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Crop responses to elevated CO_2 and interactions with H_2O, N, and temperature[☆]

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About twenty-seven years ago, free-air CO_2 enrichment (FACE) technology was developed that enabled the air above open-field plots to be enriched with CO_2 for entire growing seasons. Since then, FACE experiments have been conducted on cotton, wheat, ryegrass, clover, potato, grape, rice, barley, sugar beet, soybean, cassava, rape, mustard, coffee (C_3 crops), and sorghum and maize (C_4 crops). Elevated CO_2 (550 ppm from an ambient concentration of about 353 ppm in 1990) decreased evapotranspiration about 10% on average and increased canopy temperatures about 0.7 °C. Biomass and yield were increased by FACE in all C_3 species, but not in C_4 species except when water was limiting. Yields of C_3 grain crops were increased on average about 19%.

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Introduction

Earth's atmospheric CO_2 concentration continues to rise, and reached a milestone of 400 parts per million by volume in 2014 (http://www.esrl.noaa.gov/gmd/ccgg/trends/). That elevated levels of CO_2 can increase plant growth has been known since 1890, when de Saussure [1] first demonstrated that peas exposed to high CO_2 concentrations grew better than control plants in ambient air. Since then, there have been numerous such observations from experiments in various types of chambers and greenhouses that were first assembled and analyzed by Kimball [2], who reported an average 33% increase in agricultural yield with CO_2 enrichment. However, the walls of chambers and greenhouses introduce changes in solar and thermal radiation, wind flow, air temperature and humidity, and other artefacts [3]. Concern that plants may not respond to increasing CO_2 in open field the same as they do in chambers led to the development of free-air CO_2 enrichment (FACE) technology in the late 1980s, with the first experiment with publishable biological results conducted in 1989 [4]. Since then, there have been many FACE experiments in several countries on several crops.

The results from the first decade of such FACE experiments were first summarized and analyzed by Kimball *et al.* [5]. Marking the completion of the ten-year Swiss FACE Project, a book with chapters from many authors was edited by Nösberger *et al.* [6], which presented results available from several FACE experiments from several location and featured knowledge learned about several processes such as photosynthesis and evapotranspiration Long *et al.* [7] did another, and Ainsworth and Long [8] completed yet another meta-analysis of FACE results at the fifteen-year mark Ainsworth and Rogers [9] did another that focused on photosynthesis and stomatal conductance, and Kimball [10] presented yet another in a book chapter at two decades since the introduction of FACE.

Some of these review or meta-analytic papers have focused on particular crops. Ainsworth [11] concentrated on rice and presented data from growth chambers, sunlit controlled-environment chambers, greenhouses, open-top chambers, and FACE. Yield responses to elevated CO_2 (500–599 ppm) from the FACE experiments were about 19%, which tended to be lower than those from the chamber studies. Similarly, Wang *et al.* [12] focused on wheat and found the average yield response to FACE was about 15%. This magnitude of wheat yield response tended to be lower than those from other methods but was statistically lower only to closed growth chambers.

Recently, Bishop *et al.* [13] examined whether the responses of crops to elevated CO_2 in open-top chambers and FACE varied with seasonal temperature and water inputs. Generally, seasonal temperature was not a good predictor of CO_2 biomass and yield responses, but as predicted, responses tended to be higher in dry conditions.

Since the two-decade review [10], more than 30 pertinent papers have been published with additional results from FACE experiments. Thus, marking twenty-seven years since the first FACE experiment, herein I assemble and analyze the evapotranspiration, canopy temperature,

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biomass, and agricultural yield, results that have been reported for many FACE experiments.

Methodology

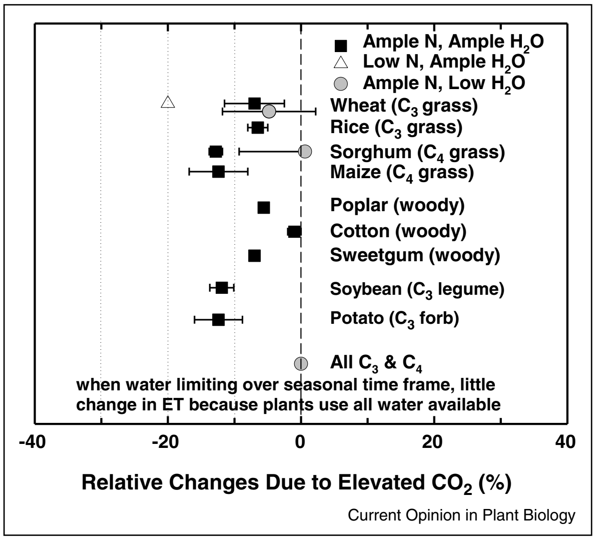
Following Kimball [2,10] and Kimball *et al.* [5], the absolute seasonal crop response values reported in the literature were extracted. Then I computed the relative increases (or decreases) due to the FACE treatments with respect to their corresponding control treatments at ambient CO_2. The various FACE experiments have not used the same target CO_2 concentration for their treatments, nor have prior reviews of the CO_2-response literature used a particular concentration for their analyses. Such lack of standardization makes it difficult to make comparisons across FACE sites and with other CO_2-enrichment-chamber type experiments. Therefore, all of the relative responses were linearly adjusted to correspond to 550 ppm (i.e. μmol mol^{-1}) or about 190 ppm above ambient (which was about 351 ppm in 1989 [14]). Such an adjustment is justified because to a first approximation growth responses by plants to elevated CO_2 are generally linear between 300 and 900 ppm [15]. The more recent FACE experiments have used target concentrations of 550 ppm or of 200 ppm above ambient, so no adjustments were made for these later FACE data. For each crop category, I then computed averages and standard errors using log-antilog transformations, which corrected for the log-normal distributions of such ratio data [2]. Each experiment was considered to be a single observation.

Results and discussion

Evapotranspiration

One commonly observed response to elevated CO_2 is partial stomatal closure with a concomitant reduction in stomatal conductance to water vapor [9]. Consequently, the rate of loss of water from the leaves or transpiration is slowed. Of course, solar radiation, wind speed, and air temperature and humidity are also important weather factors that determine rates of transpiration (T) as well as evaporation from the soil (E). Measurements of crop total transpiration plus evaporation from the soil, that is, evapotranspiration (ET), have been made in several FACE experiments (Figure 1).

Figure 1



Current Opinion in Plant Biology

Evapotranspiration (ET) responses to elevated CO_2 (+200 ppm from FACE) at ample and limited levels of soil water and nitrogen. The sources from which the data were obtained for each vegetation type are listed in Table S1.

At ample water and nitrogen, reductions in ET per unit of land area with elevated CO_2 have ranged from near zero for cotton to about 13% for sorghum (Figure 1). This large range of reductions in ET is due both to differing reductions in stomatal conductance among species and to differing increases in leaf area and in canopy temperature [16], as will be discussed in the next section. Cotton had a large growth response (Figure 3, and as will be discussed later) to elevated CO_2, and therefore it showed almost no reduction in ET under elevated CO_2. In contrast, sorghum and maize, both C_4 species, had little or no photosynthetic or growth responses to elevated CO_2, so they had large reductions in ET of about 13%. Wheat and rice were intermediate in both growth and ET responses. The two data points from mature poplar and sweetgum trees with less relative growth than annually-grown cotton show ET reductions of about 7%. The forb species, soybean and potato, had comparatively large reductions of about 12%.

When sorghum was grown under limited water supply, FACE had no effect on seasonal ET (Figure 1). This lack of season-long ET response to elevated CO_2 is because depletion of soil water caused stomata to close much of the time, and then elevated CO_2 had no effect [17]. The plants used all the water that was available to them. Thus, if water is limiting on a seasonal time scale, total seasonal ET will not be affected by elevated CO_2. However, growth will still be affected. Much of the interactive effects between elevated CO_2 and drought on growth and yield can be explained by how many extra days a crop grown at elevated CO_2 can sustain growth in a drought cycle due to water conservation from the reduced ET while water is adequate early in the cycle.

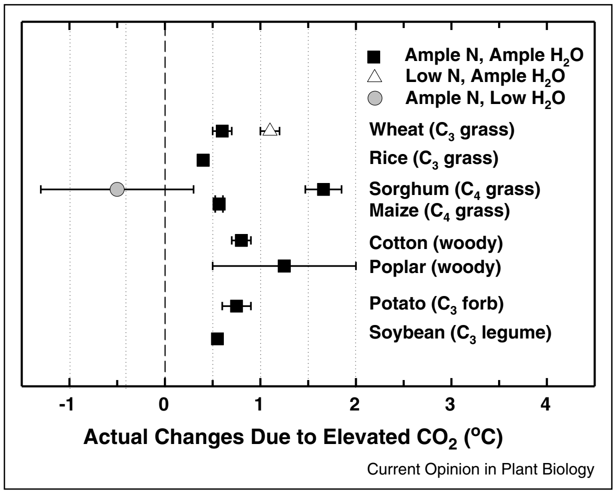
Ainsworth and Long [8] and Wall *et al.* [18] showed that when soil N was limiting, FACE caused larger reductions in stomatal conductance than under no stress conditions. Consistent with this fact, the ET of wheat grown under limited N was reduced by 20% due to FACE compared to only 6% under ample N (Figure 1). Such a larger reduction in stomatal conductance and ET due to elevated CO_2 at low N are consistent with the hypothesis that low soil N causes a reduction in rubisco (a leaf enzyme involved with photosynthesis containing N), which forces a greater reduction in stomatal conductance in order to maintain a constant ratio of internal leaf CO_2 concentration to that of outside air [18,19].

Canopy temperature

As discussed in the previous section, elevated CO_2 causes reductions in stomatal conductance [9] with consequent reductions in transpiration and evapotranspiration (Figure 1). Such reductions in transpiration result in reductions in its cooling effect on crop leaves, so crop canopy temperatures rise — about 0.4–1.7 °C at ample levels of nitrogen and water (Figure 2). When N was limited, wheat canopy temperatures rose more than at ample N: about 1.1 °C under FACE compared to 0.6 °C at ample N (Figure 2), consistent with a larger reduction in ET at elevated CO_2 (Figure 1). When water was limited, variability in sorghum canopy temperature was high, and the error bars include zero indicating no significant effect of elevated CO_2 (Figure 2), which is consistent with there being no effect of elevated CO_2 on ET when water is limited (Figure 1). One surprising feature of Figure 2 is large increase in canopy temperature of C_4 sorghum (1.7 °C), whereas C_4 maize only increased about 0.6 °C, which is about the average for all the C_3 crops (not counting poplar which has wide error bars).

These increases in canopy temperature due to the direct effects of elevated CO_2 on plants (Figure 2) are small compared to the diurnal and seasonal changes in temperature crops normally experience. On the other hand, they are in addition to the predicted increases for air temperatures globally in the future [14], for which crop growth models already predict significant yield reductions in the future (i.e. the recent paper by Asseng *et al.* [20••] suggests such a 0.6 °C increase in temperature would reduce wheat yields about 3.6%). Moreover, only a few of the plant growth models in use to date include an energy balance for the soil-plant system and thereby are able to compute such increases in crop canopy temperature and account for their consequences.

Figure 2



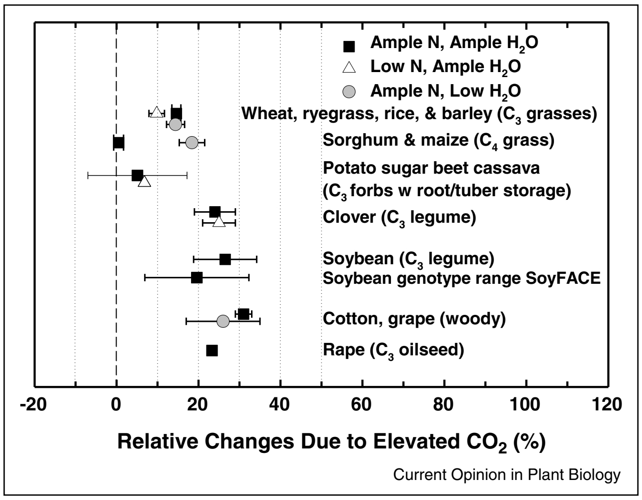
Crop canopy temperature responses to elevated CO_2 (+200 ppm from FACE) at ample and limited levels of soil water and nitrogen. The values are generally daytime values after canopy closure, so infrared thermometers viewed little soil. The sources from which the data were obtained for each vegetation type are listed in Table S1.

Shoot biomass

A fairly wide range of shoot biomass increases have been observed for various crops and ecosystems exposed to elevated CO_2 using FACE (Figure 3). C_3 grass crops (wheat, ryegrass, rice, and barley) had average increases of about 17% at ample N and H_2O, and largely due to the large number of data points (Table S1), the error bands are tight bestowing high confidence in this result. When water was limited, the increase was higher (23%), but under limited N, the increase was smaller (about 10%). However, in several of the low-N experiments, there was no prior 'N-removal' crop or other steps to assure low levels of N in the soil. Consequently, I believe the biomass response to elevated CO_2 at low N is actually lower than indicated by this data point, probably closer to 4%.

The C_4 grasses, sorghum and maize, had little or no shoot biomass response to elevated CO_2 at ample N and H_2O (Figure 3), consistent with the general lack of photosynthetic response for C_4 plants. However, when H_2O was limited, there was a substantial increase (about 18%) in biomass due to FACE. This large increase undoubtedly was due to the reduction in stomatal conductance and ET (Figure 1) following a rain or irrigation that enabled the plants to conserve water and continue growing longer into a drying cycle than control plants at ambient CO_2.

Figure 3



Shoot biomass responses to elevated CO_2 (+200 ppm from FACE) for various crops at ample and limited supplies of soil water and nitrogen. The sources from which the data were obtained for each vegetation type are listed in Table S1.

The root/tuber crops (potato, sugar beet, and cassava) exhibited a small average increase in shoot biomass (5%, Figure 3), but the error bars are wide. However, as will be presented in the next section, for these crops the yield comes from below ground, so a small shoot biomass response to elevated CO_2 is not necessarily a concern. For the case of low N, the average shoot biomass response was also small, about 6%, as expected.

Clover and soybean, both C_3 legumes, had larger increases in shoot biomass due to FACE (about 25%; Figure 3). Consistent with it being an N-fixing legume, clover showed no reduction in CO_2 response when soil N was limited.

The woody crops, cotton and grape, had comparatively large shoot biomass responses to FACE, about 31% at ample N and H_2O. When water was limited, the response tended to be slightly smaller, but not significantly so.

The single oilseed point (rape) shows a shoot biomass response of about 23%, which is similar to the legumes.

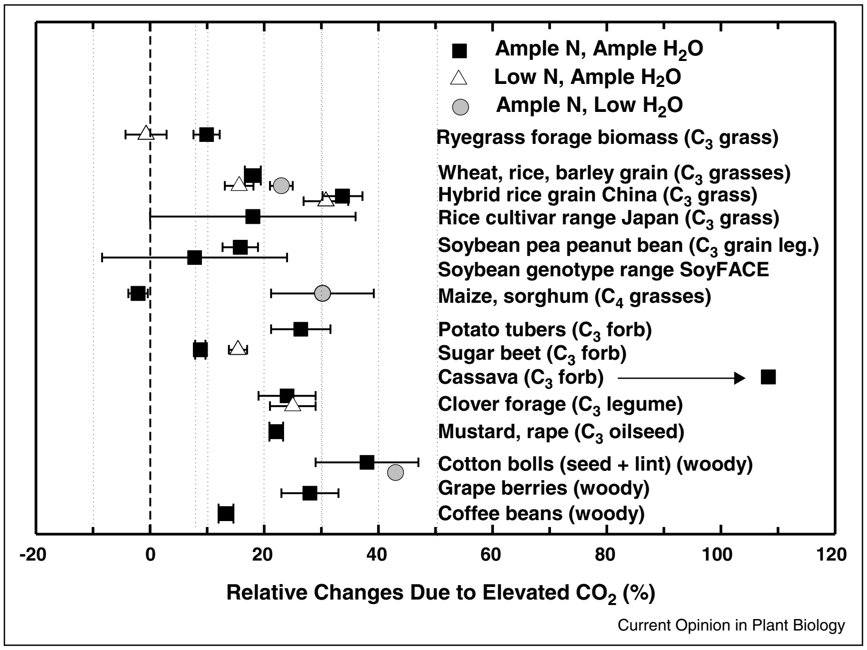
Agricultural yield

Most of the agricultural yield responses of several crops (Figure 4) to elevated CO_2 were similar to their shoot biomass responses (Figure 3), but several were different. For a forage crop like perennial ryegrass, the yield is the shoot biomass, and under ample N and H_2O, its average CO_2 stimulation (10%; Figure 4) was less than the average shoot biomass for the combined C_3 grasses (about 19%; Figure 3). Under limited N, the average ryegrass stimulation to elevated CO_2 was close to zero (Figure 4), whereas the average for the shoot biomass of C_3 grasses was about 10% (Figure 3). I think the smaller response to CO_2 under low N for the ryegrass is primarily because in most of the experiments with it, the ryegrass was grown year after year, whereas for only a few of the experiments with the other crops were there prior 'N removal' crops or other steps to assure that soil N levels were indeed low.

The average grain yield increase due to elevated CO_2 of C_3 grasses (wheat, rice, and barley) was about 19% under ample N and H_2O (Figure 4). Under limited N, it was slightly lower (16%). Again, however, in several of the low-N rice experiments, the 'low' level of N may not have been very limiting, so the true 'low' value may be lower yet. When H_2O was limited, the average yield response was slightly higher (about 22%). Although their season to season variability was high, Fitzgerald *et al.* [21••] recently reported wheat yield stimulations ranging from −17 to +79% under semi-arid conditions with and without supplemental irrigation.

However, the most exciting and important advances in regard to CO_2 enrichment are the large yield responses of hybrid rice (about 34%; Figure 4) reported from the Chinese FACE project [22–24]. These results are plotted separately in Figure 4, as well as being included in the C_3 grass averages. The hybrid varieties exhibited large yields

Figure 4



Agricultural yield responses to elevated CO_2 (+200 ppm from FACE) for various crops at ample and limited supplies of soil water and nitrogen. The sources from which the data were obtained for each vegetation type are listed in Table S1.

at ambient CO_2 as well as being highly responsive to elevated CO_2. In FACE experiments with eight cultivars of rice at two sites in Japan, Hasagawa *et al.* [25••] found a range of responsiveness to elevated CO_2 that ranged from zero to a high of 36% (Figure 4). These findings are indeed encouraging for the prospects of breeding rice varieties that can respond with higher grain yields at the elevated CO_2 concentrations expected in the future.

The average grain yield of C_3 grain legumes (soybean, pea, peanut, common bean) increased about 16% at elevated CO_2 (Figure 4), which is less than the increase of shoot biomass of soybean (26%; Figure 3). Similar to the cultivar study of Hasagawa *et al.* [25••] with rice, Bishop *et al.* [26] grew 18 genotypes of soybean under FACE conditions. The responses to elevated CO_2 ranged from −9% to 22% (Figure 4), which implies that the potential for increasing the responsiveness of soybean to elevated CO_2 by breeding is lower than for rice.

For the C_4 grass grain crops (sorghum and maize), the average response to elevated CO_2 was slightly negative at ample N and H_2O (Figure 4), consistent with the lack of photosynthetic [8,9] and shoot biomass (Figure 3) responses to elevated CO_2. However, similar to the shoot biomass response (Figure 3), when H_2O was limited, there was a substantial increase (about 30%), in grain yield due to FACE (Figure 4). As discussed previously, such an increase with limited water undoubtedly was due to the reduction in ET (Figure 1) following a rain or irrigation that enabled the plants to conserve water and to grow longer into a drying cycle than did the control plants at ambient CO_2.

Potato tuber yields were stimulated about 27% at elevated CO_2 (Figure 4). Such a large yield increase is in marked contrast to a negative stimulation observed for its shoot biomass [27], which represents a huge increase in harvest index. Sugar beet, a root crop was somewhat less responsive to elevated CO_2 than potato, with average increases of about 9% and 15% at ample and low supplies of N, respectively. Why there was a larger response at low N is puzzling, but again the soil N levels probably were not very low. The one cassava point is a surprising 109% increase in yield due to elevated CO_2 (Figure 4), whereas shoot biomass increased about 30% [28]. However, the fact that the FACE experiment under which it was grown was in the United States at a latitude of 40° N with a short growing season [28] rather than Equatorial Africa where cassava is more adapted likely influenced its growth, but that it was so responsive to elevated CO_2 is interesting.

For clover, another forage crop, the yield is the shoot biomass, and the data points for it in Figure 3 are repeated in Figure 4 for comparison. The yield stimulation was about 24% at both ample and low levels of soil N. Cotton boll yield was highly responsive to elevated CO_2 (increase of about 38%) at ample N and H_2O (Figure 4). When water was limiting, the yield response tended to be slightly larger. Although the variability was quite large, the yield increase of lint (separate from the seeds) tended to be even higher (about 55%; [10]). The yield increase of the berries of grape, another woody crop like cotton, was also fairly large (about 28%). On the other hand, coffee, another woody crop, was less responsive with a yield increase of only about 13% (Figure 4).

Interactions with temperature

Concomitant with the increase in atmospheric CO_2 concentration, Earth's temperatures are warming globally, so it is important to determine the likely effects on future agricultural productivity of increasing CO_2 and temperature in tandem. Deployment of infrared heaters over open field plots [29,30], especially in arrays to provide uniform warming over the plots [31–33], provided the feasibility to conduct T-FACE (Temperature Free-Air Controlled Enhancement) experiments. Recently, several papers have reported results from such combined FACE/T-FACE experiments. Morgan *et al.* [34] found that in prairie grazingland with a mixture of C_3 and C_4 grasses and forbs near Cheyenne, Wyoming, USA that elevated CO_2 alone (550 ppm) favored C_3 grasses, whereas warming alone (1.5 °C daytime, 3.0 °C night) favored C_4 grasses, and the combination of elevated CO_2 plus warming also favored C_4 grasses. Ruiz-Vera *et al.* [35••] reported that the interaction of CO_2 and warming on soybean in MidWest USA varied greatly according to whether the growing season was cooler or warmer than normal. During a cool season, warming (+3.5 °C) depressed yields, but elevated CO_2 (550 ppm) provided compensation for no significant net change, whereas during a warm year, additional warming depressed yields severely with no compensation from elevated CO_2. For a C_4 crop, maize, the same group [36] found no effect of either warming or CO_2 or the combination on biomass production, whereas warming caused significant reductions in grain yield, that is, a reduction in harvest index. In an experiment on wheat in China, Cai *et al.* [37] found that yields were increased by elevated CO_2 (+100 ppm) and decreased by warming (1.7 °C). In combination, yields were still somewhat lower. They also studied rice for which they reported that elevated CO_2 caused small increases in yield, but warming caused severe decreases in rice yield, both alone and in combination with elevated CO_2.

Thus, generally increasing temperature alone can stimulate or decrease plant growth depending on whether a plant is currently below or above its temperature optimum for growth. Therefore, not surprisingly, results from T-FACE experiments have shown mixed results depending on whether seasonal temperatures are below or above normal, but generally above normal temperatures have depressed grain yields. In mixtures of C_3 and C_4 grasses, both warming alone and combined warming plus elevated CO_2 favored C_4 grasses.

'Food for Thought'

Long *et al.* [38] presented an analysis of the results of experiments on cereal grain crops using FACE technology and also some enclosure experiments. They concluded that the yield responses to elevated CO_2 from the FACE experiments were half or less than those reported from the enclosure experiments. This 'Food for Thought' paper provoked controversy [39–41]. My own analysis [10] of the arguments presented and the available data did not show that responses to elevated CO_2 under FACE results were clearly lower than those from experiments using chambers. Moreover, the relatively high hybrid rice yield responses (Figure 4) and the high wheat yield responses, although variable, recently reported by Fitzgerald *et al.* [21••] also suggest less difference between FACE and other methodologies than suggested by Long *et al.* [38].

Long *et al.* [38] suggested that the FACE results were more correct because FACE conditions are more natural than those in chambers. However, if CO_2 responses under FACE are indeed lower, there may be another explanation. The CO_2 concentration in a FACE plot is not steady but instead fluctuates over a wide range due to air turbulence, and Bunce [42,43•] and a few others have shown that when elevated CO_2 is supplied in cycles or pulses, the responses of cotton, wheat, and rice are lower than if the CO_2 is supplied at a high steady level which is more characteristic of chambers. My own opinion is that the fluctuations in a FACE plot occur over a very wide range of frequencies, and a definitive experiment needs to be done to test whether such a spectrum of fluctuating CO_2 concentration actually does produce smaller responses than a steady average. In the meantime, although a much larger range of CO_2 concentrations (including sub-ambient) can be achieved in chambers, FACE obviously is the more natural technique so far as shading, wind flow, and other factors are concerned, so I think that FACE results are accurate, and we can be confident that the yield benefits measured under FACE are at least as large as we can expect in open fields under the higher future CO_2 concentrations.

Conclusions

Elevated CO_2 at concentrations of about 550 ppm from FACE {free-air CO_2 enrichment; about 190 ppm above ambient (which was about 351 ppm in 1989 [14])} decreased evapotranspiration of both C_3 and C_4 plants about 10% on average with differences among species due to varying decreases in stomatal conductance and increases in growth and leaf area. At the same time, the reduced cooling due to decreased transpiration caused increased canopy temperatures of about 0.7 °C for most crops. Biomass and yield were increased by FACE in all C_3 species, but not in C_4 species except when water was limiting and growth stimulations occurred via improved water conservation. Growth stimulations were often but not always reduced by low applications of N, although in many cases soil N may not have been limited. When water was limited, CO_2 growth and yield stimulations generally were as large or larger than under well-watered conditions. Woody perennials tended to have larger growth stimulations than the average for herbaceous crops, although coffee did not. Yields of most C_3 grain crops were increased on average about 19% by the FACE treatments. In contrast, results with hybrid rice and another rice cultivar trial showed stimulations of about 32% for cultivars that were high yielding even at ambient CO_2, which suggests potential exists for breeding varieties that yield higher at future elevated levels of CO_2.

The free-air CO_2 enrichment technique remains the best platform to test plants under the open-field conditions that future farmers will face. Following the examples of Hasagawa *et al.* [25••] and Bishop *et al.* [26] and the recommendation of Ainsworth *et al.* [44], many more FACE experiments should be done to genetically screen and select for high responses to elevated CO_2 of many genotypes of many major crops. Further, Earth continues to warm globally, which may decrease the yields of crops, such as wheat [20••]. Thus, the future FACE experiments also need to look for responses to warmer temperature and interactions with elevated CO_2. The use of arrays of infrared heater arrays now allows such T-FACE (temperature free-air controlled enhancement) experiments to be conducted [31], including having T-FACE subplots within larger FACE plots [35••,36]. Simply varying planting date can also provide a T-FACE treatment for annual crops [45] that could be accomplished within a FACE plot. At the same time, experiments with chambers that enable larger ranges of CO_2 concentrations, temperature, and other variables than are feasible in open fields also need to continue. In addition, efforts such as AgMIP [20••] need to continue to improve crop growth models so that the likely impacts of climate change on agricultural productivity can be more accurately assessed and strategies for mitigation developed.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pbi.2016.03.006.

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- • of special interest
- •• of outstanding interest

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