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Responses of soybeans and wheat to elevated CO₂ in free-air and open top chamber systems



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ABSTRACT

With increasing demand for agricultural products, more confidence is needed concerning impacts of rising atmospheric CO₂ on crop yields. Despite debate about the merits of free-air CO₂ enrichment (FACE) and open top chamber (OTC) systems, there have been no reports comparing crop yield responses to elevated CO2 in FACE and OTC systems using the same cultivar and location. In this study soybeans and winter wheat were grown for two years in FACE and OTC systems at the same time and location. An elevated CO_2 treatment of ambient plus $\sim 200 \,\mu \text{mol} \, \text{mol}^{-1}$ was applied 24 h per day for one cultivar of each species in the first year, and two cultivars of each species in the second year. Leaf area index, and midday leaf gas exchange rates were measured periodically, and total above ground biomass and seed yield were determined at maturity. In soybean, seed yield was increased by elevated CO2 in both FACE and OTC in both cultivars and years. However, the ratio of seed yield at elevated CO_2 to that at ambient CO_2 averaged significantly higher in OTC (1.49) than in FACE (1.27). In wheat, grain yield was increased by 15-30% by elevated CO₂ for both cultivars and years in the OTC, but was not increased in either cultivar or year in the FACE system. No differences in midday photosynthetic rates occurred between OTC and FACE in either species for either CO2 treatment, except one season in wheat, but stomatal conductance was more reduced by elevated CO₂ in OTC than in FACE. Short-term temporal variation in CO₂ concentration was larger in FACE than in OTC. It is not clear from these results which method produces plant responses equivalent to those which may occur with increased atmospheric CO2.

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1. Introduction

It is widely expected that there will be an increased world-wide demand for agricultural products in the coming decades because of increases in population and changes in food preferences (Gregory et al., 2005). Atmospheric carbon dioxide concentration continues to rise rapidly, and higher carbon dioxide concentrations could increase the yield of many food and forage crops, although changes in other climate factors may modify the effect (Hatfield et al., 2011). However, the amount of increase in crop yields to be expected from increased carbon dioxide alone remains a matter of debate, in part because of concerns regarding how elevated CO₂ treatments are applied experimentally.

Long et al. (2005) and Long et al. (2006) argued that crop yield increases at elevated carbon dioxide were smaller in free-air carbon dioxide enrichment (FACE) systems than in enclosure systems, such as open top chambers (OTC). However, most FACE experi-

ments increased the $[CO_2]$ to about 550 μ mol mol⁻¹, while most OTC experiments increased it to about $650-750 \,\mu\text{mol}\,\text{mol}^{-1}$ above ambient, making comparisons of plant response between FACE and OTC difficult (Bishop et al., 2014). A recent meta-analysis which restricted OTC data to experiments with about the same elevation of [CO₂] as FACE indicated smaller yield increases in FACE than in OTC systems in wheat (Wang and Feng, 2013). The same conclusion was reached for rice (Wang et al., 2015), but in rice, the average [CO₂] elevation was less in FACE than in OTC. Ziska and Bunce (2007) and Kimball (2011) both pointed out that given the large range of yield increases observed in both FACE and OTC systems, and the large known variation in response among cultivars within species, direct comparisons of FACE and OTC using the same cultivars at the same time and in the same location are needed to firmly conclude that FACE and OTC systems produce different plant responses to elevated CO₂. The only such direct comparison of FACE and OTC seems to be that of Kimball et al. (1997), with spring wheat grown in Arizona, although grain yield was not reported. This study presents additional direct comparisons of crop yield responses to elevated CO₂ in OTC and FACE, for soybeans and winter wheat grown to maturity for two years in Maryland, U.S.A.

Possible environmental differences between FACE and OTC systems are light, air temperature, humidity, wind speed, and the amount of fluctuation in $[CO_2]$ in the elevated CO_2 treatments. The magnitude of these environmental differences were assessed in this study.

2. Materials and methods

Soybeans (Glycine max L. Merr.) and winter wheat (Triticum aestivum L.) were grown for two years at the South Farm of the Beltsville Agricultural Research Center (39° 02′ N, 76° 94′ W, elevation 30 m), with both the FACE and OTC systems in the same field, with all plots within about a 100 m radius. The field site is on a nearly level flood plain with a uniform Codorus silt loam soil, a fine-loamy, mixed, mesic Fluvaquentic Dystrochrept. The site is surrounded by at least 500 m of field or forest in all directions, on a research farm surrounded by sub-urban development. In the first year, winter wheat cv. Pioneer 25 R40 (later referred to as "Pioneer") was grown from mid-October of 2012 to mid-June of 2013, and soybean cv. Spencer was grown from mid-June through mid-October 2013. In the second year winter wheat cultivars Pioneer 25 R40 and Choptank were grown from mid-October 2013 to mid-June of 2014, and the soybean cultivars Spencer and Holt were grown from mid-June to mid-October 2014. Plots were replanted within two days of harvesting of the prior crop.

In each experiment there were 3 replicate OTC and FACE plots per cultivar per CO_2 treatment. Each OTC covered 1.2 m \times 2.3 m of ground, with walls of clear acrylic sheets supported by wooden corner posts 8 cm in square cross section. Each chamber was planted with one cultivar. The row width was 30 cm for soybean and 20 cm for wheat, and there were 2 border rows and 2 interior rows for soybeans, and 2 border rows and 4 interior rows for wheat. Plant density was about $40 \,\mathrm{m}^{-2}$ for soybean and $120 \,\mathrm{m}^{-2}$ for wheat. The FACE plots were each 12 m² in area, equally split among three cultivars, and exterior border rows surrounded each FACE plot. The row spacing and plant density was the same in the FACE as in the OTC. All plant measurements were confined to plants in interior rows, and in the FACE plots, no measurements were made on plants less than 0.5 m from an outside edge. The FACE plots and the OTC were in the same positions throughout the experiment, but the CO₂ treatments were applied to plots in random positions. Plots were tilled to a depth of 20 cm with a rotary tiller just prior to planting. Wheat was fertilized in the spring with a 10-10-10 NPK fertilizer at a rate providing $25 \,\mathrm{g}\,\mathrm{N}\,\mathrm{m}^{-2}$. No fertilizer was applied to the soybean crop, because it fixes nitrogen. No pesticides were applied to the crops and no damage to the crops was apparent. Weeds were removed by hand. The plots were not irrigated, but frequent leaf gas exchange measurements indicated there was insufficient soil water stress to reduce leaf gas exchange, which is typical for this location and soil.

The elevated $[CO_2]$ treatment was applied continuously from planting, except for the winter wheat crop, where CO_2 application was stopped when either the air temperature or the soil temperature at 5 cm depth was below $0\,^{\circ}$ C. The OTCs had air blown continuously into perforated plastic pipes running the full length of the center of the bottom of each chamber. The flow rate of CO_2 into the elevated $[CO_2]$ treatment chambers was adjusted near midday every few days as necessary to maintain a $[CO_2]$ elevation of 190 μ mol mol $^{-1}$ above that of the ambient air. Air from all elevated and one ambient chamber was sampled every 45 min, using a WMA-4CO $_2$ analyzer (PP Systems, MA). The FACE plots used an area distributed free-air system (Bunce, 2015), with CO_2 emitters on a 1.2 m grid, and a target enrichment of 190 μ mol mol $^{-1}$ above the ambient $[CO_2]$ during the day and 220 μ mol mol $^{-1}$ at night,

which closely matched the [CO₂] enrichment achieved in the OTC (see Section 3). For the FACE plots, instantaneous and one minute averages of ambient and elevated [CO2] at canopy height near the center of the plots were recorded every minute. Spatial variation in [CO₂] within the FACE plots was not measured in this experiment, but has been shown to be quite small with this system (Bunce, 2011). Shaded air temperatures were measured near the center of one elevated and one ambient OTC, at canopy height. The specific chambers monitored were changed about monthly. Soil temperature at 5 cm depth was also measured in the same two chambers as air temperature. Photosynthetically active radiation (PAR) was recorded just above canopy height in one chamber. The chamber in which PAR was monitored was changed about monthly. Temperatures and PAR values were recorded every 5 min. Air and soil temperatures and PAR were also recorded at the same frequency in a standard meteorological station about 100 m from the OTC and FACE plots.

Leaf area index (LAI) in each plot was measured non-destructively on overcast days, using a Li-2200 Plant Canopy Analyzer (Li-Cor, Inc., Lincoln, Nebraska). All plots were measured on the same dates, using two above canopy and 4 below canopy measurements per plot, which were averaged to obtain one value of LAI per plot on each measurement date. LAI was measured 2 or 3 times per growing season for each crop, with one measurement date within a few days of first flowering in soybean and anthesis in wheat. The dates of anthesis in wheat and first open flower in soybean were recorded.

Mid-day leaf gas exchange rates were measured every 1-2 weeks on clear days during the spring (winter wheat) and summer (soybean) growing seasons. These measurements were made on fully expanded upper canopy leaves which were fully exposed to sunlight in situ. Leaf gas exchange was measured using a cuvette with a 2.5 cm diameter window, with either a CIRAS-1 or CIRAS-3 (PP Systems, Amesbury, MA) portable photosynthesis system. Leaves were measured in full sunlight, with the cuvette air temperature set to that of the outside air. The incoming airstream was partially dried such that the water content of air around the leaf inside the cuvette closely approximated that of the outside air. The [CO₂] external to the leaf in the cuvette was controlled to the nominal mid-day treatment concentration, either 380 or $570 \,\mu\text{mol}\,\text{mol}^{-1}$ by adjusting the supply [CO₂]. In wheat, at some stages of development, two leaves placed side-by-side were used to fill the cuvette window. Under these conditions, steady-state rates of gas exchange were achieved within about a minute of enclosing leaf material in the cuvette, which is before stomatal conductance could change in response to cuvette evaporative conditions. One measurement was made for each OTC and FACE plot for each cultivar on each measurement date. Linear regressions of midday stomatal conductance on the product of midday assimilation rate and fractional humidity divided by external [CO₂] (Ball et al., 1987) were developed for Pioneer wheat and Spencer sovbean, where two years of data were available. Regressions were also developed relating stomatal conductance to assimilation rate divided by the product of [CO₂] and the square root of leaf to air water vapor pressure difference (Medlyn et al., 2011). Slopes of these regressions are used as an index of stomatal sensitivity to environment, in this case to temperature and humidity.

At crop maturity, 4 m of interior row of soybeans, and 8 m of interior row of wheat were harvested from each OTC and FACE plot to determine the total above ground biomass and the seed biomass after drying to constant weight at 70 $^{\circ}$ C in a forced-air oven. In soybean, leaves and petioles had abscised before harvest and were not included in the harvested material.

Analysis of variance was used to test for effects of [CO₂] treatment, fumigation system, and their interaction separately for each cultivar each year for LAI and yield. The ratios of yield at elevated to

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