Effects of elevated CO$_2$ concentration on growth, water use, yield and grain quality of wheat under two soil water levels

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Abstract

Wheat (Triticum aestivum L.) is one of the most important food sources in the world. The potential impacts of elevated CO$_2$ on wheat yield and grain quality will have profound influences on the supply and nutritional value of wheat products as well as on many industrial sectors. A growth-chamber experiment was designed to estimate how soil moisture influences the potential effects of elevated CO$_2$ concentration ([CO$_2$]) on wheat growth, water use and grain yield. Spring wheat (P. aestivum cv. Gamma 8139) was grown in pots placed in controlled growth chambers and was subjected to two [CO$_2$] (approximately 350 and 700 µl/l, respectively) and two soil water levels (80 and 40% of field water capacity (FWC), respectively). High [CO$_2$] increased plant shoot dry weight by 89% under 80% FWC and by 53% under 40% FWC. Grain yield of wheat was markedly increased under elevated [CO$_2$] with greater grain number and harvest index. The ratio of plant shoot dry weight to height was increased by 75% under high [CO$_2$] at high moisture, and by 54% at low moisture. Water use efficiency of shoot (WUEs) and grain yield (WUEg) were increased under high [CO$_2$] because the magnitude of the increase in shoot dry weight and grain yield was greater than that of the cumulative consumption of water under high [CO$_2$] conditions. When wheat plants were under high [CO$_2$] conditions and maintained at high moisture, the WUEs and WUEg were increased by 62 and 128%, respectively. Elevated [CO$_2$] resulted in lower concentrations of mineral nutrients (N, P, K and Zn), lysine and crude protein in mature grains. This was probably caused by a dilution effect induced by great increment of carbohydrate in grains. The total quantity of mineral nutrients, lysine and crude protein accumulated in grains per hectare were still increased under high [CO$_2$] conditions as reflected by the increased crude starch content, and corresponding decreases in mineral nutrients, lysine and crude protein concentrations. The analysis of yield components suggested that the yield increase was mainly attributable to an increase in the number of grains. However, the effects of CO$_2$ enrichment on plants depend on the availability of soil moisture, and plants may benefit more from CO$_2$ enrichment when sufficient water is supplied.

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Keywords: Spring wheat; Triticum aestivum L.; Growth; Yield; Grain quality; Elevated carbon dioxide; Water use
1. Introduction

Atmospheric carbon dioxide concentration ([CO₂]) has increased about 30% since pre-industrial times and during this century [CO₂] levels could double or triple compared to pre-industrial levels (Houghton and IPCC, 2001). Numerous experiments have demonstrated that in many C₃ species high atmospheric [CO₂] leads to increases in photosynthetic rate, whole-plant growth and water use efficiency (WUE) and decreases in transpiration (Kimball, 1983; Drake and Leadley, 1991; Lawlor and Mitchell, 1991; Bowers, 1993; Idso and Idso, 1994; Jiang, 1995; Wang et al., 1998). From a comprehensive analysis of 437 prior observations on the yield of 37 species grown with CO₂ enrichment, Kimball (1983) concluded that a doubling of the earth’s CO₂ concentration (600 l/l) would increase agricultural yield by about 33%. However, because of the contrasting effects of elevated CO₂ on leaf transpiration rate and leaf growth, there have been inconsistent results on the whole-plant water requirements which rely greatly on the proportional changes in decline of transpiration rate and/or increase of leaf area (Allen, 1990).

Plants are the foundation of our food supply. Changes in the elemental composition of plants will affect the quality of human nutrition, especially for microelements, such as Fe and Zn, which are vital for human health (Loladze, 2002). However, there were limited reports on the effect of CO₂ enrichment on grain quality. Available literature suggested that grain protein concentration was generally decreased under elevated [CO₂] conditions (Thompson and Woodward, 1994; Rogers et al., 1998; Fangmeier et al., 1999; Pleijel et al., 2000). Loladze (2002) summarized results from published literature, and claimed that an overall decline of essential elements: C ratios induced by elevated CO₂ would intensify the already acute problems of micronutrient malnutrition.

The effect of CO₂ enrichment on crops varies under different soil moisture regimes (Ewert et al., 2002). Most studies were carried out under favorable water conditions (Cure and Acock, 1986; Amthor, 2001). However, data on the interactive effects of CO₂ and soil moisture on plants are scarce and often contradictory (Amthor, 2001). Some authors claim that the percentage increase in plant growth due to elevated [CO₂] is generally not reduced by water stress (Gifford, 1979; Idso and Idso, 1994; Kang et al., 2002) whereas the results of many other theoretical projections and field or greenhouse experiments suggest that the relative effects of CO₂ enrichment on plants are constrained by less than optimal levels of soil moisture (Kramer, 1981; Kimball, 1983; Pooetter, 1993; Hunt et al., 1995; Thompson and Woodward, 1994; Ziska et al., 1996; Bunce, 1998; Pooetter, 1998; Wu and Wang, 2000).

Water is and will be a primary limiting factor for agricultural productivity in the Loess Plateau of China due to the limited precipitation and high evapotranspiration (Xu et al., 1989; Qian, 1991; Tao et al., 2003). Thus, it is important to consider both elevated CO₂ concentrations and the differences in soil moisture when the possible effects of elevated [CO₂] on crops in China are to be assessed. In this study, we grew spring wheat under two [CO₂] and two soil moisture levels and focused on the effect of whole-season exposure of plants to elevated CO₂ on growth, water use, yield and yield quality, and its dependence on soil moisture.

2. Materials and methods

2.1. Plant materials and growth conditions

The experiment was conducted at Lanzhou University, China. Plants were grown in two identical controlled growth chambers (0.8 m × 2 m × 1.5 m) (Conviron, Controlled Environments LTD., Canada), one supplied with ambient [CO₂] (a seasonal average of 350 μl/l), and another with elevated [CO₂] (a seasonal average of 700 μl/l). There are two water level treatments (80 and 40% FWC) with six replicate pots per water level in each chamber.

The environmental variables including CO₂ concentration, temperature and light intensity inside the two chambers were continuously monitored and automatically adjusted by the same computer. Temperature and light intensity were the same in both chambers. Only [CO₂] was varied in the two growth chambers, one with ambient [CO₂] and another with doubled [CO₂]. Because there were only two growth chambers of the same model, the environmental sensors and controlling systems of the two chambers were carefully calibrated before the commencement of the experiment, and then the environmental factors in the chambers...
were periodically monitored during the entire course of experiment in order to minimize the variance induced by the between-chamber heterogeneity of environmental conditions. Electrical fans inside the chamber facilitated the circulation and thorough mixing of air, and ensured the air to be replaced twice per minute. Each chamber was provided with a combination of 16 high-pressure sodium and 12 metal halide lamps that were arranged alternatively in four rows. The above-canopy photosynthetically active radiation (PAR) inside the growth chambers was maintained constant from 7:00 a.m. to 7:00 p.m. at 450 μmol m−2 s−1 during the course of experiment. PAR across chambers was determined to be relatively uniform. The temperature inside the chambers was controlled on a diurnal sine wave with maximum of 19 °C at 2:00 p.m. and a minimum of 8 °C at 4:00 a.m. and the minimum/maximum diurnal temperatures were changed to 11/24 °C when wheat plants entering the reproductive phase, to mimic the diurnal and seasonal fluctuations of ambient air temperature. Average relative humidity inside the growth chambers was about 40% during growth seasons with it being only measured but not controlled. The environmental variables such as CO2 concentration, temperature and light intensity inside the chambers were continuously monitored and controlled by a computer.

2.2. Growth measurements

Shoot growth was assessed by periodical destructive growth analysis of three plants randomly selected from each pot. All component dry weights were obtained following oven-drying to constant weight at 65 °C. Plants were finally harvested on 19 June, 3 months (93 days) after sowing, with each treatment having an average of 170 plant. Total shoot dry weight, grain dry weight per plant, grain number per plant and thousand-seed dry weight in each pot were determined at harvest. Harvest index (HI) was derived by dividing grain mass by aboveground biomass at the conclusion of experiment.

Water consumption per plant was calculated from the records of pot weight and plants per pot. Plant water use efficiency was calculated from shoot dry weight per plant at harvest divided by cumulative consumption of water per plant (WUEs), and from grain yield per plant at harvest divided by cumulative consumption of water per plant (WUEg).

2.3. Chemical analysis of grain

Dry grain samples were ground to pass through a 0.16 mm sieve. Chemical contents of flour were determined using the method described in “National Standards of Chinese” by the Appraising Center of Grain Quality, Agricultural Science Academy of Gansu Province. Crude starch was determined using polarimetry, a national standard method. Starch was first hydrolyzed in CaCl-HOAc acid solution, then determined with a polarimeter. Concentrations of nitrogen (N), phosphorous (P), potassium (K), zinc (Zn) were determined on samples digested using the micro-Kjeldahl technique. Total nitrogen and phosphorous were measured colorimetrically on a Kjeltec Auto 1030 Analyzer (Foss Tecator) and on a spectrophotometer, respectively. Crude protein content was calculated from nitrogen content multiplying by a constant of 5.7. Potassium and zinc concentrations were measured on a Perkin-Elmer 5100 PC atomic
absorption spectrometer. Lysine was measured by dye-binding lysine method (DBL method), a simple internationally accepted method for lysine analysis (ACCAPC, 1983; Shi, 1986).

Nutritive values of grain per hectare were calculated from the concentrations of mineral nutrients (N, P, K and Zn), lysine, crude starch and crude protein multiplying by the estimated grain yield per hectare based on grain dry weight per plant.

2.4. Experimental design and statistical design

Our experiment consisted of two [CO\textsubscript{2}] levels (350 and 700 µl/l) and two soil water levels (80 and 40% FWC). A factorial design was used with a total of four treatments, which were designated as HC, HD, LC and LD, respectively, where H and L represented high (80% FWC) and low soil moisture (40% FWC), C and D represented current (350 µl/l) and doubled [CO\textsubscript{2}] (700 µl/l), respectively. Each treatment had six replicate pots within chambers. Full replicates would have been desirable, i.e., individual chambers with data from pots within chambers average, but enough chambers of the same model were not available for this form of replication. Since the environment was the same in the two chambers throughout the plant growth period, pot replication was adequate. Twelve pots were placed in each chamber and controlled with two soil water levels. H and L pots were placed alternately in the chambers and randomly changed every 2 days after weighing for soil moisture control.

Data were analyzed using SPSS 10.0 software for two-way ANOVA, t-test and standard deviation. Two-way ANOVA was carried out on shoot dry weight, shoot height, grain yield and water use data to determine the effects of CO\textsubscript{2} level, soil moisture level and their interactions. T-test was carried out on shoot dry weight, shoot height, grain yield and grain quality data to determine the effects of CO\textsubscript{2} level under the same soil moisture level. The standard deviations were shown with numerals in tables and with error bars in figures, respectively. It was considered significant when \( P \leq 0.05 \) (marked with (*)) and extremely significant when \( P \leq 0.01 \) (marked with (**)).

![Fig. 1. Effects of elevated CO\textsubscript{2} on shoot dry weight of spring wheat (g/plant) under two soil moisture levels at different developing stages.](image-url)

Shoot dry weight was obtained by harvesting three plants randomly selected from each pot and then oven-drying to constant weight. Significance levels from ANOVA (or CO\textsubscript{2}, drought, CO\textsubscript{2} × drought effects: (**), (*) NS for \( P \leq 0.01 \), \( P \leq 0.05 \), and not significant, respectively. HC, high soil moisture (80% FWC) and ambient [CO\textsubscript{2}] (350 µl/l); HD, high soil moisture and doubled [CO\textsubscript{2}] (700 µl/l); LC, low soil moisture (40% FWC) and ambient [CO\textsubscript{2}]; LD, low soil moisture and doubled [CO\textsubscript{2}]. Mean values and error bars are calculated on the six replicate pots of each treatment.
3. Results

3.1. Plant growth

High [CO₂] increased shoot dry weight by 30.7, 86.0, 133.1, 89% at elongation, booting, grain filling, and harvest stages, respectively, under high soil moisture (80% FWC) (HD versus HC, \( P < 0.05 \) at booting, grain filling, and harvest stages; not significant at elongation stage), and by 8.8, 8.4, 52.7, 53.1%, respectively, under low soil moisture (40% FWC) (LD versus LC, not significant) (Fig. 1). The positive effect of high [CO₂] on wheat growth was greater under high soil moisture than under low soil moisture conditions. As a result, the difference in shoot dry weight between the two soil moisture levels was greater under

![Graph showing effects of elevated CO₂ on plant height and shoot dry weight to height ratio under two soil moisture levels.](image URL)
elevated [CO$_2$] than under current [CO$_2$]. There was no difference in shoot dry weight under doubled [CO$_2$] + water deficit (LD) compared with under ambient [CO$_2$] + high water level (HC).

Plants grown under elevated CO$_2$ had larger ratio of shoot dry weight to shoot height (W/H ratio), while plant height was not different between the two CO$_2$ concentrations (Fig. 2). The W/H ratio of plants exposed to high CO$_2$ increased by 75.6 and 54.7% under high and low soil moisture ($P < 0.01$), respectively. On the other hand, water deficit significantly decreased plant W/H ratio by about 36.5 and 44.0%

Fig. 3. Effects of elevated CO$_2$ on the yield and its components of spring wheat under two soil moisture levels. Significance levels from ANOVA for CO$_2$, drought, CO$_2$ × drought effects; (**), (*) NS for $P \leq 0.01$, $P \leq 0.05$, and not significant, respectively: (a) grain dry weight per plant (g); (b) number of grains per plant; (c) thousand-grain dry weight (g); (d) harvest index (the ratio of grain to shoot dry weight). Mean values and error bars are calculated on the six replicate pots of each treatment.
under ambient and doubled \([\text{CO}_2]\) \((P < 0.01)\), respectively.

### 3.2. Yield and yield component analysis

Elevated \([\text{CO}_2]\) significantly increased the total grain weight per plant by 166% at high soil moisture (HD versus HC) \((P < 0.05)\), but only by 78% at low soil moisture conditions (LD versus LC) \((P < 0.01)\) (Fig. 3a).

A similar pattern was observed for the number of grains (Fig. 3b). Elevated \([\text{CO}_2]\) increased the number of grains per plant by 140% at high soil moisture (HD versus HC) \((P < 0.01)\), and by 42% at low soil moisture (LD versus LC) \((P < 0.05)\), respectively. Under \([\text{CO}_2]\) enrichment, the thousand-grain weight increased at both water levels (Fig. 3c), but the difference was not statistically significant.

The proportion of plant dry biomass allocated to grains (Harvest index, HI) increased significantly by over 30% individually by elevated \([\text{CO}_2]\) and by low soil moisture conditions (Fig. 3d) \((P < 0.05)\). The greatest relative increase in HI was found in plants under doubled \([\text{CO}_2]\) and low moisture conditions (41.9%).

Our results in Fig. 3 clearly demonstrate that elevated \([\text{CO}_2]\) can increase the per plant grain yield, primarily through positively affecting the number of grains per plant. This is clearly obvious when soil moisture was unlimited. Meanwhile, the reduction of grain yield under conditions of water deficit can be alleviated to some extent by elevated \([\text{CO}_2]\). Statistical analysis shows that there was a significantly interactive effect between soil moisture content and \([\text{CO}_2]\) on grain dry weight, grain number and harvest index, and not on thousand-grain weight (Fig. 3).

### 3.3. Water use

Under high soil moisture, wheat exposed to elevated \([\text{CO}_2]\) consumed more water during the whole growth season except for the doughing stage, with an increase of 16.7% in accumulative water consumption \((P < 0.05)\) (Fig. 4). However, the effect of elevated \([\text{CO}_2]\) on accumulative water consumption of wheat was not significant under low soil moisture. Since the enhancement of elevated \([\text{CO}_2]\) on growth was greater than on water consumption, water use efficiency of shoot (WUEs) of wheat grown at elevated \([\text{CO}_2]\) was increased by 62.6% under high soil...
Fig. 5. Effects of elevated CO₂ on water use efficiency of spring wheat under two soil moisture levels. Significance levels from ANOVA for CO₂, drought, CO₂ × drought effects; (**), (*) NS for $P \leq 0.01$, $P \leq 0.05$, and not significant, respectively: (a) water use efficiency of shoot (WUEs, shoot dry weight (g)/cumulative consumption of water (kg)); (b) water use efficiency of grain (WUEg, grain dry weight (g)/cumulative consumption of water (kg)). Mean values and error bars are calculated on the six replicate pots of each treatment.

moisture ($P < 0.05$), and by 48.3% under low soil moisture (NS) (Fig. 5a). The WUEg was increased even more by elevated [CO₂], due to the additional stimulative effect of high [CO₂] on harvest index (Fig. 5b).

3.4. Yield quality

Grains of wheat grown under elevated [CO₂] had lower content of protein (Pr), lysine, nitrogen (N), phosphorus (P), potassium (K), zinc (Zn) than those
### Table 1
Effects of elevated CO₂ on nutrition concentration in wheat grain

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Favorable soil water + current [CO₂] (HC)</th>
<th>Favorable soil water + double current [CO₂] (HD)</th>
<th>Percentage change between HD and HC (%)</th>
<th>t-test result</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crude protein (g/100 g)</td>
<td>19.02 ± 0.102</td>
<td>16.14 ± 0.081</td>
<td>−15.2</td>
<td>**</td>
</tr>
<tr>
<td>Lysine (g/100 g)</td>
<td>0.600 ± 0.008</td>
<td>0.565 ± 0.024</td>
<td>−5.8</td>
<td>NS (0.06)</td>
</tr>
<tr>
<td>Crude starch (g/100 g)</td>
<td>51.23 ± 0.3</td>
<td>56.20 ± 0.5</td>
<td>9.7</td>
<td>**</td>
</tr>
<tr>
<td>P (g/100 g)</td>
<td>3.54 ± 0.018</td>
<td>2.83 ± 0.014</td>
<td>−15.2</td>
<td>**</td>
</tr>
<tr>
<td>K (g/100 g)</td>
<td>0.625 ± 0.021</td>
<td>0.480 ± 0.042</td>
<td>−38.3</td>
<td>**</td>
</tr>
<tr>
<td>Zn (mg kg⁻¹)</td>
<td>56.03 ± 1.26</td>
<td>37.75 ± 0.63</td>
<td>−32.6</td>
<td>**</td>
</tr>
</tbody>
</table>

Within columns, values are followed by standard deviation. Three pots were chosen to analyze nutrition concentration of grains, so values are mean of three replicates.

Under ambient [CO₂], while the content of crude starch was higher (Table 1). In comparison with HC plants, protein content in grains from HD plants decreased by 15.2%. A similar trend was true for P (by 36.6%), K (by 23.2%), and Zn (by 32.6%) (P < 0.01). However, the content of crude starch in grains from HD plants was 9.7% higher than that of HC plant. Because of the positive effect of high [CO₂] on grain yield, the nutritive values of above elements in each hectare were all increased, with crude protein increased by 126%, and crude starch by 192%, respectively (Table 2).

### Table 2
Effects of elevated CO₂ on nutritive value of wheat grain on a per hectare basis

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Favorable soil water + current [CO₂] (HC)</th>
<th>Favorable soil water + double current [CO₂] (HD)</th>
<th>Percentage change between HD and HC (%)</th>
<th>t-test result</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crude protein (kg/ha)</td>
<td>211.2 ± 31.8</td>
<td>477.7 ± 104.6</td>
<td>126.2</td>
<td>*</td>
</tr>
<tr>
<td>Lysine (kg/ha)</td>
<td>6.67 ± 1.09</td>
<td>16.72 ± 3.66</td>
<td>150.7</td>
<td>*</td>
</tr>
<tr>
<td>Crude starch (kg/ha)</td>
<td>568.99 ± 87.48</td>
<td>1663.9 ± 364.6</td>
<td>192.4</td>
<td>*</td>
</tr>
<tr>
<td>N (kg/ha)</td>
<td>3.05 ± 0.58</td>
<td>8.31 ± 18.35</td>
<td>126.2</td>
<td>*</td>
</tr>
<tr>
<td>P (kg/ha)</td>
<td>37.05 ± 5.58</td>
<td>83.81 ± 18.35</td>
<td>126.2</td>
<td>*</td>
</tr>
<tr>
<td>K (kg/ha)</td>
<td>6.925 ± 0.911</td>
<td>14.20 ± 3.165</td>
<td>105.1</td>
<td>*</td>
</tr>
<tr>
<td>Zn (g/ha)</td>
<td>62.13 ± 8.65</td>
<td>111.75 ± 24.45</td>
<td>79.9</td>
<td>NS (0.059)</td>
</tr>
</tbody>
</table>

Within columns, values are followed by standard deviation. Three pots were chosen to analyze nutrition concentration of grains, so values are mean of three replicates.

Under ambient [CO₂], while the content of crude starch was higher (Table 1). In comparison with HC plants, protein content in grains from HD plants decreased by 15.2%. A similar trend was true for P (by 36.6%), K (by 23.2%), and Zn (by 32.6%) (P < 0.01). However, the content of crude starch in grains from HD plants was 9.7% higher than that of HC plant. Because of the positive effect of high [CO₂] on grain yield, the nutritive values of above elements in each hectare were all increased, with crude protein increased by 126%, and crude starch by 192%, respectively (Table 2).

### 4. Discussion

#### 4.1. Effect of CO₂ enrichment on growth and water use

In the present experiment, CO₂ enrichment significantly increased wheat growth as reported previously in many other studies (Pearcy and Björkman, 1983; Bowes, 1993; Conroy et al., 1994; Christ and Korner, 1995; Kimball et al., 1995; Rao et al., 1995; Wheeler et al., 1996; Mulholland et al., 1998a; Cardoso-Vilhena and Barnes, 2001). Kimball et al. (1995) showed that shoot biomass of wheat increased by an average of 8.4% by elevated [CO₂] in 2 years of free-air CO₂ enrichment (FACE) experiments. Sæbø and Mortensen (1996) reported that the total biomass of wheat increased by 11% at high [CO₂]. Mulholland et al. (1998a) found that stem biomass and yield in wheat under elevated [CO₂] (680 μL/L) were 27 and 30% greater, respectively, than in control plants. Cardoso-Vilhena and Barnes (2001) reported that elevated [CO₂] increased total biomass of wheat by 44%. Hocking and Meyer (1991) revealed that CO₂-enriched wheat produced about twice the dry matter of control plants. Based on a statistical analysis of ‘ESPACE-wheat’ results, Bender et al. (1999) demonstrated that the main effect of CO₂ enrichment was a significant enhancement of above-ground biomass and yield in almost all experiments. However,
CO₂ responsiveness was shown to differ considerably between different locations, with a large proportion of the observed variability remaining unexplained. Compared with existing literature, the magnitude of increase in wheat biomass and yield induced by elevated [CO₂] in our current experiment was higher. This may be attributed to the constant favorable growth conditions of temperature, soil nutrients and relative humidity in this experiment in growth chambers which are optimum for realization of the maximum effect of [CO₂] compared with the field (Conroy et al., 1994; Amthor, 2001; Cardoso-Vilhena and Barnes, 2001).

In the experiment reported here, W/H was bigger under doubled [CO₂] than under current [CO₂] (Fig. 2). This suggests that plant morphology may be somewhat altered under future high [CO₂] conditions (Müller, 1993; Christ and Körner, 1995; Sæbø and Mortensen, 1996; Mulholland et al., 1998a; Pritchard et al., 1999). High [CO₂] enhanced plants lateral growth more than vertical growth. The mechanism and consequence of this is being studied.

Generally, high [CO₂] significantly reduced transpiration (Morison, 1985, 1998; Wu and Wang, 2000). However, the reduction in transpiration induced by doubled[CO₂] is often somewhat offset by a larger leaf area induced by high [CO₂], so that the effect of high [CO₂] on whole-season water consumption is complicated (Allen, 1990; Eamus, 1991; Wu and Wang, 2000). However, WUE is generally increased under high [CO₂] in almost all previous experiments (Eamus, 1985, 1991; Wu and Wang, 2000). In the present experiment, high [CO₂] increases WUE by increasing growth more than increasing water consumption. This would be beneficial to future food production of world, especially in water-limited area (Wallace, 2000).

4.2. Effect of CO₂ enrichment on grain yield and quality

In the present experiment, CO₂ enrichment substantially increased grain yield of wheat (Fig. 4). On the one hand, elevated [CO₂] greatly increased number of grains per plant, and the harvest index (HI) on the other. High HI means that a relatively greater proportion of assimilated carbon is allocated to the seeds under high CO₂. This is in agreement with many previous experiments on wheat (Lawlor and Mitchell, 1991; Pinter et al., 1996; Wheeler et al., 1996; Mulholland et al., 1998a,b). The increased HI associated with high CO₂ may be due to the higher sensitivity of grain development to extra leaf photosynthesis induced by high CO₂ than vegetative growth (Rogers et al., 1996a). It is evolutionarily advantageous that natural plants can make full use of extra amount of assimilated carbon to promote fitness.

The grain yield of wheat is the product of individual grain weight and numbers of grains. In our experiment CO₂ enrichment slightly increased thousand-grain weight and greatly increased the number of grains per plant. Therefore, the response of wheat yield to elevated [CO₂] has been largely resulted from an increase in grain number with CO₂ enrichment. This result is similar to results reported in other experiments on wheat (Rawson, 1995; Fangmeier et al., 1996; Mulholland et al., 1998a,b; Rogers et al., 1998; Van Oijen et al., 1999; Pleijel et al., 2000) and on rice (Bugbee et al., 1994; Kim et al., 1996). Additionally, Sung and Chen (1991) observed increases in strawberry yield with CO₂ enrichment, which was associated with an increase in fruit number. The yield response of barley (Thompson and Woodward, 1994) and orange (Downton et al., 1987) to high [CO₂] was also closely related to the number of grain and fruits harvested. Rogers et al. (1996b) reported an increase in the number of flower buds in cotton grown at high [CO₂]. Wu and Wang (2000) revealed that high [CO₂]-induced increase in bean yield of broad beans could be explained by the increase in bean number. The extra carbon assimilates produced at high [CO₂] may ensure the full development of flowers and grains (Deng and Woodward, 1998). However, the effect of high [CO₂] on individual grain weight was inconsistent with increase (Van Oijen et al., 1999; Li et al., 2001), decrease (Rawson, 1995; Batts et al., 1997; Van Oijen et al., 1999; Heagle et al., 2000) and no change (Fangmeier et al., 1996; Heagle et al., 2000; Pleijel et al., 2000).

In our experiment grain harvested from high [CO₂] contained less protein and nitrogen than that from ambient [CO₂]. This agrees with most other reports on wheat (Hocking and Meyer, 1991; Thompson and Woodward, 1994; Manderscheid et al., 1995; Rogers et al., 1998; Fangmeier et al., 1999) and on rice (Seneewera and Conroy, 1997; Zhang et al., 1998). Thompson and Woodward (1994) reported wheat had...
28% less grain nitrogen in elevated [CO$_2$] (700 μl/l) compared to ambient atmospheric [CO$_2$]. Fangmeier et al. (1999) observed reductions in grain nitrogen, calcium, sulfur and iron when CO$_2$ concentrations increased from 350 to 900 μl/l, and even not changed in another cultivar, Rosella. In the reports of Sæbø and Mortensen (1996), both grain yield and the protein content of wheat was not significantly affected by CO$_2$ enrichment. In a study on rice, Zhang et al. (1998) found a decrease in protein content of grains under high [CO$_2$]. Cotrufo et al. (1998) reported that synthesis of existing data showed an average 14% reduction of N concentrations in plant tissue generated under elevated CO$_2$ regimes. A 15.2% reduction in nitrogen content in our study is very close to this average value. Reduction in plant nitrogen with elevated CO$_2$ may be resulted from increases in the concentration of storage carbohydrates and/or changes in distribution of protein or other nitrogen containing compounds due to higher photosynthetic rates. Uptake of nitrogen may also be reduced at high CO$_2$ due to lower transpiration rates (Conroy and Hocking, 1993; Manderscheid et al., 1995; Cotrufo et al., 1998).

Our experimental result indicated that the nutrient concentrations (N, P, K, Zn) in wheat grain were decreased by high [CO$_2$]. This agrees with other experiments on wheat (Fangmeier et al., 1996; Manderscheid et al., 1995) and on rice (Seneweera and Conroy, 1997). As suggested above on nitrogen reduction, both increased carbohydrate accumulation and reduced mass flow could lead to this result. The low concentrations of several essential micronutrients in modern crops contribute to the problem of micronutrient malnutrition, for instance, nearly half of the world’s population is at risk of inadequate Zn intake (Loladze, 2002). So, the lower (nutritional value): (caloric value) of crops under high CO$_2$ will aggravate the micronutrient malnutrition problem in the world (Loladze, 2002). And the effects of CO$_2$ enrichment on the elemental compositions of crops, especially on essential elements, should receive more attention, because there has been a great dearth of literature on this aspect (Loladze, 2002).

4.3. Interactive effect of CO$_2$ concentration and soil moisture content on wheat

Our results indicated CO$_2$ and soil moisture content showed significant interactive effects on wheat growth and yield. On the one hand, high CO$_2$ can alleviate the negative effect of water deficit on plants. On the other hand, the positive effect of high [CO$_2$] on plant growth was constrained by less favorable soil moisture conditions (Figs. 1–5). This is in agreement with most previous reports (Schönfeld et al., 1989; Müller, 1993; Conroy et al., 1994; Porey, 1998; Catovsky and Bazzaz, 1999; Ward et al., 1999; Wu and Wang, 2000; Amthor, 2001; Cardoso-Vilhena and Barnes, 2001; Guo et al., 2002).

Kang et al. (2002) conducted CO$_2$ enrichment experiments in two climate chambers with wheat under three soil moisture levels: 85–100% (high), 65–85% (medium), and 45–65% (low) FWC, respectively. They found that CO$_2$ enrichment led to more increase of biomass under ‘low soil moisture treatment’ (45–65% FWC) than under ‘high soil moisture treatment (85–100% FWC)’ in their experiment. We believe that the discrepancy between the results reported by Kang et al. (2002) and ours is mainly resulted from the differences in the criterion used for soil moisture treatment. It is generally acknowledged that the favorable soil moisture for wheat is 60–80% FWC. The so-assigned medium and low soil moisture treatment in Kang et al.’s experiment are by no means low in reality for wheat.

Moreover, still other reports on similar experiments suggested that growth and yield enhancement of wheat induced by high CO$_2$ was greater under drought stress than under high soil moisture (Gifford, 1979, conducted in two artificially illuminated growth cabinets; Chaudhuri et al., 1990, conducted in field; Samarakoon et al., 1995, conducted in two controlled-environment glasshouses). This may be partly attributed to the different method of water control. In their experiments, dry treatment was realized by periodically supplying a preset amount of water (very little) or given no water. The quantity of water added to maintain the soil moisture gradient was not calculated from the actual soil moisture. This may lead to actually better soil status in high CO$_2$ treatment than in ambient treatment since high CO$_2$-plants use water more economically. This effect
is more obvious under drier soil moisture treatment, which may influence the experimental results. Additionally, use of different factors, such as temperature and light intensity, may alter the interaction between CO₂ concentrations and soil moisture levels and so be partially responsible for the different results reported by different researchers.

Thus, based on the results of ours and from the literature, it is can be concluded that the positive effect of CO₂ enrichment on plants are greatest under most suitable soil moisture conditions. Depending on the life history and evolutionary traits of species, different species of wild plants and their cultivated relatives or even different cultivars of the same domesticated species may respond variously to a given soil moisture gradient as realized by the researchers. This conclusion was also supported by other experiments on trees. For instance, Catovsky and Bazzaz (1999) found that under elevated atmospheric CO₂ levels, the seedling growth of paper birch, which are often found on more xeric, well-drained soils, was enhanced more at low soil moisture treatment than at high soil moisture treatment, while yellow birch, which are usually associated with more mesic sites, showed more improved growth at high soil moisture treatment.

Cultivated wheat originally evolved from Western and Central Asia. As a C₃ plant and originated from xeric environment, cultivated wheat generally responds to increased [CO₂] more on optimal moisture conditions than under water stresses (Kramer, 1981; Kimball, 1983; Poorter, 1998; Wu and Wang, 2000), because of its high CO₂ saturation point and relatively low water use efficiency compared with C₄ species. However, the cultivar that we used in the experiment reported here is drought-resistant, and, therefore, still showed some positive responses to elevated [CO₂] under low soil moisture in our study.

5. Conclusion

1. High [CO₂] is beneficial to wheat growth, yield and WUE. This is consistent with many other studies reported in the literature.
2. CO₂ enrichment enhanced wheat grain yield mainly through increasing the grain number, and, consequently, the harvest index.
3. Morphologically, high [CO₂] enhanced the lateral growth of plants more than vertical growth.
4. Grain quality is likely to declined in a future, [CO₂]-rich world. This will aggravate the micronutrient malnutrition problem in the world. So, the effects of CO₂ enrichment on the elemental compositions of crops, especially on essential elements, should receive more attention. However, there has been a great dearth of literature on this aspect.
5. The effects of CO₂ enrichment on plants depend on soil water availability, and plants may benefit more from CO₂ enrichment when sufficient water is supplied.

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506
