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OPINION

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Comparison of crop yield sensitivity to ozone between open-top chamber and free-air experiments

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Abstract

Assessments of the impacts of ozone (O_3) on regional and global food production are currently based on results from experiments using open-top chambers (OTCs). However, there are concerns that these impact estimates might be biased due to the environmental artifacts imposed by this enclosure system. In this study, we collated O_3 exposure and yield data for three major crop species—wheat, rice, and soybean—for which O_3 experiments have been conducted with OTCs as well as the ecologically more realistic free-air O_3 elevation (O_3-FACE) exposure system; both within the same cultivation region and country. For all three crops, we found that the sensitivity of crop yield to the O_3 metric AOT40 (accumulated hourly O_3 exposure above a cut-off threshold concentration of 40 ppb) significantly differed between OTC and O_3-FACE experiments. In wheat and rice, O_3 sensitivity was higher in O_3-FACE than OTC experiments, while the opposite was the case for soybean. In all three crops, these differences could be linked to factors influencing stomatal conductance (manipulation of water inputs, passive chamber warming, and cultivar differences in gas exchange). Our study thus highlights the importance of accounting for factors that control stomatal O_3 flux when applying experimental data to assess O_3 impacts on crops at large spatial scales.

KEYWORDS
crop yield, FACE, open-top chamber, ozone, sensitivity

1 | INTRODUCTION

Tropospheric ozone (O_3) is one of the most detrimental air pollutants for vegetation at the global scale (Ainsworth, Yendrek, Sitch, Collins, & Emberson, 2012; Fuhrer et al., 2016; Paoletti, 2007). Current ambient O_3 concentrations are estimated to cause yield losses of 5%–19% in major food crops such as wheat, soybean, rice, potato, barley, and bean (Feng & Kobayashi, 2009; Osborne et al., 2016). Background O_3 concentrations have at least doubled since the pre-industrial level (Cooper et al., 2014) and projected climate change are expected to further increase concentrations by 0.5%–2% per decade during this century if the current emissions of O_3 precursors are maintained (Solomon et al., 2007).

Our knowledge on O_3 impacts on crop production is largely based on field experiments using mainly two types of experimental exposure systems: open-top chambers (OTC) and free-air O_3 concentration elevation (O_3-FACE). To date, more OTC experiments than O_3-FACE experiments have been carried out, mostly as a consequence of the considerably larger costs of the latter type of experiments. Based on the OTC experiments, dose–response relationships have been derived for several key crop species (Feng, Hu, Wang, Jiang, & Liu, 2015; Mills et al., 2007) and these relationships have been used for current estimates of O_3-induced crop yield losses at regional or global scales (Avnery, Mauzerall, Liu, & Horowitz, 2011a, 2011b; Van Dingenen et al., 2009). However, there have been concerns regarding the ecological realism of effects observed in OTC experiments due to the environmental artifacts imposed by the chamber enclosures (Ainsworth et al., 2012; Long, Ainsworth, Leakey, & Morgan, 2005; Zhu et al., 2011). Several environmental variables are altered inside the OTCs, including air turbulence, light intensity, and air temperature and humidity. The O_3 concentration is vertically uniform inside OTCs, and the leaf boundary layer resistance is low due to the high and constant turbulence caused by the chamber ventilation. These experimental artifacts likely promote increased O_3 uptake by plant leaves, which in turn has been suggested to lead to overestimation of O_3 impacts in OTC experiments compared to those occurring at similar top-of-canopy O_3 concentrations in the field (Nussbaum & Fuhrer, 2000). However, another environmental artifact may act in the opposite direction. The temperature inside OTCs may be up to 3°C higher than the outside air at noon (Leady & Drake, 1993). The warmer air inside OTCs typically has higher vapor pressure deficit (VPD), which likely leads to lower stomatal conductance and O_3 uptake, and thus a potential underestimation of O_3 impacts (Piikki, De Temmerman, Hogy, & Pleijel, 2008).

FACE is commonly considered as an ideal approach to study the responses of plants and ecosystems to elevated CO_2 or O_3 due to its small environmental artifacts (Ainsworth et al., 2012; Long et al., 2005). FACE exposure systems do not interfere with the energy and gas exchange of the plant canopy, and plant responses to elevated gas concentrations should therefore be similar to those in the natural environment. However, FACE experiments inherently require large resources with respect to funding, infrastructure, and technological know-how. So far, there are only two O_3-FACE systems of large size (>14 m in plot diameter) in the world to investigate the effects of O_3 on crops: one in China for wheat and rice, and another one in USA for soybean. Another disadvantage of FACE experiments is that they cannot decrease the O_3 concentration and thus not assess plant responses to current ambient levels. This can be achieved by air filtration treatments in OTC experiments.

Meta-analyses of CO_2 impacts on crop yield have estimated that CO_2-induced crop yield stimulation is considerably smaller in FACE experiments than in experiments with plants in chambers (Long et al., 2005; Wang, Feng, & Schjoerring, 2013) although a recent synthesis challenged this finding (Bishop, Leakey, & Ainsworth, 2014). There have been no similar multi-crop meta-analyses for O_3 impacts on crops, and we therefore do not know if the O_3 effects observed in OTC experiments differ from those found in the more ecologically realistic O_3-FACE experiments. This hampers the credibility of current estimates of O_3-induced crop yield losses, which rely on dose–response relationships based on data from OTC experiments (Avnery et al., 2011a, 2011b; Van Dingenen et al., 2009). The aim of this study was to close this knowledge gap by comparing the effects of O_3 on wheat, rice, and soybean observed in OTC and O_3-FACE experiments.

2 | MATERIALS AND METHODS

2.1 | Data collection

This analysis explored the relationship between O_3-induced relative yield and the commonly used O_3 index AOT40 (accumulated hourly O_3 exposure above a cutoff threshold concentration of 40 ppb). We included only crop species for which field experiments have been conducted with both OTC and O_3-FACE exposure systems: wheat, rice, and soybean. Osborne et al. (2016) indicated that the O_3 sensitivity may differ among regions (countries) of the experiments. To minimize confounding influences of regional differences in climate, cultivars and management practices, OTC data of a given species were only included if coming from the same region as the O_3-FACE data of that species. Thus, wheat and rice data were taken from China and soybean data from the United States. Data were searched from the Web of Science (Thompson-ISI, Philadelphia, PA, USA) and the criteria for inclusion were as follows:

1. Plants must have been rooted in the field rather than in pots.
2. Only OTC and O_3-FACE experiments were included; experiments conducted with other exposure systems were not considered.
3. For experiments which included additional non-O_3 treatments (e.g., drought, N fertilization, elevated CO_2), only data from the control and the single O_3 treatment(s) were used.
4. Ozone exposure must have been presented as the seasonal mean 7-hr (M7), 8-hr (M8), or 12-hr (M12) O_3 concentrations, or as AOT40. For experiments not reporting AOT40 values, these were estimated from M7, M8, or M12 data using conversion equations provided by Osborne et al. (2016).
5. The duration of O_3 exposure in soybean and rice must have spanned at least 60% of the total growing season, which is approximately from 3 to 4 months from sowing to maturity in rice and soybean (Pedersen & Lauer, 2004). This criterion was not applied to winter wheat, which was sown late in the preceding year and exposed to elevated O_3 usually from March through to the end of May.
6. Yield must have been measured directly, as the total harvested grain or seed mass.

The literature search found 18 studies meeting these criteria (Table 1). Based on our selection criteria, we built a database comprising 270 data points (i.e., site × species × cultivar × treatment × year combinations). Wheat, rice, and soybean data contributed 55, 44, and 171 data points, respectively, from 3, 3, and 12 experiments conducted with 8, 8, and 16 cultivars, respectively (Table 1).

2.2 | Data analysis

First, the O_3 dose was determined on an AOT40 basis. For wheat and rice, daytime hourly O_3 concentration above a threshold of 40 ppb was integrated throughout the period of 55 days (wheat) and 80 days (rice), ending at 6–7 days before maturity harvest for consistency in the period of AOT40 calculation between O_3-FACE (Zhu et al., 2011) and OTC experiments (Wang et al., 2012). For soybean, 90 days AOT40 accumulation period was used.

Second, the following model of yield response to O_3 dose was applied:

$$y = Z(1 - S\,d), \tag{1}$$

where y is the crop yield, Z is the yield at zero O_3 dose, and S is the relative sensitivity of the crop yield to the O_3 dose (d). The multiplicative model of Equation (1) is converted to an additive model by taking natural logarithm of the both sides:

$$\ln y = \ln Z + \ln(1 - S\,d). \tag{2}$$

The sensitivity parameter S can be estimated by fitting the following model iteratively to the observations:

$$\ln y_{ij} = \ln Z_i + \ln(1 - S\,d_{ij}) + \varepsilon_{ij}, \tag{3}$$

where y_{ij} is the crop yield at jth level of O_3 treatment in ith experiment, Z_i is the crop yield at zero O_3 dose in ith experiment, d_{ij} is the O_3 dose at jth level of O_3 treatment in ith experiment, and ε_{ij} is the random error. Note that, in Equation (3), Z_i and S can be estimated simultaneously as opposed to the often used two-step procedure (e.g., Osborne et al., 2016), in which Z_i and experiment-specific S_i is first estimated for individual experiments, and S is determined across the datasets in a second step. Such procedure is operationally simple, but theoretically problematic due to the inconsistency between the sensitivity estimates used for the first and the second steps. See Appendix S1 for more discussions on the theoretical problem of the two-step procedure.

Third, the above model fitting is used to test the difference of the sensitivity S between OTC and O_3-FACE as follows. Denoting the sensitivity S for OTC and O_3-FACE experiments as S_o and S_f, respectively, and the O_3 dose for OTC and O_3-FACE experiments as d_o and d_f, respectively, Equation (3) can be written as

$$\ln y_{ij} = \ln Z_i + \ln(1 - S_o\,d_{oij}) + \ln(1 - S_f\,d_{fij}) + \varepsilon_{ij}, \tag{4}$$

where $d_{oij} = d_{ij}$ for OTC experiments and $d_{oji} = 0$ for O_3-FACE experiments, and $d_{fij} = d_{ij}$ for O_3-FACE experiments and $d_{fij} = 0$ for OTC experiments. If OTC and O_3-FACE experiments share the same sensitivity (i.e., $S_o = S_f = S_c$) Equation (4) can be simplified as:

$$\ln y_{ij} = \ln Z_i + \ln(1 - S_c\,d_{ij}) + \varepsilon_{ij}. \tag{5}$$

The comparison of the above two models can be formulated such that Equation (5) represents the null hypothesis ($S_o = S_f$) and Equation (4) represents the alternative hypothesis ($S_o \neq S_f$). The test statistic (T) based on the likelihood ratio is defined as:

$$T = -2\ln(L_0/L_a), \tag{6}$$

where L_0 is the maximum likelihood for the model fitted with Equation (5) and L_a is the maximum likelihood for the model fitted with Equation (4). The test statistic asymptotically follows the Chi-square distribution with the degree of freedom = 1 (i.e., the difference between Equations (4) and (5) in the number of parameters), and the p value for the Type-I error is calculated accordingly.

In this study, the sensitivity parameter S in Equation (3) was estimated by iteratively fitting a linear model to the observations with JMP software (SAS Institute, Cary, USA). Linear relationships were fitted for all crop species and for both OTC and O_3-FACE data, since adding a quadratic term did not significantly improve any of the relationships. See Appendix S2 for details of the estimation of the model parameters in Equation (2) with the linear model fitting. The maximum likelihood (L_0 and L_a in Equation 6) was calculated from the output of the software.

3 | RESULTS AND DISCUSSION

This study is to our knowledge the first multi-species comparison of O_3 impacts reported from OTC versus O_3-FACE experiments. For all the three crops, the model with common sensitivity between O_3-FACE and OTC was rejected (Table 2).

For soybean (Figure 1a, Table 2), the sensitivity in OTC was greater than that in O_3-FACE experiments, whereas the opposite was the case for wheat and rice (Figure 1b,c, Table 2). These results indicate that current yield loss estimates (Avnery et al., 2011a, 2011b; Van Dingenen et al., 2009) based on AOT40 dose–response relationships from OTCs may be biased, positively or negatively depending on crop species. Since results were species-specific we will now discuss them species by species.

For soybean, the greater sensitivity to O_3 in OTC than O_3-FACE was likely caused by differences in water supply. Plants in all the OTC experiments but one (Mulchi, Lee, Tuthill, & Olinick, 1988) were irrigated, whereas those in O_3-FACE were not. In the non-irrigated fields of O_3-FACE, the soybean plants were likely frequently subjected to soil moisture deficit (Betzelberger et al., 2010), which should have reduced stomatal conductance and thereby O_3 uptake. Among the 6 years of O_3-FACE experiments included in the analysis of the present study, 2007 was a particularly dry year with only 233 mm rainfall during the soybean growing season (Table S1), compared to 314–432 mm in the other years. Excluding the dry year of

TABLE 1 List of experiments included in the analysis, with information on crop species and cultivar, exposure system, experimental year, O_3 treatments, location, and reference

Crops	Exposure system	Cultivar	Experimental year	O_3 treatment	Location	Reference
Wheat	OTC	Yangmai 185 Jia 002	2004[a] 2006–2008	CF, NF, E-O_3	121°18E 31°53N Jiaxing, China	Wang et al. (2012)
Wheat	OTC	Beinong 9549	2010	NF, E-O_3	116°08E 40°12N Changping China	Tong et al. (2012)
Wheat	FACE	Yangmai 15, Yangmai 16, Yangfumai 2 Yannong 9 Jia002	2007–2010	AA, E-O_3	119°42E 32°35N Jiangdou China	Feng et al. (2012)
Rice	OTC	Jiahua2 Fan3694	2004[a]–2005, 2006–2008	CF, NF, E-O_3	121°18E 31°53N Jiaxing, China	Wang et al. (2012)
Rice	OTC	Yuejingsi-2	2009	NF, E-O_3	113°45′E 23°1′N Guangzhou, China	Tong et al. (2011)
Rice	FACE	Yangdao 6 Shanyou 63 Liangyoupeijiu Wujing 15 Wuyujing 21	2007–2009	AA, E-O_3	119°42E 32°35N Jiangdou China	Zhang, Tang, Liu, and Zhu (2016)
Soybean	OTC	Essex	1999–2000	CF, E-O_3	Raleigh USA	Booker, Miller, Fiscus, Pursley, and Stefanski (2005)
Soybean	OTC	Williams Corsoy	1983	CF, NF, NF+30, NF+60, NF+90	Beltsville, USA	Heggestad, Anderson, Gish, and Lee (1988)
Soybean	OTC	Hodgson		CF, NF, NF+30, NF+60, NF+90	Beltsville, USA	Kohut, Amundson, and Laurence (1986)
Soybean	OTC	Amsoy-71, Corsoy-79	1983	CF, NF, NF+30, NF+60,	Argonne, USA	Kress, Miller, Smith, and Rawlings (1986)
Soybean	OTC	Clark	1989	CF, NF, NF+40,	Beltsville, USA	Mulchi, Lee, Tuthill, and Olinick (1988)
Soybean	OTC	Davis	1977, 1978	CF, NF	Raleigh, USA	Heagle, Letchworth, and Mitchell (1983b)
Soybean	OTC	Davis	1981	CF, NF, NF1, NF2, NF3, NF4	Raleigh, USA	Heagle, Heck, Rawlings, and Philbeck (1983a)
Soybean	OTC	Davis	1983, 1984	CF, NF, NF1, NF2, NF3, NF4	Raleigh, USA	Heagle et al. (1987)
Soybean	OTC	Davis	1982	CF, NF, NF+20, NF+40, NF+60; 1.3NF, 1.6NF, 1.9NF	Raleigh, USA	Heagle, Lesser, Rawlings, Heck, and Philbeck (1986)
Soybean	FACE	Dwight, HS93-4118, IA-3010, Loda, LN97-15076, Pana	2007–2008	AA, E-O_3	88°14W 40°02′N Champaign, USA	Betzelberger et al. (2010)

(Continues)

TABLE 1 (Continued)

Crops	Exposure system	Cultivar	Experimental year	O_3 treatment	Location	Reference
Soybean	FACE	93B15	2002–2003	AA, E-O_3	88°14W 40°02′N Champaign, USA	Morgan, Mies, Bollero, Nelson, and Long (2006)
Soybean	FACE	A mixture of Dwight, HS93-4118, IA-3010, Loda, LN97-15076, Pana, Pioneer, 93B15	2009–2010	AA, 40, 55, 70, 85, 110, 130, 160 and 200 ppb	88°14W 40°02′N Champaign, USA	Betzelberger et al. (2012)

[a]Observations in rice and wheat subjected to a very high O_3 concentration of 200 ppb for 8 hr daily (Wang et al., 2012) were excluded from the analysis to prevent the anomalously high AOT40 values from exerting overwhelming influence on the estimation of O_3 sensitivity.

TABLE 2 Comparison between the models with different (Equation 4) and common O_3 sensitivity (Equation 5) of O_3-FACE and OTC experiments. S_o is the sensitivity in OTC, S_f is the sensitivity in FACE, and S_c is the common sensitivity in both OTC and FACE

Crop species[a]	Different sensitivity		Common sensitivity	
	S_o	S_f	S_c[b]	*p* Value
Soybean	0.0102	0.0090	0.0097	.048
Wheat	0.0215	0.0259	0.0222	.023
Rice	0.0111	0.0203	0.0118	.002

[a]The sensitivities of different crop species are not readily compared since the AOT40 accumulation periods were different (see Section "2").
[b]The common sensitivity, S_c, is closer to S_o than to S_f due to differences in the number of observations as well as the range of O_3 doses for O_3-FACE compared to OTC experiments.

2007 from the analysis, there was a much more similar and statistically indistinguishable (p = .37) O_3 sensitivity of O_3-FACE (0.0098) and OTC (0.0102) experiments. This suggests that the O_3 sensitivity of soybean is similar in OTC and O_3-FACE experiments, unless the lack of irrigation in O_3-FACE experiments caused substantial soil water deficits and stomatal closure responses in unusually dry years.

It is noteworthy that Osborne et al. (2016) reported a greater sensitivity of soybean yield to O_3 dose (mean daily 7 hr concentrations) in O_3-FACE compared to OTC experiments (p = .048), which is opposite to our findings in this study. This apparent inconsistency could be attributed to differences in the datasets used. We limited ourselves to the use of published results only, and, hence, the yield data from the 2009 and 2010 O_3-FACE experiments were represented by values averaged across the seven cultivars used (as published by Betzelberger et al., 2012). Osborne et al. (2016), however, used the original experimental data for the individual seven cultivars. This allowed them to analyze the varietal differences in O_3 sensitivity in detail, but also resulted in data from 2009 and 2010 (which had seven cultivars and nine O_3 levels) dominating their analyses. We therefore argue that the apparent difference between the two studies may reflect the difference in their thrusts: varietal difference in O_3 sensitivity for Osborne et al. (2016) and OTC versus O_3-FACE contrast in this study. As noted above, our OTC-FACE contrast has been strongly affected by the results of the dry year of 2007.

Our study also differed from that of Osborne et al. (2016) with respect to data selection criteria. Osborne et al. (2016) included all data on soybean and their analysis indeed indicated that the O_3 sensitivity may differ among regions (countries) of the experiments. To allow for a stricter OTC versus O_3-FACE comparison, we therefore chose to include OTC data of a given species only if it came from the same region as the O_3-FACE data of that species. Another difference between the present study and Osborne et al. (2016) is that we excluded all data from experiments with potted plants. However, Osborne et al. (2016) compared the O_3 sensitivity of plants grown in pots versus plants freely rooted in the field and found no significant differences.

For winter wheat, the stronger sensitivity in O_3-FACE compared to OTC experiments is in line with earlier results on this species. Zhu et al. (2011) reported on a twofold higher O_3 sensitivity of grain yield in O_3-FACE compared to OTC experiments, but their dataset and methodology did not allow them to conclude that the effect was statistically significant. Compared with Zhu et al. (2011), this study included more recent results, that is, the four cultivars from studies in 2010 and the one cultivar (J002) studied from 2007 to 2010. Furthermore, the statistical power of the method used in the present study is stronger than that used by Zhu et al. (2011), which relied on simple observation of whether or not 95% CIs were overlapping (a method which can be criticized, e.g., Schenker & Gentleman, 2001). The lower O_3 sensitivity in OTC compared to O_3-FACE experiments could have been caused by higher temperature and VPD in OTCs reducing stomatal conductance and leaf O_3 uptake, as suggested by Piikki et al. (2008). Moreover, unlike for soybean, the wheat plants were not irrigated in either OTC or O_3-FACE experiments, except in one OTC study contributing two data points (Tong et al., 2012). In the other OTC experiments, the chambers had roofs

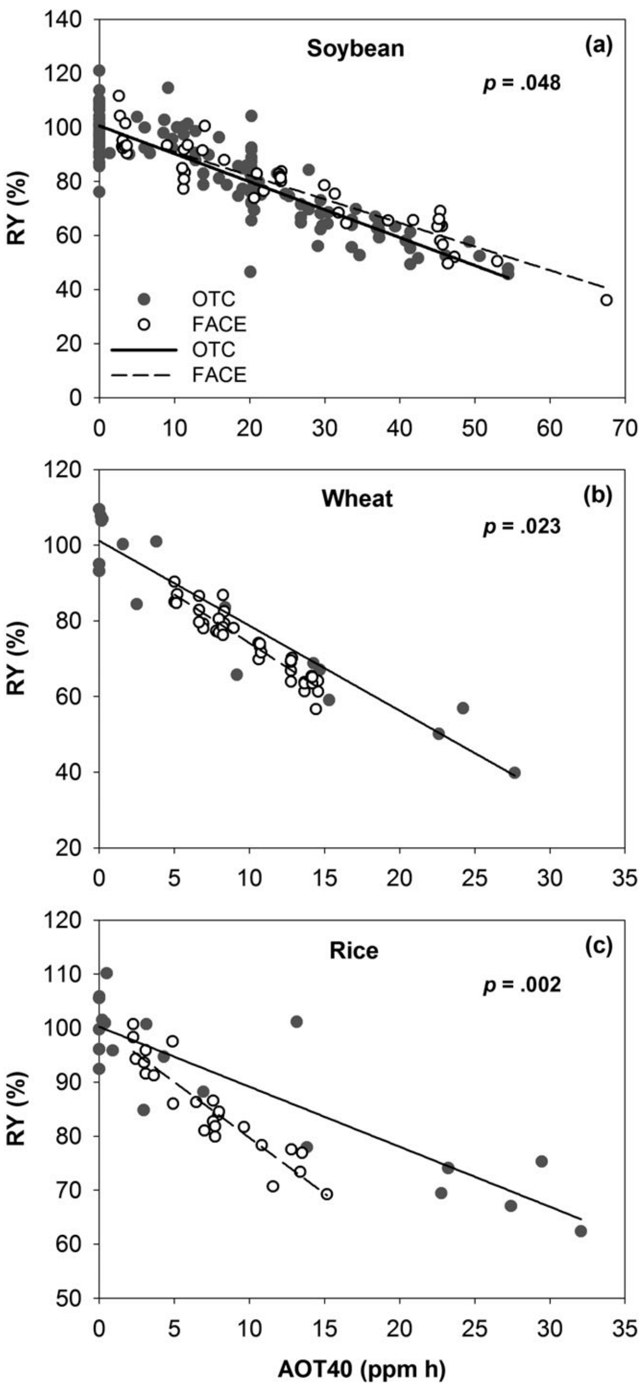

FIGURE 1 Ozone dose (AOT40)–relative yield (RY) relationships for (a) soybean, (b), wheat, and (c) rice. All slopes of the linear relationships are significantly different from zero

which were installed 30 cm above the top of the chamber walls. The roof diameter was greater than the opening at the top, and the rainfall was thus mostly excluded by the roof. Plants inside OTC got soil water from lateral flow from the soil surrounding the chambers as well as from the shallow ground water (<1 m), but soil moisture should have been lower in OTC than in O_3-FACE experiments. This experimental artifact thus likely limited the stomatal O_3 uptake and contributed to the lower O_3 sensitivity in OTC compared to O_3-FACE experiments with wheat. In contrast to the situation for soybean, O_3 was released at the top of the canopy in both OTC and O_3-FACE experiments with wheat and rice, leaving the VPD and soil moisture effects to dominate over that of possible vertical O_3 profiles within the canopy.

Cultivar differences may also have contributed to the difference in O_3 sensitivity for wheat, but this is very difficult to assess properly with the present dataset since most cultivars are different between the O_3-FACE and OTC experiments. However, a comprehensive meta-analysis on wheat investigating this issue concluded that the large variation in O_3 sensitivity among experiments were related to neither year of experiment nor year of cultivar release (Pleijel, Broberg, Uddling, & Mills, 2018).

For rice, this is the first analysis to compare the difference in O_3 sensitivity between OTC and O_3-FACE experiments. The higher O_3 sensitivity in O_3-FACE compared to OTC experiments was likely linked to cultivar differences. A previous study reported that hybrid cultivars of rice showed higher stomatal conductance (Pang, Kobayashi, & Zhu, 2009) and greater yield responses to O_3 than inbred cultivars (Shi et al., 2009). In the present dataset, hybrid cultivars were used in O_3-FACE experiments only. When excluding these from the analysis, the difference between OTC and O_3-FACE experiments was no longer statistically significant (p = .457, Table S2). This suggests that the apparent difference in O_3 sensitivity between OTC and O_3-FACE for rice could be attributed to the difference in sensitivity between hybrid and inbred cultivars. Since rice plants in both OTC and O_3-FACE were grown in flooded soil, it is unlikely that soil water availability limited stomatal O_3 uptake in either of the exposure systems. Furthermore, the passive OTC warming artifact likely had a smaller effect on VPD in rice experiment than those with upland crops. Since rice plants in both OTC and O_3-FACE were grown in flooded soil, the temperature increase in OTC caused increased evaporation from the flooded water surface, with actual vapor pressure increasing along with the increase in saturated vapor pressure due to the temperature rise.

4 | CONCLUSION

This study has demonstrated that three major crops showed apparent differences in O_3 sensitivity between OTC and O_3-FACE experiments. In wheat and rice, O_3 sensitivity was higher in O_3-FACE compared to OTC experiments, while the opposite was the case for soybean. These differences could be linked to two factors: differences in environmental artifacts and differences in O_3 sensitivity of the cultivars used in OTC and O_3-FACE experiments. In soybean, irrigation likely increased the sensitivity to O_3 in OTC experiments, whereas in wheat OTC experiments, removal of rainfall inputs by partial roofs together with increased temperature and VPD likely decreased stomatal O_3 uptake and impacts. In rice, the higher sensitivity in O_3-FACE experiments was linked to the inclusion of hybrid cultivars with higher stomatal conductance and O_3 sensitivity than inbred cultivars (Pang et al., 2009), and the sensitivity difference between OTC and O_3-FACE experiments disappeared when only inbred cultivars were considered. These differences in O_3 sensitivity between OTC and O_3-FACE experiments could to a large extent have been accounted for using a stomatal flux-based O_3 dose metric, instead of AOT40 which only considers O_3 concentrations in the air. This study thus demonstrates that accounting for factors that control stomatal conductance is important when applying experimental data to assess O_3 impacts on crops at large spatial scales, supporting the use of a stomatal flux-based O_3 index for improved regional and global O_3 impact assessments on crops.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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