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Effects of CO$_2$ Enrichment on Biomass Yield and Response to Drought In Radish and Winter Wheat

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ABSTRACT
Atmospheric CO$_2$ levels have been increasing since the industrial revolution. There are many questions about the impacts of elevated CO$_2$ levels and how the subsequent rise in average global temperature will ultimately impact the planet. One change that many climate scientists are confident about is a global redistribution of precipitation. This study specifically addressed the coupled effects of elevated CO$_2$ and drought stress for two species, radish, *Raphanus sativus*, and winter wheat, *Triticum hybernum*. To understand how future climate changes might affect plants, radish and winter wheat were grown in simulated conditions of elevated CO$_2$ at 400 and 800 ppm. After reaching maturity, each species was subjected to water stress. The radish did not exhibit much of an increase in biomass in response to elevated CO$_2$. Both radish treatments exhibited an expected decrease in wet biomass in response to drought. In contrast, the winter wheat exhibited a decline in water content over the experimental period but dry biomass increased throughout the drought. The winter wheat results were consistent across both treatments.

INTRODUCTION
For much of the planet’s history, the concentration of carbon dioxide (CO$_2$) in the Earth’s atmosphere has been at about 285 µmol mol$^{-1}$ (parts per million; ppm) (Reddy et al., 2010). Since the industrial revolution, that number has climbed steadily until reaching its current level at roughly 385 µmol mol$^{-1}$. Because much of that CO$_2$ has anthropogenic origins (Mann & Kump, 2008), that number will continue to rise as developing countries continue to industrialize and burn increasing amounts of fossil fuels. Recent estimates even suggest that the concentration of atmospheric CO$_2$ is likely to reach 700-800 µmol mol$^{-1}$ by the end of this century (Usuda & Shimogawara, 1998; Usuda, 2006). While many questions still surround the issue of what impacts elevated CO$_2$ levels and how the subsequent rise in average global temperature will ultimately impact the planet, one change that many climate scientists are confident about is a global redistribution of precipitation (Solomon et al., 2008). With this shift in global water distribution, many regions that are now typically arid will likely receive much more precipitation. While those regions may see this increase in precipitation as a positive change, the implications of that shift are serious. If more water is precipitated in the desert or other arid regions, not only does it do little to aid local flora and fauna since most of it evaporates before becoming groundwater, less of it is being distributed to regions where livelihoods already depend on there being consistent, and largely unrestricted, access water for agriculture. One critical
issue that arises is how plants will respond to this change, especially those that are cultivated for food. Determining how plants will respond to increased CO2 coupled with changes in water availability is a critical research question.

In consideration of the projected rise in atmospheric CO2 and the resulting changes in global water distribution, the experiment was designed to address the question of how drought might affect the growth rate and biomass accumulation of plants subjected to conditions of elevated CO2 and increased drought frequency. One possible response to elevated concentrations of atmospheric CO2 is the “CO2 fertilization effect,” whereby plants undergo more active photosynthesis due to conditions that allow them to increase their intake of CO2. For many plant species, that enrichment of atmospheric CO2 causes a marked increase in growth rate and biomass accumulation (Usuda, 2006; Huang et al., 2007). Evidence also suggests that elevated levels of atmospheric CO2 may increase a plant’s water-use efficiency by reducing the rate of stomatal conductance, which indirectly limits water loss (Huang et al., 2007; Leakey et al., 2009; Morison, 1985). This begs the question of whether conditions of high levels of CO2, which have been documented to close stomata, might also provide better water use efficiency (WUE) due to fewer ports through which water can escape.

The objective of this study was to test how radish, Raphanus sativus, and winter wheat, Triticum hybernum, growing in an enriched CO2 environment, will respond under conditions of prolonged drought. The hypothesis was that the plants grown under elevated CO2 levels would undergo the CO2 fertilization effect; whereas the plants in the control group growing under ambient conditions would not. It was also hypothesized that additional biomass reserves would make plants grown under elevated CO2 better equipped to deal with drought, as evidenced by a larger biomass yield at the end of the experimental period (Usuda & Shimogawara, 1998).

MATERIALS AND METHODS
PLANTS AND EXPERIMENTAL CONDITIONS

Seeds of radish and winter wheat were planted and grown in Conviron growth chambers at DePaul University. Light was provided by a combination of incandescent and fluorescent bulbs, and each chamber was set for a photon irradiance (light intensity) of 600 µmol m⁻² s⁻¹ for a daily light cycle of 18 hours of light/6 hours of darkness. Both chambers were programmed to maintain a constant temperature of 25°C at approximately 60% relative humidity. For the control and experimental treatments, two different concentrations of atmospheric CO2 were employed. In the control, which will be called the ambient concentration (AC), the growth chamber was set to maintain a CO2 concentration of 400 µmol mol⁻¹, which serves as an analog for the actual current CO2 concentration of approximately 385 µmol mol⁻¹. The other growth chamber used in the experimental treatment conditions, which will be called the elevated concentration (EC), was set for a CO2 concentration of 800 µmol mol⁻¹—double what is present today—to reflect the level of atmospheric CO2 that climatologists expect will exist by the end of the century.

EXPERIMENTAL DESIGN

This experiment was conducted over the course of 103 days, from February 25, 2011 to June 7, 2011, and was divided into two main stages. At the beginning of the initial stage of germination and maturation that began on February 25, 96 winter wheat seeds and 96 radish seeds were planted in 1 pint planting cups approximately ½ inch below the surface of the soil. Half the pots were placed in each of the two growth chambers (control: n=48 radish, 48 winter wheat; experimental: n=48 radish, 48 winter wheat). During this initial period watering and monitoring of the digital readout of the conditions within each growth chamber were conducted daily. Weekly measurements of growth (height and number of leaves) and monitoring of the digital readout of the conditions within each growth chamber were conducted daily. Weekly measurements of growth (height and number of leaves) were also collected during this time. This initial period lasted for 41 days, and ended on April 6th. During the “growth analysis” stage, destructive harvesting was used to acquire the data on growth rate and biomass yield, began at 42 days.
For each harvest, a quarter of the specimens from each sample group were selected by random. Excess dirt from the roots was then removed and the mass of each individual plant was measured to determine its wet biomass. Samples were then placed in a drying oven set at approximately 105°C, left overnight to remove any moisture, and then massed to determine their dry biomass. This procedure was repeated at intervals of roughly three weeks (20-22 days) for three subsequent destructive harvests, which were completed on June 7, 2011.

GROWTH ANALYSIS
The growth analysis stage, (April 7th – June 7th, 2011), was divided into three, three-week-long harvest periods. At the conclusion of each of these harvest periods, plants were destructively sampled to compare biomass accumulation between the AC and EC samples. Though there are only three harvest periods, we conducted four destructive harvests in total. The first harvest on April 7, 2011, which was conducted prior to subjecting the plants to the drought stress treatment, was used to establish a baseline level of growth and biomass accumulation, which we used to evaluate the effects of the drought treatment applied to harvest 2, 3 and 4 (occurring on April 29th, May 19th and June 7th respectively). In these subsequent Harvests, both the control and experimental treatments were subjected to conditions of drought stress by reducing the frequency of their water allocation from once daily to once every two to three days (depending on how dry the soil was).

To accurately and effectively compare the data collected from each harvest period the average mass of the samples from the initial harvest (harvest 1) was determined. Because pots were used as experimental units, the value for average biomass per plant is replicated across pots. Upon the second harvest, the masses of the experimental units were divided by the average mass from Harvest 1, creating ratios of the averages of Harvest 2 to Harvest 1. The average of those ratios was then used to conduct the statistical tests and make graphs (Table 1). These steps are subsequently repeated for Harves 3 and 4.

After each sample from harvest 2 has been compared to the harvest 1 average to find its ratio, the average of all the harvest 2 ratios was then calculated. By determining these ratios the effects of confounding variables between harvests were eliminated (ex: plants grown under elevated CO2 were larger at the beginning of the drought than those grown under ambient conditions). Converting biomass data to ratios allowed comparisons to be made between data points of different harvests and treatment conditions. To determine whether biomass ratios were significantly different between the elevated and control treatments t-tests were used to compare the treatments.

RESULTS
Radish: Prior to drought stress, radish biomass increased under enhanced CO2 conditions. The dry weight of radish in the control treatment group averaged across all four harvests was 2.91 grams; ranging from 2.69 grams to 3.24 grams. The dry biomass of radish in the experimental treatment averaged across harvests is 5.62 grams, ranging from 5.03 grams to 6.57 grams (Figure 2). Upon inducing drought, both treatments exhibited an expected decrease in wet biomass. At harvest 1, the average wet biomass yield was 62.78 grams in the experimental treatment, and 28.83 grams in the control treatment (Figure 1). However, in the control treatment, the average amount of wet biomass at the time of harvest decreased by only 10.49 grams from harvest 1 to harvest 4; but, in the experimental treatment from harvest 1 to harvest 2 alone, the average wet biomass decreased by 9.56 grams, from 62.78 to 53.22 grams (which is nearly as much water as was lost over the course of the entire control treatment). From harvest 2 to harvest 3 in the experimental treatment, the average wet biomass decreased by an additional 22.64 grams, from 53.22 grams to 30.58 grams. By the final harvest, the average wet biomass of radishes in the experimental treatment had fallen 40.17 grams from harvest 1, settling at 22.61 grams (Figure 1).
Winter Wheat: For each destructive harvest from Harvest 1 to Harvest 4, the average mass of the wet weight for each destructive harvest decreased by a total of only 7.09 grams. After losing an average of 7.18 grams of water between harvest 1 and harvest 2, the rate of water loss plateaued, and even recovered slightly during harvests 2-4, in which we recorded three average wet biomass yields within ±1.0 gram of each other. Water loss was slightly more pronounced in the experimental treatment than in the control, but the difference was not statistically significant (See Table 1 for p-values). The experimental treatment also lost 7.09 grams of water between the harvest 1 and harvest 2, decreasing from an average of 56.33 grams at harvest 1 to 49.24 grams by harvest 2. During the remainder of the experimental treatment, the winter wheat only lost an additional 5.90 grams of water, decreasing the average wet biomass yield from 49.24 grams at harvest 2 to 43.34 grams by harvest 4 (Figure 3).

From harvest 1-4, the control treatment for the winter wheat actually increased in average dry biomass accumulation by 8.32 grams—from 3.50 grams at harvest 1 to 11.82 grams by harvest 4—even in spite of being stressed for water. This trend is further supported by the experimental treatment group, which also increased in dry biomass by a total of 19.30 grams—from 8.93 grams at harvest 1, to 28.23 grams by harvest 4 (Figure 4).

Ratios for dry biomass from harvest 2 were higher for the radish in the experimental treatment, but these differences were not statistically significant. The winter wheat dry biomass ratios were higher in the experimental treatment for harvest 3 and 4, but the differences were not statistically significant. The dry biomass ratio for the winter wheat in harvest 2, however, was higher in the experimental treatment and statistically significant (Table 1). All of these ratios refer to data collected after the drought treatment.

DISCUSSION

Both the radish and the winter wheat experimental treatment groups responded to the increased levels of CO2 with signs showing some degree of the CO2 fertilization effect. These effects include greater biomass accumulation resulting from more active photosynthesis due to increased CO2 uptake. However, the responses to increased CO2 varied greatly between the radish and the winter wheat. One main aspect of the CO2 fertilization effect is that elevated CO2 will induce an increased rate of growth and result in a greater biomass yield. This was the case for the radish: dry biomass was higher in the elevated treatment than in the control throughout the experiment (see Figure 2). Interestingly, the radish dry biomass was highest in harvest 2, then decreasing slightly and leveling off in subsequent harvests. This may have been due to down regulation, though this is unlikely during such a short experiment. Radish wet biomass, however, was the same in both control and experimental treatments by harvest 4, indicating that growth under elevated CO2 did not reduce water loss.

Winter wheat dry biomass was also higher in the experimental treatment throughout the experiment. However, wet biomass in the experimental treatment was also higher during all harvests, potentially indicating an ability to withstand drought conditions. From harvests 1 through 4, winter wheat's wet biomass decreased by only 7.09 grams in the control treatment and by 12.99 grams in the experimental treatment (Figure 3). In comparison, over the same period, the wet biomass of radish only decreased by 10.49 grams in the control treatment, but it fell by 40.17 grams in the experimental treatment. This illustrates not only how vulnerable the radish plant is to drought in conditions of increased CO2; it also shows how well equipped winter wheat is to deal with such conditions. Indeed, when biomass ratios were compared between radish and winter wheat grown at ambient CO2 concentrations, ratios were significantly higher in winter wheat at harvest 3 (p < 0.001) and 4 (p = 0.019). Winter wheat grown under elevated CO2 had higher dry biomass ratios than radish at harvest 2 (p < 0.001).
(p < 0.001) and 4 (p < 0.001). Not only was winter wheat much better at retaining water throughout the drought period, but also during that time it was able to increase its biomass in spite of being water stressed (Figure 4). These results indicating a positive response to the CO2 fertilization reflect those of previous studies (Usuda & Shimogawara, 1998; Usuda, 2006). The combination of being able to weather lengthy periods of drought conditions, while maintaining substantial growth rates, together make winter wheat an ideal crop that can be counted on to not only survive, but also thrive in a wide range of conditions.

Though the results were largely statistically insignificant, a greater understanding of the nature of these plants can still be gained from the findings. Some elements of the experimental design could be improved in future experiments. First, a reduction in the amount of sunlight provided is necessary, decreasing from 18 hours of sunlight to 14 hours of sunlight and 10 hours of darkness.

Also, the racks inside the growth chambers were set at different heights in relation to the light source, which was not realize until well into the experiment; so it is possible that proximity to the light may have impacted one group disproportionately. The drought treatment could have been executed more strictly as well. Although it was not our intent to prematurely kill the radishes, they were stressed to the point where some died off quickly as a result and many those that survived began putting all of their remaining energy into producing flowers and seeds in a final to reproduce before dying. In that instance, it would have been wise to have already tested radish on a smaller scale to determine a basic range of how much drought a radish can take before dying. Had that been done, and had we adhered to a stricter watering schedule, the water could have been dosed more accurately. Conversely, it is likely that the winter wheat was not subjected to a severe enough drought to negatively affect its biomass accumulation. Similar research with a longer drought period is a potential subject for future research.
FIGURE 3
Results from an experiment to compare biomass accumulation of winter wheat grown under ambient (400 ppm) and elevated (800 ppm) atmospheric CO2 then subjected to drought stress. Figure shows a slight decrease in wet biomass during the drought.

FIGURE 4
Results from an experiment to compare biomass accumulation of winter wheat grown under ambient (400 ppm) and elevated (800 ppm) atmospheric CO2 then subjected to drought stress. Figure shows an increase in dry biomass during the drought in both treatments.

FIGURE 5
Results from an experiment to compare biomass accumulation of winter wheat grown under elevated (800 ppm) atmospheric CO2 then subjected to drought stress. Figure shows a decline in water content but shows increasing dry biomass throughout the drought.

FIGURE 6
Results from an experiment to compare biomass accumulation of winter wheat grown under ambient (400 ppm) atmospheric CO2 then subjected to drought stress. Figure shows a decline in water content but shows increasing dry biomass throughout the drought.
### TABLE 1

Results from an experiment to compare biomass accumulation under drought stress of species grown under ambient (400 ppm) and elevated (800 ppm) atmospheric CO2. Biomass ratios were calculated by dividing biomass at a given harvest by pre-drought biomass. We then used t-tests to see whether ratios were significantly different between treatments. P-values are reported in the t-test column.

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WORKS CITED


