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Global food insecurity. Treatment of major food crops with elevated carbon dioxide or ozone under large-scale fully open-air conditions suggests recent models may have overestimated future yields

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Predictions of yield for the globe's major grain and legume arable crops suggest that, with a moderate temperature increase, production may increase in the temperate zone, but decline in the tropics. In total, global food supply may show little change. This security comes from inclusion of the direct effect of rising carbon dioxide (CO_2) concentration, [CO_2], which significantly stimulates yield by decreasing photorespiration in C_3 crops and transpiration in all crops. Evidence for a large response to [CO_2] is largely based on studies made within chambers at small scales, which would be considered unacceptable for standard agronomic trials of new cultivars or agrochemicals. Yet, predictions of the globe's future food security are based on such inadequate information. Free-Air Concentration Enrichment (FACE) technology now allows investigation of the effects of rising [CO_2] and ozone on field crops under fully open-air conditions at an agronomic scale. Experiments with rice, wheat, maize and soybean show smaller increases in yield than anticipated from studies in chambers. Experiments with increased ozone show large yield losses (20%), which are not accounted for in projections of global food security. These findings suggest that current projections of global food security are overoptimistic. The fertilization effect of CO_2 is less than that used in many models, while rising ozone will cause large yield losses in the Northern Hemisphere. Unfortunately, FACE studies have been limited in geographical extent and interactive effects of CO_2, ozone and temperature have yet to be studied. Without more extensive study of the effects of these changes at an agronomic scale in the open air, our ever-more sophisticated models will continue to have feet of clay.

Keywords: global change; atmospheric change; crop production; food security; harvest index

1. INTRODUCTION

Ever more refined world and regional maps estimating crop production and global food supply under Intergovernmental Panel on Climate Change (IPCC) climate change scenarios continue to be developed (Rosenzweig & Iglesias 1998; Parry *et al.* 2004; Thomson *et al.* 2005). These suggest that in the absence of a direct fertilization effect of rising CO_2, crop production by 2050 and 2080 will decline across the globe. When CO_2 fertilization is included, crop production in temperate zones is increased while production in the arid and sub-humid tropics declines. In sum, global food supply would remain similar to today. Estimations of temporal and spatial variation in future food production are linked into further models to estimate economic impacts (Parry *et al.* 2004). These efforts depend on sound data on the responses of the major crops to the key variables of climatic and atmospheric change, singly and in combination, and in different locations. Records of spatial and temporal variation in yields at the field-scale provide powerful datasets for prediction of the responses of crops to rising temperature and altered precipitation (Gitay *et al.* 2001). Tropospheric carbon dioxide ([CO_2]) and ozone ([O_3]) concentrations are predicted to increase 50 and 20% by 2050 (Prather *et al.* 2001; Prentice *et al.* 2001). Both gases have strong direct effects on photosynthesis and crop production. Knowledge of crop responses to both gases is predominantly from small plot trials using laboratory-controlled environments, greenhouses and closed- and open-topped

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transparent field chambers (Kimball 1983; Cure & Acock 1986; Ainsworth *et al.* 2002; Morgan *et al.* 2003). While use of these facilities was pragmatic, and often for comparative questions, major limitations in making quantitative yield predictions are well recognized. No agrochemical company would base its decision on whether to market a new product on tests in such facilities without field testing at an acceptable agronomic test scale, yet estimates of the ability of the globe to feed itself are almost entirely dependent on data gained in such facilities.

This paper will show that failure to examine the impacts of these gases on our major crops in open-air field trials could have led to a serious overestimation of future global food production. It will show that the fertilization effect of [CO_2] has probably been overestimated, while omission of [O_3] effects from most models could have led to a 20% overestimation of future crop production in the Northern Hemisphere.

2. WHY MIGHT CHAMBER STUDIES BE INSUFFICIENT?

Thousands of experimental studies have evaluated the response of crops to the increases in atmospheric [CO_2] expected to occur this century (reviewed in Kimball 1983; Drake *et al.* 1997; Amthor 2001; Ainsworth *et al.* 2002; Jablonski *et al.* 2002; Kimball *et al.* 2002). Most information about crop responses to elevated [CO_2] has been derived from experimental studies that have used greenhouses, artificially illuminated controlled environmental chambers, transparent field enclosures or open-top chambers (OTCs). While all of these methods provide an atmosphere with enriched [CO_2], they also significantly alter other aspects of the environment surrounding the plant. Many of these studies, including some field studies, used plants grown in pots. Arp (1991) showed that rooting volume altered the response of plants to elevated [CO_2], and further experiments have reported a strong feedback when roots encounter a physical barrier (Masle *et al.* 1990; Thomas & Strain 1991).

Most field studies used OTCs, transparent walled chambers, of up to 2 m diameter. Despite the fact that the top of the chamber is open to the atmosphere, there are environmental differences between even the best-engineered OTCs and the adjacent unclosed crop. The effect of the OTC itself may exceed that of elevation of [CO_2] or [O_3] (Drake *et al.* 1989; Day *et al.* 1996). Whitehead *et al.* (1995) compared microclimatic conditions within and outside OTCs. When the outside photon flux was 1600 $\mu mol\,m^{-2}\,s^{-1}$ (about three-quarters of full sunlight in summer at mid-latitudes), air temperature within the chamber was 4.3 °C higher and vapour pressure deficit 0.8 kPa higher. The transmission of total solar irradiance into the chambers was lower and the ratio of diffuse to total solar irradiance in the chambers was altered. Further, OTCs reduce airflow and intercept rainfall. Also, lower canopy leaves, which are poorly coupled to the atmosphere under natural conditions, are as well coupled as upper canopy leaves within an OTC. This is because circulation within the OTC will ensure turbulent transfer of gases to the upper and lower leaves alike, while in the open frictional drag will result in the lower leaves being more poorly coupled to the atmosphere. This artificial coupling potentially exaggerates the effect of decreased stomatal conductance, and overestimates improved soil water status and crop yield (Long *et al.* 2004). The migration of pathogens and pests is also restricted by enclosures. It may be argued that the OTCs in which [CO_2] is maintained at current atmospheric level provide sufficient experimental control. However, temperature, humidity and light modify the response of plants to elevated [CO_2] and [O_3] (Curtis 1996; Curtis & Wang 1998; Ainsworth *et al.* 2002). Therefore, even if chamber effects do not change the direction of a response, they will probably alter its magnitude.

Additionally, small isolated plots in agronomic trials and ecological experiments often overestimate treatment effects on biomass, production and yields (Roberts *et al.* 1993). Gaps caused by sampling within a small area exacerbate this problem. Increased radiation interception at the edges of small plots can exaggerate the effect of a treatment. The maximum practical size of OTCs limits each plot to a ground surface area of less than 3.1 m^2. Therefore, in a 2 m diameter chamber, more than 50% of the vegetation is less than 30 cm from the chamber wall and 75% is within 50 cm of the wall. The recommended border or buffer area for agricultural trials is typically twice the vegetation height (Roberts *et al.* 1993). Therefore, even a 50 cm high semidwarf wheat crop would require a 1 m buffer zone, and thus no area within an OTC would be free from edge effects (Long *et al.* 2004). Consequently, knowledge of crop responses to elevated [CO_2] and [O_3] is currently derived from experiments that are considered unacceptable in standard agronomic trials (McLeod & Long 1999).

3. FREE-AIR CONCENTRATION ENRICHMENT

A free-air concentration enrichment (FACE) apparatus is a circular or octagonal system of pipes that release treatment gas, or air enriched with the treatment gas, just above the top of the crop canopy, and for tall canopies (greater than 1 m) at one or two additional heights below the canopy. Wind direction, wind velocity and [CO_2] or [O_3] are measured at the centre of each plot and this information is used by a computer-controlled system to adjust gas flow rate, controlled by a massflow control valve, to maintain the target elevated [CO_2] or [O_3]. Only pipes on the upwind side of the plots release gas, unless wind velocity is less than 0.4 $m\,s^{-1}$ when it is released alternately from adjacent release points (McLeod & Long 1999). Quantities of released gas decrease with depth into the canopy to reflect the profile of wind speed. The fast feedback proportional integral differential algorithms avoid large overshoots in response to fluctuations in [CO_2] or [O_3] and provide a stable elevation of concentration. The first large-scale FACE systems diluted CO_2 or ozone with air, which was pumped into the ring (Hendrey *et al.* 1993; Lewin *et al.* 1994). More recent designs have either pumped out of the ring to baffle upwind of the outlets (Karnosky *et al.* 1999) or released pure CO_2 or a high concentration of ozone at supersonic velocity into the wind. At this speed the exiting air is immediately turbulent, entraining and mixing with the surrounding air (Miglietta *et al.* 2001). Although several FACE experiments have been conducted with crops, only five locations have used large rings or plots (greater than or equal to 8 m diameter) with fully replicated ($n \geq 3$) designs in each year of the experiment (Long *et al.* 2004). Mini-FACE systems as small as 1 m diameter have been developed (Miglietta *et al.* 1996), but they do not escape many of the problems of enclosures outlined above. For example, substantial differences in the photosynthetic response of wheat to elevated [CO_2] were observed in a mini-FACE (Miglietta *et al.* 1996) versus a full-size FACE system (Nie *et al.* 1995*a*,*b*; Wall *et al.* 2000). This review is therefore limited to full-size FACE systems of more than 8 m diameter plots and with the five major food crops at the global scale; i.e. wheat, rice, maize, sorghum and soybean.

FACE is not without limitations (McLeod & Long 1999). Long-term continuous records of [CO_2] within FACE rings show that 1 min averages of actual [CO_2] are typically within $\pm 10\%$ of the target concentration for about 90% of the time in low stature vegetation, including most arable crops (McLeod & Long 1999). On shorter time-scales (i.e. less than 1 min), as in OTCs, there are larger fluctuations around the target elevated [CO_2] (Nagy *et al.* 1992; Hendrey *et al.* 1999). An important issue is whether these fluctuations are perceived by the plant, and in particular whether they affect net CO_2 exchange. The response of photosynthesis to [CO_2] is nonlinear, so if [CO_2] fluctuates, the measured rate of photosynthesis at a given [CO_2] will decrease as the amplitude of variation around the mean [CO_2] increases (Long *et al.* 2004). In an experiment to address this issue, Hendrey *et al.* (1997) found that oscillating [CO_2] by 225 μmol mol^{-1} around a mean of 575 μmol mol^{-1} had no effect on whole-chain electron transport through photosystem II when the oscillation frequency was 1 min or less, but lower frequency oscillations resulted in progressively greater decreases in electron transport. Given that 1 min averages are usually within 10% of the target [CO_2] in FACE, these results suggest that the low frequency oscillations in [CO_2], necessary to decrease the response of photosynthesis to elevated [CO_2], are uncommon.

The advantage of using the wind as the carrier gas, as in FACE, is that the perturbation of the natural microclimate is minimal in contrast to enclosure methods. The disadvantages are that a dilution gradient is generated across the treatment plot and the system is dependent on continuous air movement. So, although the centre of the plot is maintained close to the target, the upwind site may be 100 μmol mol^{-1} above and the downwind 100 μmol mol^{-1} below the target. With a strong prevailing wind, a gradient effect would occur across each plot. However, analysis of isotopic composition across FACE plots shows a remarkable uniformity. This suggests that although transient gradients occur, when averaged over growing seasons, these gradients are not detectable (Leavitt *et al.* 1996).

A further potential disadvantage of FACE is its dependence on continuous air movement. During daylight hours the continual flux of solar radiation and resulting convective currents ensure that still periods are rare, except around dawn. However, at night, still conditions commonly occur. Some FACE systems mix pure CO_2 into an airstream which is then pumped into the plots at the release points. This flow of CO_2-enriched air moves air into the plot under still conditions. These systems can therefore enrich the atmosphere under still conditions. However, still conditions also result in a climatic inversion, where cold air forms at the surface overlain by warm air. Pumping air into the plot brings the warm air to the surface thus disrupting the inversion (Pinter *et al.* 2000). Enrichment can be achieved under still conditions, but only by significantly altering the microclimate. The system described by Miglietta *et al.* (2001) does not predilute CO_2 but releases pure CO_2 at supersonic velocity through minute nozzles into the wind. The energy of these turbulent jets generates a predilution of the CO_2 before the wind carries it back over the treatment plot. This system depends completely on some air movement and cannot operate under perfectly still conditions.

4. CARBON DIOXIDE

Plants can only perceive a change in atmospheric [CO_2] through tissues that are exposed to the open air. The protective cuticle of higher-plant leaves and other photosynthetic organs means that only the inner surfaces of the guard cells of stomata and the mesophyll can directly sense a change in atmospheric [CO_2]. While many steps in metabolism use or respond to CO_2, the only sites where there is convincing evidence for a response in the concentration range of relevance (240–1000 μmol mol^{-1}) are ribulose 1 : 5 bisphosphate carboxylase/oxygenase (Rubisco) and a yet undefined metabolic step affecting stomatal aperture, that may also involve Rubisco (Buckley *et al.* 2003; Long *et al.* 2004).

The direct increase in C_3 photosynthesis due to elevation of [CO_2] results from two properties of Rubisco. (i) The enzyme is not saturated by present atmospheric [CO_2], and so elevated [CO_2] will increase the velocity of carboxylation and net photosynthesis. (ii) CO_2 is a competitive inhibitor of the oxygenation reaction which leads to photorespiration. Photorespiration typically releases 20–40% of recent photosynthate as CO_2. This significantly reduces net photosynthesis of C_3 crops, and will be suppressed in favour of greater carbon gain by rising [CO_2]. Because the kinetic properties of Rubisco are highly conserved across C_3 crops, the improvement in photosynthetic gain with rising [CO_2] can be calculated for all C_3 crops with some confidence. An increase in atmospheric [CO_2] from today's 372 to 550 μmol mol^{-1} would increase net leaf photosynthesis by 12–36%, while elevation to 700 μmol mol^{-1} would generate a stimulation of 18–63%, for a leaf temperature of 25 °C. The lower end of these ranges represents light-limited photosynthesis, while the greatest stimulation occurs under light-saturated conditions, when the amount of Rubisco is assumed to be limiting. Since crop canopies in the field gain their carbon in roughly equal quantities from light-limited and light-saturated photosynthesis,

Table 1. Comparison of chamber and FACE findings on percentage increase in yield with elevation of [CO_2] to 550–575 μmol mol^{-1}.
(n.s., not significantly different from zero.)

crop	linear[a]	hyperbolic[b]	FACE	some recent model projections[c]
wheat	22	25	8[d]	19[e], 23[f], 33[g]
rice	16	18	10[h]	26[i]
maize	6	7	n.s.[j]	10[f]
sorghum	23	34	n.s.[k]	
soybean	17	19	15[l]	16[f]
mean (C_3)	23	25	11	19[m] – 27[n]

[a] Mean projected increase in yield reported linearly extrapolated to 550–575 μmol mol^{-1} from the averages provided by Kimball (1983) for 660 μmol mol^{-1} and for wheat from the average observed in open-top chambers across western Europe in the 'ESPACE-wheat' project (Bender *et al.* 1999).
[b] Mean projected increase assuming a hyperbolic response of yield to increasing [CO_2], saturating at 2000 μmol mol^{-1}, e.g. Amthor (2001).
[c] Effect of elevation to 550 μmol mol^{-1} extracted by comparison of projections with and without a direct effect of [CO_2].
[d] Irrigated spring wheat, Arizona (Kimball *et al.* 1995).
[e] Europe (Ewert *et al.* 2005).
[f] USA (Thomson *et al.* 2005).
[g] USA & Canada (Rosenzweig & Iglesias 1998).
[h] Rice, Honshu Island, average of 3 years and three nitrogen treatments, reported in fig. 4 of Kim *et al.* (2003).
[i] ORYZA1 model projection (Matthews *et al.* 1997).
[j] Rainfed maize, central Illinois (A. D. B. Leakey, M. Uribelarrea, E. A. Ainsworth, S. L. Naidu, A. Rogers, D. R. Ort & S. P. Long, unpublished data).
[k] Irrigated sorghum, Arizona (Ottman *et al.* 2001).
[l] Rainfed soybean, central Illinois, average of 3 years (Morgan *et al.* 2005).
[m] Mean of all major crops in Europe, including C_4.
[n] USA (Darwin & Kennedy 2000).

actual gains are likely to be in the middle of these ranges (Long 1991; Long *et al.* 2004). Also, this theoretical stimulation increases with temperature because photorespiration increases as a proportion of photosynthesis with temperature. Actual increases are likely to be lower than theoretically possible given feedbacks both within the plant and at the ecosystem level. This will be further complicated by decreased transpiration, which may provide an additional gain due to improved plant water status (reviewed in Long *et al.* 2004).

How large are the actual yield increases due to [CO_2]? Kimball (1983) showed from an exhaustive survey of over 1000 chamber studies that elevation of [CO_2] to 660 μmol mol^{-1} caused an average 33% increase in yields for C_3 crops, with 99% confidence limits of 24–43%. This review will consider the effect of elevation to the estimated 2050 [CO_2] of *ca* 560 μmol mol^{-1}, which approximates the level used in large-scale FACE experiments with food crops. The 33% increase observed at 660 μmol mol^{-1} equates to 23% at 560 μmol mol^{-1} assuming a linear response, or 25% if a more realistic hyperbolic response with saturation of yield response at 2000 μmol mol^{-1} is assumed (table 1). Most of the models and studies that have fed into recent assessments, such as the UN–IPCC third assessment report of future staple crop production, derive their 'CO_2-fertilization' effect from Kimball (1983) (Gitay *et al.* 2001). The models used to predict future crop yields mathematically approximate carbon gain from either radiation use efficiency or net photosynthesis (e.g. CERES-wheat, Ritchie & Otter 1985; Godwin *et al.* 1989; CERES-rice, Singh *et al.* 1989; CERES-maize, Jones & Kiniry 1986; Ritchie *et al.* 1989; SOYGRO, Jones *et al.* 1989; EPIC, Stockle *et al.* 1992). To estimate the effects of greater [CO_2] on yield in the future, a CO_2-fertilization factor is applied to reflect the direct physiological stimulation of these processes by elevated [CO_2]. The CO_2-fertilization factor applied in most CERES or SOYGRO modelling exercises (e.g. Parry *et al.* 1999) is based on the methods of Peart *et al.* (1989), which used the ratio of photosynthetic carbon gain under elevated [CO_2] compared with ambient [CO_2] from early literature reviews (Kimball 1983; Cure & Acock 1986; Allen *et al.* 1987). For example, the direct stimulation of photosynthesis at *ca* 550 ppm has been assumed to be +21% for soybean, +17% for wheat, +17% for rice and +6% for maize (Rosenzweig & Iglesias 1998), +29% for soybean, +21% for wheat and +8% for maize (Adams *et al.* 1990) and +10% for maize (Dhakwa *et al.* 1997). In most EPIC applications (e.g. Brown & Rosenberg 1999; Izaurralde *et al.* 2003; Thomson *et al.* 2005), the CO_2-fertilization factor for radiation use efficiency uses the method of Stockle *et al.* (1992), which parameterized a CO_2-response function to reproduce the mean yield stimulations reported for elevated [CO_2] by Kimball (1983). This corresponds to a yield stimulation at *ca* 550 ppm of +20% for soybean, +28% for wheat and +8% for maize.

The extensive survey of Kimball (1983) suggests that with an increase in [CO_2] to 550 μmol mol^{-1} C_3 yield should increase by 25% with a 99% lower confidence interval of 18%. Yet, not one of the three major C_3 crops showed an actual yield increase that reached this lower confidence limit of 18% when tested under large scale replicated open-air elevation of [CO_2] in FACE. For wheat actual values were a third of that observed in chambers, for rice two-thirds and soybean four-fifths. For the two major C_4 crops, there was no significant increase in yield at all in FACE compared to the chamber-predicted increase of 7% and modelled increase of 10% (table 1). Evidence from chamber experiments has been contradictory regarding direct effects of elevated [CO_2] on C_4 photosynthesis (reviewed in Ghannoum *et al.* 2000). As described above, models for C_4 crops currently assume a direct increase in photosynthesis or radiation use efficiency in elevated [CO_2] in addition to reduced stomatal conductance and water-use efficiency. However, FACE experiments with maize under optimal growing conditions indicate no direct response of C_4 enzyme activity, photosynthetic flux or yield to elevated [CO_2] (A. D. B. Leakey, M. Uribelarrea, E. A. Ainsworth, S. L. Naidu, A. Rogers, D. R. Ort & S. P. Long, unpublished data). Removing a direct CO_2-fertilization effect on C_4 photosynthesis and radiation use efficiency from the models may correct for this overestimate by basing yield estimates under elevated [CO_2] solely on improved water-use efficiency.

Averaged across the FACE experiments of table 1, the yield increase is 11% for C_3 crops and 7% for all five major food crops, which is one-third to one-quarter of the direct effect of [CO_2] modelled in the recent assessment for Europe and the USA by Darwin & Kennedy (2000) (table 1). Overall, these FACE results suggest that the fertilization effect of [CO_2] used in current models of global food production is seriously overestimated. However, this is based on just five fully replicated full-scale FACE experiments (see d, h, j, k, l in table 1). With such a small sample there is the possibility that these results are unrepresentative, but the fact that they all fall below the lower 99% confidence interval established from chamber studies, suggests that this is unlikely. While it might be argued that spring wheat in Arizona is unrepresentative of the major wheat growing areas, sorghum in Arizona, rice in Japan and soybean and maize in Illinois are all in near-ideal climate zones for the respective crops, and yet yield stimulations by elevated [CO_2] all fall below expectations. This conclusion suggests a larger difference between FACE and chamber studies, than noted in the earlier reviews by Amthor (2001) and Kimball *et al.* (2002). What might explain this difference? Amthor (2001) reviewed all previously published studies of wheat grown throughout its life cycle in elevated [CO_2]. In common with this study, the yield increase in FACE was less than in chamber studies. It indicates an overestimation in chamber studies relative to FACE, although the difference is considerably less than indicated by table 1. However, most chamber studies used [CO_2] of *ca* 680–700 ppm and Amthor (2001) assumed a linear increase in yield with increase in [CO_2] from 350 to 700 ppm. This would underestimate the yield increase that would be observed in chambers at 550 ppm if the response is curvilinear. For example, Fangmeier *et al.* (1996) observed an increase in yield for spring wheat of 28% when growth [CO_2] in OTCs was increased from 360 to 540 ppm, but only observed a further 4% increase in yield when [CO_2] was increased from 540 to 650 ppm, suggesting the response to be strongly curvilinear. Kimball *et al.* (2002) reviewed all prior FACE crop studies, and noted that while the response was less than in chamber studies the difference was not significant. Long *et al.* (2004) were able to use the larger database of FACE studies that had become available with a further 2 years of primary publications and applied statistical meta-analysis to show a significantly lower seed yield for the major crops, as in table 1.

Despite further publications, unfortunately the current FACE experiments are not adequate to re-parameterize the existing models. They cover far too small an area of the ranges of these crops. FACE experiments have shown increased response of wheat to elevated [CO_2] in drought, and of both wheat and rice under low N conditions, as anticipated (reviewed in Kimball *et al.* 2002; Ainsworth & Long 2005). A major omission is any information on how temperature interacts with elevated [CO_2] under the fully open-air conditions of FACE. Based on the kinetics of Rubisco a much larger increase in dry matter production should occur at higher temperatures and a reduced response at low temperatures. This interaction is either not represented or poorly represented in the major models of crop production. It may be significant that cotton grown during the summer at the FACE site in Arizona showed a 42% increase in yield compared to 8% for wheat grown over the winter and spring (reviewed in Kimball *et al.* 2002; Ainsworth & Long 2005).

5. OZONE

Although elevated tropospheric ozone concentrations ([O_3]) have been recognized as a factor lowering the yields of the major food crops since the 1970s and 1980s (reviewed in Ashmore 2002), the major current projections of global food production under atmospheric change scenarios (Gitay *et al.* 2001; Parry *et al.* 2004) *do not* account for the damaging effect of rising [O_3]. While elevated background levels are often insufficient to produce the visible lesions apparent after acute exposures, these elevations will lower photosynthetic rate, accelerate leaf senescence and decrease ovule fertilization (McKee *et al.* 1997). In industrialized countries of the Northern Hemisphere, tropospheric [O_3] has risen by 1–2% per year (Chameides *et al.* 1994). Nearly one-quarter of the Earth's surface is currently at risk from tropospheric ozone in excess of 60 nmol mol^{-1} during mid-summer, with even greater concentrations occurring locally (Fowler *et al.* 1999*a*,*b*). The croplands of western Europe, the midwest and eastern US and eastern China are being exposed to some of the highest background [O_3] (Prather *et al.* 2001). Although the risks of acute ozone exposure around large cities are well known, it is often not appreciated that background [O_3] has been rising in rural areas, distant from centres of industrialization. Tropospheric [O_3] forms as a result of the action of sunlight on polluted air masses containing nitrogen oxides, hydrocarbons and carbon monoxide. These polluted air masses can be transported thousands of miles both across and between continents (Prather *et al.* 2001). Increasing fossil fuel consumption is predicted to raise the production of nitrogen oxides, while increased temperature and hydrocarbon concentrations are expected to cause further increases in tropospheric [O_3] (Pritchard & Amthor 2005). The IPCC Third Assessment Report projected an increase in surface [O_3] across the globe, with a 2100 July mean increase of *ca* 40 nmol mol^{-1} in the Northern Hemisphere and *ca* 30 nmol mol^{-1} in the tropics (Prather *et al.* 2001). These projections also suggest an increase in tropospheric [O_3] of 20–25%

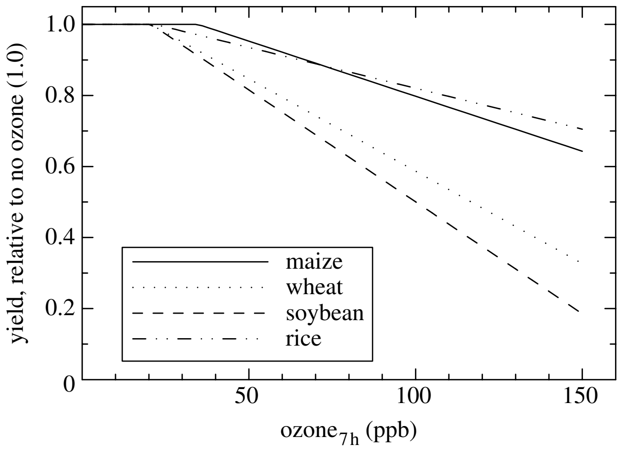

Figure 1. Yield declines due to tropospheric ozone $[O_3]$ for the staple crops maize (*Zea mays*; $n=20$), rice (*Oryza sativa*; $n=26$), soybean (*Glycine max*; $n=41$) and wheat (*Triticum aestivum*; $n=33$). Estimates were constructed from the equations of Kobayashi *et al.* (1995), Mills *et al.* (2000), Ashmore (2002) and Wang & Mauzerall (2004). The number of independent treatments on which the above authors developed each line is indicated after species name. Ozone concentration is based on exposure at the stated average for the highest 7 h of each day.

by 2050, with greater regional increases projected for midwest US, China, Arabia and western Europe. Currently, these areas experience a mean daytime growing season concentration of *ca* 50–60 nmol mol^{-1}. Extensive trials in the USA and western Europe using standardized designs of OTCs have established yield reduction equations for the major crops, except sorghum (reviewed in Ashmore 2002; figure 1). Yield reduction can begin at concentrations as low as 20 nmol mol^{-1}. At 50–60 nmol mol^{-1}, yield losses of 7, 8, 18 and 22% are projected for maize, rice, wheat and soybean, respectively. The reality of such losses is clearly demonstrated when OTCs with charcoal filters to remove ozone are placed in the field next to control OTCs which blow the unfiltered ambient air into the chamber (Ashmore 2002). The 20% increase in surface $[O_3]$ by 2050 would result in yield losses relative to today's yields of 5, 4, 9 and 12% for maize, rice, wheat and soybean, respectively (figure 1), and approximately double these losses by the end of the century. Using similar data to that shown in figure 1, Wang & Mauzerall (2004) project that with the very large increases in surface $[O_3]$ projected for east-central China, crop losses for maize, rice and soybean will each exceed 30% by 2020.

Again these responses have been established in small chambers that differ substantially from the outside, natural field conditions. Some environmental differences between the chamber and the open air could ameliorate the effect of elevated $[O_3]$, while others could exacerbate the effect (reviewed in Morgan *et al.* 2003). Recognition of this limitation led to the development of FACE systems that elevated pollutants rather than CO_2, almost two decades ago (McLeod & Long 1999), but the systems were never deployed with crops until now. Morgan (2004) used a FACE system adapted to elevate $[O_3]$ by 20% to examine whether the decreases in yield for soybean projected from chamber experiments occurred in the open air. In 2002, the ambient (control) growing season 8 h average $[O_3]$ was 62 nmol mol^{-1} and the treatment was 75 nmol mol^{-1}, a 21% elevation. In 2003, the ambient growing season 8 h average was 50 nmol mol^{-1} and the treatment 63 nmol mol^{-1}, a 25% elevation. Seed yield was significantly decreased by 15% in 2002 and by 25% in 2003. How does this compare to expectations established from chamber studies? Based on the equations of Mills *et al.* (2000) and Ashmore (2002), the expected decreases were 12 and 9% for 2002 and 2003, respectively. Therefore, on average the observed decrease in the open air (20%) was substantially greater than expected. This single and only FACE study of the effect of elevated $[O_3]$ suggests that, at least in the case of soybean, not only will the substantial decreases found in chamber studies be realized, but they may be even greater under fully open-air exposure. Should this extrapolate across all major food crops, then even the alarming future yield losses projected by Wang & Mauzerall (2004) may be underestimates.

6. CONCLUSIONS

In the absence of any physiological effect of elevated $[CO_2]$, global climate change is expected to decrease yields of the major grain crops across the globe (Gitay *et al.* 2001; Parry *et al.* 2004). Elevated $[CO_2]$ is projected to rescue this situation to the extent that temperate North and South America, western Europe, Australia and China would all see yield increases by 2050 and 2080. As has been noted in such projections, the direct effect of elevated $[CO_2]$ on crop yields is one of the largest uncertainties (Parry *et al.* 2004; Thomson *et al.* 2005), which is the reason for calculating future yields with and without a physiological effect of elevated $[CO_2]$. Unfortunately, the inclusion makes a *world* of difference in a very literal sense, a world with sufficient food versus one perhaps without. Here, we show that the database of chamber studies, which has been the mechanistic basis for crop yield models, overestimates the yield gain that is observed under fully open-air conditions in the field. Worse however, current projections of world food supply (e.g. Gitay *et al.* 2001; Parry *et al.* 2004) do not account for the damaging effect of rising surface $[O_3]$ concentrations. Chamber studies suggest that with the estimated $[O_3]$ increase for the Northern Hemisphere, yield loss due to $[O_3]$ would numerically offset any increase due to rising $[CO_2]$. There has only been one replicated large-scale fully open-air study of the effects of season-long elevation of $[O_3]$ on a grain crop, and this revealed a loss substantially greater than even the large losses recorded in chamber studies. Should this be representative of other major crops and growing areas, it suggests that the yield losses due to rising $[O_3]$ will outweigh any gains due to rising $[CO_2]$. This is especially relevant to the projected increase in future crop production in eastern China (Parry *et al.* 2004), where these gains would almost certainly be reversed if the effects of rising $[O_3]$ as projected by Wang & Mauzerall (2004) are included.

Chamber experiments have shown that elevated $[CO_2]$ may provide some protection against elevated

$[O_3]$. Elevated $[CO_2]$ decreases stomatal conductance and therefore decreases uptake of O_3 into the leaf. Will this operate in the open? The only FACE experiment to report elevated $[O_3]$ and $[CO_2]$ effects within a factorial design has been an investigation of deciduous trees in North Wisconsin (Karnosky *et al.* 2005). Here, it was found that although elevated $[CO_2]$ decreased stomatal conductance, the relative decrease in dry matter production and photosynthesis caused by elevated $[O_3]$ was the same at ambient and at elevated $[CO_2]$. Since less O_3 will have been assimilated, the result suggests that elevated $[CO_2]$ grown tissue was metabolically less tolerant of O_3 (Karnosky *et al.* 2005). McKee *et al.* (1995, 1997) found that with wheat grown in chambers, elevated $[O_3]$ had less affect on dry matter production and photosynthesis at elevated $[CO_2]$, but yield was similarly depressed because of a direct effect of elevated $[O_3]$ on ovule fertilization. Consequently, if we are to have any confidence in projections of future global food security, whether elevated $[CO_2]$ provides any protection against rising $[O_3]$ in the major food crops under fully open-air conditions requires urgent investigation.

While chamber and glasshouse experiments are important qualitative guides, it is well established both for trials of agrochemicals and transgenic plants that chamber performance is an unreliable quantitative, and sometimes qualitative, predictor of field performance. New agrochemicals apparently effective in a chamber may be ineffective in the field (Anand *et al.* 2003; Black 2004) and disease resistance apparent in transgenes in the greenhouse may be absent in the field (e.g. Anand *et al.* 2003). Based on this long-standing agronomic experience it should be no surprise that chamber versus fully open-air treatments on a large scale do not agree. No agrochemical or biotechnology company would base its business plan on chamber studies alone, yet the UN–IPCC (Gitay *et al.* 2001) bases its projections of future food supply for the whole globe on such potentially flawed data.

Unfortunately, our existing FACE studies of the major crops are too few to provide any real basis for correction. There is good reason to expect significant interactions between $[CO_2]$, $[O_3]$, temperature and soil moisture, requiring improved technologies for open-air treatment. FACE experiments may have been avoided for cost, but a design based on that of Miglietta *et al.* (2001) is likely to cost under 180 000€ in components for a four replicate facility. CO_2 would be the major recurrent cost, with 20 m plots requiring about 1 t of CO_2 each per day. This cost can be greatly decreased if a facility is sited near a natural or industrial source of CO_2. A network of such facilities are required first to obtain reliable estimates of the $[CO_2]$ and $[O_3]$ effects on our major food crops, and then as a means for adapting our crops to these changes. Whatever the cost, it is small compared to the cost of uncertainty. For four midwestern states, losses of \$2.03 billion with climate change are projected without a CO_2-fertilization effect and gains of \$645 million with CO_2 fertilization (Crosson 1993). Without these facilities coupled with improved mechanistic understanding of crops responses to rising $[CO_2]$ and $[O_3]$, our ever-more sophisticated models for projecting future food production and vegetation–atmosphere interactions will continue to rest on feet of clay.

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