Assessing the impacts of current and future concentrations of surface ozone on crop yield with meta-analysis

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ABSTRACT

Meta-analysis was conducted to quantitatively assess the effects of rising ozone concentrations ($[O_3]$) on yield and yield components of major food crops: potato, barley, wheat, rice, bean and soybean in 406 experimental observations. Yield loss of the crops under current and future $[O_3]$ was expressed relative to the yield under base $[O_3]$ (≤ 26 ppb). With potato, current $[O_3]$ (31–50 ppb) reduced the yield by 5.3%, and it reduced the yield of barley, wheat and rice by 8.9%, 9.7% and 17.5%, respectively. In bean and soybean, the yield losses were 19.0% and 7.7%, respectively. Compared with yield loss at current $[O_3]$, future $[O_3]$ (51–75 ppb) drove a further 10% loss in yield of soybean, wheat and rice, and 20% loss in bean. Mass of individual grain, seed, or tuber was often the major cause of the yield loss at current and future $[O_3]$, whereas other yield components also contributed to the yield loss in some cases. No significant difference was found between the responses in crops grown in pots and those in the ground for any yield parameters. The ameliorating effect of elevated $[CO_2]$ was significant in the yields of wheat and potato, and the individual grain weight in wheat exposed to future $[O_3]$. These findings confirm the rising $[O_3]$ as a threat to food security for the growing global population in this century.

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1. Introduction

Ozone (O_3) is currently the most important air pollutant that negatively affects growth of both agricultural and native species in most parts of the world (Ashmore, 2005; Benton et al., 2000; Clarke et al., 1990; Fuhrer and Booker, 2003; Karnosky et al., 2007; Krupa et al., 2001; Wahid et al., 1995; Wang et al., 2007a). Limited measurements suggest that pre-industrial ground-level O_3 concentration ($[O_3]$) was about 10 ppb (Volz and Kley, 1988). The rapid economic growth during the second half of the last century has seen increased emission of O_3 precursors, e.g. nitrogen oxides and volatile organic compounds, and the increase in surface $[O_3]$ at an annual rate of 0.5–2% over the past decades (Vingarzan, 2004). The surface $[O_3]$ has now reached a global mean of approximately 50 ppb (8-h summer seasonal average) (Fiscus et al., 2005) exceeding the concentration against which the anthropogenic ozone impacts on plants are measured (Fuhrer et al., 1997). Ozone concentration in the Northern Hemisphere is projected to increase further by 20–25% between 2015 and 2050, and by 40–60% by 2100, if current emission trends continue (Meehl et al., 2007). Such levels of $[O_3]$ could damage most crop species, and would largely reduce

food production in the future. Indeed a conservative estimate of the crop losses to elevated $[O_3]$ indicates an increase to 2–16% for wheat, rice and corn, and to 28–35% for soybeans in China, Japan and South Korea for 2020 (Wang and Mauzerall, 2004).

The increased crop losses to O_3 will make it more difficult to meet the food demand of the global population, which is projected to increase from current ca. 6 billion to ca. 8 billion in 2025 (USBC, 2001), against the increasing risks of climatic changes and diminishing resources of land and fresh water (Gilland, 2002; Gregory and Ingram, 2000).

Numerous studies have shown that elevated $[O_3]$ generally results in reduced photosynthesis and whole-plant growth, decreased stomatal conductance, altered antioxidant system, and accelerated senescence, although the extent of the effects varies by species or even cultivars (Ainsworth, 2008; Ashmore, 2005; Biswas et al., 2008; Clarke et al., 1990; Feng et al., 2006, 2007, 2008; Kobayashi et al., 1995; Long and Naidu, 2002; Morgan et al., 2003, 2006). Furthermore, elevated $[O_3]$ can increase respiration rates and affect carbon allocation patterns, resulting in a decreased root: shoot ratio (Andersen, 2003; Biswas et al., 2008; Feng et al., 2006; Nouchi et al., 1995), or decreases in the leaf area ratio and specific leaf area (e.g. Morgan et al., 2003). Ozone can directly affect biochemical and/or physiological processes that might subsequently influence plant response to other biotic or abiotic stresses (e.g. Dixon et al., 1995; Fincher et al., 1989).

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Some research programs in the U.S. (National Crop Loss Assessment Network, NCLAN, see review by Heagle, 1989) and Europe (European Crop Loss Assessment Network, EUCLAN, review by Jäger et al., 1992) have derived relationships between “O₃ dose” or “O₃ exposure” and the yield of major crop species through controlled O₃ fumigation experiments under near-field conditions using open-top chambers. Crop losses to O₃ have been estimated with O₃ monitoring data being input into the empirical O₃ exposure–response functions. For example, the NCLAN program investigated 14 crop species across the U.S. in a total of 41 studies during a 7-year period and indicated an approximate 5% yield loss and annual economy loss in excess of \$1 billion at the national level (Heagle, 1989; Murphy et al., 1999).

Outside North America and Europe also, significant effects of elevated [O₃] on crop yield have been estimated. In the Kanto region including the Tokyo Metropolitan area of Japan, yield loss in rice was estimated to range from 0% to 7% across the locations, and a 3% loss of rice production of the region was estimated on average across the 5 years from 1981 to 1985 (Kobayashi, 1992). The yield loss estimate was based on the relationship between the [O₃] and the crop growth derived from a 3-year study of ozone exposure of rice plants in field chambers (Kobayashi et al., 1995). In the Yangtze River Delta region of China, yield losses in 1999 due to O₃ pollution were estimated to be 10.0% and 2.8% for wheat and rice, respectively (Feng et al., 2003), which was calculated from dose–response functions based on local open-top chamber studies and monitoring data in that region. Wang and Mauzerall (2004) estimated the O₃-induced yield losses in major agricultural crops in China, Japan and South Korea for 1990 and 2020 using outputs of an air chemistry–transport model and the dose–response functions based on the NCLAN studies.

The dose–response functions have thus been quite useful in estimating the crop losses, but it must be noted that they represent only a portion of the large number of studies that have been conducted on the yield responses to ambient and elevated [O₃] with a variety of crops. These studies provide a large database from which it is feasible to obtain the mean response of crop yield to [O₃] by using meta-analysis. This approach has been used to examine soybean responses to elevated [CO₂] (Ainsworth et al., 2002) and elevated [O₃] (Morgan et al., 2003), wheat responses to elevated [O₃] (Feng et al., 2008), and rice responses to elevated [CO₂] and [O₃] (Ainsworth, 2008).

Here in this study, we use the meta-analysis as a means of quantitative estimate of the yield response to current and future [O₃] in major food crops. Our aims are to (1) summarize and synthesize the results of the numerous studies on the responses of yield and its components to current and future [O₃]; and to (2) determine if different rooting environment and additional treatments, e.g. elevated [CO₂], significantly alter the responses of the crops to [O₃].

2. Materials and methods

2.1. Database

Relevant journal articles were searched for by a variety of keywords in the Web of Science (ISI) and by the list of references in reviews and meta-analyses. The search covered all peer-reviewed literature published on this topic between 1980 and 2007. To include an article in this meta-analysis, we examined if it met the following criteria: (1) the O₃ fumigation period was longer than 10 days; (2) plant species were agricultural or horticultural crops; (3) [O₃] in the control treatment of the experiment was less than 26 ppb; (4) elevated [O₃] was in the range between 31 and 75 ppb during exposure; and (5) measured responses included yield and its components such as individual grain, seed, or tuber weight,

number of grains or seeds per unit harvested organ. The yields and individual grain, seed, or tuber mass were reported on dry weight basis except for potato, whose yield was sometimes, if not always, expressed on fresh weight basis.

We found studies with 17 crop species in total, but we report here the results with six major food crops: potato (*Solanum tuberosum* L.), barley (*Hordeum vulgare* L.), wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), bean (*Phaseolus vulgaris* L.), and soybean (*Glycine max* (L.) Merr.). Appendix 1 lists the 81 publications used in this meta-analysis. The variables were considered independent if the data were obtained from separate experiments or from different treatments within a single experiment (e.g. different [O₃] treatments, years, species, cultivars, or additional treatments). There were 406 observations in total covered in this meta-analysis. Mean values for each variable were taken directly from tables or text, when reported. Data given only in the figures were digitized using GRAFULA software (Wesik SoftHaus, St. Petersburg, Russia).

To determine effects of ambient [O₃] on crop yield, we set the upper boundary of the base [O₃] level at 26 ppb, which was observed in charcoal-filtered (CF) air plots in some open-top chamber studies (e.g. Heck et al., 1988), and is very close to 25 ppb that was used as the base [O₃] (B-O₃) in the NCLAN studies (Lesser et al., 1990). We then defined the current ambient 7 or 12 h daily [O₃] (C-O₃) as being in the range from 31 to 50 ppb. The low end of this range corresponds to the ambient atmospheric [O₃] at less-polluted areas while the upper bound is close to current global daily mean [O₃] (Fiscus et al., 2005). The future ambient [O₃] (F-O₃) is assumed in the range from 51 to 75 ppb, based on the projections of Assessment Report Four (AR4) that [O₃] could further rise by 40–60% by the year 2100 (Meehl et al., 2007). The boundaries are admittedly arbitrary, but are based on predictive studies with air chemistry–transport models (Meehl et al., 2007), whereas some projections suggest an even greater increase to 80 ppb by 2100 (Fiscus et al., 2005). Indeed, [O₃] in some regions already exceeds the projections intermittently during the cropping season (Fiscus et al., 2005).

2.2. Meta-analyses

Each crop species was analyzed separately to obtain an estimate of the mean effect of elevated [O₃] on that species. The meta-analysis was conducted by using the MetaWin 2.0 statistical software (Rosenberg et al., 2000). To estimate the treatment effect, the natural log of the response ratio ($r = \text{value in elevated [O}_3\text{]} / \text{value in the base [O}_3\text{]}$) was used as the metric for analysis (Hedges et al., 1999; Rosenberg et al., 2000) and reported as the percentage changes from B-O₃ as $(r - 1) \times 100\%$ (Ainsworth et al., 2002; Curtis and Wang, 1998). Negative percentage changes indicate a decrease in the plant variable in response to elevated [O₃] treatment, whereas positive values indicate an increase.

Because many studies did not report information that would allow computation of sample variance (standard deviations or standard errors with replicate size), we had to use an un-weighted approach in which 95% confidence intervals of the effect size were calculated by re-sampling the data using 9999 bootstrap replicates for each analysis (Adams et al., 1997). Estimates of the effect size were assumed to be significant if the 95% confidence intervals did not overlap with zero (Curtis and Wang, 1998; Morgan et al., 2003).

To explain the variation in crop yields response to elevated [O₃], the data were divided into categories, such as different rooting environments (‘pot’ – rooted within a container, or ‘ground’ – rooted directly in the earth), and additional treatments (drought, elevated [CO₂], and additional stress). Heterogeneity among levels of these categorical variables was assessed by re-sampling following Adams et al. (1997). For multiple comparisons, groups were considered to differ significantly if their 95% confidence

intervals did not overlap, providing a conservative test of group differences (Feng et al., 2008; Grantz et al., 2006; Morgan et al., 2003; Taub et al., 2008). Each categorical level for all crops was included in this analysis if there were at least two papers and five observations.

3. Results

3.1. Current ambient $[O_3]$ versus base $[O_3]$

All of the crops included in this analysis showed significant yield losses when grown at C- O_3 relative to B- O_3 (Fig. 1). For potato, the mean yield loss was 5.3%, whereas the yield losses for cereal crops: barley, wheat and rice, were 8.9%, 9.7% and 17.5%, respectively. For the grain legumes: bean and soybean, the yield losses were 19.0% and 7.7%, respectively. The average ambient $[O_3]$ for all crops was within a range of 41–49 ppb. Among the six crops investigated, the largest yield loss was found in bean, with a mean response of -19.0% ($n = 43$) and a 95% CI from -12% to -26% (Fig. 1).

Response of the yield components to $[O_3]$ varied with species (Fig. 2). In potato, C- O_3 did not significantly decrease the individual tuber weight or tuber number per plant. In barley, C- O_3 significantly reduced the individual grain weight (3.5%) and ears per plant (4.8%), but not number of grains per ear. In wheat, individual grain weight (-6.2%) and number of grains per ear (-5.9%) were both significantly decreased when exposed to a mean $[O_3]$ of 39 ppb. In rice, the yield loss resulted from a combination of significant decreases in individual grain weight (-3.1%), number of grains per panicle (-8.4%) and panicles per plant (-8.9%). In bean, C- O_3 induced the yield loss as a result of significant decrease in individual seed weight (-10.5%) and seeds per pod (-12.3%), whereas only individual seed weight (-5.1%) was significantly reduced by C- O_3 in soybean.

No significant difference was found for any variables between crops grown in pots and those grown in the ground (Table 1). In potato, soybean and wheat, the three species with the largest sample size, we categorized treatments into up to four different groups: no additional stress treatment, combination of C- O_3 with drought, combination of C- O_3 with elevated $[CO_2]$, and combination of C- O_3 with other stress treatments including low nitrogen, low or high temperature, low light, enhanced UV-B radiation, and elevated $[NH_3]$ or $[NO_2]$. Additional stress did not aggravate the O_3 -induced

Fig. 1. Response of crop yields to current $[O_3]$ (31–50 ppb) for six crops. Symbols represent the mean percent change at current ambient $[O_3]$ relative to base $[O_3]$ (≤ 26 ppb) and the bars show the 95% confidence intervals (CIs). Degree of freedom (d.f.) for each species is given in parenthesis. Mean $[O_3]$ is expressed on y-axis.

Fig. 2. Response of yield components to current ambient $[O_3]$ (31–50 ppb) for six crops. See Fig. 1 for explanation of the notations.

negative effects on any variables. To the contrary, elevated $[CO_2]$ ameliorated the detrimental effects of C- O_3 relative to those under ambient $[CO_2]$, although significant difference was found only in individual grain mass of wheat (Fig. 3).

3.2. Future $[O_3]$ versus base $[O_3]$

As noted before, F- O_3 was assumed to range from 51 to 75 ppb. Our results demonstrated that F- O_3 of 63 ppb significantly decreased yield by 41.4%, 21.6% and 21.1% in bean, soybean and wheat, respectively, relative to B- O_3 (Fig. 4). The largest loss was observed in bean with the mean response being 41.4% and its 95% CI of 27.7–52.7%, which was significantly greater than all other crops but rice (Fig. 4). There were no significant differences among barley, wheat, rice, or soybean with respect to the yield response to F- O_3 . Consistent with the results with current ambient $[O_3]$, potato yield loss at F- O_3 was the smallest (11.9%).

Responses of the yield components to F- O_3 (Fig. 5) differed from those to C- O_3 (Fig. 2). In potato, O_3 -induced reduction in individual tuber weight (7.2%) contributed to the yield loss more than tuber number per plant (4.4%) (Fig. 5). In barley, F- O_3 significantly reduced individual grain weight (3.6%) and number of ears per plant (10.7%). Yield loss (21%) in wheat resulted from a combination of decreased individual grain weight (12.9%), fewer ears per plant (6.35%) and less grains per ear (6.8%). In rice, F- O_3 significantly reduced individual grain weight (4.0%) and grains per panicle (5.8%), but did not affect number of panicles per plant. In legumes, the yield losses in bean (41.4%) and soybean (21.6%) resulted from reduced individual seed weight (25.6% for bean and 14.0% for soybean) and fewer pods per plant (20.5% for bean and 11.1% for soybean) (Fig. 5).

Table 1

Results of the meta-analysis of current ambient [O₃] (31–50 ppb) effects on crop yield, and its yield components, e.g. seed number per pod (seed no.), individual seed mass, pod number per plant (pod no.) under different rooting environments.

Crop	Variable	Rooting Environment	d.f.	% Change from base [O ₃]	95% CI		Mean [O ₃] (ppb)
					Minimum	Maximum	
Potato	Tuber Yield	Pot	7	−6.46	−11.5	−1.41	44
		Ground	15	−3.01	−8.06	2.06	45
Bean	Seed Yield	Pot	32	−19.2	−27.7	−10.4	42
		Ground	9	−18.5	−28.0	−6.69	43
	Pod No.	Pot	14	−5.77	−10.5	−1.16	44
		Ground	7	1.33	−6.93	9.90	41
Soybean	Seed Yield	Pot	38	−6.73	−11.8	−1.12	42
		Ground	21	−9.31	−15.6	−3.09	41
	Seed Mass	Pot	38	−6.30	−8.78	−3.78	42
		Ground	20	−2.79	−5.08	−0.30	40
	Seed No.	Pot	38	1.33	−0.55	3.27	42
		Ground	12	0.45	−3.93	5.02	37
	Pod No.	Pot	38	−1.20	−4.76	2.48	42
		Ground	12	−7.11	−13.3	−0.92	37
Barley	Grain Yield	Pot	8	−10.9	−19.9	−3.46	46
		Ground	8	−6.72	−11.4	−1.85	38
	Grain Mass	Pot	7	−3.45	−6.53	0.04	45
		Ground	9	−3.60	−5.36	−1.79	37
	Ear No.	Pot	8	−6.70	−11.73	−2.11	46
		Ground	9	−3.09	−7.04	1.53	37
Wheat	Grain Yield	Pot	24	−9.34	−14.5	−4.16	42
		Ground	35	−9.90	−15.9	−4.52	39
	Grain Mass	Pot	20	−2.98	−7.27	1.17	41
		Ground	33	−8.18	−11.5	−5.09	39
	Grain No.	Pot	9	−7.54	−11.4	−3.63	44
		Ground	16	−4.93	−9.38	−0.89	37
	Ear No.	Pot	19	−3.52	−7.42	0.23	41
		Ground	8	−1.52	−11.2	9.37	35
Rice	Grain Mass	Pot	10	−2.14	−3.36	−1.09	35
		Ground	5	−4.8	−10.4	−1.24	40

Degrees of freedom (d.f.) for each estimate, % change from base [O₃] (≤ 26 ppb) and the 95% confidence intervals (CIs) are reported. The mean ambient [O₃] for different rooting environment is also reported.

Comparing all studies performed in pots with those involving plants rooted in the ground, no variables showed a significant difference in any crops (Table 2). There were some indications that elevated [CO₂] or drought ameliorated the detrimental effects of F-O₃ on the yield and its components (Fig. 6). However, only the yield of wheat and potato, and individual grain weight of wheat showed significantly smaller response to F-O₃ under elevated [CO₂], compared with that in ambient [CO₂]. Surprisingly, the other stress treatments including low nitrogen and low light did not significantly alter the O₃ response for any variables in any crops species included (Fig. 6).

4. Discussion

4.1. Are current ambient levels of O₃ causing yield loss in major food crops?

This meta-analysis indicated that surface [O₃] at the current ambient-level induced an average yield loss of 11.3% in the range from 5% to 19% in the six major food crops including cereals, grain legumes and tubers. The results are compared with those reported in previous quantitative reviews. Morgan et al. (2003) indicated a mean yield loss in soybean of about 10% exposed to 30–60 ppb [O₃], which is comparable to the 7.7% decrease seen in this study relative to the width of the confidence intervals.

With wheat, our previous meta-analysis found the mean yield loss of 17.5% and the range from 11.2% to 24.0% in response to mean [O₃] of 43 ppb with a range of 30–59 ppb (Feng et al., 2008), whereas we found only 9.7% (5.8–13.8%) yield loss in this study. The

difference between this and the previous studies can be mostly attributed to the difference in the reference [O₃]. Our main concern in this paper is the impacts of current and future [O₃] on crops. The base [O₃] was hence defined as being less than 26 ppb, which is very close to the base [O₃] in the NCLAN studies (Lesser et al., 1990) as mentioned earlier. The base [O₃] in this study included both charcoal-filtered and non-filtered [O₃] below 26 ppb, and hence it ranged from 3 to 25 ppb with the mean across studies being 13.8 ppb. In the previous study (Feng et al., 2008), on the other hand, we focused on the contrast between control and elevated [O₃], and hence setting the reference [O₃] equal to the charcoal-filtered [O₃], which was on average 6 ppb and ranged from 3 to 10 ppb. The lower reference [O₃] in the previous study should have contributed to the larger effect of [O₃] than the present study. Inclusion of the observations under elevated [CO₂] into this study has only slightly reduced the effects of elevated [O₃] as compared with the previous one, which evaluated the effect of elevated [CO₂] separately. Without [CO₂] enrichment, the wheat yield loss ranged from 6% to 16% with mean yield loss being 11% (Fig. 3), which is only slightly greater than the yield loss including the elevated [CO₂] treatment.

Most studies indicated that rice was less sensitive to chronic O₃ exposure than other major food crops (Feng et al., 2003; Kobayashi et al., 1995; Mills et al., 2007; Wang et al., 2007b). Nevertheless, this analysis demonstrated that the yield loss in rice was as high as 17.5% at mean [O₃] of 41 ppb. This is primarily because of the results with the Pakistani varieties: IRRI-6 and Basmati 385, which showed a yield reduction of 36–57% when exposed to the mean [O₃] of 40–44 ppb (Maggs et al., 1995; Maggs and Ashmore, 1998). Noting the

Fig. 3. Responses of crop yield and yield components to current ambient [O₃] (31–50 ppb) in combination with additional treatments. See Fig. 1 for explanation of the notations.

Fig. 4. Response of crop yields to future ambient [O₃] (51–75 ppb) for six crops. See Fig. 1 for explanation of the notations.

Fig. 5. Response of yield components to future [O₃] (51–75 ppb) for six crops. See Fig. 1 for explanation of the notations.

anomalously low harvest index, e.g. 0.16 in the filtered-air treatment, in those studies (Maggs et al., 1995; Maggs and Ashmore, 1998), we reanalyzed the data excluding them. The results showed that current [O₃] reduced yield in rice by 7.4%, with a 95% CI of 5.75–9.33%, which is smaller than that found initially (Fig. 1), and is comparable to other species. It is thus suggested that rice is no less sensitive to current ambient [O₃] than other species. Similar results with rice have also been reported by Ainsworth (2008).

In the Yangtze River Delta of China, surface [O₃] measurements demonstrated that mean [O₃] across the rice growing season (July–October) ranged from 38 to 46 ppb and the average across the locations was 43 ppb (Wang et al., 2006), which is higher than the mean current ambient [O₃] (41 ppb) in this meta-analysis. Therefore, it can be inferred that O₃ has already been reducing rice production in China, where the farmers produce approximately one-third of the global rice crop (Coats, 2003).

The largest yield loss in our results was 19% with bean, along with a 95% CI of 12–26%, which is based on 43 measurements and 13 individual studies, 22 cultivars and/or lines and across seven countries under [O₃] in the range of 30–50 ppb. This result indicated that bean is very sensitive to O₃, in agreement with the study of Mills et al. (2007), who ranked bean as the most sensitive among agricultural crops according to O₃ critical levels (AOT40 for 5% yield reduction). Filtration studies at Mediterranean sites, where O₃ exposures are among the highest in Europe, have shown yield loss above 20% of *P. vulgaris* L. (Schenone et al., 1992).

Fresh or processed potato tubers already form a major component of the human diet and may become increasingly important for human nutrition, especially in developing countries, because the ratio of edible to non-edible components (harvest index) is much

Table 2

Results of the meta-analysis of elevated $[O_3]$ (51–75 ppb) effects on crop yield, and its yield components, e.g. seed number per pod (seed no.), individual seed mass, pod number per plant (pod no.) under different rooting environments.

Crop	Variable	Rooting Environment	d.f.	% Change from base $[O_3]$	95% CI		Mean elevated $[O_3]$ (ppb)
					Minimum	Maximum	
Bean	Seed Yield	Pot	11	–41.4	–51.8	–28.1	63
		Ground	4	–41.2	–65.6	0.39	68
Soybean	Seed Yield	Pot	33	–24.6	–30.2	–18.3	66
		Ground	50	–19.5	–23.2	–15.5	63
	Seed Mass	Pot	28	–16.4	–19.7	–12.9	67
		Ground	26	–11.3	–13.5	–9.04	65
	Seed No.	Pot	27	–0.81	–3.16	1.53	67
		Ground	16	–1.60	–3.68	0.82	66
	Pod No.	Pot	27	–11.0	–15.7	–5.76	67
		Ground	16	–11.4	–15.7	–6.44	66
Wheat	Grain Yield	Pot	15	–20.0	–26.4	–14.1	65
		Ground	25	–21.8	–27.4	–15.9	65
	Grain Mass	Pot	16	–10.1	–13.9	–6.08	68
		Ground	28	–14.5	–19.0	–9.99	63

Degrees of freedom (d.f.) for each estimate, % change from base $[O_3]$ (≤ 26 ppb) and the 95% confidence intervals (CIs) are reported. The mean elevated $[O_3]$ for different rooting environment is also reported.

greater than in cereals such as wheat, rice and maize (Vandermeiren et al., 2005). CHIP was a large-scale OTC project to provide field-based data spanning a wide range of climatic conditions and O_3 concentrations in Europe using a common cultivar, Bintje (De Temmerman et al., 2002). Our results supported the model simulations based on the CHIP dataset, and indicated that elevated $[O_3]$ would reduce potato tuber yield by 3–5% across Europe (Wolf and Van Oijen, 2003).

The exposure–response relationships have allowed the yield losses for different crops to be estimated for a given ozone exposure (Ashmore, 2002). According to the linear dose–response model (Mills et al., 2000, 2007), we estimated the yield loss of individual crop, and compared with the results of this meta-analysis (Table 3). Among the crop species, rice, bean and soybean exhibited responses to elevated $[O_3]$ comparable between the two methods. For wheat, the mean yield loss from dose–response function was greater than that from this meta-analysis. This is possibly because this study included observations conducted in greenhouses and controlled growth chambers as well as those in open-top chambers, whereas the dose–response functions were derived from open-top chamber experiments (Mills et al., 2000, 2007). It has been found that the effects of ozone on wheat growth tend to be less in indoor growth chambers than in open-top chambers (Feng et al., 2008).

A larger difference was found between the two approaches in potato yield response to $[O_3]$ (Table 3). Our results showed lower yield loss possibly due to the observations under elevated $[CO_2]$. Fig. 3 shows that the O_3 -induced yield loss in potato is less when combined with elevated $[CO_2]$ (–2%) than in ambient $[CO_2]$ (–8%), and that the yield loss in ambient $[CO_2]$ has the CI that overlaps with the yield loss estimate from the exposure–response relationship. For barley, the yield loss estimated from Mills et al. (2000, 2007) studies is based on a very weak correlation ($r^2 = 0.0012$, $n = 47$) between the relative yield and the ozone dose, and, hence,

should be subject to a large estimation error. The apparent difference between the two approaches for barley (Table 3) should therefore be considered non-significant.

Numerous studies have shown that O_3 frequently reduces yield in grain crops by decreasing ear and pod numbers, seed numbers per ear, spikelet or pod (and hence seed number per plant), and individual seed weight (see review by Black et al., 2000). From our meta-analysis, response of different yield components to $[O_3]$ varied by crop species and treatment $[O_3]$. It is noteworthy that reduced weight of individual grain or seed is often the major cause of the yield loss to O_3 in cereals and grain legumes (Figs. 2 and 5). This yield component is under genetic control, and usually most conservative among the yield components against the environmental stresses. It is affected by occurrence of stresses only during the grain filling stage. The results in Figs. 2 and 5 hence imply that the effect of ozone on crop yield is exerted through accumulation of the damages or that the plants are more sensitive to ozone at the later stages.

4.2. To what extent will future levels of surface O_3 reduce yield of major food crops?

In this meta-analysis, we assumed that future $[O_3]$ is represented by a daytime concentration of 51–75 ppb during the crop growth. The average daytime $[O_3]$ in the studies reviewed in this analysis increased from 42 ppb for current ambient air to 63 ppb for future air. Given the current emission trends, surface $[O_3]$ is projected to rise globally by 20–25% between 2015 and 2050, and 40–60% by 2100 (Meehl et al., 2007), supporting our assumptions on current and future $[O_3]$. Compared with yield loss at current ambient $[O_3]$, future $[O_3]$ could drive a further 10% decrease in yield for soybean, wheat and rice, and 20% for bean, indicating the future

Table 3

Comparison of yield losses estimated from this meta-analysis and dose–response function, based on average $[O_3]$ of all observations for specific crop species.

	Potato	Barley	Wheat	Rice	Bean	Soybean
$[O_3]$ (ppb) ^a	44.7	41.9	40.5	41	42.3	41.8
Yield loss (%) ^b	12.1	3.87	14.4	8.95	17.9	9.13
Yield loss (%) ^c	1.5–9.24	4.15–14.2	5.83–13.8	5.75–9.33 ^d	12–26.2	3.53–11.7

^a Average $[O_3]$ from all observations for specific crop species.

^b Estimated from exposure–response function (Mills et al., 2000, 2007).

^c Calculated from this meta-analysis.

^d The data were estimated excluding the studies of Maggs et al. (1995), due to lower HI.

Fig. 6. Responses of crop yield and yield components to future [O₃] (51–75 ppb) in combination with additional treatments. See Fig. 1 for explanation of the notations.

[O₃] as a significant threat against food production in the world (Ashmore et al., 2006).

It must be noted that O₃ is not the only element of global change, and that O₃ will interact with other factors such as water stress, [CO₂] and temperature. Previous meta-analyses showed that elevated [CO₂] and drought significantly lessen the yield loss due to elevated [O₃] in soybean (Morgan et al., 2003) and wheat (Feng et al., 2008). In this study also, elevated [CO₂] ameliorated the detrimental effects of elevated [O₃] (Fig. 6). The interacting effects of elevated [CO₂] are very important when predicting the O₃ impacts on crop production under higher [CO₂] in the future (Fiscus et al., 2005). The elevated [CO₂] will reduce stomatal conductance and, thereby, O₃ uptake into leaves. The O₃ impacts will be less than those predicted from [O₃] under current [CO₂] (Fiscus et al., 2005), because of the reduced O₃ uptake in combination with other changes due to elevated [CO₂] (Booker and Fiscus, 2005; Cardoso-Vilhena et al., 2004). Other factors than [CO₂] could also change in the future, and alter the impacts of increasing [O₃]. In this study, however, they did not change the O₃ impact significantly (Fig. 6), possibly because of the smaller number of observations for the

interactive effects than the previous studies (Feng et al., 2008; Morgan et al., 2003).

To address the interacting effects of elevated [CO₂] and other factors on the O₃ impacts, the flux-based dose–response relationships (Pleijel et al., 2007) would be better suited than the concentration-based approach (Pleijel et al., 2004). This is clearly a step forward toward the mechanism-based estimation of the crop losses. However, the estimation of O₃ uptake requires extra pieces of information for stomatal conductance, and therefore the flux-based approach is currently limited to wheat and potato, for which the relevant data are available across a number of studies (Pleijel et al., 2007). The same limitation applies to the meta-analysis to an even greater extent. If the O₃ dose were to be flux-based rather than concentration-based, the meta-analysis would lose its virtue of being based on all available publications, most of which lacks the information to estimate the O₃ uptake. As a more feasible approach in meta-analysis, the observations were grouped according to additional treatments, some of which alter the O₃ uptake, and the O₃ impacts were compared between the groups. The ameliorating effects of elevated [CO₂] due largely to reduced O₃ uptake (Fiscus et al., 2005) have been confirmed in this and other meta-analyses (Feng et al., 2008; Morgan et al., 2003).

The distinction between [O₃] and O₃ uptake also raises a concern about the alteration to the O₃ impacts by chambers. It has been shown that, in open-top chambers, O₃ uptake by plants is either larger (Nussbaum and Fuhrer, 2000) or smaller (Piikki et al., 2008) than in the field to the extent that would alter the resultant impacts on plants. Free-air controlled environment (FACE) technology provides a means to examine the impact of elevated [O₃] relative to current background [O₃] without the alterations to O₃ uptake by chambers (McLeod and Long, 1999). Using a FACE system, Morgan et al. (2006) showed that a 23% increase in [O₃] from an average daytime ambient level of 56 ppb to the elevated level of 69 ppb over two growing seasons caused a 20% decrease in soybean yield. This is much larger than the 8% yield loss expected from the chamber results. It must therefore be noted that the detrimental effects of elevated [O₃] may be larger than those estimated in this study as well as other studies based on the exposure–response functions derived from chamber experiments. FACE experiments are urgently needed for major crop species to better predict the impacts of increasing surface [O₃]. It is of particular importance to study rice under elevated [O₃] and [CO₂], for which studies are lacking even in chambers (Ainsworth, 2008). Rice is the most important staple crop in Asia, where we could see a large increase in surface [O₃] in the near future (Wang and Mauzerall, 2004; Yamaji et al., 2008). As we found in this study, rice is no less sensitive to elevated [O₃] than other species.

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Appendix. References used in meta-analysis of current and future ozone effects

Soybean

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Wheat

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