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Rice production in a changing climate: a meta-analysis of responses to elevated carbon dioxide and elevated ozone concentration

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Abstract

Rice is arguably the most important food source on the planet and is consumed by over half of the world's population. Considerable increases in yield are required over this century to continue feeding the world's growing population. This meta-analysis synthesizes the research to date on rice responses to two elements of global change, rising atmospheric carbon dioxide concentration ([CO_2]) and rising tropospheric ozone concentration ([O_3]). On an average, elevated [CO_2] (627 ppm) increased rice yields by 23%. Modest increases in grain mass and larger increases in panicle and grain number contributed to this response. The response of rice to elevated [CO_2] varied with fumigation technique. The more closely the fumigation conditions mimicked field conditions, the smaller was the stimulation of yield by elevated [CO_2]. Free air concentration enrichment (FACE) experiments showed only a 12% increase in rice yield. The rise in atmospheric [CO_2] will be accompanied by increases in tropospheric O_3 and temperature. When compared with rice grown in charcoal-filtered air, rice exposed to 62 ppb O_3 showed a 14% decrease in yield. Many determinants of yield, including photosynthesis, biomass, leaf area index, grain number and grain mass, were reduced by elevated [O_3]. While there have been too few studies of the interaction of CO_2 and O_3 for meta-analysis, the interaction of temperature and CO_2 has been studied more widely. Elevated temperature treatments negated any enhancement in rice yield at elevated [CO_2], which suggests that identifying high temperature tolerant germplasm will be key to realizing yield benefits in the future.

Keywords: cultivar, face, global change, *Oryza sativa*, photosynthesis, stress, yield

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Introduction

Rice (*Oryza sativa* L.) is produced in at least 95 countries across the globe and provides a staple food for more than half of the world's current population (IRRI, 2002; Coats, 2003). As population increases over this century, the demand for rice will grow to an estimated 2000 million metric tons by 2030 (FAO, 2002). Meeting this $\sim$ 35% increase in demand will require significant improvements in rice production. However, achieving these improvements will be a challenge as the future climate changes and water scarcity increases (Bouman *et al*., 2007).

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Current Intergovernmental Panel on Climate Change (IPCC) projections indicate that atmospheric CO_2 concentration ([CO_2]) will increase over this century, reaching 730–1020 ppm by 2100 (Meehl *et al*., 2007). An increase in global temperature, ranging from 1.1 to 6.4 °C depending on global emissions scenarios, will accompany the rises in atmospheric [CO_2] (Meehl *et al*., 2007). In China, where farmers produce approximately one-third of the global rice crop (Coats, 2003), these anticipated changes in temperature and [CO_2] have been modeled to have opposite effects on the production (Erda *et al*., 2005). Increasing temperatures shortened the growing season leading to decreased yields, while elevated [CO_2] increased the yields (Erda *et al*., 2005). Using the CERES rice model adopted for Northern India, Lal *et al*. (1998) projected that a 2 °C increase in temperature would cancel out the positive effect of elevated [CO_2] on rice yields, and that increasing water shortage in combination with rising temperature will likely limit rice production, even with rising [CO_2]. China and India are the two largest producers of rice globally (Coats, 2003), and these modeling efforts demonstrate the significant challenge of increasing rice production to meet the needs of growing populations.

Along with [CO_2], tropospheric ozone concentration ([O_3]) has also risen since the industrial revolution (Forster *et al*., 2007). Unlike CO_2, O_3 is a short-lived and highly variable atmospheric constituent. Ozone is a secondary pollutant formed from oxidation of carbon monoxide (CO), methane (CH_4) or nonmethane volatile organic compounds in the presence of nitrogen oxides (NO_x; Fowler *et al*., 1999). During the 1990's, there were five global 'hot spots' where 3-month mean [O_3] reached 60–70 ppb, and two of the hot spots were in rice-growing regions of China and India (Emberson *et al*., 2001). Wang & Mauzerall (2004) estimated that O_3-induced yield loss in rice in China was 4% in 1990, equivalent to a profit loss of roughly $1.2 billion. O_3-induced yield loss in China is conservatively projected to double by 2020 (Wang & Mauzerall, 2004) as emissions and O_3 precursors substantially increase (Streets & Waldhoff, 2000; Unger *et al*., 2006).

In order to improve modeling and breeding efforts in the future, it is increasingly important to quantify how rice physiological and yield parameters will respond to anticipated changes in the atmosphere. The components of harvestable yield in rice are the number of panicles on unit ground area, the number of filled spikelets per panicle, and grain weight. A change in any of these parameters at elevated [CO_2] or elevated [O_3] will alter the final yields. While there have been surprisingly few studies that have investigated the combined effects of elevated [CO_2] and elevated tropospheric [O_3] on rice (Olszyk & Wise, 1997), there have been a number of studies that investigated the individual effects of elevated [CO_2] or elevated [O_3] on rice physiology and production. These studies provide a large database from which it is possible to distill the mean response of rice parameters to elevated [CO_2] and elevated [O_3] using meta-analysis, and thereby improve understanding of the mechanisms that determine yield. This approach has been used to study the response of soybean to elevated [CO_2] (Ainsworth *et al*., 2002) and elevated [O_3] (Morgan *et al*., 2003). It has also been used to synthesize crop responses to elevated [CO_2] in FACE experiments (Ainsworth & Long, 2005; Long *et al*., 2006), but the mean response of rice to climate change has not been quantitatively assessed.

Here, the response of rice to two global changes that directly affect photosynthesis and productivity is quantitatively reviewed using meta-analysis. Over the past four decades, the methods for fumigating crops with elevated [CO_2] or elevated [O_3] have changed and the major cultivars have changed. Individual studies have also used different target CO_2 and O_3 treatment concentrations and different nutrient or stress conditions. While these differences pose challenges to distilling a mean response of rice to elevated [CO_2] or elevated [O_3], the meta-analytic approach allows a statistical test of whether experimental factors like cultivar or fumigation method significantly alter the mean response to elevated [CO_2] or elevated [O_3] (Curtis & Wang, 1998). The aims of this study are first to synthesize the mean response of rice physiological and yield characteristics to elevated [CO_2] and elevated [O_3], and second to test if different methods of fumigation, different cultivars or different stress treatments significantly alter the mean response of rice to elevated [CO_2].

Materials and methods

Development of databases

The Web of Science® citation database (ISI, Thomson Inc., Philadelphia, PA, USA) and the Agricola database (SilverPlatter International) were searched for all peer-reviewed primary literature of rice photosynthesis, biomass and yield responses to elevated [CO_2] or elevated [O_3]. The search included peer-reviewed journal articles from 1980 to 2007. Seventy manuscripts provided relevant data investigating the CO_2 response of rice yield, individual grain mass, grain number, panicle number, harvest index (HI; the ratio of grain weight to total plant weight), aboveground biomass, leaf area index (LAI), leaf nonstructural carbohydrates (TNC), light-saturated photosynthetic rate (A_{sat}) and/or stomatal conductance to water vapor (g_s) (Appendix S1). Twelve manuscripts provided data investigating the response of rice to elevated [O_3] (Appendix S2). The majority of studies investigated rice grown under flooded conditions. Mean values for each variable from treatment (elevated [CO_2] or elevated [O_3]) and control (ambient [CO_2] or charcoal-filtered air) conditions were recorded from each study, along with standard deviations of the means and sample sizes. Within an individual study, different cultivars, stress or nutrient treatments, or treatment concentrations of CO_2 or O_3 were considered to be independent (Curtis & Wang, 1998; Ainsworth *et al*., 2002).

Meta-analysis

The natural log of the response ratio (r = response in elevated [CO_2]/response in ambient [CO_2]) was used as the metric for analysis (Hedges *et al*., 1999; Rosenberg *et al*., 2000). The meta-analysis procedure followed the techniques of Curtis & Wang (1998), using the statistical software, METAWIN (Rosenberg *et al*., 2000). The mixed-model analysis was used based on the assumption of random variation in responses among studies, and a weighted parametric analysis was used whenever possible (i.e. when the standard errors or variances and sample sizes were reported). In the weighted analysis, each individual observation was weighted by the reciprocal of the mixed-model variance (Curtis & Wang, 1998; Gurevitch & Hedges, 1999). Normal quantile plots were plotted to check normality of the data before proceeding with the weighted analyses. A weighted parametric analysis was conducted for all measures, except panicle number, where data limitations only allowed an unweighted analysis in which the variance was calculated by resampling (Adams *et al*., 1997; Gurevitch & Hedges, 1999; Morgan *et al*., 2003). In the O_3 study, all variables except panicle number were analyzed using weighted parametric analysis. For all analyses, 95% confidence intervals that did not overlap with zero were considered significant.

To test whether different cultivars or growth conditions quantitatively altered the CO_2 response, the data were divided into categories, such as different cultivars, or for continuous variables such as [CO_2], ranges of concentration. Heterogeneity (Q_T) was partitioned within and between levels of categorical variables [i.e. cultivar, concentration of CO_2, method of CO_2 fumigation and stress treatment (Curtis & Wang, 1998; Ainsworth *et al*., 2002)]. Between-group heterogeneity (Q_B) for each categorical variable was first examined across all data, then the dataset was subdivided according to levels of those categorical variables with significant Q_B. Means of different categories were considered significantly different from one another if their 95% confidence intervals did not overlap (Curtis & Wang, 1998; Ainsworth *et al*., 2002). This categorical analysis was not possible with the elevated [O_3] database due to the limited sample sizes.

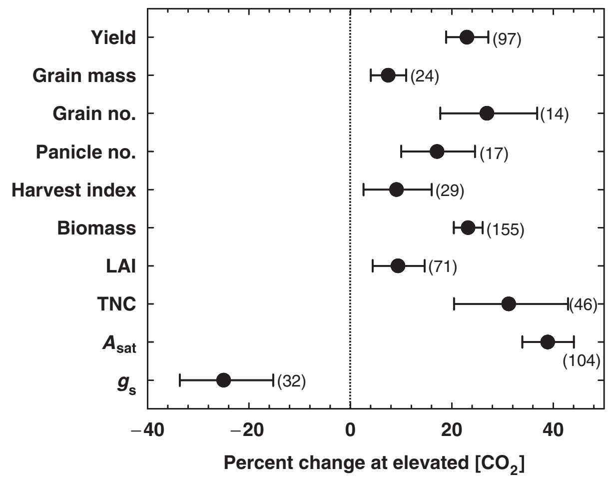

Fig. 1 Rice responses to elevated [CO_2]. Symbols represent the percent change at elevated [CO_2] and are surrounded by 95% confidence intervals. The degrees of freedom for each agronomic or physiological parameter are given in parentheses on the right axis. LAI, leaf area index; TNC, total leaf nonstructural carbohydrates; A_{sat}, light-saturated photosynthetic rate; g_s, stomatal conductance to water vapor.

Table 1 Between-group heterogeneity (Q_B) for CO_2 effect size across different categorical variables

Variable	*k*	Elevated [CO_2]	Method	Cultivar	Stress
Yield	98	7.52*	68.62**	100.7***	10.22*
Grain number	15	3.98	2.68	3.32	19.16**
Grain weight	25	12.97*	11.00*	14.47**	13.64**
Panicle number	18	6.87	0.19	0.591	2.23
Harvest index	30	15.33**	24.62***	37.79***	11.81*
Biomass	156	2.79	5.84	68.20***	3.48
LAI	72	5.20	0.24	10.04	1.22
TNC	47	4.95	5.62	7.49	0.49
A_{sat}	105	9.90**	174.4***	139.9***	4.37
g_s	33	0.02	0.12	0.07	—

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
k represents the number of studies for each variable.

Results

When averaged across all studies, increasing [CO_2] from an average of 365 to 627 ppm increased rice yields by 23% (Fig. 1). The increase in rice yields at elevated [CO_2] came from a combination of increased individual grain mass (+ 7%), greater panicle number (+17%), and greater grain number (+27%; Fig. 1). HI increased by 9% at elevated [CO_2], despite the significant increase in aboveground biomass (Fig. 1). Examination of the physiological mechanisms of response revealed that A_{sat}, TNC, and LAI were all significantly higher at elevated [CO_2], while g_s was 25% lower at elevated [CO_2] (Fig. 1).

All experiments were subdivided into three treatment [CO_2] categories: 500–599, 600–699, and ≥700 ppm. The treatment [CO_2] significantly affected the magnitude of the response of yield, grain mass, HI, and A_{sat} (Table 1; Fig. 2) with a consistent trend towards a greater stimulation with higher treatment [CO_2] (Fig. 2). For elevated [CO_2] between 500 and 599 ppm, there was no significant enhancement of grain mass or HI (Fig. 2). For both variables, a significant enhancement

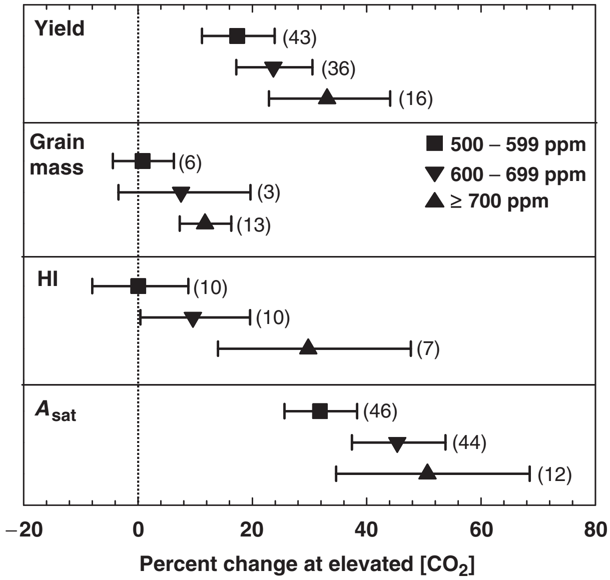

Fig. 2 The effect of CO_2 treatment concentration on rice yield, individual grain mass, harvest index (HI), and light-saturated photosynthetic rate (A_{sat}). Symbols represent the percent change at elevated [CO_2] and are surrounded by 95% confidence intervals. The degrees of freedom are given in parentheses.

Table 2 Between-group heterogeneity (Q_B) and significance (P) for subgroups of response variables

Variable	Elevated [CO_2] (ppm)	Method	Cultivar	Stress
Yield	500–599	*4.175, 0.063*	0.57, 0.709	6.41, 0.244
	600–699	44.41, 0.001	34.75, 0.025	1.35, 0.680
A_{sat}	500–599	16.06, 0.004	15.39, 0.011	1.66, 0.491
	600–699	0.03, 0.893	–	1.18, 0.118

Data were first partitioned according to different treatment CO_2 concentrations, then categories were tested for heterogeneity.

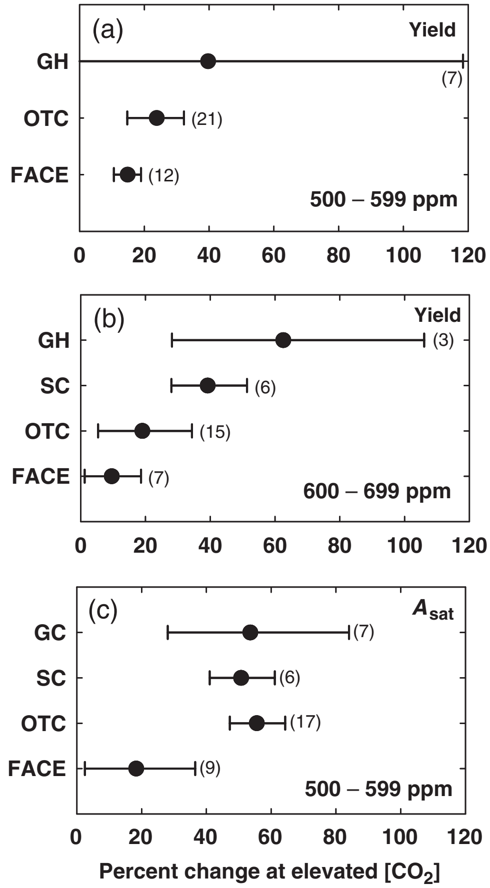

Fig. 3 Variation in rice yield (upper panel) and light-saturated photosynthetic rate (A_{sat}; lower panel) with method of fumigation. Elevated [CO_2] treatments were first divided into two categories: 500–599 and 600–699 ppm, then methods of fumigation were tested for differences in response (Table 2). Symbols represent the percent change at elevated [CO_2] and are surrounded by 95% confidence intervals. The degrees of freedom are given in parentheses. GH, greenhouse; GC, growth chamber; SC, closed sunlit chamber; OTC, open-top chamber; FACE, free air concentration enrichment.

was only apparent at elevated [CO_2] ≥ 700 ppm (Fig. 2).

Method of fumigation, cultivar, and stress treatment affected the mean response of yield and A_{sat} to elevated [CO_2] within each CO_2 treatment category (Table 2; supplementary Table S1). The method of fumigation significantly altered rice responses to elevated [CO_2] when studies were subdivided to those between 500–599 and 600–699 ppm (Table 2). Rice yield was stimulated to a greater magnitude when plants were exposed to elevated [CO_2] in greenhouses or closed sunlit chambers [SC; e.g. Soil-Plant-Atmosphere-Research chambers (Baker *et al.*, 1997)], compared with open-top chambers (OTCs) or FACE (Fig. 3b). While the percent stimulation in rice yield was higher in OTCs compared with FACE (Fig. 3a and b), the 95% confidence intervals overlapped. However, the percent stimulation in A_{sat} at elevated [CO_2] was significantly greater in rice plants grown in OTCs (56%) compared with FACE (18%) for elevated concentrations of 500–599 ppm (Fig. 3c).

Yield, grain mass, grain number, and HI responses to elevated CO_2 were also affected by additional stress treatments (Table 1; Fig. 4). Rice grown under low N or high-temperature conditions lacked a yield response to elevated [CO_2] (Fig. 4); however, there were a limited number of studies that investigated the interactions. When rice was grown under low-P conditions, the percent change in grain mass and grain number at elevated [CO_2] was nearly three times that of rice grown with no additional stress treatment (Fig. 4). The HI of

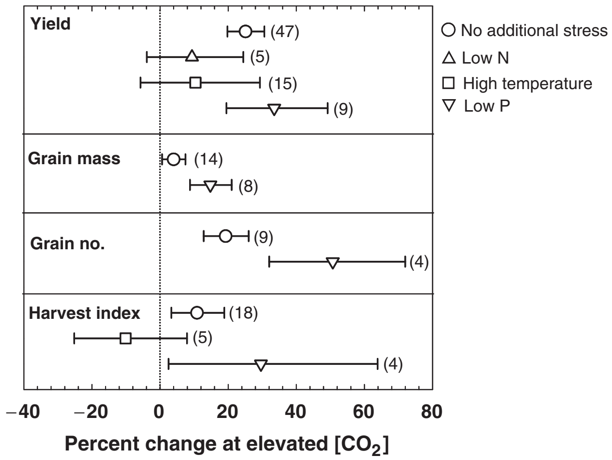

Fig. 4 The effect of different stress treatments of the response of yield, grain mass, grain number, and harvest index to elevated [CO_2]. Symbols show percent change at elevated [CO_2] surrounded by 95% confidence intervals. The degrees of freedom are given in parentheses.

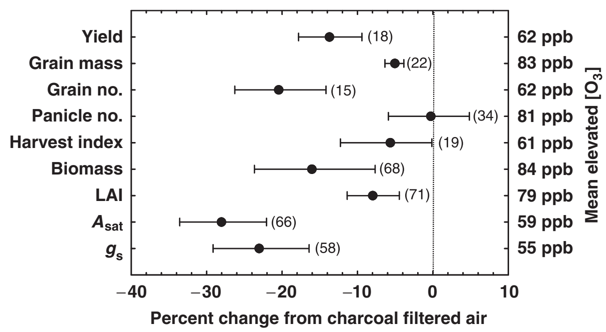

Fig. 5 Rice responses to elevated [O_3]. Symbols represent the percent change at elevated [CO_2] and are surrounded by 95% confidence intervals. The mean treatment O_3 concentrations for each variable are given on the right axis and degrees of freedom for each agronomic or physiological parameter are given in parentheses.

plants grown at elevated [CO_2] with no additional stress treatment increased by 11%. When plants were challenged with high temperature, there was no change in HI at elevated [CO_2], but when plants were grown at low P, HI increased nearly 30% (Fig. 4).

While elevated [CO_2] stimulated rice yield and yield determinants (Fig. 1), elevated [O_3] negatively impacted nearly every aspect of rice performance (Fig. 5). When compared with charcoal-filtered air, chronic, elevated [O_3] (62 ppb) decreased rice yields by 14%. The yield components driving this response were a 5% decrease in the mass of individual grains and a 20% decrease in grain number. Panicle number was not significantly affected by elevated [O_3]. Aboveground biomass decreased by 16% on an average at elevated [O_3], LAI decreased by 8%, and HI also significantly decreased (Fig. 5). Photosynthetic rates were 28% lower when rice was grown at elevated [O_3] compared with charcoal-filtered air and g_s was reduced by 23% (Fig. 5).

Discussion

The world's annual rice production needs to markedly increase over the next 30 years in order to meet the projected demand from population growth (IRRI, 2002). This meta-analysis shows that an increase in rice production will be aided by rising atmospheric [CO_2] (Fig. 1), but hindered by rising background [O_3] (Fig. 5). Perhaps the most critical results from this study are that both low-N treatments and high-temperature treatments negated any enhancement in rice yield at elevated [CO_2] (Fig. 4); however, there were a limited number of studies that investigated these important interactions. Kim *et al*. (2003b) showed a linear relationship between the % increase in yield at elevated [CO_2] and the % increase in spikelet number. Low N fertilization limited N uptake during vegetative growth, which constrained any increase in spikelet number, thereby limiting the yield response (Kim *et al*., 2003b). Low N may also cause more pronounced acclimation of photosynthesis to elevated [CO_2], which can limit total dry matter and leaf area increases at elevated [CO_2] (Suter *et al*., 2001; Ainsworth *et al*., 2003). There are a variety of mechanisms of rice responses to high temperature which limit the yield response to elevated [CO_2]. Matsui *et al*. (1997) demonstrated that high temperatures during flowering increased pollen sterility. Such high spikelet temperatures might be exacerbated by reductions in transpiration and therefore evaporative cooling of the leaf canopy at elevated [CO_2] (Bernacchi *et al*., 2007). Further, panicle weight and HI were adversely affected by high temperatures in three different rice cultivars regardless of growth [CO_2] (Moya *et al*., 1998). Without continued use of N-fertilizer and identification of rice germplasm that is tolerant to high temperatures, CO_2-induced yield gains will most likely be limited in the future.

There has been ongoing debate in the literature about the extent to which different methods of fumigation alter the measured response of crops to elevated [CO_2] and whether this might impact predictions of future food supply (Long *et al*., 2005, 2006; Tubiello *et al*., 2007; Ziska & Bunce, 2007). This meta-analysis statistically tested if method of fumigation altered the mean response of different yield parameters to elevated [CO_2] in rice (Table 1). The mean response of yield, HI, grain weight, and A_{sat} all varied with method of fumigation (Table 1). However, studies with different fumigation techniques also used different cultivars, which may potentially confound the interpretation of results. When elevated CO_2 concentrations were limited to those between 500 and 599 ppm or 600 and 699 ppm, method still had a significant effect on the percent stimulation of yield and A_{sat} (Table 2; Fig. 3). Unfortunately, not all studies have been done at the same control [CO_2]. This is primarily because atmospheric [CO_2], which serves as the control in open-top chamber and FACE studies, has increased from 339 ppm in 1980 to a present concentration of 385 ppm (Dr Pieter Tans, NOAA ESRL, www.cmdl.noaa.gov/gmd/ccgg/trends). Therefore, the possibility remains that these results are confounded by the fact that ambient [CO_2] ranged from 365 to 385 ppm in FACE studies (e.g. Kim *et al*., 2003a; Yang *et al*., 2006a, b; Shimono *et al*., 2007), while ambient [CO_2] in earlier chamber studies was more frequently controlled to 330–360 ppm (e.g. Baker *et al*., 1990, 1992, 1997; Teramura *et al*., 1990; Ziska & Teramura, 1992; Seneweera *et al*., 1996). In this meta-analysis, the average ambient [CO_2] for FACE and OTC studies was 372 and 369 ppm, respectively, so this did not pose a problem for the comparison of FACE and OTC studies. However, the average ambient [CO_2] for SC studies was 346 ppm, which likely exacerbated the differences in response (Fig. 3).

Scaling all of the data to a common ambient or elevated [CO_2] using a linear scaling approach or a beta factor has been suggested as a method to control for the differences in ambient [CO_2] (Amthor & Koch, 1996; Tubiello *et al*., 2007; Ziska & Bunce, 2007). The beta factor is calculated as

$$\beta = \frac{[(Y_{Ele} - Y_{Amb})/Y_{Amb}]}{\ln([CO_2]_{Ele}/[CO_2]_{Amb})},$$

where yield at elevated [CO_2] is represented by Y_{Ele}, yield at ambient [CO_2] is represented by Y_{Amb}, and elevated and ambient [CO_2] are $[CO_2]_{Ele}$ and $[CO_2]_{Amb}$, respectively. After the beta factor is calculated for each individual experiment, it can then be used to estimate the [CO_2] stimulation for a given experiment at any [CO_2]. The approach of using beta factors to scale data has major limitations. First, beta factors presume that the shape of the response curve is fixed and known, *a priori*, and second, only two points are used to predict the response over a large range of CO_2 concentrations. This has the problem of extending conclusions well outside of the range of original measurements. Further, a very large range of potential response curves are predicted by the data, any of which might or might not be accurate (Fig. 6), and all of which are subsequently used to adjust individual data points to common [CO_2]. The advantage of the meta-analytic approach is that both ambient and elevated [CO_2] can be grouped into similar ranges and a statistical test of the difference in those ranges can be made (Fig. 3; supplementary Table S1). While the comparison of FACE and SC studies was affected by the ambient [CO_2] as described earlier in the text, applying 'correction factors' such as the beta factor would introduce more error.

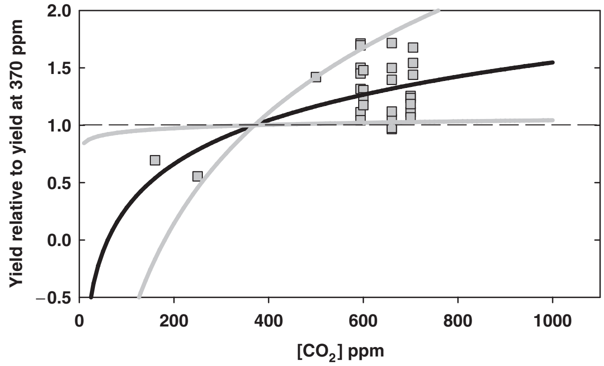

Fig. 6 The range of responses of individual SC studies, scaled to 370 ppm (gray squares). The mean predicted response from the average beta factor ($\beta = 0.68$) for SC studies is illustrated by the black line. The upper and lower ranges of predicted responses from SC beta factors ($\beta = 0.04$, 1.39) are illustrated by the gray lines.

The responses of both soybean and rice to elevated [CO_2] and elevated [O_3] have now been quantitatively reviewed using meta-analysis (Ainsworth *et al*., 2002; Morgan *et al*., 2003), and provide an interesting basis for comparison of two of the world's major food crops. In both the crops, elevated [CO_2] stimulated photosynthetic carbon uptake, aboveground biomass, and final harvestable yield; however, there were differences in the components of yield. On an average, individual seed mass was not affected by elevated [CO_2] in soybean, but grain mass was significantly higher in elevated [CO_2] in rice. Notably, HI was significantly decreased by elevated [CO_2] in soybean, and was significantly increased by elevated [CO_2] in rice. These differences suggest that while some mechanisms of response to [CO_2] are conserved between species, others differ significantly. One possibility is that rice's ability to produce multiple stems provides a greater capacity for improvements in HI compared with species with one stem (Seeneweera *et al*., 1994).

The responses of rice and soybean to elevated [O_3] were very similar, with both crops showing significant decreases in stomatal conductance, carbon assimilation, aboveground biomass, individual grain number and mass, and final harvestable yield (Morgan *et al*., 2003). This is quite surprising given that previously rice has been estimated to be less sensitive to chronic O_3 exposure than other major crops (Wang & Mauzerall, 2004). Monitoring stations in some parts of rural areas of China have measured current annual concentrations as high as 74 ppb, with hourly maximums nearing 200 ppb (Wang *et al*., 2007). These concentrations exceed the mean concentration of O_3 from this meta-analysis, which showed a significant 14% decrease in rice yield at 62 ppb. Current rice yield losses from O_3 are estimated at 4%, but on a regional scale, these are probably substantially greater (Wang *et al*., 2007). This meta-analysis reviewed rice responses to chronic low-level [O_3] treatments, but concentrations are already reaching levels that cause acute damage; therefore, the decreases projected by this analysis are probably underestimates of potential future O_3-induced yield loss.

As [CO_2] rises in the future, it may protect against yield loss from the increase in ground-level [O_3]. However, studies of the interaction of elevated [CO_2] and [O_3] have been very limited (Olszyk & Wise, 1997). Olszyk & Wise (1997) found that elevated [CO_2] ameliorated some of the detrimental effects of elevated [O_3] on plant growth and leaf injury; however, rice plants were not grown to maturity and the authors warn that the results should be considered preliminary because of the greenhouse environment in which the study was conducted. Therefore, attention must be given to understanding the interactive effects of elevated [CO_2], rising tropospheric [O_3], rising temperature and nitrogen supply, if we are to be able to forecast with any confidence future supply of the world's most important food cereal.

Conclusions

This meta-analysis provides a synthesis of rice responses to elevated [CO_2] and elevated [O_3]. While future yields have the potential to be stimulated by [CO_2], the degree of stimulation will be dampened by increasing temperatures and increasing tropospheric [O_3]. As rice is consumed by more than half of the world's population and provides the major calorie source for the bulk of the world's poor (IRRI, 2002), identifying germplasm that can maximize the benefits of elevated [CO_2] in a future of high temperatures and high [O_3] demands more research attention.

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Supplementary material

The following material is available for this article online:

Appendix S1. References included in rice-elevated [CO_2] database.

Appendix S2. References included in rice-elevated [O_3] database.

Table S1. Results of the meta-analysis of [CO_2] effects on rice yield, grain number (grain no.), individual grain mass, panicle number (panicle no.), harvest index (HI), biomass, leaf area index (LAI), total leaf nonstructural carbohydrate content (TNC), light-saturated photosynthesis (A_{sat}), and stomatal conductance to water vapor (g_s). The main effects of elevated [CO_2] on each variable are shown in bold. Categorical groups are reported if they were statistically significant (see Tables 1 and 2). Degrees of freedom for each estimate (df), % change at elevated [CO_2], and the 95% confidence intervals (CI) are reported. The mean ambient and elevated [CO_2] for each category and level are also reported.

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