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# Crop response to elevated $CO_2$ and world food supply A comment on "Food for Thought..." by Long et al., Science 312:1918–1921, 2006

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**Abstract**

Recent conclusions that new free-air carbon dioxide enrichment (FACE) data show a much lower crop yield response to elevated $CO_2$ than thought previously – casting serious doubts on estimates of world food supply in the 21st century – are found to be incorrect, being based in part on technical inconsistencies and lacking statistical significance. First, we show that the magnitude of crop response to elevated $CO_2$ is rather similar across FACE and non-FACE data-sets, as already indicated by several previous comprehensive experimental and modeling analyses, with some differences related to which "ambient" $CO_2$ concentration is used for comparisons. Second, we find that results from most crop model simulations are consistent with the values from FACE experiments. Third, we argue that lower crop responses to elevated $CO_2$ of the magnitudes in question would not significantly alter projections of world food supply. We conclude by highlighting the importance of a better understanding of crop response to elevated $CO_2$ under a variety of experimental and modeling settings, and suggest steps necessary to avoid confusion in future meta-analyses and comparisons of experimental and model data.


*Keywords:* $CO_2$ crop response; FACE; Chambers; Experimental and model data; Climate change; World food supply

## 1. Introduction

A recent review of free-air carbon dioxide enrichment (FACE) studies concluded that the positive effects of elevated $CO_2$ on several food crops are roughly half those shown by earlier experiments conducted in non-FACE environments (Long et al., 2006). On the basis of such strong differences, it was argued that crop models – based on the old data – may simulate response to elevated $CO_2$ too strongly, thereby downplaying otherwise potentially large negative effects of future projected changes in temperature and precipitation on crop yields. Thus, estimates of world food supply for the 21st century, as reviewed by IPCC (2001), might be too optimistic and in need of substantial downward revisions (Long et al., 2006, 2005).

While discussions focusing on uncertainties of crop model projections of yield under climate change and elevated $CO_2$ are important (e.g., IPCC TAR, 2001; Reilly et al., 2001; Tubiello

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and Ewert, 2002), current literature shows that these recent conclusions are incorrect, for several reasons. Here we argue that:

(1) The meta-analysis of Long et al. (2006) does not show significantly lower crop yield response to elevated $CO_2$ in FACE compared to non-FACE experiments.
(2) Simulated yield responses to elevated $CO_2$, as implemented in most crop models used for climate change impact assessment, are consistent with FACE results.
(3) Any remaining differences in $CO_2$ response based on FACE results would not significantly alter projections of world food supply in the 21st century.

## 2. Material and methods

### 2.1. Measures of crop yield response

We define the *yield response ratio* of a given crop, $RR[C, C_0] = Y(C)/Y(C_0)$, as the yield of that crop at elevated $CO_2$ concentration $C$, divided by the yield at a reference concentration, $C_0$. An alternative measure characterizing crop response is the *percent enhancement factor*, $E[C, C_0] = 100 \times (RR[C, C_0] - 1)$, defined as the percentage yield *increase* from $C_0$ to $C$. Response ratios or enhancement factors discussed herein were re-scaled to a reference $CO_2$ concentration $C_0 = 350$ ppm, unless noted otherwise. This is necessary for proper data comparisons across many studies. To this end, we note that because atmospheric $CO_2$ concentration has risen in the last several decades at about 0.5% per annum—i.e., from 330 ppm in the mid-1970s, to 350 ppm in the mid-1980s, and to over 380 ppm today[1]—comparing yield response ratios of similar experiments made in different periods requires re-scaling of the apparent, smaller responses obtained using higher reference $CO_2$ concentrations, as shown below in this section.

### 2.2. Non-rectangular hyperbolas

In addition to linear scales, studies of crop yield response to elevated $CO_2$ have routinely used classes of non-rectangular hyperbolas for data analysis. Such curves have the following form:

$$y = \frac{(aC + y_{max}) - \sqrt{(aC + y_{max})^2 - 4\xi aCy_{max}}}{2\xi}$$

where $y = RR[C, C_0]$ is the crop response ratio at $CO_2$ concentration $C$, $y_{max}$ is the asymptotic maximum response, $a$ is the initial slope of the response ratio, and $\xi$ is the non-rectangular parameter,[2] usually set around 0.9 in photosynthesis studies (e.g., Thornley, 1998). For $\xi = 0$ the non-rectangular hyperbola becomes a rectangular hyperbola; for $\xi = 1$ it becomes a set of two straight lines.

### 2.3. Scaling response ratios to different $CO_2$ concentrations

Scaling of crop response ratios or enhancement factors is often useful for comparison across existing datasets. For instance, scaling may be performed to infer yield responses at elevated $CO_2$ concentrations that are different from those used in a given experiment. It is important to note however that "predictions" made with such methods are not necessarily bio-physically based, as they depend on the particular scaling method used. For instance, older non-FACE datasets were typically reported at either 660 ppm, from a reference concentration of 330 ppm (as in Kimball, 1983), or at 700 ppm, from 350 ppm (as in Amthor, 2001); more recent FACE datasets are usually reported at 550 ppm, with reference concentrations in the 350–370 ppm range. Specifically, the two non-FACE datasets mentioned above provide, under doubled $CO_2$ concentration, crop yield enhancement factors of 33% (many-crops analysis, Kimball, 1983) and 31% (wheat analysis, Amthor, 2001), respectively. Scaling these responses to 550 ppm and reference concentrations of 350 ppm provides a useful basis for comparison to FACE data. Depending on whether straight lines, rectangular or non-rectangular hyperbolas are used for such scaling, the following "predictions" at 550 ppm $CO_2$ are made: the 33% enhancement of Kimball (1983) scales to 20%, 21% or 23%, respectively. The enhancement for wheat, 31% (Amthor, 2001), scales to 18%, 21% or 24% (Fig. 1).

In general, non-linear hyperbolic scaling predicts higher responses because of more convexity compared to rectangular and linear methods. Yet there is no *a priori* reason for yield response ratios to follow either linear or hyperbolic curves—yield being such a complex integrator over a plant's life cycle. Understanding the metadata characteristics of the crop responses to be scaled may help in choosing an appropriate scaling method. For instance, the 33% figure of Kimball

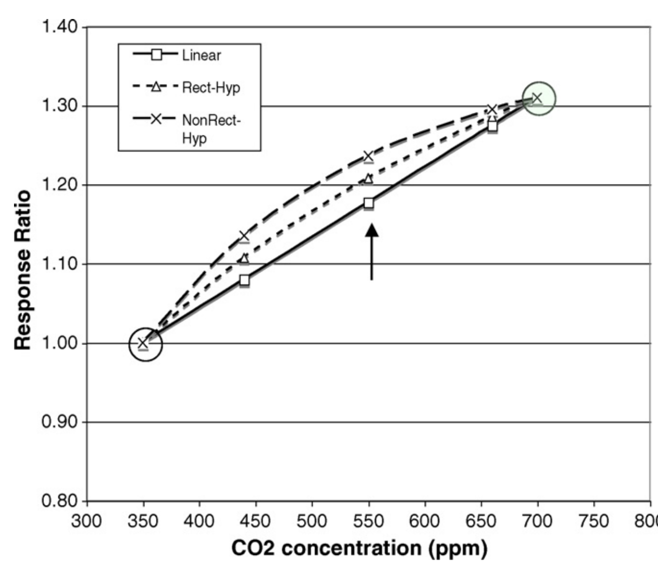


Fig. 1. Scaling of response ratio. The arrow indicates "predictions" at 550 ppm obtained with linear and hyperbolic curves, derived from observed data points (open circles) representing a response ratio of 1.31 at 700 ppm with reference to 350 ppm. Parameters for hyperbolic scaling were $\xi = 0.9$ or $\xi = 0$, and $y_{max} = 1.5$.

[1] http://cdiac.esd.ornl.gov/ftp/trends/co2/maunaloa.co2.

[2] Forcing a response ratio of 1 at a reference $CO_2$ concentration $C_0$ effectively reduces a three-parameter curve-fitting problem to a two-parameter problem. Specifically, two parameters become linked by the equivalence: $\xi - (aC_0 + y_{max}) + aC_0y_{max} = 0$.

Table 1
Response ratios of crop yield at 550 ppm elevated $CO_2$ as a function of increasing reference atmospheric $CO_2$ concentrations, computed using either linear or hyperbolic scaling

| Year | Reference ambient $CO_2$ (ppm) | Response ratio to 550 ppm | | |
|---|---|---|---|---|
| | | Linear | Rectangular hyperbola | Non-rectangular hyperbola |
| 1975 | 330 | 1.17 | 1.18 | 1.19 |
| 1985 | 350 | 1.15 | 1.15 | 1.16 |
| 2000 | 370 | 1.13 | 1.13 | 1.13 |
| 2005 | 380 | 1.12 | 1.12 | 1.12 |
| 2025 | 400 | 1.11 | 1.10 | 1.09 |

Historical atmospheric $CO_2$ concentrations data are from the Mauna Loa dataset, while projections to 2025 assume a 0.5% per annum growth rate. An average response ratio of 1.13 and 370 ppm reference level was reported by Long et al. (2006) for C3 crops rice, wheat and soybean.

(1983) was obtained by computing linear slopes at many concentrations; the consistent way of scaling this number to other concentrations would thus be linear. In discussing FACE versus non-FACE data from Long et al. (2006), a range indicating the gap between linear and non-hyperbolic scaling will nonetheless be provided.

Scaling is also necessary to normalize results collected against reference $CO_2$ concentrations that differ between experiments, due to rising ambient atmospheric levels over time. Table 1 shows the errors made by not normalizing such results against a common reference, estimated by assuming linear or hyperbolic behavior. To this end, examples pertinent to elevated $CO_2$ studies are FACE experiments, in particular those using a fixed enrichment level at 550 ppm; their reference $CO_2$ concentrations rose from about 355 ppm during the early 1990s to over 380 ppm today (Amthor, 2001).

## 3. Crop response to elevated $CO_2$

### 3.1. FACE data compared to earlier studies and reviews in IPCC TAR

#### 3.1.1. The meta-analysis of Long et al. (2006) does not show significantly lower crop yield response to elevated $CO_2$ in FACE compared to non-FACE experiments, and is consistent with reviews in IPCC TAR (2001)

Long et al. (2006) stated that results from free-air $CO_2$ enrichment (FACE) were 50% lower than found in other studies. By contrast, previous meta-analyses of both FACE and enclosure studies by several authors, including these, had shown that FACE data may be consistent with observations in non-FACE experiments, such as glasshouses, closed and open-top field chambers, and laboratory studies: at 550 ppm enrichment, mean yields increased 17–20% in FACE, compared to 19–23%[3] in non-FACE experiments (Kimball et al., 2002; Long et al., 2004; Ainsworth and Long, 2005; Gifford, 2004; Amthor, 2001).

Conclusions in Long et al. (2006) were based mainly on data presented in Table 1 and Figure 2 of that article, summarizing response ratios at 550 ppm for several crops. There are important discrepancies in both Table 1 and Figure 2 in Long et al. (2006) that affect comparisons with non-FACE results. Once allowed for, we show below that values reported by Long et al. (2006) are consistent with earlier analyses.

In general, it was not clear what reference concentration was associated with the yield response ratios of FACE data reported in Table 1 and Figure 2 of Long et al. (2006). This is a critical piece of information, since non-FACE data used for comparison were referenced to either 330 or 350 ppm $CO_2$. The reference level for both Table 1 and Figure 2 of Long et al. (2006) was indicated as "ambient" concentration; this was given as 380 ppm in the introduction; as ∼370 ppm, and then as 372 ppm, in their materials and methods section. With reference to earlier computations, we note that an enhancement factor of 13%, reported for FACE experiments at 550 ppm and a reference $CO_2$ of 370 ppm, would correspond to 15–16% if normalized to 350 pm, using either linear or hyperbolic scaling.

In their Table 1, Long et al. (2006) reported enhancement factors at 550 ppm for five main crops – rice, wheat, soybean, sorghum and maize (the latter two pooled as "C4 crops") – comparing FACE and non-FACE data from various meta-analyses. In particular, the non-FACE data were derived from both old and more recent analyses, such as Kimball (1983), Cure and Acock (1986), Amthor (2001) and Ainsworth et al. (2002). Based on such table, Long et al. (2006) concluded that FACE data showed 50% less enhancement than non-FACE data. We indicate below a number of inconsistencies with these data comparisons and related conclusions.

First, although meta-analyses of many-crop data have proved useful for comparing across experimental settings (e.g., Ainsworth and Long, 2005; Long et al., 2004), they are problematic for single crop comparisons: in fact, they have little statistical power, once the large standard errors and the small sample size of FACE (typically $n = 4$–10) compared to non-FACE data are considered (Amthor, 2001).

Nevertheless, an argument could be made – as in Long et al. (2006) – that although single-crop comparisons of FACE versus non-FACE data are statistically weak, the fact that reported FACE data were found to be lower than non-FACE data in 11 out of 12 cases in Table 1 of Long et al. (2006) points to a low probability of this happening by chance alone ($P = 0.0019$).[4] However, we note that those 12 separate cases arise from combinations of

[3] A $CO_2$ response of 20% magnitude at 550 ppm is consistent with current theoretical understanding of photosynthesis. Since crops derive about half of their production under light-limited conditions, with the remainder produced under high light levels, mean crop response should fall roughly at mid-point between the levels of stimulation of light-limited photosynthesis (RubP regeneration), or +12% at 550 ppm (Long et al., 2004), and those of light-saturated photosynthesis (Rubisco activity), or +36% at 550 ppm (Long et al., 2006, 2004).

[4] Demonstrating that FACE data are lower that non-FACE data may simply point to differences in experimental settings and not to actual "true" differences in physiological responses. For instance, trace-ethylene gas is not scrubbed from the $CO_2$ used for enrichment, and could be a cause for lower yields than found in other experimental settings (e.g., Gifford, 2004). In addition, $CO_2$ concentrations fluctuate at high frequencies within FACE fields, potentially leading to lower mean effective concentrations than originally set for the experiment. Fluctuating $CO_2$ concentrations have also the potential to limit plant $CO_2$ response (Holtum

four crops and three physiological parameters—photosynthesis, biomass, and yield. The latter three are not independent: lower photosynthesis rates in one set of data (e.g., FACE versus non-FACE data) are mechanistically connected to lower biomass production, and ultimately lower yields, across those same comparisons. More appropriately, considering only one of these parameters as independent, FACE data reported in Table 1 of Long et al. (2006) would be lower than non-FACE data in only three out of four cases; the probability of this outcome happening by chance ($P = 0.16$) is clearly not remote.

Second, in their evaluation of recent FACE data, Long et al. (2006) included comparisons to older non-FACE results, such as Kimball (1983) and other pre-1990s analyses. Yet many recent analyses of non-FACE data had already revised these earlier numbers downwards—for instance, reporting enhancements of 15% for rice at 550 ppm (Nakagawa and Horie, 2000); 18% at 550 ppm for wheat (Amthor, 2001); and 24% at 689 ppm for soybean (Ainsworth et al., 2002). The numbers in the "enclosure studies" row in Table 1 of that paper – summarizing such more recent analyses – were by comparison quite high: the value reported for wheat, 31%, corresponded to the enhancement factor reported by Amthor (2001) at 700 ppm compared to 350 ppm $CO_2$, not at 550 ppm compared to "ambient." The enhancement factor reported for soybean, 32%, was even higher than the value reported by some of these same authors at 689 ppm, e.g., 24% (Ainsworth et al., 2002). Based on the latter analyses, the correct scaled enhancement factor for soybean at 550 ppm, referenced to 350 ppm, should have been reported as 14–19%, indeed quite close to the recent FACE values in Table 1 of Long et al. (2006).

Values reported in the "enclosure studies" row of Table 1 in Long et al. (2006), were in fact based on their Figure 2, in which non-rectangular hyperbolic scaling was used to further show that FACE-derived enhancement factors were lower than those "predicted" from earlier, non-FACE data. This conclusion however would be correct only by assuming that a curve-fit of data collected from many different experimental settings had physiologically-based prediction power, rather than simply providing a way to summarize those data in a coherent and useful manner. We argue that several inconsistencies characterize this figure.

Results of curve-fitting in Long et al. (2006) depended on the data-pooling methods used. We clarify this statement by focusing on the "wheat" curve in Figure 2 of Long et al. (2006), for which the entire dataset used by these authors was also available to us (Fig. 2 of this manuscript), i.e., over 100 data points for wheat yield response to elevated $CO_2$ over the range 140–1100 ppm (Amthor, 2001). Long et al. (2006) fitted these data with a non-rectangular hyperbola, apparently using a reference $CO_2$ concentration of 370 ppm; we likewise used a reference concentration of 370 ppm in this data analysis, for consistency. The "wheat" curve in Figure 2 in Long et al. (2006) was replicated by pooling the original data in 100 ppm intervals to get a mean value, and by choosing growth classes centered

and Winter, 2003)—although existing FACE data indicate responses similar to those obtained in chamber experiments.

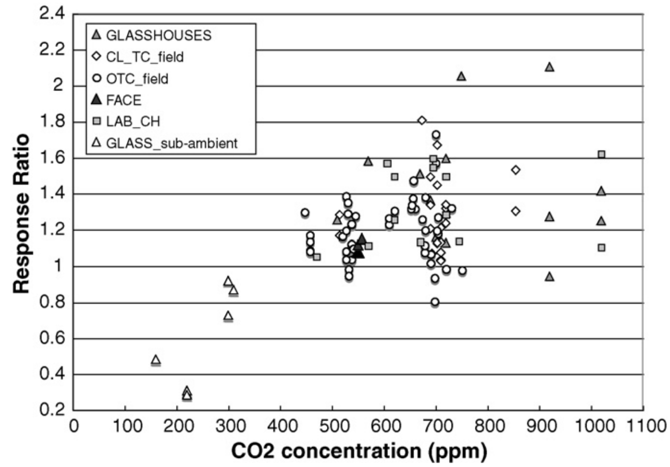


Fig. 2. Response ratio of wheat yield to elevated $CO_2$, relative to 370 ppm, as derived from experiments in glasshouses (for experiments at either above or sub-ambient $CO_2$); field closed top chambers (CL_TC_field); field open-top chambers (OTC_field); laboratory controlled environments (LAB_CH); and FACE (data from Amthor, 2001).

around the same eight points as shown in the Long et al. (2006) paper; the four FACE points in the dataset were excluded from these computations. By the same token, a non-rectangular hyperbola was employed for curve-fitting. As shown in Fig. 3, our data pooling technique reproduced most points in Long et al. (2006). Specific small differences are not important in terms of our discussion, since a single non-rectangular hyperbola provided the least mean-square error (LMSE) fit to both sets of data, with $y_{max} = 1.5$, $\xi = 0.94$ ($R^2 = 0.90$ and LMSE = 0.035 for the Long et al., 2006 data points; $R^2 = 0.97$ and LMSE = 0.026 for our pooled set).

Based on such a curve, Long et al. (2006) "predicted" response ratios of non-FACE data at 550 ppm, comparing the

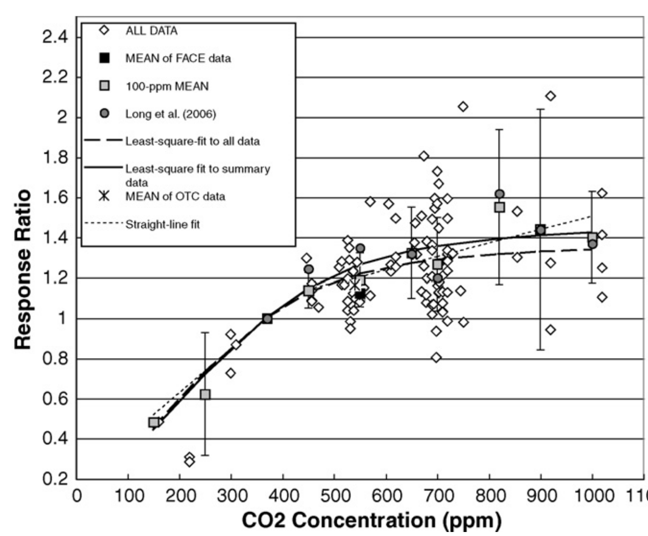


Fig. 3. Response ratio of wheat yield to elevated $CO_2$ relative to 370 ppm. Open symbols: observed data from Fig. 2. Closed square symbols: mean response ratios computed from observed data in 100-ppm intervals, centered at $CO_2$ concentration specified in Long et al. (2006); bars indicate standard errors of the computed means. Full circles: mean response ratios reported by Long et al. (2006). Non-rectangular hyperbolas were those used for data summary.

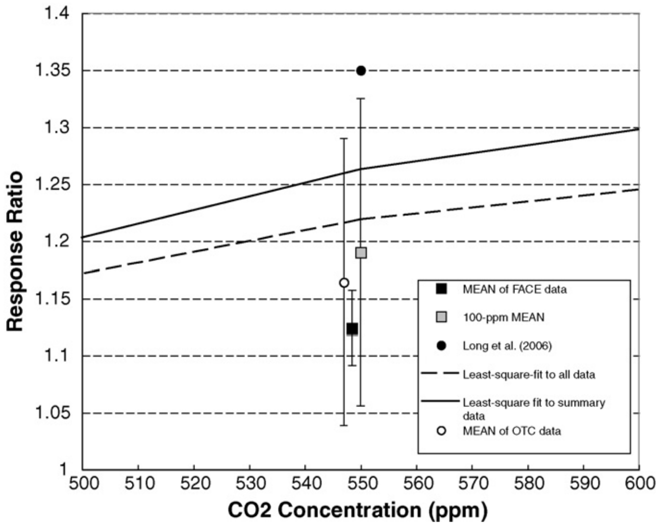


Fig. 4. Details of wheat response ratios at 550 ppm $CO_2$ relative to 370 ppm, as computed respectively from FACE, open-top chamber (OTC), and all observed data in the Amthor dataset (2001). The summary point reported by Long et al. (2006) at 550 ppm is indicated for comparison.

results to observed FACE data. However, such a curve was not the only possible choice for describing the Amthor (2001) data compilation, depending on how the latter is represented. Specifically, as also shown in Fig. 3, when fitting the full dataset as opposed to fitting the pooled subsets, a different hyperbola was found to provide the best fit, with $y_{max} = 1.40$, $\xi = 0.94$ ($R^2 = 0.38$; LMSE = 0.021). Similarly to what was already discussed for scaling methods, we note that curves obtained by fitting techniques are not necessarily explanatory of the physiology underlying a given dataset, since different curves may equally well describe such datasets—for instance as a function of different pooling criteria. Depending on which curve is chosen, "predictions" of $CO_2$ wheat yield enhancement at 550 ppm were 26% using the hyperbola fitting the pooled data, but only 21% for the curve fitting all data. By contrast, computing a response from the original data alone – by averaging data points within a 100 ppm window centered around 550 ppm – gave a mean enhancement factor of 19%.[5]

The implication of these documented dependencies on curve fitting methods and data pooling choices is that response ratios should be computed, whenever possible, using the observed data—rather than "predicted" from curves lacking full biophysical explanatory power. When "prediction" is the only available option, however, results should be weighted against the standard errors of the underlying dataset and pooling techniques, as opposed to comparing single mean values, as done in Long et al. (2006). For instance, with reference to Fig. 4, the mean enhancement of wheat in FACE experiments at 550 ppm was 12.4%; by contrast, the mean of open-top field chamber data for wheat – computed by considering all OTC points in a 100 ppm window around 550 ppm – was 16.4%, i.e., also lower than the mean of all data. Importantly, the standard error bars of the means computed for FACE, open-top chamber, and all data, overlapped each other, so that the conclusion in Long et al. (2006), i.e., that enhancements computed from FACE data were significantly lower than suggested by non-FACE data, is statistically incorrect.

Finally, although instantaneous photosynthesis can be modeled with non-rectangular hyperbolas, there is no reason to assume that yield response to elevated $CO_2$ would necessarily follow such curves. In the case of the data for wheat, one straight line for sub-ambient data and a cubic for above-ambient data was shown to be the best-fit to a larger version of this dataset—including data up to 10,000 ppm $CO_2$ (Amthor, 2001). Limiting the analysis to the 140–1100 ppm range, we found that two straight lines (see again Fig. 3) would have fitted the pooled dataset almost as well as the non-rectangular hyperbola ($R^2 = 0.95$ and LMSE = 0.027).

### *3.2. Parameterizations of crop response to elevated $CO_2$*

#### *3.2.1. Simulated crop responses to elevated $CO_2$, as implemented in the key crop models used for climate change impact assessment, are consistent with FACE results*

Conclusions in Long et al. (2006) – that crop models overestimate response to elevated $CO_2$ in light of recent FACE results – were based on the assumption that these models were strictly based on older, non-FACE experimental data and equations; in addition, results from a select number of published crop modeling simulations under climate change were provided as indirect indication of too strong a $CO_2$ effect on crop growth and yield. We note at the outset that it is risky to deduce crop model performance at elevated $CO_2$ by analyzing results of a small number of unconstrained crop simulations at either local or regional scales, because simulations of crop response are critically modified by multiple, non-linear interactions with soil, climate and management variables. Instead, model equations and parameters for $CO_2$ effects should be directly analyzed.

Here we show that parameters for simulating crop response to elevated $CO_2$, as implemented in most models used in integrated assessments, are in fact consistent with published FACE data. Crop models used in impact assessment studies simulate the effects of elevated $CO_2$ on crop growth and yield with a variety of methods (Tubiello and Ewert, 2002), ranging from simple multipliers of final biomass and yield to more elaborate ones, such as mechanistic models of leaf photosynthesis scaled to canopy; or variable multipliers of daily biomass, based on water and nutrient stress, phenological stage, leaf area feedback, etc. Many of these models have been shown to reproduce rather well-without changing parameterization—observed yields at higher $CO_2$ (660 ppm and above, tested using chamber or greenhouse data), as well as FACE results for 550 ppm. Examples are: CROPGRO (Boote and Pickering, 1994); ecosys (Grant et al., 1999); Demeter (Kartschall et al., 1995); a modified CERES-wheat model (Tubiello et al., 1999); APSIM (Asseng et al., 2004); AFR-Wheat, LINTULC and SIRIUS (Ewert et al., 2002).

Some key crop models used in climate change impact assessment, such as AEZ (Fischer et al., 2002a), CERES (Tsuji et al.,

[5] This value was consistent with the mean response of wheat originally computed by Amthor (2001), i.e., 31% at 700 ppm, which scales to 18–24% at 550 ppm, as previously shown.

1994), and EPIC (Williams, 1995; Stockle et al., 1992), have not been evaluated against FACE data. Nonetheless, in these models, simulated yield response to elevated $CO_2$ was set at the lower range suggested by the older, non-FACE experimental data upon which they are empirically based—recognizing that crop response in farmers' fields would be lower than found under the optimal growth conditions of many experimental settings (e.g., Warrick et al., 1986). Coincidentally, these empirically based model parameters are also rather consistent with FACE data. For example, under 550 ppm $CO_2$ and with no water or N stress, simulated crop yield increases with DSSAT, EPIC and AEZ range from 9% to 17% for C3 crops, and from 3% to 7% for C4 crops. We note that parameter values used in EPIC were higher than those used in DSSAT, and especially in AEZ. While all three models have been used to project climate change impacts on crop yields, only the latter two have been used extensively for projections of world food supply.

*3.2.1.1. DSSAT-CERES.* This family of widely used cereal grain models (wheat, maize, barley, sorghum) employs constant multipliers for daily total crop biomass under elevated $CO_2$, equally applied to either stressed or unstressed growth conditions. As shown in Table 2 a, for C3 crops, the assumed response ratios change almost linearly with $CO_2$ level from 330 to about 660 ppm, but diminish at higher levels, reaching a plateau of 1.5 beyond 1000 ppm. For C4 crops, the response ratio relative to 330 ppm plateaus at 1.10 beyond 990 ppm. Thus, the combined response of C3 and C4 crops in DSSAT is lower than reported in Kimball (1983). In that review, the mean $CO_2$ enhancement over all agricultural crops was 33% from 330 to 660 ppm, compared to a value for DSSAT of 25% in the same $CO_2$ range.

In particular, the DSSAT response ratio for increases from 350 to 550 ppm $CO_2$ is 1.15, or a 15% enhancement (response at 350 ppm was obtained by interpolating values at 330 and 440 ppm in Table 2a). For C4 crops, the response ratio from 350 to 550 ppm is 1.045, i.e., a 4.5% enhancement. These enhancement factors are closer to values reported by Long et al. (2006), i.e., +13% for C3 crops and ∼0% for C4 crops, than to those deduced from Kimball (1983), i.e., 19–23% at 550 ppm, as previously calculated.

*3.2.1.2. DSSAT-CROPGRO and APSIM.* The DSSAT-CROPGRO family of crop models for legumes (soybean, peanut, etc.), in contrast to the CERES models, uses mechanistic equations for leaf photosynthesis, which are then scaled to canopy level (Boote and Pickering, 1994). The leaf-level equations were shown to give accurate response to elevated $CO_2$ (Alagarswamy et al., 2006). APSIM simulates crop growth via radiation-use efficiency, transpiration efficiency and a range of limiting factors, which are modified under elevated $CO_2$ using leaf-level mechanistic equation (vonCammerer and Farquhar, 1981). Model parameters are not easily analyzed in these cases, as interactions of many environmental and management factors would alter response ratios of harvest yield through the plant growth cycle. We note however that such parameters are in line with current mechanistic understanding of leaf photosynthesis, and have allowed these models to well reproduce FACE data in some instances (e.g., Asseng et al., 2004).

Table 2
Response ratios for $CO_2$ (ppm) crop response in three major crop models

| $CO_2$ | (a) CERES | | (b) EPIC | | (c) AEZ | | | |
|---|---|---|---|---|---|---|---|---|
| | C3 | C4 | C3 | C4 | Wheat | Rice | Soybean | Maize |
| 330 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| 440 | 1.08 | 1.03 | 1.11 | 1.05 | 1.05 | 1.03 | 1.07 | 1.01 |
| 550 | 1.17 | 1.06 | 1.19 | 1.08 | 1.11 | 1.10 | 1.16 | 1.04 |
| 660 | 1.25 | 1.10 | 1.25 | 1.10 | 1.16 | 1.15 | 1.21 | 1.06 |
| 770 | 1.32 | 1.13 | 1.30 | 1.12 | 1.18 | 1.17 | 1.24 | 1.08 |
| 880 | 1.38 | 1.16 | 1.33 | 1.13 | 1.18 | 1.17 | 1.24 | 1.08 |
| 990 | 1.43 | 1.18 | 1.36 | 1.14 | 1.18 | 1.17 | 1.24 | 1.08 |

Sources for model codes: DSSAT-CERES (K. Boote, Pers. Commun.); EPIC/CropSyst (Tubiello et al., 2000); AEZ (G. Fischer, Pers. Commun.).

*3.2.1.3. EPIC/CropSyst.* Depending on model versions of EPIC (Williams, 1995) or CropSyst (Stockle et al., 2003) this family of crop models – which also includes CENTURY in terms of simulated response to elevated $CO_2$ – uses multipliers for either daily biomass or final yield (Stockle et al., 1992; Tubiello et al., 2000). As shown in Table 2b, response ratios of crop yield are nearly linear from 330 to 660 ppm, for both C3 and C4 crops, diminishing in strength at higher concentrations, and reaching a maximum response ratio of 1.36 (C3) and 1.14 (C4) at 990 ppm. The mean enhancement factors in the range 330–660 ppm are similar to those computed for DSSAT-CERES, i.e., 25% for C3 crops (EPIC and CropSyst include legumes with cereals), and 10% for C4 crops. The corresponding yield increases from 350 to 550 ppm are +16.7% for C3 crops, and +7.0% for C4 crops, respectively, i.e., higher than those reported by Long et al. (2006) for FACE experiments, though still lower than the multi-crop response values reported by Kimball (1983).

*3.2.1.4. AEZ.* The IIASA-FAO AEZ, or agro-ecological zone model of Fischer et al. (2002a), has been employed in the majority of assessment studies of climate change impacts on world food supply reviewed in IPCC TAR (2001). In this approach, AEZ-computed crop yield changes are coupled to a world food trade model, BLS (e.g., Fischer et al., 2005). The BLS food trade model was also used in other studies of world food supply and climate change (e.g., Rosenzweig and Parry, 1994; Parry et al., 2004), although these had incorporated DSSAT results for yield responses, rather than AEZ projections.

In order to simulate crop response to elevated $CO_2$, the AEZ model employs multipliers of final biomass production – which translate directly into yield via a harvest index – and distinguishing among major crops. Unlike DSSAT-CERES, such multipliers are reduced under stress conditions. As shown in Table 2c, values for response ratios are lower than in either DSSAT or EPIC/CropSyst; percent enhancement factors at 550 ppm are less than 11% for wheat; 10% for rice; 16% for soybean, and 4% for maize. The AEZ enhancement factors are thus close to, and some even lower than, those presented by Long et al. (2006), namely 13% for wheat, 12% for rice, 14% for soybean, and 0% for C4 crops.

### *3.3. Projections of world food supply in the 21st century*

#### *3.3.1. Any remaining differences in $CO_2$ response based on new FACE data would not significantly alter projections of world food supply in the 21st century*

Concerns about the ability of the world to feed itself under climate change and the modest $CO_2$ effects reported by Long et al. (2006, 2005) are not supported by the current literature. Although projections under climate change of crop models are sensitive to the assumed effects of elevated $CO_2$ (e.g., Reilly et al., 2003; Tubiello and Ewert, 2002), they are only one component of the complex integrated frameworks necessary to project trends in world food supply, demand and trade.

Crop models have been used extensively to quantify impacts of climate change on crop yield, indicating that positive $CO_2$ effects may counterbalance negative impacts of small levels of climate change (e.g., IPCC, 2001; Reilly et al., 2003). As atmospheric $CO_2$ levels continue to rise, however, progressive saturation of the $CO_2$ response of crops will lead to smaller positive $CO_2$ effects, at the same time as the changes in temperature and precipitation grow larger. A variety of studies thus find that negative climate effects may begin to outweigh beneficial effects of $CO_2$ sometimes after the middle of this century—or once the mean global temperature rise extends beyond about 2 °C warming (Hitz and Smith, 2004). Yet these crop yield results cannot be simply extended to derive projections of global and regional food supply—the latter being largely determined by socio-economic factors, such as the interplay of land, capital and labor in response to population growth, technological and economic development (Rosenzweig and Parry, 1994; IPCC, 2001; FAO, 2003; Parry et al., 2004; Fischer et al., 2002b; Tubiello and Fischer, 2006).

Pressures from a growing population and increasing income alone imply a doubling of current global cereal demand by 2080, requiring an increase in production from 2 to slightly over 4 billion tonnes (e.g., Fischer et al., 2005). Within this context, analyses of the impacts of climate, $CO_2$, and other environmental changes on food supply must include, in addition to effects on crop yields, explicit representations of land availability as well as the market dynamics of demand and supply. From an economic perspective, food demand is relatively price-inelastic and commodity supply is relatively price-elastic—price elasticity being a common summary measure defined as the percentage change in quantity divided by the percentage change in price. It follows that, globally, the actual quantity of commodity production needed to meet a given demand may not be very sensitive to changes in crop yields, either positive or negative (Reilly et al., in press). If anything, yield changes will tend to modify the prices of agricultural commodities and food, rather than the quantities produced or consumed. In addition under climate change, global trade may lessen negative impacts by moving food from climate-advantaged to climate-disadvantaged regions.

These mechanisms will tend to minimize the effects on world food supply implied by differences in $CO_2$ effects between FACE and non-FACE data, if any. For instance, as shown in Table 3, the effect on global cereal production of socio-economic pathways that include different population and economic growth is about 10%, expressed as CV across IPCC SRES scenarios.

Table 3
Projections of world cereal production (million metric tonnes) from 1990 to 2050 and 2080, under different socio-economic scenarios (IPCC, 2000)

| | 2000 | 2050 | 2080 |
|---|---|---|---|
| A1 | 2100 | 3406 | 3884 |
| B1 | 2100 | 3334 | 3729 |
| B2 | 2100 | 3474 | 4115 |
| A2 | 2100 | 3763 | 4791 |
| A2_IIASA | 2100 | 3550 | 4215 |
| H3A2 | 2100 | 3767 | 4749 |
| H3A2no | 2100 | 3723 | 4668 |
| H3A2_IIASA | 2100 | 3557 | 4178 |
| H3A2_IIASAno | 2100 | 3520 | 4117 |

Projections are for cases with no climate change (A1, A2, B1, B2, A2_IIASA); with climate change – predicted by the Hadley Had3 model – including effects of elevated $CO_2$ on crops (H3A2, H3A_IIASA); and with climate change, but no $CO_2$ effects (H3A2no, H3A2_IIASAno). Data from Fischer et al. (2005) and Tubiello and Fischer (2006).

For any specific socio-economic pathway and climate change, including or not including the effects of elevated $CO_2$ on crops changes the global cereal production results by less than 2%.

Current simulations also show that climate change may significantly increase disparities between developed and developing countries, with negative consequences in terms of malnutrition and the number of people at risk of hunger. Such projected disparities are somewhat more sensitive to the assumed strength of the $CO_2$ response than the global results (Table 4), but depend for the most part on physical features of climate change – i.e., warming may favor agriculture in developed high-latitude regions, while increasing heat and moisture stress in developing tropical regions – as well as on socio-economic ones, for instance a greater ability to adapt in richer versus poorer economies (IPCC, 2001). As an example from Table 4, the variation in the projected number of people at risk of hunger in 2080 across socio-economic scenarios was large at 85%, expressed as CV across IPCC scenarios, compared to a range of 5–25% due

Table 4
Projections of number of people undernourished (millions) from present to 2050 and 2080, under different socio-economic SRES scenarios (IPCC, 2000)

| | 2000 | 2050 | 2080 |
|---|---|---|---|
| A1 | 824 | 208 | 108 |
| A2 | 824 | 721 | 768 |
| A2s | 824 | 988 | 1065 |
| B1 | 824 | 239 | 91 |
| B2 | 824 | 348 | 233 |
| B2s | 824 | 502 | 458 |
| H3A1f | 824 | 219 | 136 |
| H3A2 | 824 | 730 | 885 |
| H3A2no | 824 | 788 | 950 |
| H3A2s | 824 | 1001 | 1144 |
| H3B1 | 824 | 242 | 99 |
| H3B2 | 824 | 336 | 244 |
| H3B2no | 824 | 356 | 257 |

Projections are for cases with no climate change (A1, A2, B1, B2); with climate change – predicted by the Hadley Had3 model – and including effects of elevated $CO_2$ on crops (H3A1f, H3A2, H3B2, H3B1); and with climate change, but no $CO_2$ effects (H3A2no, H3B2no). Scenario A2s and B2s have lower economic growth than A2 and B2. Data from Fischer et al. (2005).

to climate change. Assuming or not assuming positive effects of elevated $CO_2$ on crops modified the projected climate impacts by 5–7%. Thus, the $CO_2$ fertilization effect is only moderately important in determining large-scale effects of climate change on key agricultural economic variables. In particular, differences between FACE and other experimental results of the magnitude discussed by Long et al. (2006) would not be large enough to significantly alter projections of world food supply for the 21st century.

## 4. Conclusions

Several decades of research on the effects of elevated $CO_2$ concentration on crop growth and yield have produced a wealth of valuable information, critically increasing understanding of the dynamics of photosynthesis, biomass accumulation and crop yield that are necessary to project future impacts of climate change on agriculture. In particular, some key interactions between elevated $CO_2$ effects and crop management, especially irrigation and fertilization regimes, are fairly well understood. Yet the jury is still out concerning the real strength of the effects of elevated $CO_2$ on crop yields in farmers' fields, due to several key uncertainties. To this end, much more research is needed to increase understanding of the interactions of elevated $CO_2$ with increasing temperatures, worsening air pollution, changes in moisture availability and mineral nutrition, and altered incidence of pests, diseases and weeds.

It is also necessary to assess response of crops other than the key cereal grains, and in climate regimes other than temperate, especially those of importance to developing countries in the sub-tropics. The strength of the $CO_2$ effect in comparison to other drivers of change in the world food system (e.g., market forces) needs to be further assessed.

Our analyses show that crop yield responses to elevated $CO_2$ are similar across FACE and non-FACE experimental data. Not only is this important for interpreting existing projections of global food supply, but it also has implications for the future of experimental work on plant response to elevated $CO_2$ and environmental stress. In particular, our results indicate that many experimental frameworks, from controlled environments to FACE, have useful roles. While FACE systems are invaluable in many respects, several considerations—for instance cost, interest in evaluating $CO_2 \times$ temperature interactions, or the need to test at $CO_2$ levels higher than 550 ppm—make it important to know that controlled environmental chamber, greenhouse, closed-top or open-top field chambers, or gradient tunnel approaches can continue to be used with reliable results. Such approaches can provide at least valuable initial screening of the effects of multiple environmental stresses on crop yields, even if eventually one might hope to examine field-level consequences in a FACE environment.

Importantly, even greater co-operation is warranted between experimentalists and modelers, and across disciplines, so that key questions of importance to crop yield, crop production and food supply under future climate, environmental and socioeconomic change can be framed within comprehensive and mutually beneficial research programs.

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