Tansley review

Predicting the impact of changing CO_2 on crop yields: some thoughts on food

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Summary

Recent breakthroughs in CO_2 fumigation methods using free-air CO_2 enrichment (FACE) technology have prompted comparisons between FACE experiments and 'enclosure studies' with respect to quantification of the effects of projected atmospheric CO_2 concentrations on crop yields. On the basis of one such comparison, it was argued that model projections of future food supply (some of which are based on older enclosure data) may have significantly overestimated the positive effect of elevated CO_2 concentration on crop yields and, by extension, food security. However, in the comparison, no effort was made to differentiate 'enclosure study' methodologies with respect to maintaining projected CO_2 concentration or to consider other climatic changes (e.g. warming) that could impact crop yields. In this review, we demonstrate that relative yield stimulations in response to future CO_2 concentrations obtained using a number of enclosure methodologies are quantitatively consistent with FACE results for three crops of global importance: rice (*Oryza sativa*), soybean (*Glycine max*) and wheat (*Triticum aestivum*). We suggest, that instead of focusing on methodological disparities *per se*, improved projections of future food supply could be achieved by better characterization of the biotic/abiotic uncertainties associated with projected changes in CO_2 and climate and incorporation of these uncertainties into current crop models.

Key words: carbon, crops, elevated CO_2, food security, rice, soybean, wheat.

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Table 1 Comparison of different methods used to simulate future climate, and their spatial/temporal scales

Method	[CO_2]	Temperature	Nutrients	Water	Air quality	Spatial/temporal scales
Growth chamber	+/–	+/–	+/–	+/–	+/–	Plant, weeks–months
Glasshouse	+/–	+/–	+/–	+/–	+/–	Plant/canopy, months
SPAR unit	+/–	+/–	+/–	+/–	+/–	Plant/canopy, months
Tunnels	+	+/–	+	+/–	+/–	Ecosystem, months–years
OTC	+	+/–	+	+/–	+/–	Ecosystem, months–years
FACE	+		+	+	+/–	Ecosystem, months–years

For a given method, '+' indicates that a given parameter can be added (i.e. supra-ambient); '–' means that subambient levels of the parameter can be achieved. The spatial scale is the highest (and subsequent lower) organizational levels represented by the system (e.g. 'whole plant' includes leaf and cellular responses). Air quality refers to the addition (or scrubbing) of ozone or other aerobic pollutants.
FACE, free-air CO_2 enrichment; OTC, open-top chambers; SPAR, soil–plant–atmosphere research.

I. Rising CO_2 and agricultural crop yields

Although terrestrial plants evolved at a time of high atmospheric CO_2 (4–5 times present values), concentrations appear to have declined to relatively low values during the last 25–30 million yr (Amthor, 1995; Bowes, 1996). However, records of atmospheric CO_2 concentration beginning in the late 1950s on Mauna Loa provided proof that the global atmospheric concentration of CO_2 was increasing (Keeling *et al.*, 1976). These recent increases, and the projected concentrations of atmospheric CO_2 (i.e. 500–1000 μmol mol^{-1} by the end of the 21st century; see Houghton *et al.*, 2001), therefore represent an upsurge of an essential resource, exceeding anything plants have experienced since the late Tertiary (Pearson & Palmer, 2000; Crowley & Berner, 2001).

Although scientists have known for 200 yr that enhanced concentrations of CO_2 stimulate the growth of plants (T. De Sassure, 1804, as cited in Kimball, 1983), the number of studies involving CO_2 fumigation of agricultural and horticultural plants increased markedly in the 1960s and 1970s (Allen, 1979). By the early 1980s, Kimball (1983) had documented over 400 observations with respect to agricultural yield in response to elevated CO_2 conditions, data that could potentially be used to forecast the impact of rising CO_2 on crop productivity.

However, many of these observations involved the response of individual agronomic plants grown in pots in glasshouse or growth cabinet conditions. It seems unlikely that the response of single plants to CO_2 could act as a reasonable surrogate for prediction of the future of global agriculture given the spatial and temporal aspects of plant function, from the molecular to the ecosystem level. In addition, CO_2 is not just the source of carbon in the biosphere, but a longwave-radiation trapping gas, with consequences for surface temperature and precipitation, climatic variables that affect crop productivity.

II. Expanding methodologies

Clearly, a better and more thorough analysis of how plant growth and yield would respond to CO_2/climate was needed. To that end, a number of methodological papers throughout the 1980s and early 1990s described new, innovative means to simulate future CO_2/temperature/climate such as soil–plant–atmosphere research (SPAR) units (e.g. Mortensen, 1982), temperature gradient tunnels (TGT; e.g. Horie *et al.*, 1991), open-top chambers (OTC; e.g. Rogers *et al.*, 1983; Drake *et al.*, 1989) and free-air CO_2 enrichment (FACE) systems (e.g. Allen *et al.*, 1985; Hileman *et al.*, 1992a). The FACE technology was developed, in large part, because earlier results using enclosures (laboratory and field) indicated that small plot size and artificial enclosure could produce microclimatic and edge effects that would influence crop responses (Hendrey, 1994). However, as with all simulations, each methodology is able to add (or subtract) various abiotic parameters from the system (Table 1). In general, as the spatial/temporal scale increases, microclimatic effects do diminish, but short-term control of variables becomes more difficult. For example, a 5-s sample of air from an elevated CO_2 OTC was within ± 10% of the set point 80% of the time (L. H. Ziska, unpublished data; Hileman *et al.*, 1992b), whereas a 5-s air sample from an elevated rice (*Oryza sativa*) FACE system in Japan was within ±10% of the set point only 50% of the time (Table 2; Okada *et al.*, 2001).

III. Which methodology gives the 'truest' prediction of future yields?

As systems for simulating future atmospheric composition and/or climates have become more sophisticated over greater spatial scales, is it fair to state that the results from such newer systems represent (or are closer to representing) the 'true' response of crop yields to projected changes in CO_2/climate? In a recent hypothesis first published in the *Philosophical Transactions of the Royal Society* (Long *et al.*, 2005), and later reiterated in *Science* (Long *et al.*, 2006), Long and colleagues argued that current modeling efforts overestimate the impact of increasing CO_2 on future crop yields, because the models used are parametrized with data obtained from earlier 'enclosure studies' and not from the more sophisticated FACE systems.

However, Long *et al.*'s (2005, 2006) hypothesis made no distinction among 'enclosure studies' which would include

Table 2 Mean relative enhancement of rice (*Oryza sativa*) yields at 700 relative to 370 μmol mol^{-1} CO_2 for a range of methodologies

Methodology	Relative yield (700/370)[a]	Comments/reference
Various	1.13	Cure & Acock (1986)[b]; review of three studies
Glasshouse	1.44 (0.91–3.41)	Average of 20 experiments[c]
Tunnels	1.24 (1.18–1.37)	Average of 6 experiments[d]
SPAR	1.19 (1.04–1.27)	Average of 10 experiments[e]
OTC	1.26 (0.91–1.57)	Average of 6 experiments[f]
FACE	1.20 (1.11–1.22)	Average of 6 experiments[g]

Minimum and maximum values are shown in parentheses.
Rice data were determined only for rice growing under nonlimiting conditions of temperature, water, nutrients, etc.
[a]Because different experiments use different concentrations of 'ambient' and 'elevated' CO_2, we scaled the published data to a 700 relative to 370 μmol mol^{-1} comparison using a beta factor $\beta = [(Y_H - Y_L)/Y_L]/\ln(C_H/C_L)$, where C_L is the 'low' (always approximately ambient; 315–408 ppm) CO_2 concentration used, C_H is an elevated CO_2 concentration used, Y_L is yield in the C_L treatment, and Y_H is yield in the C_H treatment. Following calculation of the beta factor for a given experiment, the relative stimulation of yield $(1 + [(Y_H - Y_L)/Y_L])$ was then solved for using 700 and 370 μmol mol^{-1} as C_H and C_L, respectively (Tables 2–4). The appropriateness of using a beta response function (curvilinear response) for these species is consistent with published yield response curves over a range of CO_2 values (e.g. fig. 1 in Baker *et al*., 1996 for rice; fig. 14 in Baker & Allen, 1993 for soybean (*Glycine max*); Amthor, 2001 for wheat (*Triticum aestivum*); for a more detailed explanation of β, please see Amthor & Koch, 1996).
[b]The Cure & Acock (1986) reference is used for comparison to the Long *et al*. (2006) study.
[c]Alberto *et al*. (1996); Imai *et al*. (1985); Teramura *et al*. (1990); Ziska & Teramura (1992); Ziska *et al*. (1996).
[d]Kim *et al*. (1996); Nakagawa & Horie (2000).
[e]Baker *et al*. (1996); Sakai *et al*. (2004).
[f]DeCosta *et al*. (2003); Moya *et al*. (1998).
[g]Kim *et al*. (2003); Yang *et al*. (2006).
FACE, free-air CO_2 enrichment; OTC, open-top chambers; SPAR, soil–plant–atmosphere research.
(See the Supplementary Material Appendix S1 for references grouped by crop type.)

crop yield data obtained from a variety of sources, including single plant experiments in growth chambers or glasshouses, as well as assemblages of plants grown in field-based open-top chambers. As we have already pointed out, single plant data are unlikely to reflect global crop responses to CO_2 and/or climatic change; hence, the comparison of 'enclosure studies' *in toto* with FACE systems requires further elucidation as to what exactly is meant by the term 'enclosure studies' and whether, in fact, all enclosure studies overestimate the impact of rising atmospheric CO_2 on crop yields.

For a more precise comparison, we examined relative yield response to elevated CO_2 for a number of enclosure methodologies for three crops of global significance: rice, soybean (*Glycine max*) and wheat (*Triticum aestivum*). In examining the literature we have defined 'experiment' as a single replicated

Table 3 Mean relative enhancement of soybean (*Glycine max*) yields at 700 relative to 370 μmol mol^{-1} CO_2 for a range of methodologies

Methodology	Relative yield (700/370)[a]	Comments/reference
Various	1.27	Cure & Acock (1986); review of 12 studies
Glasshouse	1.34 (1.09–1.91)	Average of 17 experiments[b]
Growth chamber	1.36 (1.08–1.59)	Average of 11 experiments[c]
SPAR	1.28 (0.96–1.63)	Average of 13 experiments[d]
OTC	1.37 (1.19–1.50)	Average of 30 experiments[e]
FACE	1.40 (1.24–1.87)	Average of four experiments[f]

Minimum and maximum values are shown in parentheses.
Data were determined only for optimal conditions of temperature, water, nutrients, and unmanipulated ozone concentrations. In studies where multiple CO_2 concentrations were used, including an elevated concentration near 700 μmol mol^{-1} CO_2, only the data for 700 μmol mol^{-1} CO_2 are included here.
[a]Calculated as determined in Table 1.
[b]Ferris *et al*. (1999); Teramura *et al*. (1990); Ziska *et al*. (1998); Ziska *et al*. (2001).
[c]Cure *et al*. (1988a); Cure *et al*. (1988b); Heinemann *et al*. (2006); Sionit *et al*. (1987).
[d]Allen *et al*. (1991); Baker *et al*. (1989); Boote *et al*. (2005); Nakamoto *et al*. (2004).
[e]Booker *et al*. (2005); Bunce (2005); Deepak & Agrawal (2001); Heagle *et al*. (1998); Heagle *et al*. (1999); Prior *et al*. (2005); Rogers *et al*. (1986); Torbert *et al*. (2004); Ziska (2000); Ziska & Bunce (2000); Ziska & Goins (2006).
[f]Miglietta *et al*. (1993), Morgan *et al*. (2005).
FACE, free-air CO_2 enrichment; OTC, open-top chambers; SPAR, soil–plant–atmosphere research.
(See the Supplementary Material Appendix S1 for references grouped by crop type.)

study of one cultivar, i.e. multiple years or cultivars are multiple 'experiments' (cf. Ainsworth *et al*., 2002). In addition, as most comparisons of yield enhancement (relative to ambient, background concentration) have been made at ~700, rather than 550 μmol mol^{-1} CO_2 (i.e. the concentration used in the FACE experiments), it is easier to use 700 μmol mol^{-1} as a common point of comparison. It should also be stressed that ambient CO_2 concentration itself has changed appreciably during the experimental era (e.g. from ~320 in early enhancement studies to a current concentration of ~380 μmol mol^{-1}), such that we have scaled the relative yield to a ratio of 700 to 370 μmol mol^{-1} CO_2 (Tables 2–4). (The use of 370 rather than 380 μmol mol^{-1} is a consequence, in part, of the fact that many recent papers still list ambient CO_2 concentration as 370 μmol mol^{-1}; e.g. Morgan *et al*., 2005.) Scaling the observed (published) response to these concentrations was accomplished using a beta (β) factor ($\beta = [(Y_H - Y_L)/Y_L]/\ln(C_H/C_L)$, where C_L is the 'low' (always approximately ambient; 315–408 ppm) CO_2 concentration used, C_H is an elevated CO_2 concentration used, Y_L is yield in the C_L treatment, and Y_H is yield in the C_H treatment for any published experiment). Following calculation of the beta factor for a given experiment, the relative

Table 4 Mean relative enhancement of wheat (*Triticum aestivum*) yields at 700 relative to 370 μmol mol^{-1} CO_2 for a range of methodologies

Methodology	Relative yield (700/370)[a]	Comments/reference
Various	1.33	Cure & Acock (1986)[b]; review of eight studies
Growth chamber	1.33 (0.96–1.58)	Average of 12 experiments[c]
Glasshouse	1.47 (1.12–1.85)	Average of 10 experiments[d]
Tunnels	1.26 (1.03–1.69)	Average of 18 experiments[e]
OTC	1.31 (0.99–1.99)	Average of 49 experiments[f]
FACE	1.19 (1.13–1.23)	Average of four experiments[g]
FACE	1.23 (1.22–1.23)	Results for the two experiments with proper FACE-infrastructure ambient-CO_2 control plots (see Amthor, 2001)

Minimum and maximum values are shown in parentheses.
Data are from experiments with favorable temperature, water, ozone concentration, and nutrient supply.
[a]Calculated as determined in Table 2.
[b]The Cure & Acock (1986) reference is used for comparison to the Long *et al*. (2006) study.
[c]Amthor (2001) experiments L2a, L2e, L4, L5a, L7a (three ambient/elevated CO_2 combinations), L11a, L11b, L13a, L14a and L14b.
[d]Amthor (2001) experiments G2a, G3a, G4, G5a, G6, G7a, G8 and G9a; Derner *et al*. (2004) second- and third-generation plants.
[e]Closed-top field chambers, including temperature gradient tunnels. Amthor (2001) experiments C1a (two ambient/elevated CO_2 combinations), C1c (two ambient/elevated CO_2 combinations), C2a, C2b, C3a, C3c, C3e, C3g, C3i, C3k, C5a, C5b, C5d, C5f, C5h and C5j.
[f]Amthor (2001) experiments O3a (four ambient/elevated CO_2 combinations), O3b (four ambient/elevated CO_2 combinations), O4, O5a (two ambient/elevated CO_2 combinations), O5b (two ambient/elevated CO_2 combinations), O6a, O7a (two ambient/elevated CO_2 combinations), O7c (two ambient/elevated CO_2 combinations), O7e (three ambient/elevated CO_2 combinations), O8a (two ambient/elevated CO_2 combinations), O9d, O9e, O9f, O10a (two ambient/elevated CO_2 combinations), O11a, O12, O13a, O14a, O14d (two ambient/elevated CO_2 combinations), O14e, O15, O17a (two ambient/elevated CO_2 combinations), O17b (two ambient/elevated CO_2 combinations), and O18; Donnelly *et al*. (2005); Manderscheid *et al*. (2003); Ravi *et al*. (2001), with the unspecified ambient CO_2 concentration assumed to be 370 ppm; Schutz & Fangmeier (2001).
[g]Amthor (2001) experiments F1a, F1c, F1e and F1g.
(See the Supplementary Material Appendix S1 for references grouped by crop type.)
FACE, free-air CO_2 enrichment; OTC, open-top chambers.

stimulation of yield ($1 + [(Y_H - Y_L)/Y_L]$) was then solved for 700 and 370 μmol mol^{-1} as C_H and C_L, respectively (Tables 2–4). The appropriateness of using a beta response function for these species is consistent with published yield response curves over a range of CO_2 values (e.g. fig. 1 in Baker *et al.*, 1996 for rice; fig. 14 in Baker & Allen, 1993 for soybean). In addition, we have only included data for plants under favorable conditions of temperature, water, light, nutrients, and unmanipulated ozone concentrations. There are obvious complications imposed by both abiotic and biotic interactions with regard to stimulation of crop yields by elevated CO_2, but these will be discussed in greater detail in the latter part of this review.

IV. Comparing responses among methodologies

1. Rice

We determined the relative yield enhancement of rice for five different methodologies. The relative response of rice under glasshouse conditions appears to be high, in part as a result of the very large enhancement effect observed for two cultivars (Ziska *et al.*, 1996); however, overall, the relative stimulation of yield in rice is consistent for tunnels, SPAR units, OTCs and FACE methodology (Table 2). Long *et al.* (2006) also reported small differences in relative yield stimulation for rice between enclosure studies and FACE at a common CO_2 concentration of 550 μmol mol^{-1}.

2. Soybean

The relative enhancement of soybean yield has, on average, been quite consistent among exposure systems (Table 3). There are two FACE publications for soybean yield. Miglietta *et al.* (1993), using a natural CO_2 spring, reported a relative enhancement effect of 1.85 at an average daytime CO_2 of 652 μmol mol^{-1}, and Morgan *et al.* (2005) reported an average enhancement effect of 1.15 at 550 μmol mol^{-1} CO_2 over 3 yr. Normalizing the Morgan *et al.* (2005) data based on their quoted ambient value of 370 μmol mol^{-1}, their response ratios would extrapolate to values of 1.24, 1.24, and 1.25 for 3 yr at 700 relative to 370 μmol mol^{-1}. We obtained the same scaling using the soybean response curve given in Long *et al.* (2006). Overall, the mean response ratio of the four free-air studies would be 1.40, slightly higher than the overall mean from the other enrichment systems (1.34; Table 3).

It could be argued that the Miglietta *et al.* (1993) study is suspect because it used plants in pots. However, a greater relative CO_2 response in this pot experiment would be inconsistent with the generalization that plants in pots show a reduced CO_2 response when compared with field-grown plants (e.g. Ainsworth *et al.*, 2002, but see also Booker *et al.*, 2005). Another possibly significant difference between the open-air studies is that the Miglietta *et al.* (1993) system produced high night-time CO_2 concentrations (as a result of low wind speed), while in the Morgan *et al.* (2005) SoyFACE system, no CO_2 was added at night. Recent OTC data for soybean over a 4-yr period indicate that additional CO_2 only given during the daytime stimulated seed yield of soybean only half as much as elevated CO_2 given continuously when compared with ambient conditions (Bunce, 2005; but see also Heagle *et al.*, 1999). However, even if only the three values from the Illinois SoyFACE system are considered, equal or lower response ratios were obtained in about a third (24 of 71) of the other enrichment studies from enclosed systems in Table 3. The mean response ratio (extrapolated to 700 µmol mol^{-1}) of 1.24 for SoyFACE is, in fact, identical to the overall response ratio reported in the soybean meta-analysis of Ainsworth *et al.* (2002) (i.e. 1.24 at 689 µmol mol^{-1} among all enclosure studies examined).

3. Wheat

The estimated effect of increasing CO_2 concentration from 370 to 700 ppm (by mathematical extrapolation) was a 23% increase in yield in the wheat FACE experiments that used proper ambient CO_2 control systems. This 23% compares to 33% for growth chamber experiments, 47% for glasshouse experiments, 26% for closed-top field chambers (including temperature gradient tunnels), and 31% for open-top field chambers. Thus, the stimulation of yield for the given CO_2 concentration increase in glasshouses for individual plants was double that for FACE (as was the case for rice; Table 2), but for the two non-FACE field methodologies yield stimulation was only 13 and 35% greater than for FACE. Overall, these values are consistent with the CO_2 enhancement values reported previously for FACE studies (Long *et al.*, 2006).

While field enclosure studies in wheat have produced modestly greater yield stimulation for a given CO_2 concentration increase relative to FACE (Table 4), the small number of wheat FACE experiments (all conducted in a single field in Arizona, USA) makes a general comparison difficult. Also, the wheat FACE experiments were not conducted in a major wheat-growing region, so the applicability of FACE results to major wheat-growing areas remains unknown. In any case, the elevated-CO_2 stimulation of wheat yield in FACE experiments has been only modestly smaller than the yield stimulation produced by the same CO_2 concentration increase in field enclosure studies. Moreover, the ranges of results from the different methodologies overlap, indicating that a significant methodological bias in the CO_2 fertilization effect on yield has not been established for wheat.

4. Overall

We could find no support for a consistent, large (~2×) overestimation of relative yield response to elevated CO_2 in rice, soybean or wheat in (field) enclosure methodologies relative to FACE systems as reported by Long *et al.* (2005, 2006). Does this mean that there are no methodological 'artifacts' related to enclosures that could influence plant response? Hardly. For example, a SPAR unit, because of its small size, is almost certainly subject to edge effects. However, SPAR units typically provide neutral density shadecloth to minimize unrealistic side lighting and are also quite sophisticated in being able to provide precise control over a range of air temperatures, CO_2 concentrations (even subambient concentrations) and soil types – certainly useful information in improving model projections of effects of CO_2 and/or climatic change on crop yields.

Does this mean, then, that SPAR units are the superior methodology for obtaining the 'true' response of crop yields to projected changes in CO_2/climate? It would be easy enough to highlight the benefits of SPAR methodology (e.g. it allows independent control of temperature, light, nutrients and CO_2) while stressing the limitations of a FACE system (e.g. CO_2 fluctuations may underestimate the yield response of plants; Holtum & Winter, 2003). But such subjective parsing of benefits and limitations would, in effect, simply create a specious argument (i.e. SPAR units are inherently superior to all other methodologies).

If methodological and technological considerations are a concern, we suggest that the way to determine differences and establish 'superiority' is not through parsing the benefits and limitations of a particular methodology, but by direct scientific inquiry. That is, a side-by-side comparison of different methodologies should be performed using the same soil, cultivar, temperature, nutrition level, etc. Surprisingly, in all of the debate regarding the 'realism' of CO_2 enrichment methodologies, we could find only one study (Kimball *et al.*, 1997) that attempted such a comparison. They report an experiment with wheat in Arizona where OTCs operated concurrently in the same field as a FACE experiment. Data from this comparison demonstrated that the relative responses of the aboveground biomass (unfortunately, yield was not measured or reported) and absolute growth relative to elevated CO_2 were nearly identical in the two systems. In a later review, Kimball *et al.* (2002) suggested that microclimatic effects, while important with respect to absolute yields under field conditions, probably did not dominate the first-order linear effects of elevated CO_2 concentration *per se*. Kimball concluded, 'for the most part, the FACE- and chamber-based results have been consistent, which gives confidence that conclusions drawn from both types of data are accurate'. This conclusion is in line with the observations reported here (i.e. Tables 2–4).

V. Methodology vs future uncertainty

In the methodology debate, there is another, larger, consideration. The goal of any of the methodologies discussed so far is to quantify how crop yields will respond to projected changes in CO_2 and associated changes in climate in order to assess the potential threat to future food security. Suppose that, in a side-by-side comparison between methods, that one of the methods (call it 'A') could be shown to be the superior technology for simulating future CO_2 concentrations. Would the response of a given crop cultivar to a single elevated CO_2 concentration provide an accurate picture of future yield? Probably not. It is still unclear if smaller increases in CO_2 concentration provide a similar response to that found in larger 'doubling' experiments, and it is likely that different varieties, probably with different responses to a change in CO_2 concentration, will be grown in the future.

But is any quantification of yield in response to increasing CO_2 by itself sufficient to provide us with an accurate estimate of future yields? It is becoming increasingly clear that any effect of CO_2 concentration on yield will be modulated by other abiotic variables such as temperature, moisture, and nutrient availability. In addition, biotic factors such as weeds, insects, and diseases might modify the effect of increasing CO_2 concentration on yield. Indeed, the large range of responses obtained with all methodologies, as documented in Tables 2–4, for experiments under nominally optimal conditions suggests that large abiotic and/or biotic interactions exist. Both abiotic and biotic factors, in turn, are also likely to be directly or indirectly altered by changes in CO_2 and/or climate.

Therefore, if our goal is to achieve greater consistency between experimental and model results for crop yield in a future climate, then an improved understanding of how abiotic and biotic parameters alter the response of crop yield to CO_2 concentrations may also be crucial in providing a more accurate estimate of agricultural productivity and potential threats to food security. For the remainder of this review, we would like to focus on what we perceive as key areas of biotic and abiotic uncertainty; and to address, in a preliminary fashion, how questions associated with such uncertainties could be used to improve yield forecasts of rice, soybean, and wheat with increasing CO_2 concentration.

VI. Abiotic uncertainties

Two of the most important edaphic factors related to crop yields are soil moisture and nutrient availability. For rice and wheat, there are now sufficient data to indicate that any stimulation of crop yield by increasing CO_2 will be dependent on nitrogen (N) availability (e.g. see Kim *et al.*, 2003 for rice; Wolf, 1996 for wheat) whereas stimulation of yield by CO_2 in soybean appears to be independent of supplemental N (Cure *et al.*, 1988a). However, a number of questions remain unaddressed. What is the optimal application of N needed with increasing CO_2 to maximize rice and wheat yields? If root growth is stimulated by CO_2, how will this affect the timing of N application and temporal exploitation of soil resources? If, for economic reasons, N is limiting for a given region, what will be the expected impact on crop yield as CO_2 rises? What about the supply of other nutrients, particularly phosphorous?

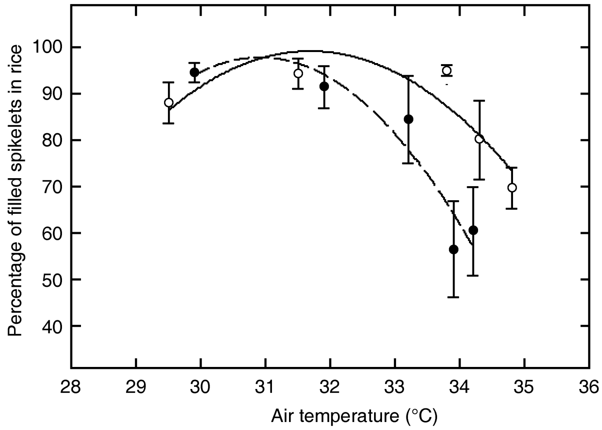

Fig. 1 Relationship between percentage of filled spikelets (with 10 or more germinated pollen grains) and increasing air temperature at ambient (open circles) and elevated (closed circles; ambient +300 μmol mol^{-1}) atmospheric CO_2 concentration. Data are from paddy rice (*Oryza sativa* cv. IR 72) grown in open-top chambers in the Philippines. Bars are ± standard error. Additional details can be found in Matsui *et al*. (1997). Recent data obtained by Peng *et al*. (2004) indicate that higher night relative to daytime temperatures may already be limiting rice yields globally.

In contrast to nutrients, there is a surfeit of data indicating that, under water-limiting conditions, the indirect effect of CO_2 on stomatal aperture (and potential reductions in transpirational water use) may enhance the relative effect of elevated CO_2 on crops (see Polley, 2002 for a review). However, here too there are a number of unresolved questions. How will elevated CO_2 affect crop yields under flooded conditions? Will yield sensitivity to water quality (e.g. salinity) be similar at higher CO_2 concentrations to the yield sensitivity today?

One of the largest uncertainties remains air temperature. Initial assessments based on photosynthetic biochemistry suggested a positive interaction between projected increases in temperature and CO_2 (e.g. Long, 1991). However, such positive interactions do not necessarily translate into additional seed yield with simultaneous increases in CO_2 and temperature as opposed to elevated CO_2 alone (e.g. Matsui *et al.*, 1997; Batts *et al.*, 1998; Amthor, 2001). For rice, increasing CO_2 and temperature may, in fact, negate any yield enhancement related to increasing CO_2 (Moya *et al.*, 1998; Ziska *et al.*, 1996) as a result, in part, of reductions in transpirational cooling, higher canopy temperatures and increased pollen sterility (Fig. 1). The interaction of temperature and CO_2 seems more complex for wheat, with a majority of experiments indicating a reduction in yield with elevated CO_2 in combination with warming compared with elevated CO_2 alone (table 7 in Amthor, 2001). A few studies have compared responses of soybean crops grown for the full season under different temperature regimes (Sionit *et al.*, 1987; Baker *et al.*, 1989; Boote *et al.*, 2005; Heinemann *et al.*, 2006) but have found only minor effects of these treatments on the yield response to elevated CO_2.

Another atmospheric uncertainty is anthropogenic pollution. Ozone concentrations have certainly risen precipitously throughout the 20th century (Marenco *et al.*, 1994), although some evaluations indicate that ozone may be declining, particularly in the eastern states (Fiore *et al.*, 1998; EPA, 2004). Because ozone is phytotoxic, a number of studies have examined whether the increase in ozone will offset any positive effect of CO_2 on crop yield. In a review of studies of wheat, Amthor (2001) evaluated experimental protocols and concluded that four studies (all OTC experiments) were relevant with respect to a combination of possible future ozone and CO_2 concentrations. Recent work with soybean has indicated that ozone fluxes that suppressed net photosynthesis, growth and yield of soybean were generally much less harmful if plants were grown simultaneously with elevated CO_2 (Booker & Fiscus, 2005). Heagle *et al.* (1998) found that increasing ozone concentration above the ambient outdoor concentration increased the seed yield response to elevated CO_2. Although Heagle *et al.* (1999) also reported a significantly smaller yield response to enhanced CO_2 at low ozone, it is unlikely that high ozone is necessary for CO_2 stimulation of yield; otherwise, there would be little CO_2 response of soybean in SPAR, glasshouse or growth chamber experiments. The fact that consistent responses to CO_2 were observed for a wide range of methodologies, some of which filter ozone, indicates that ambient ozone concentrations *per se* may not impose a significant limitation to CO_2 enhancement of yield in soybean, contrary to some reports (e.g. Long *et al.*, 2005). In contrast to soybean and wheat, almost no data have been published for ozone, CO_2 and rice yields. Overall, given the spatial and temporal distribution of ozone, and the fact that different stages of plant growth will exhibit different sensitivities, a satisfactory understanding of how ozone could modify crop yield response to rising CO_2 has not been forthcoming, and should be a priority for further research.

VII. Biotic uncertainties

Since the inception of agriculture, insects and diseases have limited crop yield potential. Will such limitations increase or decrease in response to future changes in CO_2/climate? Certainly it is reasonable to expect that climate stability with respect to temperature and precipitation is likely to affect the range of specific species of insects and diseases for a given crop growing region. For example, Cannon (1998) has suggested that migratory insects could colonize crops over a larger range in response to temperature increases, with subsequent reductions in yield. Gutierrez (2000) has suggested that predator and insect herbivores are likely to respond differently to increasing temperature, with possible reductions in insect predation (i.e. greater insect numbers). Unfortunately, while there is evidence suggesting that insect damage could increase as a function of climate, specific experimental results related to rice, soybean and wheat remain scarce. Similarly, while we recognize plant–pathogen interactions as a factor affecting crop yields, our ability to predict CO_2/climate change impacts on pathogen biology and the impact of subsequent changes on the yield of rice, soybean or wheat is tenuous at best as specific experimental data are not available.

Given the importance of weeds to crop production, it is surprising to find so few assessments of how changes in CO_2/climate will alter their impact on agriculture (a recent review of all crop/weed competition studies is given in table 2.2 in Ziska & Bunce, 2006). Yet, we are aware of only a handful of weed/crop competition studies with respect to soybean (Ziska, 2000; Ziska & Goins, 2006), one study with respect to rice (Alberto *et al.*, 1996) and no studies with respect to wheat, where the effects of projected changes in CO_2/climate on seed yield have been quantified (Fig. 2). As with pests and diseases, CO_2/climate effects on weed biology and crop/weed

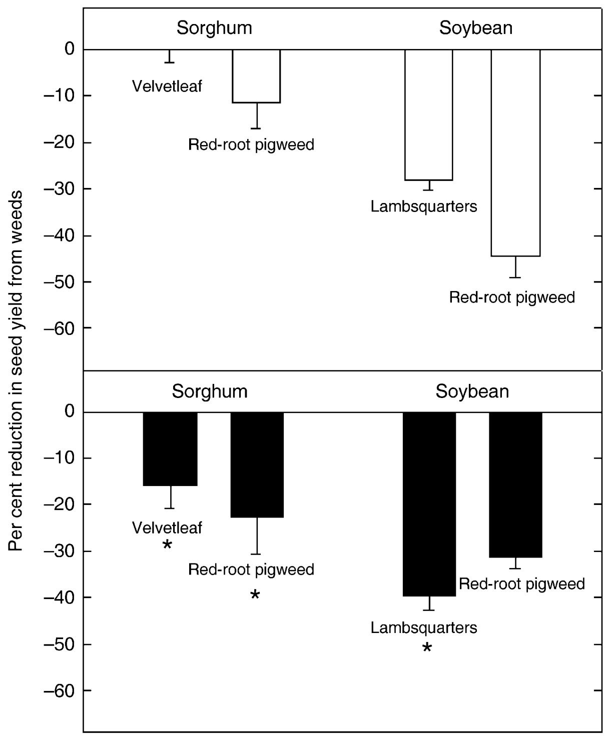

Fig. 2 Per cent reduction in seed yield for sorghum (*Sorghum bicolor*) and soybean (*Glycine max*) (a C_4 and C_3 crop, respectively) as a function of competition from C_3 (velvetleaf (*Abutilon theophrasti*) and lambsquarter (*Chenopodium album*)) and C_4 (red-root pigweed (*Amaranthus retroflexus*)) weeds at ambient CO_2 (open bars) and at ~250 µmol mol^{-1} above ambient (closed bars). Weed spacing was two plants per meter of crop row in all cases. Increasing CO_2 resulted in a greater loss in crop seed yield from weedy competition (indicated by the asterisk) in all cases, except for red-root pigweed in soybean. See Ziska (2000, 2003) for additional details.

competition represent a significant biological uncertainty with respect to predicting future yields of rice, soybean and wheat.

Another biological uncertainty is the range of intraspecific variability within a given crop to changes in CO_2 and/or climate. Morgan *et al.* (2005) suggested that variation among soybean cultivars in yield response to enhanced CO_2 was small and unlikely to be a factor in soybean response in a FACE system. This is in contrast to cultivar comparisons that have shown large differences in response ratios in glasshouse and OTC studies for soybean (Heagle *et al.*, 1998; Ziska & Bunce, 2000; Ziska *et al.*, 2001). Overall, in fact, there are at least enough preliminary data to suggest that genotypic variation in the response of rice, soybean and wheat yields to CO_2 could be substantial (e.g. Manderscheid & Weigel, 1997; Moya *et al.*, 1998; Ziska *et al.*, 2001, 2004; for a recent review, see Newton & Edwards, 2006). Analysis of cultivar differences in CO_2 responsiveness and exploitation of such differences could significantly improve global food security as CO_2 increases. Much of the US Department of Agriculture, Agricultural Research Service (USDA-ARS) effort for soybean in this regard was switched to the SoyFACE system at its inception, because that system is better suited to field comparisons among multiple cultivars, but no reports of comparative yield responses from FACE have been published to date.

However, to properly assess intraspecific variation, other variables in addition to CO_2 need to be examined. These data are noticeably lacking, particularly for soybean and wheat. In a glasshouse study involving 17 different rice varieties, genotypic variation in response to CO_2 was negated as temperature increased, because, for all cultivars, high temperature resulted in pollen sterility no matter the CO_2 concentration (Ziska *et al.*, 1996). Similarly, for a field OTC study, the combination of increasing CO_2 and air temperature resulted in reduced grain yield and declining harvest index compared with increased CO_2 alone for three rice cultivars (Moya *et al.*, 1998). Still, given that there are over 100 000 rice cultivars (and thousands of soybean and wheat cultivars), it seems reasonable to suggest that a more thorough evaluation of the response of crop germplasm to CO_2/climate is warranted. Unfortunately, at present, we are unaware of any such systematic evaluation in regard to CO_2/climate at the government, university or corporate level. Yet such an assessment is imperative for identifying those cultivars that could maintain, or improve, yields in response to changes in CO_2/climate and improve food security.

VIII. Uncertainty vs methodology

The uncertainties listed here are not meant to be inclusive, but illustrative. If our goal is to improve our predictive capacity regarding crop yields with respect to CO_2/climate, then a better understanding/quantification of these (and other) uncertainties would seem to be a high priority. Which methodology, then, is best suited to studying these uncertainties? At present, no one methodology is capable of providing a perfect evaluation of future CO_2/climate with precise control (i.e. all current methodologies have limitations). However, given that CO_2/climate is likely to affect a range of biological properties over spatial and temporal scales, a number of methodologies could, and should, be used to improve our knowledge of these uncertainties. For example, superambient changes in CO_2 for a range of temperatures could be assessed for crop yields using SPAR units; greenhouses or growth chambers could be used to assess genetic and proteomic differences and responses among crop lines to CO_2/climate; FACE could be used to assess ecosystem interactions among weeds, pests and diseases, etc. Ultimately, appropriate technologies should be determined by the specific level(s) of organization the researcher wishes to investigate and/or the relative ability to adequately control the environmental variable of interest.

This does not mean that we should ignore methodological deficiencies. New and innovative strategies to simulate and control a range of projected environments using methodologies that include control of abiotic/biotic uncertainties over large spatial scales are crucial in bettering our understanding of the underlying plant processes likely to be affected by projected changes in CO_2/climate. Understanding of such processes, in turn, will allow us to extrapolate experimental data to improve model scenarios for a wide range of crop yields with respect to global climate change. To that end, improvement of current systems, such as inclusion of heaters to allow warming to be included as an experimental variable in large FACE rings, and improved technology to minimize microclimate effects in SPAR units and OTCs, as well as new approaches (e.g. urbanization as a surrogate for climate change; see Ziska *et al.*, 2003), need to be explored and characterized.

IX. Modelers and experimentalists

Given the unprecedented scale and scope of anticipated changes in CO_2/climate, it is tempting to ignore the large number of uncertainties as being unquantifiable, and to focus on one or two parameters (e.g. CO_2 in isolation from other changes) that can be well defined. In general, such an approach is consistent with that of many experimentalists who work in large part on quantifying one or two variables, usually in the short term (1–2 yr). Such an approach is also certainly valid as it provides key information, but only for a specific set of circumstances.

However, given the large adjustment in scale, uncertainties in crop yields may be magnified in global change models. This is not an expression of the modeler's aptitude; rather, it is a reflection of experimental unknowns. For example, early projections by Kropff *et al.* (1993) of the effect of climate on rice yields assumed that rising CO_2 and temperature acted independently (i.e. the response to CO_2 did not change with temperature). Yet, since these early assessments, it has become apparent that elevated CO_2 may exacerbate the negative effects of temperature, particularly on pollen sterility (Kim *et al.*, 1996; Matsui *et al.*, 1997), and that higher night-time temperature may limit rice yields (Peng *et al.*, 2004). Incorporation of temperature/CO_2 interactions might, of course, improve the efficacy of model projections regarding the consequences of CO_2/climate changes on rice yield (as might incorporation of weeds, pests and disease impacts, or cultivar variability, or nitrogen deposition, etc.).

X. Final thoughts

Given a current population of more than six billion with a projected increase of an additional billion every 12 yr, being able to reliably predict the impact of changing CO_2/climate on global crop productivity certainly should be 'food for thought' for scientists and policy makers (Long *et al.*, 2006). How, then, do we improve our predictive capacity? Long *et al.* (2005, 2006) contended that re-evaluation of crop yields in response to elevated CO_2 concentration using FACE technology is a key means to improve model reliability. While FACE technology can offer some advantages to the experimentalist, we have also shown that the relative effect of CO_2 on yield stimulation of rice, soybean and wheat is, with the exception of single plant evaluations, consistent across a range of CO_2 concentration control methodologies.

Given the importance of models in predicting the impact of CO_2 and/or climate change on food security, it is of obvious interest to try, whenever possible, to improve the efficacy of existing models (Tubiello *et al.*, 2007). However, in addition to the concerns related to methodology (Long *et al.*, 2005, 2006), we would suggest a broader evaluation and inclusion of more of the biotic and abiotic factors mentioned here into any integrated assessment of rising CO_2 and crop yields. Incorporation of these factors will certainly require unprecedented cooperation and data sharing between modelers and experimentalists of all disciplines at the government, university and private sector levels – a daunting task in an age of specialization and increased competition for diminished resources. Nevertheless, by more precisely defining the impact of CO_2/climate on crop yield, we hope to be able to reduce uncertainty regarding global food supply in an uncertain and changing environment.

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Supplementary Material

The following supplementary material is available for this article online:

Appendix S1 References for Tables 2–4 Grouped by Crop Type (Rice, Soybean and Wheat)

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-8137.2007.02180.x
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