to total plant biomass. The number of tillers was determined at harvest. Data presented in Fig. 1 relate to the 18 d CO_2 enrichment experiment to the right. Error bars show the variance (s.d., $n=10$) among cohorts of individuals. The variance between individuals was substantially greater than the variance between chambers. When all individuals per chamber are pooled ($n=2$ chambers per treatment) differences of dry matter are only significant (t-test) at the 10% level in shoots and at the 5% level in roots.

Discussion

The results of this series of short-term CO_2 enrichment experiments with plants growing under unlimited mineral nutrient supply and favourable temperature indicate an enormous discrepancy between the stimulation of plant photosynthesis and biomass accumulation. In this respect the results obtained with this rather artificial experimental system are similar to results with field-grown plants in general and even whole ecosystems, including those with poor mineral nutrient supply (Diemer, 1994; Körner, 1995). While the daytime photosynthetic carbon fixation by the shoot remained at least doubled as long as twice control CO_2 levels were provided, and whole plant carbon balance almost tripled in the second CO_2 enrichment phase (Fig. 1; Table 1), biomass accumulation after 12–18 d of treatment was increased by only 20–75% (depending on the light regime) compared to controls in these fast-growing young plants (Fig. 3). Ingvardsen and Veierskov (1994) also reported a 250% stimulation of photosynthesis compared to a 25% stimulation of dry matter production in *Hordeum* seedlings of similar age and duration of exposure to twice ambient CO_2 concentrations. Since allocation patterns were not significantly altered at harvest, there is a need to explain the fate of a large amount of additional carbon taken up under elevated CO_2 every day, which is not ending up in the biomass pool. A large fraction of this carbon may be accounted for by an increase in respiration of both the whole shoot and whole root systems. When comparing the results with the literature it should be noted that the whole shoot and whole root rates of respiration refer to actively growing and undisturbed tissue, whereas the majority of published data are either for non-growing mature tissue (e.g. fully developed leaves only) or detached organs. A large part, if not the only part, of the respiratory stimulation which was found under elevated CO_2 is possibly due to increased respiration associated with growth and transport processes. It takes several days for this stimulation to cease

Table 1. *CO_2 balance of whole wheat seedlings under elevated CO_2 for two 48 h periods depicted from the experiment illustrated in Fig. 1*

Period 1 for 2 and 3 October, period 2 for 8 and 9 October (mmol CO_2 per plant for 48 h).

	Net photosynthetic CO_2 assimilation	Respiratory CO_2 losses			CO_2 balance
		Shoot[a]	Root[b]	Shoot + root	
Period 1					
Low CO_2	9.2	1.0	0.9	1.9	7.3
Elevated CO_2	17.7	1.6	1.5	3.1	14.6
Relative difference	+92%	+60%	+67%	+63%	+100%
Period 2					
Low CO_2	11.0	1.5	1.1	2.6	8.4
Elevated CO_2	28.8	2.3	2.4	4.7	24.1
Relative difference	+162%	+53%[c]	+118%[c]	+181%	+187%

[a] CO_2 losses during the night only, daytime losses are accounted for in net photosynthetic assimilation.
[b] Sum of day and night values calculated by using the temperature response curve obtained from night-time data shown in Fig. 1.
Note that the mean biomass at harvest, 2 d after the second period had ended, was 1.97 g for shoots and 0.36 g for roots in the low-CO_2 treatment and reached 3.02 g for shoots and 0.66 g for roots in the elevated-CO_2 treatment. Hence, per unit biomass respiration did not change much.

when CO_2 is switched back to control levels and, afterwards, rates of respiration per unit dry mass appear to be even lower in high-CO_2-treated plants, similar to what was found by Gifford *et al.* (1985). Pooling the stimulation of respiratory fluxes under elevated CO_2 in intact plants, roughly one-third of the additional CO_2 taken up under elevated CO_2 is lost again by respiration. The fraction of carbon released to the hydroponic solution is unknown (amounts may be substantial as indicated by the studies of Lekkerkerk *et al.* (1990) with soil-grown wheat), but here the CO_2 evolution from the whole solution without the roots at the end of the experiment was negligible (data not shown). There was also no significant slime or debris deposition in the containers.

The finding that leaf expansion growth in wheat is insensitive to CO_2 enrichment agrees with earlier findings by Kemp and Blacklow (1980) who found that leaf expansion in wheat is not carbohydrate-limited. A number of investigations have shown that leaf expansion in wheat is directly controlled by temperature (Gallagher, 1979; Hay and Wilson, 1982). Jolliffe and Ehret (1985) found that leaf expansion in bean is also not limited by assimilate supply. On the other hand, Leadley and Reynolds (1989) found that leaf expansion in soybean could be stimulated by CO_2 enrichment similar to what Sasek and Strain (1989) found for *Pueraria lobata* ('Kudzu', Fabaceae). The data clearly support the view that tillering is the key to understanding the CO_2 responses of wheat, which highlights the significance of CO_2 effects during the early life phase. In the field, such an effect would either reduce the amount of seed required to achieve a certain crop leaf area index, or be diminished by mutual shading of tillers. It may also lead to altered phasing between tillering, tiller expansion and canopy closure, the consequences of which should be investigated under competitive field conditions. Such interactions in the early phase of crop development may have greater effects on yield response of wheat to elevated CO_2 than direct CO_2 fertilization effects at later stages of development.

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