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Large crop production losses induced by global ozone stress based on interval evaluation

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Abstract

Global crop yield loss due to ground-level ozone (O₃) concentrations is a major challenge to food security, but a dose-response association is not easy to quantify. Here, we propose using a new metric, O₃ sensitivity of crop yield (Yₒ), to estimate yield loss under different O₃ time intervals using four observational databases. The Yₒ metric shows a non-linear parabola with elevated atmospheric O₃ for wheat, maize, rice, soybean, and assorted vegetables. Spatial heterogeneity of yield loss varies as a function of crop type and O₃ intervals. Estimates of yield loss from ozone suggest recent losses (2017-2019) may reach as high as 537 million tonnes, with a significant proportion coming with lower (30-40 ppb) exposure (325 million tonnes). Our results suggest that previous research, which only included higher (>40 ppb ozone), may have had grossly underestimated the negative effect of atmospheric O₃ on crop production. Suppose these results are endemic to global crop production. In that case, additional research will be necessary to reassess ozone sensitivity and dose-responses, both spatially and temporally, to determine future air pollution impacts.
Introduction

Air pollution, including atmospheric (or ground-level) concentrations of ozone (O\textsubscript{3}), can significantly damage plant growth and biomass accumulation in terrestrial ecosystems\textsuperscript{1, 2, 3}. Atmospheric O\textsubscript{3} enters the plant body through leaf stomata and stimulates a series of biochemical reactions, which destroy the cell structure and initiate physiological and metabolic disorders\textsuperscript{4, 5}. Such adverse reactions can decrease stomatal conductance and net photosynthetic rate and further result in losses of biomass and yield. Since the late 1800s, atmospheric O\textsubscript{3} has risen from approximately 10 ppb to 50 ppb today and will increase by 40-60% until 2100\textsuperscript{6}.

For agroecosystem, an accurate assessment of how elevated atmospheric O\textsubscript{3} affects crop productivity, especially crop yield, is crucial for global food security\textsuperscript{3, 7}. Most researchers have focused on the total loss of crop yield caused by atmospheric O\textsubscript{3} while turning out to have considerable variation and high uncertainty\textsuperscript{8, 9, 10}. The value of 40 ppb O\textsubscript{3} is generally considered a threshold. Beyond 40 ppb, atmospheric O\textsubscript{3} could cause significant crop yield loss\textsuperscript{11, 12}. Nonetheless, atmospheric O\textsubscript{3} may be unlikely to fall directly below the crop threshold by taking measures in the short term\textsuperscript{1}. The knowledge gap on crop yield change under different atmospheric O\textsubscript{3} intervals swamps the evaluation and prediction of future atmospheric O\textsubscript{3} pollution on crop productivity. It thus is not conducive to the establishment of effective mitigation strategies and policies.

As atmospheric O\textsubscript{3} rises, crop O\textsubscript{3} absorption does not increase proportionally because of stomatal resistance\textsuperscript{4}. Crops have specific adaptability and resistance to atmospheric O\textsubscript{3} damage through their natural defenses (e.g., antioxidants, detoxification, and nocturnal remediation capabilities) and the specific triggering responses\textsuperscript{13}. These differences in ozone sensitivity may lead to significant variation of yield responses relative to low and high O\textsubscript{3} concentrations and for a time of exposure to those concentrations. However, this phenomenon to date is poorly noticed and understood when evaluating O\textsubscript{3} impact\textsuperscript{4, 9, 14}. Here we propose a new approach with the O\textsubscript{3} sensitivity of crop yield (Y\textsubscript{o}) by estimating crop yield loss rate (%) per increase in O\textsubscript{3} concentration of 1 ppb above ambient levels for one hour. Although individual experiments have reported average values of Y\textsubscript{o} based on the relationship between O\textsubscript{3} dose (hour mean of O\textsubscript{3} or accumulated O\textsubscript{3} over a threshold concentration) and crop yield loss rate\textsuperscript{3, 14, 15}, explicit quantification of the values under smaller O\textsubscript{3} intervals is still scant and remains a major challenge in formulating dose-responses for crop yield assessment. Due to the lack of observational O\textsubscript{3} data, part of this challenge has been met using atmospheric models to predict
regional and global O3-induced crop yield losses$^3,8,16$. However, with the establishment of numerous O3 monitoring stations in recent years, more accurate global real-time O3 concentration data could be obtained (Supplementary Fig. 5). An interval evaluation of $Y_o$ based on observational real-time O3 data is crucial to consistent predictions of crop yield response to changes in atmospheric O3.

Based on an evaluation of over 900 O3 fumigation experiments, we present a detailed analysis to provide a dose-response of O3 exposure on yield of major crops (wheat, maize, rice, and soybean) based on seven interval evaluations. 7246 hourly atmospheric O3 monitoring stations, distribution of crop cultivation, and crop production observational databases (see “Methods” section; Supplementary Data). We first calculate the $Y_o$ under different crop types and O3 intervals (30-40, 40-50, 50-60, 60-70, 70-80, 80-90, and >90 ppb). Then we map the global distribution of yield loss rates for major crops under 7 O3 intervals. In addition, we provide a metric for the dose-response of O3 for yield loss on a regional crop basis. Finally, we discuss direct and indirect pathways by which atmospheric O3 affects crop yield through photosynthetic and agronomic indexes using a structural equation model$^{17}$. In general, the sizes of $Y_o$ show a non-linear parabola with atmospheric O3 elevation. Larger crop production loss caused by atmospheric O3 is estimated compared to the previously suggested value.

**Results and discussion**

The O3 sensitivity of crop yield. Our synthesis quantified the $Y_o$ of primary crop yield (wheat, maize, rice, soybean, and vegetable) under 7 O3 intervals at the global scale by involving 960 O3 fumigation experiments (Fig. 1). Previous studies have established different O3 indicators to estimate the impact of atmospheric O3 on crop yield$^3,12,18,19$. However, those O3 indicators are mainly divided into two categories: O3 dose indicators (M7 or M12: 7-hr or 12-hr mean O3; AOT$_{40}$, or SUM$_{60}$, hourly average O3 concentration higher than 40 or 60 ppb) and O3 stomatal absorption flux indicator (POD$_Y$, hourly O3 stomatal flux higher than the cumulative flux of Y nmol m$^{-2}$ s$^{-1}$)$^3,20$. The O3 dose indicators unify the atmospheric O3 with the crop yield, ignoring the crop's resilience and adaptation to different atmospheric O3. The O3 stomatal absorption flux indicator considers the influence of biological and environmental factors on the stomatal O3 absorption of plants; however, it is difficult to obtain the actual value from observational data, especially at the global or regional level scale$^3$. Based on a large number of experimental data, the $Y_o$ under different O3 intervals can overcome the above defects better to understand crop yield response to elevated atmospheric O3.

At the global scale, the average of $Y_o$ was -11.1×10$^{-6}$ ppb h$^{-1}$, with a low 95% confidence of -10.7 to
-11.4×10^{-6} \text{ ppb h}^{-1} (N = 960, \text{ Fig. 1b}). The $Y_o$ among crop types was significantly different with an average of -18.2, -15.3, -11.2, -10.6, and -8.4×10^{-6} \text{ ppb h}^{-1} for soybean, vegetables, wheat, maize, and rice, respectively (Fig. 1b). These differences may be due to different responses of crops in photosynthesis with leaf stomatal and non-stomatal limitations under $O_3$ stress. For example, leaf stomata can regulate $O_3$ absorbed doses, thus affecting crop sensitivity to $O_3$. The decrease in stomatal conductance under $O_3$ stress is considered the major reason for reducing the photosynthetic rate. Generally, the stomatal conductance of soybean is more significant, and its response to $O_3$ was significantly weaker than wheat and rice (Supplementary Fig. 10)\textsuperscript{9, 21, 22}. In terms of non-stomatal factors, the mesophyll of dicotyledonous (e.g., soybean and most vegetables) is differentiated into palisade tissue and spongy tissue compared with monocotyledonous (e.g., wheat, maize, and rice). Palisade tissue is close to the upper epidermis and contains more chlorophyll. High $O_3$ can firstly damage the palisade tissue and then cause cytoplasmic wall separation and cell content dispersion, inhibiting crop growth and yield formation\textsuperscript{23}. Therefore, soybean and vegetable were more sensitive to elevated $O_3$ than wheat, maize, and rice.

There were significant differences in the $Y_o$ for the same crop type among $O_3$ fumigation concentrations (Fig. 1c, Supplementary Fig. 6-9). Previous researches mainly focused on the overall size and did not explicitly distinguish the different effects of $O_3$ levels\textsuperscript{11, 24}. Many studies indirectly showed that different $O_3$ fumigation concentrations showed diverse impacts on crop growth and yield formation based on data integration (Meta-analysis)\textsuperscript{21, 22}. In this study, we also demonstrate a non-linear parabola between the $Y_o$ and $O_3$ fumigation concentration (Fig. 1c). Our result provides evidence of biological evolutionism to $O_3$ stress. This viewpoint can be supported by the crop's photosynthetic physiologies, antioxidant system, and other multiple pathways resulting in adaptation and recovery to $O_3$ stress\textsuperscript{4}. As $O_3$ concentration increases, the detrimental effect of unit $O_3$ concentration on photosynthesis decreases gradually\textsuperscript{9}. High $O_3$ stress can minimize stomatal conductance through the plasma membrane, slow anion channel preferential response in guard cells, and even cause stomatal closure, inhibiting leaf photosynthesis and lowering crop productivity\textsuperscript{4}. Simultaneously, the activities of superoxide dismutase, catalase, and peroxidase increase rapidly under $O_3$ stress, which is the first step to defend against reactive oxygen species damage caused by $O_3$\textsuperscript{4, 25}. Other pathways enhance crop resistance and lead to the parabola relationship between the $Y_o$ and $O_3$ concentration, i.e., high $O_3$ stress can accelerate crop respiratory metabolisms and promote
nutrient absorption by stimulating related enzymes.\textsuperscript{4, 26}

Interestingly, when O\textsubscript{3} concentration exceeded 100 ppb, the crop yield loss rate increased with an elevated O\textsubscript{3} concentration of 1 ppb h\textsuperscript{-1} (Fig. 1c). Long-term high O\textsubscript{3} exposure can reduce stomatal resistance and destroy the antioxidant system\textsuperscript{26}, which would lead to irreversible damage to the crop. Overall, the parabola relationship between the Y\textsubscript{o} and O\textsubscript{3} concentrations is an advanced indicator of how crop yield responds to different O\textsubscript{3} concentrations.

Fig. 1 Ozone sensitivity of crop yield. a, global distribution of the 960 experiments from 208 published papers in which the effect of elevated ozone concentration on crop yield was assessed. The size of black circles represents the sample size ranging from 1 to more than 19. Crop types include wheat (in brown), maize (in red), rice (in green), soybean (in turquoise), and vegetable (in blue). b, response ratio (natural logarithm-transformed ratio of treatment to control) of the ozone sensitivity of crop yield (ppb h\textsuperscript{-1}). Dot and bar represent the mean and range at 95% confidence intervals of ozone sensitivity of crop yield. The value in parentheses represents the sample sizes. c, the relationship between ozone sensitivity of crop yield and ozone fumigation concentration. Each dot represents the average effect size under ozone fumigation intervals with <30, 30-40, 40-50, 50-60, 60-70, 70-80,
80-90, >90 ppb for each crop type according to the treatment groups in the database.

**The magnitude of crop production loss.** To our knowledge, this study is the first to present global distribution maps of major crop yield (wheat, maize, rice, and soybean) loss under 7 O\textsubscript{3} intervals (30-40, 40-50, 50-60, 60-70, 70-80, 80-90, and >90 ppb) based on integrating available observation-based databases. Global annual crop yield loss rate (2017-2019) added up to 23.8, 12.2, 12.3, and 26.8\% for wheat, maize, rice, and soybean, respectively (Fig. 2, Supplementary Fig. 6-9).

Although previous studies have estimated crop yield losses associated with O\textsubscript{3} exposures using a meta-analysis method\textsuperscript{21, 22, 27}, their results are unlikely to be widely applied for two reasons. First, the meta-analysis' findings were calculated using existing literature with a limited sample size (N<150)\textsuperscript{21, 22, 27}. The key factors causing variation in meta-analysis results, as stated in their articles\textsuperscript{21, 22, 27}, are that they used the different O\textsubscript{3} fumigation concentrations and duration of O\textsubscript{3} fumigation. For example, some experimental fumigations did not last for the entire crop growth period, which would underestimate the O\textsubscript{3} stress. Second, the crop yield loss rate is caused by the accumulation of O\textsubscript{3} concentration. The atmospheric O\textsubscript{3} concentration and duration are different at the global and regional scales\textsuperscript{1, 28}. The meta-analysis findings did not map the rate of crop yield loss caused by atmospheric O\textsubscript{3} in various regions.

The U. S. Environmental Protection Agency and European researchers have suggested that atmospheric O\textsubscript{3} concentrations above 60 and 40 ppb would affect local crop yields\textsuperscript{12}. Currently, most studies estimate the crop yield loss rate caused by atmospheric O\textsubscript{3} based on AOT\textsubscript{40}\textsuperscript{28, 29}. Our study showed that O\textsubscript{3} concentration over 30 ppb had a significant effect on crop yield than O\textsubscript{3} concentration below 30 ppb (Supplementary Fig. 3). Previous results based on AOT\textsubscript{40} are most likely underestimate the impact of O\textsubscript{3} on crop production. Therefore, the crop yield loss rate evaluated with different O\textsubscript{3} intervals was robust by using the accurate Y\textsubscript{0} and hourly O\textsubscript{3} data from more than 7,000 O\textsubscript{3} monitoring stations in our study (Supplementary Fig. 4). The crop yield loss rate differed significantly among divergent O\textsubscript{3} intervals (Fig. 2, Supplementary Fig. 6-9). This was mainly because the occurrence frequency of low O\textsubscript{3} concentration was much higher than that of high concentration (Supplementary Table 1). It is also affected by the relationship between the Y\textsubscript{0} and O\textsubscript{3} concentration (Fig. 1c). Our estimation based on the Y\textsubscript{0} can provide a reference to diagnose the response of crop yield to atmospheric O\textsubscript{3} change predicted by other empirical methods.
Fig. 2 Global annual loss rate (%) of crop yield (2017-2019) due to atmospheric ozone concentration. The maps showed the spatial distribution of cumulative crop yield loss (%) in the case of ozone concentration above 30 ppb for wheat (a1), maize (b1), rice (c1), and soybean (d1), averaged for the period 2017-2019. The spatial distribution of crop yield loss in the case of ozone above 30, 40, 50, 60, 70, 80, and 90 ppb for wheat, maize, rice, and soybean were also shown in Supplementary Fig. 6-9, respectively. All data were presented for the 0.0083° grid squares based on global 7246 real-time ozone monitoring stations (see Supplementary Fig. 5). a2, b2, c2, and d2 indicated crop yield loss of wheat, maize, rice, and soybean in the case of ozone concentration ranged with 30-40, 40-50, 50-60, 60-70, 70-80, 80-90, and >90 ppb for global and 5 countries or regions (ranked top five in grain production) averaged value, respectively. The percentage of ozone monitoring stations involved in calculating the effects of ozone on crop yield at each range of ozone concentration was shown in Supplementary Table 1.
Global annual crop production loss (2017-2019) caused by atmospheric O₃ added up to 537 million tonnes, of which 177, 182, 82, and 96 million tonnes for wheat, maize, rice, and soybean, respectively (Table 1). The yield loss in our study (537 million tonnes) was about double that of a recent global study (227 million tonne) that used the European Monitoring and Evaluation Programme model according to global crop production data for 2010-2012. This difference is mainly because the chemical transport model does not accurately predict hourly O₃ concentration, especially for a multi-year time series of atmospheric O₃ concentrations at a global scale of 30, 31. Atmospheric O₃ concentrations have been increasing at an annual rate of 0.5-2.0% for the past few decades 32. The data of global hourly O₃ concentration and continued increase in O₃ over time are the main reasons leading to the rise in crop yield loss estimated by our study (537 million tonnes) compared with Mills, Sharps 3 (227 million tonnes). Despite that good practices and advanced technologies were adopted in crop cultivation, crop yield in many world regions stagnated in recent years. This might be partly explained by the growing severe O₃ pollution, which damaged the yield formation of the crop. Atmospheric O₃ may be unlikely to fall directly below the injury threshold in the short term 1. Our results also indicate that low levels of O₃ have a non-negligible effect on yield loss (Supplementary Figure 3). Hence, O₃ mitigation strategies and policies in agriculture are crucial for global food security.
Table 1 Global and five areas (ranked top five in grain production) annual loss amount of wheat, maize, rice, and soybean production (million tonnes) in the case of ozone 30-40 ppb and above 40 ppb. Each country's annual loss rate of crop yield in the case of ozone above 30, 40, 50, 60, 70, 80, and 90 ppb and total yield for wheat, maize, rice, and soybean were shown in Supplementary Table 2-6.

| Wheat | 30-40 ppb | >40 ppb | Maize | 30-40 ppb | >40 ppb | Rice | 30-40 ppb | >40 ppb | Soybean | 30-40 ppb | >40 ppb |
|-------|-----------|---------|-------|-----------|---------|------|-----------|---------|---------|-----------|---------|
| Area  |           |         | Area  |           |         | Area |           |         | Area    |           |         |
| Global| 112.44    | 64.94   | Global| 99.51     | 82.76   | Global| 48.08     | 33.49   | Global  | 64.87     | 30.93   |
| China | 28.17     | 23.42   | America| 42.09     | 27.44   | China | 22.59     | 18.97   | America | 29.93     | 13.46   |
| Europe| 25.37     | 12.62   | China | 23.40     | 32.77   | India | 6.15      | 3.59    | Brazil  | 21.74     | 9.35    |
| America| 11.74    | 5.97    | Europe | 6.86     | 4.39    | Vietnam| 2.00      | 1.23    | China   | 3.20      | 3.11    |
| Russia| 10.48     | 5.93    | Brazil | 6.43     | 3.75    | Indonesia| 1.68     | 1.77    | Argentina| 2.99     | 1.75    |
| India | 8.27      | 6.15    | Argentina| 3.08    | 2.39    | Bangladesh| 1.37     | 0.75    | India   | 0.31      | 0.18    |
| Other | 28.40     | 10.86   | Other  | 17.64    | 12.02   | Other | 14.29     | 7.19    | Other   | 6.70      | 3.08    |
The mechanisms of crop production loss. The magnitudes of $Y_o$ varied greatly among experimental sites, ranging from $-44.9 \times 10^{-6}$ to $-4.8 \times 10^{-6}$ ppb h$^{-1}$ (Fig. 1). Path analysis showed a network of inter-correlation of atmospheric $O_3$ concentration, photosynthetic indexes, and agronomic indexes in determining the $Y_o$ (Fig. 3a), implying that the effect size of $Y_o$ was regulated by multiple factors rather than a single factor. Agronomic indexes, especially aboveground biomass and grain number per ear, are the most critical factors directly determining crop yield under elevated $O_3$. Photosynthesis indexes play their roles mainly by affecting agronomic indexes. When atmospheric $O_3$ particularly enters the crop body through the stomata, it can stimulate a series of biochemical reactions (photosynthetic rate, stomatal conductance, and enzyme activity), which further reduce the agronomic indexes leads to crop yield loss$^4,5$. Breeding new cultivars which have better resistance to $O_3$ damage is recognized widely$^{33}$. The inter-correlation between atmospheric $O_3$ concentration, photosynthetic indexes, and agronomic indexes in determining the $Y_o$ suggested in our study can provide a scientific reference for crop breeding and $O_3$-crop models optimization.

**Fig. 3** Influence of ozone ($O_3$) and ozone sensitivity of photosynthetic ($P_o$) and agronomic ($A_o$) indexes on the ozone sensitivity of crop yield ($Y_o$). a, path analysis results on the direct and indirect effects of $O_3$, $P_o$, and $A_o$ on the $Y_o$. Numbers show the path coefficients. Grey path and number indicate that the effect is insignificant. Arrow width is proportional to the standardized coefficient. The $P_o$ includes ozone sensitivity of light-saturated rate, ozone sensitivity of stomatal conductance, and ozone sensitivity of chlorophyll (See supplementary Fig. 11). The $A_o$ has the ozone sensitivity of above ground biomass, the ozone sensitivity of grain number per ear, and the ozone sensitivity of leaf area. b, the standardized total effect of $O_3$, $P_o$, and $A_o$ on the $Y_o$.

**Limitation.** Although we have rigorously reviewed and synthesized multiple datasets from the available literature and public data to estimate global crop production losses and underlying potential
drivers, there are limitations to the current study. One area of importance is acknowledging intra-specific variation to O₃ among crop cultivars. In recent years, many crop cultivars have been developed to achieve higher yields and better resilience to O₃. Variation in crop cultivar response will, in turn, provide uncertainties for Yₒ. Secondly, we derived crop yield loss rates from observed stations' global real-time atmospheric O₃ concentration data (see “Methods”). However, not all countries or regions have established real-time atmospheric O₃ observatory stations or provided access to the observational data. Consequently, atmospheric O₃ stations in Asia, Europe, and North America are better represented than South America and Australia, with data from other Africa, the Middle East, and Russia being problematic (Supplementary Fig. 5). Therefore, estimates of the crop yield loss rates in Africa and Russia may be less accurate. Thirdly, although the crop yield loss rates with the 0.0083 x 0.0083° grid squares are reported based on MAPSPAM and the atmospheric O₃ database, the global crop production in our study is based on country-specific FAO data and does not provide the exact resolution. Such resolution can result in a mismatch between crop yield loss rates and crop production and may affect the final estimates of food production loss. While we recognize these limitations, our combined databases define and provide accurate values of the Yₒ and robust estimate of crop production loss under different atmospheric O₃ intervals than previous studies.

In summary, our global synthesis verifies that the Yₒ, defined as yield loss rate (%) with an elevated O₃ concentration of 1 ppb h⁻¹, shows a non-linear parabola with atmospheric O₃ increase and significant differences among crop types. This indicator provides a new perspective and method for improving the crop system models to predict yield loss by using real-time atmospheric O₃ accurately. The crop yield responses to different atmospheric O₃ concentrations present significant variations and indicate that low O₃ stress (30-40 ppb) has considerable damage to crop yield. Based on an interval evaluation, we demonstrate the spatial quantification of crop yield loss rate under O₃ stress globally, including much more significant crop production losses than previously reported. Finally, the co-regulation of crop yield response to elevated O₃ by crop photosynthetic and agronomic indexes signifies the necessity of comprehensive measures to improve crop resistance against O₃ stress. These results are crucial to identifying crop yield-sensitive regions under global O₃ pollution and may help facilitate an appropriate response at the scientific and policy level.

Methods

Experimental data collection. To establish a standardized and unified database of responses of crop
yield to atmospheric O$_3$ concentration, experimental data that met the following criteria were collected
through Web of Science (http://apps.webofknowledge.com), Google Scholar (https://scholar.google.com), and China Knowledge Resource Integrated Database (http://www.cnki.net/). A wide range of keywords ("ozone* yield", "ozone* wheat", "ozone* maize or corn", "ozone* rice", "ozone* vegetable", "ozone* production", and "grain yield") were used. The target literature was obtained directly from the corresponding authors because of paper download and subscription permissions. The PRISMA flow chart showed the process of literature collection until November 2020 (Supplementary Fig. 1).

To standardize the database, experimental data were only when the following criteria were met: (1) the experiment included O$_3$ fumigation and no O$_3$ fumigation (control) treatments; (2) no anthropogenic simulation (e.g., elevated carbon dioxide was included; (3) experimental period, O$_3$ fumigation concentration, O$_3$ exposure time (hour day$^{-1}$), and crop yield were reported via figures, tables and text; (4) crop was planted directly in the soil, and the variety was given; (5) data were excluded if they were previously reported. Get Data Graph Digitizer 2.24 (free software) was used to derive data from figures. Data presented as equations were excluded.

To make the database consistent, units of partial data were converted. For crop yield, if the target literature described only the percentage of O$_3$ fumigation effects on crop yield under O$_3$ fumigation treatment, then the value of 1 and 1 - the percentage was recorded under control and O$_3$ fumigation treatments. For O$_3$ concentration, the unit of part per billion (ppb) was considered as the only unit of O$_3$ concentration under O$_3$ fumigation and control treatments. The parts per million (ppm) and nmol mol$^{-1}$ were converted to ppb by using the following equation:

\[ 1 \text{ ppb} = 0.001 \text{ ppm} \tag{1} \]
\[ 1 \text{ ppb} = \frac{22.4}{48} \text{ ug/m}^3 \tag{2} \]

The data represented 960 O$_3$ fumigation experiments reported in 208 published articles/reports that tested the effect of elevated O$_3$ concentration on crop yield. This included 363 experiments for wheat, 31 experiments for maize, 305 experiments for rice, 147 experiments for soybean, and 114 experiments for various vegetables, respectively. Besides the experimental period, O$_3$ fumigation concentration, exposure time, and crop yield measures, photosynthetic and agronomic indexes were also included in the database, which explained the variation in $Y_o$. Photosynthetic indexes had a light-saturated rate (191 experiments), stomatal conductance (169 experiments), leaf chlorophyll content (170
experiments), and leaf injury (41 experiments), correspondingly. Agronomic indexes included aboveground biomass (266 experiments), total biomass (218 experiments), grain number per ear (316 experiments), ear number per plant (343 experiments), grain-setting percentage (180 experiments), 1000-grain weight (379 experiments), and harvest index (225 experiments), and leaf area index (190 experiments), respectively. The mean, standard deviations (SD), and sample size (N) of photosynthetic and agronomic indexes under O₃ fumigation and control treatments were recorded in the database together with the crop yield. If only the standard error (SE) was reported in the target literature, SD was transformed by: $SD = SE\sqrt{N}$. If SD or SE was not reported, the missing SD was replaced by multiplying the corresponding mean times with the coefficient of 0.05. If N was not reported, the disappeared N was replaced as the mean sample sizes of each crop type. Additionally, latitude and longitude were extracted only to show the global distribution of the 960 experiments (Fig. 1a). In cases where latitude and longitude were not reported across the target literature of the O₃ fumigation experiments (34% of target literature did not report latitude and longitude), the approximate latitude and longitude were obtained by inputting the name of the experimental site into Google Earth 7.0 (the free version). It did not affect the major results. Furthermore, the author and publication year were recorded and used to test the publication bias (Supplementary Fig. 2). Overall, the sites of our global study spanned from -1.26° to 57.92° and -123.23° to 140.21° in latitude and longitude, respectively.

The O₃ sensitivity of crop yield. The $Y_0$ is crop yield loss rate (%) relative to elevated O₃ concentration per 1 ppb h⁻¹. This is applied to normalize the effects of atmospheric O₃ on crop production. One primary objective of our study was to precisely define the $Y_0$ under different O₃ intervals using a meta-analysis approach. Meta-analysis is a comprehensive statistical strategy to systematically combine and quantitatively evaluate multiple independent research results with a common research purpose, which is particularly suitable for the large-scale study.

Before performing the meta-analysis, the quality of experimental data was using the "metainf" package (Supplementary Fig. 2). This is a method of combining publication bias and treatment to explore any source of publication bias. Such discrimination could reduce the small-sample effects by publication bias and ensure the credibility of the results. If a control corresponds to more than one experimental treatment at a study site, such treatments are considered non-independent of sampling. Previous studies have shown that the non-independence of the sample can significantly affect the research results, but such studies have also offered solutions. According to the principles of
statistics and study purpose, the data of different O\textsubscript{3} concentrations under O\textsubscript{3} fumigation treatment was regarded as non-independence of sampling compared with the same control treatment. Therefore, the mean and SD of non-independence were weighted based on the concentration of different O\textsubscript{3} fumigation. The following equation calculated the weight of O\textsubscript{3} fumigation concentrations (W\textsubscript{f}):

\[ W_f = \frac{C}{\sum_{i=1}^{n} C_i} \]  

where C is the concentration of different O\textsubscript{3} fumigation (ppb); n is the number of O\textsubscript{3} fumigation concentrations under the same control treatment.

To quantify the magnitude of O\textsubscript{3} sensitivity of crop yield, we first calculated the response ratio (RR) of O\textsubscript{3} fumigation on crop yield. The RR of treatment was calculated as the following equation:

\[ RR = \frac{X_f}{X_c} \]  

where \( X_f \) and \( X_c \) are the crop yield under O\textsubscript{3} fumigation and control treatments, respectively.

The value of RR less than 1 indicates a negative effect of O\textsubscript{3} fumigation on crop yield. The meta-analysis is the comparison of treatments including even different variables. The RR is natural log-transformed to approach the normal distribution:

\[ \ln(\text{RR}) = \ln \left( \frac{X_f}{X_c} \right) = \ln(X_f) - \ln(X_c) \]  

The overall response ratio (\( \ln(\text{RR}) \)) of a group was calculated as follow:

\[ \ln(\text{RR}_g) = \frac{\sum_{i=1}^{n} \ln(\text{RR}_i) * W_i}{\sum_{i=1}^{n} W_i} \]  

where n is the number of a group. W\textsubscript{i} is the weighting factor of the \( i \)th data in the group. The W\textsubscript{i} is calculated as the following equation:

\[ W_i = \frac{1}{V_i} \]  

where V\textsubscript{i} is the variance of \( i \)th data. The V\textsubscript{i} was calculated as the following equation:

\[ V_i = \frac{SD_f^2}{n_f X_f^2} + \frac{SD_c^2}{n_c X_c^2} \]  

where \( n_f \) and \( n_c \) are the numbers of samples for O\textsubscript{3} fumigation and control treatments, respectively. SD\textsubscript{f} and SD\textsubscript{c} are the standard deviations for O\textsubscript{3} fumigation and control treatments, respectively.

The standard error (SD(\( \ln(\text{RR}_g) \))) and 95% confidence interval (CI) of the \( \ln(\text{RR}_g) \) were calculated by the following equations:

\[ \text{SD}(\ln(\text{RR}_g)) = \sqrt{\frac{\sum_{i=1}^{n} W_i}{\sum_{i=1}^{n} W_i}} \]
\[ 95\% \text{CI} = \ln(RR+) \pm 1.96 \text{SD} \left( \ln(RR+) \right) \] (10)

O₃ fumigation significantly affects the crop yield if the 95% confidence interval does not overlap with 1. If the 95% confidence interval of two variables does not overlap, they are considered significantly different. The following equation transformed the effect size (ES, %):

\[ ES = \left( e^{\ln(RR+)} - 1 \right) \times 100\% \] (11)

A value of ES less than 0 indicates a negative effect of O₃ fumigation on crop yield. A meta-analysis should be performed to correctly and effectively detect heterogeneity in data before merging it, i.e., heterogeneity test. Previously, a chi-square test was used as a tool for testing heterogeneity. However, it has been found that the chi-square test lacks efficacy and has no statistical significance for the existence of heterogeneity for small samples. At present, the most commonly used heterogeneity testing methods can be divided into two kinds: the graphical method and the systematic measurement method. For latter, if \( P > 0.1 \) and \( I^2 < 50\% \) (no heterogeneity), the fixed-effect model is selected for meta-analysis. Otherwise, the random effect model is selected. The meta-analysis was performed using the MetaWin 2.0.

The \( Y_o \) (ppb h⁻¹) was calculated as follows:

\[ Y_o = \frac{ES}{(O_f - O_c)d\times h} \] (12)

where \( O_f \) and \( O_c \) are O₃ concentrations (ppb) for O₃ fumigation and control treatments, respectively. \( d \) and \( h \) are the days of O₃ fumigation and hours of O₃ fumigation per day, respectively.

Previous studies indicated that atmospheric O₃ concentrations above 40 ppb could significantly affect crop yield²⁸,⁴³. Based on our dataset, atmospheric O₃ can dramatically affect crop yield even at 30-40 ppb (Supplementary Fig. 3). Therefore, we calculated the \( Y_o \) of different crop (wheat, maize, rice, soybean, and vegetable) yield under 7 intervals (30-40, 40-50, 50-60, 60-70, 70-80, 80-90, and >90 ppb) according to O₃ concentration of fumigation treatment (Fig. 1c). The \( Y_o \) of maize under the 30-40 ppb interval was obtained using a fitting equation due to the missing data (Supplementary Fig. 4). Based on the above principles and methods, we also calculated the O₃ sensitivity of photosynthetic indexes (light-saturated rate, stomatal conductance, leaf chlorophyll, and leaf injury) and agronomic indexes (aboveground biomass, total biomass, grain number per ear, ear number per plant, setting percentage, thousand seed weight, harvest index, and leaf area index), respectively. This was done to try and determine the mechanistic basis for any O₃ damage relative to proportional changes in crop yield.

Global real-time O₃ concentration data. The global crop yield loss rate is dependent on global
real-time $O_3$ concentrations during the crop growing season. In this study, we used hourly $O_3$
concentrations as the standard unit. The hourly $O_3$ concentrations, in turn, were derived by searching
and/or directly accessing air quality monitoring stations in each country. An air quality monitoring
station had to meet the following three criteria in our database: (1) air quality monitoring station must
report the exact latitude and longitude; (2) $O_3$ concentration must be recorded on an hourly basis. If
only the average of one day was given, data were excluded; (3) a complete record of at least two years
of data from 2017 to 2019. Any air quality monitoring station reported in the parts per million, or nmol
mol$^{-1}$ units were converted to ppb using equations 1-2. Overall, the hourly $O_3$ database includes about
160 million data pairs (latitude, longitude, time, and $O_3$ concentration) from 7246 stations in more than
60 countries or regions (Supplementary Fig. 5). Except for missing data for some countries (e.g., Japan
for 2019), the integrity rate of the database is more than 94%.

The hourly $O_3$ concentration was divided into 7 intervals (30-40, 40-50, 50-60, 60-70, 70-80, 80-90,
and >90 ppb). If the $O_3$ concentration is below 30 ppb for an hour, the 7 intervals are assigned 0 ppb. If
the $O_3$ concentration for an hour is more than 90 ppb, the first 6 intervals are assigned 10 ppb, and the
7th interval (>90 ppb) is the difference of $O_3$ concentration of that hour and 90 ppb. For every air
quality monitoring station, the crop yield loss rate (%) of total and each $O_3$ interval was calculated as
follows:

$$\text{Crop yield loss rate} = \sum_{g=1}^{ng} \left( \sum_{m=1}^{nm} \left( \sum_{i=1}^{ni} \left( -\Delta Y_{ith} \times O_{ith} \right) \right) \right) \times 100\% \quad (13)$$

where $i$, $m$, and $g$ are the $i$th $O_3$ intervals, the $m$th hour and $g$th day, respectively. $ni$ is total $O_3$ intervals
for an hour. $nm$ is 12, meaning 12 hours per day (08:00-20:00). $ng$ is the number of days of crop
growing season.

Although we have tried to obtain crop yield loss rate for more than 7,000 stations worldwide,
however, the distribution of those stations is limited. To get the spatial predictions of the crop yield loss
rate in each country or region, kriging classifications combined with regression were used in ArcGIS
10.4.1 (version). The result was presented for 0.0083×0.0083° grid squares across the entire terrestrial
system of the globe$^{44}$. Meantime, different crop distribution data (about 2 million) were obtained at the
MAPSPAM (https://www.mapspam.info/) and used to get the spatial distribution of the crop yield loss
rate in the cropland (Supplementary Fig. 6-9).

**Global crop production data.** To estimate the crop production loss caused by atmospheric $O_3$, the
global crop production was obtained from the Food and Agriculture Organization of the United Nations
(FAO, http://www.fao.org/faostat/en/#data/QC). The FAO reports wheat, maize, rice, and soybean crop productions for 200 countries or regions for the years 1961-2019. However, crop production data for 2017-2019 have been selected under real-time O\textsubscript{3} data as the national crop production data is not consistent with that of the crop yield loss rate data on a grid square. Furthermore, this is the most recent and complete observational data which we can get. Therefore, crop production loss of total and each O\textsubscript{3} interval was estimated on a national basis using the following equation:

\[
\text{Crop production loss} = \sum_{i=1}^{n_i} (\text{Crop production} \times \text{Crop yield loss rate}_{ith})
\]  

(14)

**Structural equation model analysis.** Structural equation model (SEM) analysis was performed for quantitative partitioning the direct and indirect pathways and determining whether atmospheric O\textsubscript{3} concentration influences the Y\textsubscript{o} through crop indexes\textsuperscript{17}. The 7 O\textsubscript{3} intervals (30-40, 40-50, 50-60, 60-70, 70-80, 80-90, and >90ppb) and four crop types (wheat, maize, rice, and soybean) were regarded as treatment gradient to conducted the SEM analysis focusing on the overall effect. To simplify the model framework, crop indexes were divided into two categories: agronomic indexes and photosynthetic indexes. For agronomic indexes, the O\textsubscript{3} sensitivity of the aboveground biomass, grain number per ear, and leaf area index were retained as latent variables according to loading scores. For the latent variable photosynthetic indexes, three potential indicators were: O\textsubscript{3} sensitivity of light-saturated rate, stomatal conductance, and chlorophyll (Supplementary Fig. 11). The following possible pathways were hypothesized: first, O\textsubscript{3} concentration, agronomic indexes, and photosynthetic indexes have a direct effect on the Y\textsubscript{o}; second, O\textsubscript{3} concentration may indirectly affect the Y\textsubscript{o} via its impact on agronomic and photosynthetic indexes. Finally, photosynthetic indexes may indirectly affect the Y\textsubscript{o} via their effects on agronomic indexes. SEM analysis assumes that the variance-covariance matrix of the observed variable is a function of a set of parameters. Its estimation requires minimizing the difference between the variance-covariance value of the sample and the value estimated by the model and taking the difference as the residual. The maximum likelihood (estimate means and intercepts) was used to assess the path parameter. A nonparametric bootstrap method was adopted to calculate the accuracy of parameter estimate\textsuperscript{17}. The standardized total effect was shown to express the relative impact of O\textsubscript{3}, photosynthetic indexes, and agronomic indexes on the Y\textsubscript{o}. Amos 17.0 for Windows (version) was used to perform the SEM analysis.

**Data availability**

All data related to this manuscript are available from the Dryad Digital Repository:
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Figure Legends

Fig. 1 Ozone sensitivity of crop yield. a, global distribution of the 960 experiments from 208 published papers in which the effect of elevated ozone concentration on crop yield was assessed. The size of black circles represents the sample size ranging from 1 to more than 19. Crop types include wheat (in brown), maize (in red), rice (in green), soybean (in turquoise), and vegetable (in blue). b, response ratio (natural logarithm-transformed ratio of treatment to control) of the ozone sensitivity of crop yield (ppb h⁻¹). Dot and bar represent the mean and range at 95% confidence intervals of ozone sensitivity of crop yield. The value in parentheses represents the sample sizes. c, the relationship between ozone sensitivity of crop yield and ozone fumigation concentration. Each dot represents the average effect size under ozone fumigation intervals with <30, 30-40, 40-50, 50-60, 60-70, 70-80, 80-90, >90 ppb for each crop type according to the treatment groups in the database.

Fig. 2 Global annual loss rate (%) of crop yield (2017-2019) due to atmospheric ozone concentration. The maps showed the spatial distribution of cumulative crop yield loss (%) in the case of ozone concentration above 30 ppb for wheat (a1), maize (b1), rice (c1), and soybean (d1), averaged for the period 2017-2019. The spatial distribution of crop yield loss in the case of ozone above 30, 40, 50, 60, 70, 80, and 90 ppb for wheat, maize, rice, and soybean were also shown in Supplementary Fig. 6-9, respectively. All data were presented for the 0.0083° grid squares based on global 7246 real-time ozone monitoring stations (see Supplementary Fig. 5). a2, b2, c2, and d2 indicated crop yield loss of wheat, maize, rice, and soybean in the case of ozone concentration ranged with 30-40, 40-50, 50-60, 60-70, 70-80, 80-90, and >90 ppb for global and 5 countries or regions (ranked top five in grain production) averaged value, respectively. The percentage of ozone monitoring stations involved in calculating the effects of ozone on crop yield at each range of ozone concentration was shown in
Fig. 3 Influence of ozone (O₃) and ozone sensitivity of photosynthetic (Pₒ) and agronomic (Aₒ) indexes on the ozone sensitivity of crop yield (Yₒ). a, path analysis results on the direct and indirect effects of O₃, Pₒ, and Aₒ on the Yₒ. Numbers show the path coefficients. Grey path and number indicate that the effect is insignificant. Arrow width is proportional to the standardized coefficient. The Pₒ includes ozone sensitivity of light-saturated rate, ozone sensitivity of stomatal conductance, and ozone sensitivity of chlorophyll (See supplementary Fig. 11). The Aₒ has the ozone sensitivity of above ground biomass, the ozone sensitivity of grain number per ear, and the ozone sensitivity of leaf area. b, the standardized total effect of O₃, Pₒ, and Aₒ on the Yₒ.

Tables

Table 1 Global and five areas (ranked top five in grain production) annual loss amount of wheat, maize, rice, and soybean production (million tonnes) in the case of ozone 30-40 ppb and above 40 ppb. Each country’s annual loss rate of crop yield in the case of ozone above 30, 40, 50, 60, 70, 80, and 90 ppb and total yield for wheat, maize, rice, and soybean were shown in Supplementary Table 2-6.

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Author contributions

A.D., B., W.J., and Y.E. designed the study. A.D. and T.J. collected the data. A.D. analyzed the data. All authors contributed significantly to the writing of the manuscript.

Competing interests

The authors declare no competing interests.
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