Effects of CO2 Increase on Wheat Growth and Yield under Different Atmospheric Pressures and Their Interaction with Temperature

Shigeto Fujimura1, Peili Shi2, Kazuto Iwama3, Xianzhou Zhang2, Jai Gopal4 and Yutaka Jitsuyama3

1Fukushima Agricultural Technology Centre, Koriyama 963-0531, Japan; 2Institute of Geography Science and Natural Resources, Chinese Academy of Sciences, Beijing 100101, P. R. China; 3Division of Bioresources and Product Science, Hokkaido Univ., Sapporo 060-8589, Japan; 4Division of Crop Improvement, Central Potato Research Institute, Shimla, 171001, India

Abstract: To determine the effects of CO2 under different atmospheric pressures, we assessed the effects of elevated CO2 on the growth of spring wheat (Triticum aestivum L.) in a field experiment in Lhasa (3688 m above sea level), the Tibet Plateau, China, and in a growth chamber (GC) experiment in Sapporo (15 m above sea level), Japan. Open-top chambers (OTCs) were installed at Lhasa and spring wheat was grown under CO2 at a partial pressure of 23.4 Pa (ambient CO2) and 38.5 Pa (elevated CO2, equivalent to a 200 µmol mol-1 increase). In the OTC experiments, CO2 was elevated with gas-firing equipment and a blower, so that the air temperature inside the OTC for elevated CO2 was raised 0.8ºC. In the GC experiment in Sapporo, we used three CO2 partial pressure levels; 24.8, 39.8 and 59.3 Pa and two air temperature regimes, 11/19ºC and 11/21ºC (night/day). In the OTC experiment, dry weight at harvest was lower in the elevated CO2 than in the ambient CO2. In the GC experiment, the effect of the elevation of CO2 from 24.8 to 39.8 Pa on biomass was greater than that from 39.8 to 59.3 Pa. A 2ºC increase in temperature reduced dry weight at all CO2 levels and offset the positive effect of CO2 increase from 39.8 to 59.3 Pa. The difference between the results obtained in the experiments in OTC and GC was not clear and might have involved artifacts such as blower and/or ethylene effects.

Key words: Dry matter production, High altitude, Low partial pressure of CO2, Temperature, Triticum aestivum L., Yield.

Atmospheric CO2 levels are predicted to rise from the current 380 µmol mol-1 (38.5 Pa in partial pressure at sea level) to 460–560 µmol mol-1 (46.5–56.7 Pa at sea level) by year 2050, with an increase in average air temperature (IPCC, 2007). The predicted multi-model ensemble mean temperature rise from 2046 to 2065 is 1.65, 1.75 and 1.29ºC for IPCC Special Report on Emission Scenarios A2, A1B and B1, respectively (IPCC, 2007). Global warming could adversely affect the present conditions for cereal production in the world. Wheat yield has been predicted to decrease approximately 3–4% for each 1ºC rise in temperature above 15ºC during the grain filling period (Wardlaw and Wrigley, 1994), because high temperatures generally reduce the growth duration by accelerating phenological development (Marcellos and Single, 1972; Butterfield and Morison, 1992; Asseng et al., 2004), enhancing respiration rate (Wardlaw et al., 1980), and consequently reducing dry matter production (Monteith, 1981; Batts et al., 1998; Asseng et al., 2004). On the other hand, the increase in CO2 level is predicted to increase crop production and modify the adverse effect of global warming. Field experiments have demonstrated that an increase in CO2 from 350–380 to 680–700 µmol mol-1 increased net photosynthetic rate (Pn) by 30–50%, resulting in a 15–30% increase in total dry matter production and grain yield in spring wheat (Mulholland et al., 1997, 1998; van Oijen et al., 1999). Thus, the combined effects of CO2 increase and global warming on cereal growth and yield are significant for world food production. Batts et al. (1998) cultivated winter wheat in a temperature gradient tunnel and analyzed the combined effect of CO2 elevation and temperature increase. They concluded that the 2.6ºC
increase in mean seasonal temperature nullified the beneficial effect of a 340 µmol mol⁻¹ increase in CO₂. Amthor (2001) reviewed the combined effect of CO₂ elevation and temperature increase on wheat, and concluded that the combined effect of an increase in CO₂ by 300–350 µmol mol⁻¹ and temperature increase of 1–4ºC adversely affected yield.

Since the solubility of CO₂ in a liquid is proportional to its partial pressure above the liquid (Henry’s law), the photosynthetic rate as well as the concentration of CO₂ in chloroplasts depends on the partial pressure of CO₂. The partial pressure of CO₂ at high altitudes is lower than that at low altitudes. For example, at 0 m and 4000 m above sea level, the air pressure is 1013 hPa and 617 hPa respectively (National Astronomical Observatory, 2004), and the partial pressure of CO₂ is about 38.5 Pa and 23.4 Pa, respectively. Since the response to the increase in partial pressure of CO₂ is greater at a lower partial pressure of CO₂ in photosynthetic rate (Farquhar et al. 1980) and grain yield (Amthor, 2001), the effect of elevated CO₂ on cereal production may be greater at a higher altitude. If so, the combined effect of elevated CO₂ and global warming would be greater at a higher altitude. On the other hand, the increase in partial pressure of CO₂ is smaller at a higher altitude for a given increase in mole fraction (in moles CO₂ per mole), because air pressure is lower at a higher altitude. When the CO₂ concentration is elevated from 380 µmol mol⁻¹ to 600 µmol mol⁻¹, the partial pressure of CO₂ increases by 22.3 Pa and 13.6 Pa at 0 m and 4000 m above sea level, respectively. Therefore, the effect of CO₂ increase on cereal production would be smaller at a higher altitude.

To resolve this controversy on the effect of increasing CO₂ concentration with the altitude, in this study, we examined the effects of an elevated CO₂ level on cereal production under different atmospheric pressure conditions. To predict the effect of an elevated CO₂ level at a high altitude on spring wheat growth and yield, we constructed open-top chambers (OTCs) in Lhasa (3688 m above sea level), which is the capital of Tibet Province on the Tibet Plateau and is one of the highest regions in the world where crop cultivation is practiced. An additional experiment using growth chambers was carried out in Sapporo (15 m above sea level), Japan, to further analyze the results obtained in Lhasa. Since the temperature in plots under elevated levels of CO₂ was increased by the blower in the OTC experiment, the combined effect of CO₂ elevation and temperature increase at subambient CO₂ partial pressure was also examined.

### Materials and Methods

The spring wheat cultivar 3u90, widely cultivated in Lhasa, was used in the OTC experiment in Lhasa and in the growth chamber experiment in Sapporo. The OTC experiment was carried out at the Lhasa Plateau Ecological Research Station (29° N, 91° E, 3688 m above sea level) of the Chinese Academy of Sciences, China, in 2001. Twelve OTCs (each 3×3 m, 2 m height; consisting of aluminum frames and polyethylene wall) were used for the two treatments, i.e., six OTCs with ambient levels of CO₂ (ambient CO₂) and six replicate OTCs with increased levels of CO₂ (elevated CO₂). Inside each OTC, we planted wheat in a 2×2 m area, 0.5 m apart from the chamber side. The treatments were arranged in a randomized block design with six replications. CO₂ for the elevated levels was supplied with a liquefied petroleum gas-firing equipment (CG-253S2G, Nepon, Japan) and was injected into a blower that supplied 1800 m³ hr⁻¹ air (approximately 2500 µmol CO₂ mol⁻¹) through plastic pipes placed about 15 cm above the canopy. The CO₂ level was increased from 16 days after sowing (DAS) (19 May 2001) for 13 hr per day (0500–1800 solar time) until the day before the final harvest (2 October 2001). Long-term gas detector tubes (GASTEC, Japan) did not detect carbon monoxide (measuring range 0.4–400 µmol mol⁻¹), nitrogen dioxide (0.1–30 µmol mol⁻¹) and sulfur dioxide (0.2–100 µmol mol⁻¹) in the air directly from the gas-firing equipment. Hydrocarbons, including ethylene, were not measured. The average temperature outside of OTGs during the crop period (May to September) was 14.1ºC and the monthly average temperature ranged from 11.7 (May) to 15.4ºC (July) (Table 1). The monthly precipitation was high in June and July, and was low in May and September. Total precipitation during the cropping period was 490 mm. For measurement of CO₂ concentration, air temperature and relative humidity, air was pumped into a portable open gas-exchange system (LI-6400, LI-COR, USA) from the center of the plot using a polyethylene tube (around 3 m long, 1/4 inch diameter) and the average values for ten minutes were logged. Measurements were conducted on seven days during growth in 2–3 plots for each treatment. The mean CO₂ partial pressure measured from 0800 to 1600 averaged over seven days was 24.1±0.6 Pa (means±SD, n=7) (374 µmol mol⁻¹ in mole fraction), 24.4±0.8 Pa (378 µmol mol⁻¹) and 37.2±4.1 Pa (576 µmol mol⁻¹) outside of OTCs, in ambient and in elevated CO₂, respectively. The air

| Month | Minimum | Maximum | Average | Precipitation (mm) |
|-------|---------|---------|---------|-------------------|
| May   | 18.5    | 5.0     | 11.7    | 34                |
| June  | 20.2    | 7.7     | 14.0    | 169               |
| July  | 21.6    | 9.2     | 15.4    | 131               |
| August| 20.8    | 9.5     | 15.2    | 103               |
| September | 20.4 | 7.7     | 14.0    | 53                |
| Average/Total | 20.3 | 7.8 | 14.1 | 490 |

---

**Table 1.** Air temperature and precipitation measured out of open-top chambers during the crop period in the OTC experiment.
temperature was highest in elevated CO₂ (25.1 ± 4.2°C), followed by ambient CO₂ (24.3 ± 3.7°C) and outside of OTCs (24.0 ± 3.0°C). The relative humidity was almost the same outside of OTCs, in ambient CO₂ and in elevated CO₂ (35.1 ± 12.4%, 36.0 ± 11.9%, and 34.2 ± 12.4%, respectively). Seeds were sown on 3 May 2001 at a rate of 550 seeds per m². As practiced by local farmers, nitrogen (N), phosphorus (P) and potassium (K) were applied at 40.0, 7.9 and 9.1 g m⁻², respectively, at sowing, and at 35.0, 2.6 and 3.3 g m⁻², respectively, at heading. Sheep manure was also applied at 1 kg m⁻² at sowing. The crop was irrigated when needed.

The growth chamber experiment was conducted in a glasshouse at the Field Science Center for Northern Biosphere of Hokkaido University, Sapporo (15 m above sea level). Nine seeds were sown per pot (16 cm diameter, 20 cm height) and the plants were thinned to three plants per pot when the second leaf emerged. The pots were transferred to the growth-chambers (1.2 m wide, 0.8 m depth, 1.8 m height; KG50-HLA, Koito, Japan) at 10 DAS. Pots were filled with Andosol soil, which was mixed with 0.50 g of N, 0.26 g of P and 0.42 g of K per pot at sowing. A dose of 0.36 g N, 0.16 g P and 0.30 g K per pot was applied at 32 DAS and a dose of 0.18 g N was applied at 83 DAS. The chamber was illuminated by using white fluorescent tubes for 13 hr a day. The photosynthetic photon flux density (PPFD) at the canopy level was about 500 µmol m⁻² s⁻¹ and the relative humidity in the chambers was about 80%. Gaseous CO₂ (purity 99.5%) was injected into the chambers to control the CO₂ concentration. To keep the CO₂ concentration below the ambient level, ambient air was injected after trapping CO₂ with soda lime. The following treatments were applied in factorial combinations after transferring the plants to the growth chambers without chamber replication. Data were analyzed as two-way factorial ANOVA without replication. (i) Three partial pressure levels of CO₂ (during day): 24.8, 39.8 and 59.3 Pa, about 250, 400 and 600 µmol mol⁻¹, respectively, were examined in Sapporo to represent the current, high and very high partial pressure levels of CO₂, respectively, in Lhasa. (ii) Two temperature regimes 11/19°C and 11/21°C (night/day maximum and minimum temperature cycle) at each partial pressure of CO₂ were examined: First, 24.8 and 39.8 µmol mol⁻¹ CO₂ at 11/19°C, second, 24.8 and 39.8 µmol mol⁻¹ at 11/21°C, and third at 600 µmol mol⁻¹ CO₂ at 11/19°C and 11/21°C.

Heading stage, dry matter production and chlorophyll content (SPAD value) were determined. Grain yield, yield components and Pₚ were also determined in the OTC experiment. Heading was assigned to a date when 70% of stems had headed. In the OTC experiment, the number of headed stems in 0.125 m² was counted once every two days, and each count was replicated three times. The total aboveground dry weight was recorded on 85 DAS (i.e., at the heading stage) and 153 DAS (i.e., at the final harvest) for 0.33 and 1 m², respectively. At final harvest, grain yield and yield component were also determined. In the growth chamber experiment, the total aboveground dry weight was determined at 83 DAS (i.e. at about the heading stage) and 128 DAS (i.e., when most of the leaves had turned yellow). Pₚ was measured at PPFD of 1600 µmol m⁻² s⁻¹ for flag leaf after heading by using the LI-6400 in the OTC experiment. Two leaves each were measured in three plots per treatment. Measurements were conducted under each growth CO₂ concentration. The leaf temperature and relative humidity was controlled at 25°C (actual value achieved was 24.7–25.2°C) and 50–60% (actual value achieved was 33–59%), respectively. SPAD value was measured after heading on upper three leaves by using SPAD-502 (Konica Minolta Sensing, Japan) in both the OTC and growth chamber experiments. Measurements were conducted for 4–8 plants in three plots per treatment in the OTC experiment and for one plant in each pot in the growth chamber experiment.

Results

1. Open-top chamber experiment in Lhasa

The effect of the treatment on phenological development was not detected in the OTC experiment (at 74.7 DAS in elevated CO₂ and 78.3 DAS in Ambient, P = 0.33). Pₚ was significantly higher in elevated CO₂ than in ambient CO₂ at 90 DAS i.e. about 10 days after heading (Fig. 1a). After that, Pₚ decreased in elevated CO₂ to the level in ambient CO₂ at 103 DAS and remained at this level until harvest.
The effects of treatment on the SPAD value of flag, upper second and third leaves were similar; hence the results of only the flag leaf are presented here (Fig. 1b). SPAD values of flag leaves were similar in both treatments up to 117 DAS, and started to decline around 117–124 DAS in both treatments. The SPAD value in elevated CO₂ was significantly lower than that in ambient CO₂ at 130 DAS. Although the interaction effect of treatment × stage was not significant (P=0.43), plants in elevated CO₂ tended to have lower SPAD values than those in ambient CO₂ at 130-144 DAS.

Total dry weight was unaffected by treatment at 85 DAS but it was significantly lower in the elevated CO₂ than in ambient CO₂ at 153 DAS (Table 2). Although there was no significant effect, grain yield was lower in elevated CO₂ than in ambient CO₂ (Table 3). Grain number per spike, grain number per area and thousand grain weight were also lower in elevated CO₂ than in ambient CO₂. Spike number per area and harvest index were similar in both treatments.

2. Growth chamber experiment in Sapporo

CO₂ effect on phenological development was not detected in the growth chamber experiment (P=0.39). Days from sowing to heading was 79.5, 78.6 and 75.4 in CO₂ levels of 24.8, 39.8 and 59.3 Pa, respectively. Days to heading in the growth chamber experiment were almost the same as that in the OTC experiment. The effects of the treatments on SPAD value after heading were similar in flag, upper second and third leaves; hence the results of only flag leaf are presented (Fig. 2a). SPAD values of flag leaves were similar at all CO₂ levels at 86 DAS. It started to decline around 93-100 DAS at all CO₂ levels, but SPAD value decreased more at higher CO₂ levels. Total dry weight at 83 and 128 DAS was increased by CO₂ elevation (Table 4). It was the highest at 59.3 Pa followed by 39.8 and 24.8 Pa, in this order.

The effect of temperature on phenological development
was not detected in the growth chamber experiment (P=0.37). Days from sowing to heading were 79.0 and 76.7 in 11/19ºC and 11/21ºC temperature regime, respectively. High temperature adversely affected wheat dry matter production. The SPAD value was similar in both temperature regimes around heading (Fig. 2b). SPAD value tended to be lower in the high temperature regime than in the low temperature regime after 123 DAS but the differences were not significant. There was no significant temperature effect on total dry weight at 83 DAS while total dry weight at 128 DAS was significantly decreased by the high temperature.

To analyze the combined effect of CO₂ and temperature on dry matter production, we plotted total dry weights at 128 DAS against the partial pressure of CO₂ (Fig. 3). The effect of temperature on total dry weight was similar within the range of CO₂ partial pressure tested in the growth chamber experiment. The effect of a given increase in CO₂ partial pressure was greater at a lower CO₂ partial pressure than at a higher CO₂ partial pressure.

### Discussion

We investigated the effects of CO₂ increase on spring wheat growth under low air pressure conditions in Lhasa. To further analyze the results obtained in Lhasa, we examined the effects of CO₂ level and temperature regime in the growth chamber in Sapporo. Since pots were used for the cultivation in the growth chamber experiment, there was a possibility that root restrictions caused acclimation of photosynthesis to CO₂ elevation and decrease the stimulation of dry matter production. Pₙ measured before heading and previously reported by Fujimura et al. (2010) was significantly increased by CO₂ elevation. Pₙ before heading in 59.3 Pa stimulated by 39% compared with that in 39.8 Pa (Fujimura et al., 2010). In free-air CO₂ enrichment and OTC experiments, the Pₙ was enhanced by 30−50% with the increase in CO₂ from the current level to 550−700 μmol mol⁻¹ (Kimball et al. 2002; van Oijen et al., 1999; Mulholland et al., 1997). In the growth chamber experiment in this study, total dry weight at 128 DAS was significantly increased by CO₂ elevation. The percentage of total dry weight at 128 DAS at 24.8 Pa and 59.3 Pa, CO₂ was 74% and 120%, respectively. Amthor (2001) reviewed the effects of CO₂ increase on wheat yield. The relative value of grain yield at 250 and 580 μmol mol⁻¹ CO₂ relative to that at 350 μmol mol⁻¹ CO₂ was about 0.7 and 1.2, respectively, which is consistent with our results. The stimulations of Pₙ and total dry weight in this study were consistent with the previous studies, suggesting that root restrictions due to pot cultivation were not too much of a problem.

In the growth chamber experiment, wheat plants were grown at three CO₂ levels (24.8, 39.8 and 59.3 Pa) and two temperature regimes (11/19ºC and 11/21ºC). CO₂ at a partial pressure of 24.8 and 39.8 Pa is equivalent to current levels of CO₂ at 4000 m above sea level and 0 m above sea level, respectively, and that at 39.8 and 59.3 Pa is equivalent to 200 μmol mol⁻¹ CO₂ at an altitude of 4000 m and at 0 m, respectively. When the partial pressure of CO₂ was increased from 24.8 Pa to 39.8 Pa and from 39.8 Pa to 59.3 Pa, the total dry weight at 128 DAS was increased by 24.7 g per pot (38% of total dry weight at 24.8 Pa) and 18.1 g per pot (20% of total dry weight at 39.8 Pa), respectively. These results suggested that the effect of elevated CO₂ on dry matter production was greater at an altitude of 4000 m than at 0 m. Mayeux et al. (1997) cultivated wheat in soil containers located across a subambient CO₂ gradient chamber. Total dry weight was

---

**Table 4. Effects of treatments on total dry weight at 83 and 128 days after sowing in the growth chamber experiment.**

| Treatment | CO₂ Levels | Total dry weight (g per pot) |
|-----------|------------|-------------------------------|
| 83 DAS    | 128 DAS    |                               |
| CO₂       |            |                               |
| 24.8 Pa   | 29.6 (77) b| 64.9 (72) c                   |
| 39.8 Pa   | 38.5 (100) ab| 89.6 (100) b                   |
| 59.3 Pa   | 47.8 (124) a| 107.7 (120) a                  |
| Temperature | 11/19ºC | 40.2 (100) a                   |
|           | 11/21ºC | 37.1 (92) a                    |
| Statistical effect | CO₂ | *                                |
|           | Temperature | ns *                           |

Significance: * P<0.05; ns, no significant difference. Figures in parentheses indicate percentages to the value of 39.8 Pa CO₂ and in 11/19ºC treatments, respectively. Means with the same letters were not significantly different from each other at P<0.05 (Tukey HSD).
increased by 136–193% by the shift from 200 to 350 μmol mol⁻¹. The stimulation of dry matter production by the elevated CO₂ under subambient CO₂ was much less in the present study. Mayeux et al. (1997) did not examine the effects of a CO₂ increase above ambient CO₂ levels.

We analyzed the combined effect of CO₂ elevation and temperature increase on dry matter production in spring wheat. The effect of a 2°C increase in daytime temperature on total dry weight at 128 DAS was similar within the range of partial pressure of CO₂ tested in the growth chamber experiment, suggesting that the effect of temperature increase was independent of the partial pressure of CO₂. Therefore, there was a more negative combined effect of CO₂ elevation and temperature increase at a higher partial pressure of CO₂. The combined effect of a 200 μmol mol⁻¹ increase in CO₂ concentration and 2°C increase in daytime air temperature increased dry matter production under the CO₂ partial pressure of CO₂ at 4000 m above sea level, i.e., the dry matter production was higher with CO₂ at 34.9 Pa at 11/21°C than that at 24.8 Pa at 11/19°C. On the other hand, the combined effect did not increase dry matter production at 0 m above sea level, i.e., the dry matter production with 34.9 Pa CO₂ at 11/19°C was similar to that with 59.3 Pa at 11/21°C. Batts et al. (1998) concluded that the increase in mean seasonal temperature of up to 2.6°C nullified the beneficial effect of CO₂ increase by 340 μmol mol⁻¹. Amthor (2001) reported that the combined effect of CO₂ elevation by 300–350 μmol mol⁻¹ and temperature increase by 1–4°C adversely affected the yield. We found a more negative combined effect of CO₂ elevation and temperature increase than that reported by Batts et al. (1998) and Amthor (2001).

A 2°C increase in daytime temperature decreased total dry weight at 128 DAS in the growth chamber experiment. High temperatures generally reduce the growth duration by accelerating phenological development (Marcellos and Single, 1972; Butterfield and Morison, 1992; Asseng et al., 2004), enhance respiration rate (Wardlaw et al., 1980), and consequently reduce dry matter production (Monteith, 1981; Batts et al., 1998; Asseng et al., 2004). The reason for the decrease in dry matter production by temperature increase was not clear in the growth chamber experiment. The SPAD value was similar in both temperature regimes except at 123 DAS and 128 DAS, and the difference was not significant during measurements. The SPAD value suggested that growth duration was not reduced by a high temperature. On the other hand, the dry weight suggested that the crop growth rate was lower at 11/21°C than at 11/19°C during the later phase of growth. The dry weight was similar at 83 DAS in both temperature regimes while it was significantly lower at 11/21°C than at 11/19°C at 128 DAS. Although Pₐ before heading measured and previously reported by Fujimura et al. (2010) was significantly lower at 11/21°C (24.5 μmol m⁻² s⁻¹) than at 11/19°C (26.3 μmol m⁻² s⁻¹), it was not clear whether the respiration rate was responsible for the difference in Pₐ between temperature regimes or not.

The results obtained on dry matter production in the OTC experiment were not consistent with those obtained in the growth chamber experiment. In the OTC experiment, Pₐ before heading was 47% higher in elevated CO₂ than in ambient CO₂ (Fujimura et al., 2010) and it was significantly higher in elevated CO₂ than in ambient CO₂ at about 10 days after heading. However, the elevated CO₂ neither improved total dry weight nor grain yield at final harvest. Total dry weight in the OTC experiment was significantly lighter in elevated CO₂ than in ambient CO₂ at 153 DAS. One possible reason leading to lower dry matter production in elevated CO₂ was the acceleration of leaf senescence indicated by a lower SPAD value after 130 DAS. However, a lower SPAD value at the end of growth at a higher CO₂ level was also observed in the growth chamber experiment. Another possible reason was that the temperature in the elevated CO₂ plot was 0.8°C higher than that in the ambient CO₂ plot. However, the results of the growth chamber experiment indicated that the combined effect of a 200 μmol mol⁻¹ increase in CO₂ concentration and 2°C increase in daytime temperature at an altitude of 4000 m caused an increase in dry matter production. In the OTC experiment, the liquefied petroleum gas-firing equipment was used to supply CO₂, but hydrocarbons, including ethylene, were not measured. Ethylene is a gaseous plant hormone, and improperly adjusted or uncleaned heating units, leaky gas lines and exhausts from combustion engines were the major nonliving sources of ethylene (Gibson et al. 2000). The growth of tomato, rice, mung bean and phalaris was reduced by ethylene in the range of 20 to 60 nmol mol⁻¹. Wheat and rice exposed to ethylene at higher than 50 nmol mol⁻¹ became sterile and had lower yield (Klassen and Bugbee, 2002). Sterility due to the elevated CO₂ might not occur because the harvest index was similar in the elevated CO₂ and ambient CO₂ plots. However, the adverse effect of ethylene on growth, including dry matter production, could not be denied.

Air temperature during the daytime was 0.8°C higher in the elevated CO₂ chamber compared with the ambient CO₂ chamber due to the warm air from the gas-firing equipment and possibly due to the blower effect and elevated CO₂ level. Pinter et al. (2000) analyzed the blower effect on wheat development in free-air CO₂ enrichment (FACE). The results indicated that plots with blowers were warmer at night than plots without blowers, suggesting that the blowers disrupted air near the ground entraining warmer air from above. In the OTC experiment, air was supplied to the elevated CO₂ chamber by the blower during the daytime, thus air near the ground was disrupted only during the daytime. Therefore, the blower effect on air temperature in the elevated CO₂ plots would be...
smaller than that in the experiments in Pinter et al. (2000). Pinter et al. (2000) also analyzed the effect of stomatal closure due to elevated CO₂ on temperature. Foliage temperature in the elevated CO₂ plots with a blower was on the average 0.6°C warmer than that in the ambient CO₂ plots with a blower during the daytime, while the differences between these plots was small during the nighttime. Air temperature at 10 cm above the canopy during the daytime was also higher in the elevated CO₂ plots than in the ambient CO₂ plots although the difference was smaller than that in foliage temperature. These results suggested that the air temperature in the elevated CO₂ chamber was warmer than that in the ambient CO₂ chamber because of the warm air from the gas-firing equipment and the closure of stomata due to elevated CO₂.

The results of the growth chamber experiment in this study suggested that dry matter production was more enhanced by CO₂ elevation at a lower partial pressure of CO₂. Although no CO₂ effect on days from sowing to heading was detected, leaf senescence was accelerated at a higher CO₂ level in both the OTC experiment and the growth chamber experiment. The acceleration of leaf senescence did not nullify the beneficial effect of CO₂ elevation on dry matter production in the growth chamber experiment. On the other hand, dry matter production was lower in the elevated CO₂ than in ambient CO₂ in the OTC experiment. The reason for the decrease in dry matter production in the elevated CO₂ condition was not clear and might have involved artifacts such as blower and/or ethylene effects.

Acknowledgements

We thank Dr. Z. Zhong, Dr. J. Yamaguchi, Mr. T. Ebisawa, Dr. X. Wang, Dr. Y. Liu, Dr. K. Terauchi, Mr. Y. Izawa, Mr. H. Koike, Mr. S. Saitou and Dr. I. Terashima for discussion and assistance.

References

Amthor, J.S. 2001. Effects of atmospheric CO₂ concentration on wheat yield: review of results from experiments using various approaches to control CO₂ concentration. Field Crops Res. 73: 1-34.

Asseng, S., Jamieson, P.D., Kimball, B., Pinter, P., Snyre, K., Bowden, J.W. and Howden, S.M. 2004. Simulated wheat growth affected by rising temperature, increased water deficit and elevated atmospheric CO₂. Field Crops Res. 85: 85-102.

Batts, G.R., Ellis, R.H., Morison, J.I.L., Nkemka, P.N., Gregory, P.J., and Hadley, P. 1998. Yield and partitioning in crops of contrasting cultivars of winter wheat in response to CO₂ and temperature in field studies using temperature gradient tunnels. J. Agric. Sci. 130: 17-27.

Butterfield, R.E. and Morison, J.I.L. 1992. Modelling the impact of climatic warming on winter cereal development. Agric. For. Meteorol. 62: 241-261.

Farquhar, G.D., von Gaemmerer, S. and Berry, J.A. 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. Planta 149: 78-90.

Fujimura, S., Shi, P., Iwama, K., Zhang, X., Gopal, J. and Jitsuyama, Y. 2010. Effect of altitude on the response of net photosynthetic rate to carbon dioxide increase by spring wheat. Plant Prod. Sci. 13: 141-149.

Gibson, J.L., Whipker, B.E., Blankenship, S., Boyette, M., Cresswell, T., Miles, J. and Peet, M. 2000. Ethylene: sources, symptoms, and prevention for greenhouse crops. North Carolina State University, Horticulture Information Leaflet 530.

IPCC. 2007. Cambridge University Press, Cambridge and New York.

Klassen, S.P. and Bugbee, B. 2002. Sensitivity of wheat and rice to low levels of atmospheric ethylene. Crop Sci. 42: 746-753.

Kimball, B.A., Kobayashi, K., Bindi, M. 2002. Responses of agricultural crops to free-air CO₂ enrichment. Adv. Agram. 77: 293-306.

Marcellos, H. and Single, W.V. 1972. The influence of cultivar, temperature, and photoperiod on post-flowering development of wheat. Aust. J. Agric. Res. 23: 533-540.

Mayeux, H.S., Johnson, H.B., Polley, H.W., Malone, S.R. 1997. Yield of wheat across a subambient carbon dioxide gradient. Glob. Change Biol. 3: 269-278.

Monteith, J.L. 1981. Climate variation and the growth of crops. Quart. J. R. Met. Soc. 107: 749-774.

Mulholland, B.J., Craigon, J., Black, C.R., Colls, J.J., Atherton, J. and Landon, G. 1997. Impact of elevated atmospheric CO₂ and O₃ on gas exchange and chlorophyll content in spring wheat (Triticum aestivum L.). J. Exp. Bot. 48: 1853-1863.

Mulholland, B.J., Craigon, J., Black, C.R., Colls, J.J., Atherton, J. and Landon, G. 1998. Growth, light interception and yield responses of spring wheat (Triticum aestivum L.) grown under elevated CO₂ and O₃ in open-top chambers. Glob. Change Biol. 4: 121-130.

National Astronomical Observatory. 2004. Chronological Scientific Tables 2005. Maruken, Tokyo, Japan*

Pinter, P J Jr., Kimball, B.A., Wall, G.W., LaMorte, R L., Hunsaker, D J., Adamsen, F J., Frumau, K F A., Vugs, H F., Hendrey, G R., Lewin, K F., Nagy, J., Johnson, H B., Wechsung, F., Leavitt, S W., Thompson, T L., Matthias, A D. and Brooks, T J. 2000. Free-air CO₂ enrichment (FACE): blower effects on wheat canopy microclimate and plant development. Agric. For. Meteorol. 103: 319-333.

van Oijen, M., Schapendonk, A.H.C.M., Jansen, M.J.H., Pot, C.S. and Maciorowski, R. 1999. Do open-top chambers overestimate the effects of rising CO₂ on plants? An analysis using spring wheat. Glob. Change Biol. 5: 411-421.

Wardlaw, I.E., Sofield, L. and Cartwright, P.M. 1980. Factors limiting the rate of dry matter accumulation in the grain of wheat grown at high temperature. Aust. J. Plant Physiol. 7: 387-400.

Wardlaw, I.E. and Wrigley, C.W. 1994. Heat tolerance in temperate cereals an overview. Aust. J. Plant Physiol. 21: 695-703.

* In Japanese.