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An Intermittent Exposure Regime Did Not Alter the Crop Yield and Biomass Responses to an Elevated Ozone Concentration

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Abstract: The intermittent ozone (O_3) exposure of crops to alternating high and low concentrations is common in fields, but its impact on crop production has not been thoroughly investigated. In this study, two widely planted and O_3-sensitive crops, winter wheat and soybean, were intermittently exposed to elevated O_3 concentrations in open-top chambers. The results showed that the winter wheat and soybean yields significantly decreased with O_3 exposure (AOT40, cumulative hourly O_3 concentration above 40 ppb) ($p < 0.001$). The relative yield losses were 0.99% per AOT40 for winter wheat and 1.2% per AOT40 for soybean, respectively. The responses of the crop biomasses to elevated O_3 concentrations were lower than that of crop yield. Although the O_3-induced crop yield and biomass losses under continuous O_3 exposure were greater than those under intermittent O_3 exposure, the differences were not statistically significant. Therefore, we can conclude that the effects of elevated O_3 concentrations on crops are closely related to the exposure dose but not significantly related to the temporal distribution of elevated O_3 concentrations. This study improves our understanding of how crop production responds to intermittent O_3 exposure.

Keywords: ozone; intermittent exposure; wheat; soybean; yield; biomass

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1. Introduction

Ozone (O_3), a widely distributed air pollutant, has significant negative impacts on human health, crop yields, and visibility. Due to substantial efforts to reduce the emissions of O_3 precursor gases such as nitrogen oxides (NOx), carbon monoxide, and hydrocarbons, the O_3 concentrations over Europe and North America have slightly decreased or plateaued since 2000 [1–5]. However, the O_3 concentrations in eastern Asia continued to increase after 2000 [6–8]. In China, with rapid economic growth and increasing NOx emissions, O_3 concentrations have been increasing significantly. Xu et al. [9] reported that the summer O_3 concentrations at the Shangdianzi background site in North China increased at rates of more than 2%/yr during 2004–2016. The warm-season daily maximum 8 h average (MDA8) O_3 levels increased by 2.4 ppb (5.0%)/yr, with more than 90% of the sites showing positive trends and 30% exhibiting trends greater than 3.0 ppb/yr [7]. O_3-induced leaf injuries have frequently been observed in and around Beijing, North China [10–12], indicating that high O_3 exposure has caused significant damage to plants in China. Many experiments have confirmed that staple crops worldwide, such as wheat, soybean, rice, and maize, are O_3-sensitive [13–15]. The O_3-induced global crop losses are estimated at 277 Tg, and the global annual crop yield is estimated to be reduced by 12.4%, 7.1%, 4.4%, and 6.1% for soybean, wheat, rice, and maize, respectively, due to elevated O_3 concentrations [14]. Crop losses induced by elevated O_3 concentrations have attracted particular attention in China, because any reduction in crop production in China might threaten global food security. The most recent estimates showed that the national mean relative yield losses induced by O_3 in China were 11.45–19.74%, 7.59–9.29%, 0.07–3.35%, and 6.51–9.92% for wheat, rice, maize, and soybean, respectively, from 2010 to 2017 [16]. This shows that mitigating the impact of increasing O_3 concentrations is crucial to increase global crop supplies.

At present, the assessment of crop losses caused by O_3 has mostly been carried out through dose–response relationships. Available investigations have shown that crop losses have a good correlation with metrics of O_3 exposure, such as AOT40, which is one of most widely used metrics [17–19]. However, this knowledge on the impact of O_3 on crops is derived from experiments in which crops are continuously exposed to target O_3 concentrations. However, the concentration of O_3 in the atmosphere is not continuously increasing but exhibits different patterns, because the generation of ozone is influenced by many factors. O_3 is photochemically produced through the oxidation of carbon monoxide, methane, and nonmethane hydrocarbons in the presence of nitrogen oxides [20]. The ambient O_3 concentrations fluctuate depending on weather conditions and more readily form on warm, sunny days when the air is stagnant. Along with temporal variations in sun light, ambient O_3 concentrations exhibit two temporal patterns: one is a significant diurnal variation in O_3 concentrations that increases from morning, reaches a peak after noon, and then decreases [21]; the other is a sequential alternation on days in which high and low O_3 concentrations occur depending on sunny and cloudy skies, respectively [22,23]. The temporal variation in O_3 concentration is likely to alter the impact of O_3 on plants. To improve estimates of crop losses or explore safeguards to crop production, it is essential to understand how crops respond to these patterns of O_3 exposure. A previous study revealed differences in crop losses between crops that are exposed to O_3 diurnal variation and a constant O_3 concentration [24]. However, how plants respond to sequential exposure to different O_3 concentrations (i.e., intermittent O_3 exposure) has been investigated less.

When unfavorable conditions occur, plants can adjust their metabolism to modulate their growth and development via defense and homeostasis pathways to resist and adapt to environmental stresses. Plants' resilience to environmental stress is determined by acclimation not only to stress but also to recovery after the stress is relieved. As stress ceases, plants can show growth patterns of partial, full, or compensatory recovery. Available reports show that plants can recover from drought [25], flooding [26], and metal pollution [27]. O_3 entering plant leaves through stomata can trigger a reaction chain involving reactive oxygen species (ROS), which causes lipid peroxidation to damage the cell membrane, biochemical metabolism processes, and growth. With an increasing O_3 concentration, the damage becomes more serious. When plants are exposed to low O_3 concentrations, the damage might be minor or even hermetic [28]. Under cloudy and rainy weather conditions, which are not conducive to forming O_3 in the air due to a lack of ultraviolet radiation [29,30], crops can not only avoid the impact of high O_3 concentrations but also recover from previous stress from high O_3 concentrations. O_3 exposure can thus be viewed as a sequential stress, in which both high O_3 concentrations and low O_3 concentration (i.e., intermittent exposure) alternatively impose distinct stressors. To date, information on O_3-induced crop loss due to such intermittent exposure is limited. In this study, unlike in traditional continuous O_3 exposure experiments, we carried out crop growth experiments with intermittent exposure to high O_3 concentrations. The study aims at investigating whether the crop response to O_3 was altered by different intermittent low-O_3-exposure regimes.

2. Materials and Methods

2.1. Experimental Site

The experimental site was located 30 km north of downtown Beijing, China (40°12′ N, 116°08′ E). It has a typical temperate and monsoonal climate with four distinct seasons. The annual mean precipitation is 550.3 mm, and the mean air temperature is 11.8 °C [31].

2.2. O_3 Exposure Facility

Open-top chambers (OTCs) for O_3 exposure were established as previously described [32]. Nine cylindrical OTCs (2.5 m in height and 2 m in diameter, with an inside area of 3.14 m^2), 2 m apart from each other, were made of an aluminum alloy frame that was covered with 2 mm transparent plastic (85% transparency). A rain cap was placed 25 cm above the frustum and attached on top of the OTCs to prevent rain and wind from entering the chamber while allowing ambient air to freely circulate. The difference in the average air temperature from 9:00 a.m. to 17:00 p.m. inside and outside the chamber was no more than 2 °C [33].

O_3 was generated from pure hospital-grade oxygen using a high-voltage discharge method (CFG-140, Jinan Sankang Envi-tech, Jinan, China). Ambient air or O_3-containing air delivered by a 750 W centrifugal blower was released through a 13 cm diameter three-way connector, which was placed in the center of each chamber with an aluminum tube. The O_3 concentration in each chamber was monitored sequentially for 10 min using an automated time-sharing system connected to an ozone analyzer (Model 49i, Thermo Scientific, Thermo Fisher Scientific Ltd., Franklin, MA, USA), and all the data were stored in the analyzer. The Model 49i O_3 analyzer was calibrated every month with a Model 49i-PS O_3 analyzer, which is a transfer standard for the calibration of ozone analyzers (Model 49i-PS, Thermo Scientific, USA). The precision, response time, and span drift were 1.0 ppb, 20 s, and <1% per month for both O_3 analyzers. When the O_3 concentration within the OTC exceeded 10% of the target O_3 concentration, a glass rotameter (LZB-2, Suzhou Chemical Instrument, Suzhou, China) was used to manually tune the flow of oxygen entering the O_3 generator to achieve the target O_3 concentration. Pretests showed that O_3 concentrations were evenly distributed, both vertically and horizontally, within the OTCs.

2.3. Experimental Design

The OTCs were randomly assigned to each of the three O_3 treatment groups: ambient O_3 as the control, ambient plus 40 ppb O_3, and ambient plus 80 ppb O_3. For each O_3 treatment, 3 replicates of the OTCs were used. Three temporal regimes of O_3 exposure were established: continuous (CE, O_3 exposure continuous), a 5-day cycle (5 dC, O_3 exposure for 5 days, then interrupted for 5 days) and a 10-day cycle (10 dC, O_3 exposure for 10 days, then interrupted for 10 days). These regimes were established by moving plant pots between the OTCs of the control group and those with elevated O_3 concentrations. For example, in the 5 dC treatment, we placed the pots in an OTC with an elevated O_3 concentration for 5 days and then moved these pots to the OTC of the control for 5 days. Afterwards, a new cycle was initiated until the crop ripened.

2.4. Crops and Management

In North China, the cropping system is maturations of two types of crops within a year. Winter wheat is sown in later autumn and harvested in the next early summer, after which soybean is sown in summer and harvested in later fall. Winter wheat and summer soybean plants were sown in plastic pots that were 30 cm in diameter and 30 cm high. The popular planted wheat cultivar Jing 411 (*Triticum aestivum* L. jing411) was selected. This cultivar is cold-tolerant and amenable to maturation [34]. Wheat plants were sown on 6 October 2020 and harvested on 28 May 2021. The soybean cultivar used was Jidou 12 (*Glycine max* (Linn.) Merr. Jidou12), which is widely planted in North China and matures early [35]. The soybeans were sown on 15 June 2021 and harvested on 15 October 2021.

All pots were filled with composite soil mixed with commercial organic soil. Eight grams of complex fertilizer was applied per pot. Other practices, such as irrigation and pesticide application, were carried out as necessary so that the crops could grow without stress from drought, insects, pests, or nutrient deficiency.

After the wheat and soybean plants were 10 cm high, the plant pots were transferred to the OTCs for O_3 fumigation. For each treatment, at least 9 pots were used as replicates. Fumigation was carried out from 16 March until 20 May, when the leaves became yellow in winter wheat, and from 6 July until 19 October, when the leaves became yellow in soybean. The daily O_3 fumigation time was from 9:00 a.m. to 17:00 p.m. The cumulative O_3 exposure was described as AOT40, which was calculated as the cumulative hourly mean O_3 concentration over 40 ppb during O_3 fumigation (Table 1).

Table 1. Cumulative values of AOT40 for each treatment (ppm·h).

Crop	Control	40 ppb			80 ppb		
		5 dC	10 dC	CE	5 dC	10 dC	CE
Winter wheat	3.60	14.44	15.05	25.51	23.43	23.42	43.60
Soybean	3.71	11.61	13.25	19.94	21.77	23.65	38.68

2.5. Harvest and Yield Measurements

Three individuals were harvested from each pot after the crop ripened. The roots, stems, leaves, and grains were separated, and their dry weights were determined as the root, stem, and leaf biomass and yields, respectively, after oven-drying at 70 °C to a constant weight.

2.6. Statistical Analyses

All statistical analyses were performed in R v 4.2.1 (R Core Team, 2022). To test whether biomass and yield responded differently to elevated O_3 concentrations under different O_3 exposure regimes, we fitted linear models with the lm function in the nlme package. In the models, root, stem, and leaf biomass and yield per individual plant were specified as response variables, while O_3 effects were measured based on statistically significant (p) responses for each treatment, with O_3 exposure doses (AOT40)er as independent factors. The 95% confidence intervals (CIs) derived from the slopes of the linear models were compared to determine whether there were significant differences in the effects of O_3 on crop biomass and yield among the different treatments. If the 95% CIs overlap among the different treatments, it means that there is no significant difference in the response to AOT40 among the different treatments.

3. Results

3.1. Winter Wheat

An elevated O_3 concentration significantly reduced the yield (grain weight) of winter wheat under the CE treatment ($p < 0.05$), significantly increased the yield under the 5 dC treatment ($p < 0.1$), and did not significantly influence the yield under the 10 dC treatment (Figure 1a). However, the 95% CI of the regression slopes of crop yield to AOT40 overlapped among the different treatments (Figure 1b), suggesting that intermittent exposure did not change the response of the winter wheat yield to O_3 exposure. There were significant linear regressions between the relative yield and AOT40 for all the treatments as follows:

$$RY = 1.20 - 0.0099\ AOT40\ (r2 = 0.304,\ p = 0.009) \tag{1}$$

Elevated O_3 concentrations did not significantly influence the root, stem, leafor total biomass of winter wheat under the CE or 10 dC treatment ($p > 0.05$), but they did significantly increase the root ($p < 0.05$), stem ($p < 0.1$), leaf ($p < 0.1$), and total biomass ($p < 0.1$) under the 5 dC treatment (Figure 1c,e,g,i). However, the 95% CI of the regression slopes of the crop biomass to AOT40 overlapped among the different treatments, indicating that there was no significant difference in the responses of the biomass to O_3 exposure among the different exposure regimes (Figure 1d,f,h,j) and suggesting that intermittent exposure (5 dC and 10 dC treatments) did not change the response of winter wheat biomass to O_3 exposure.

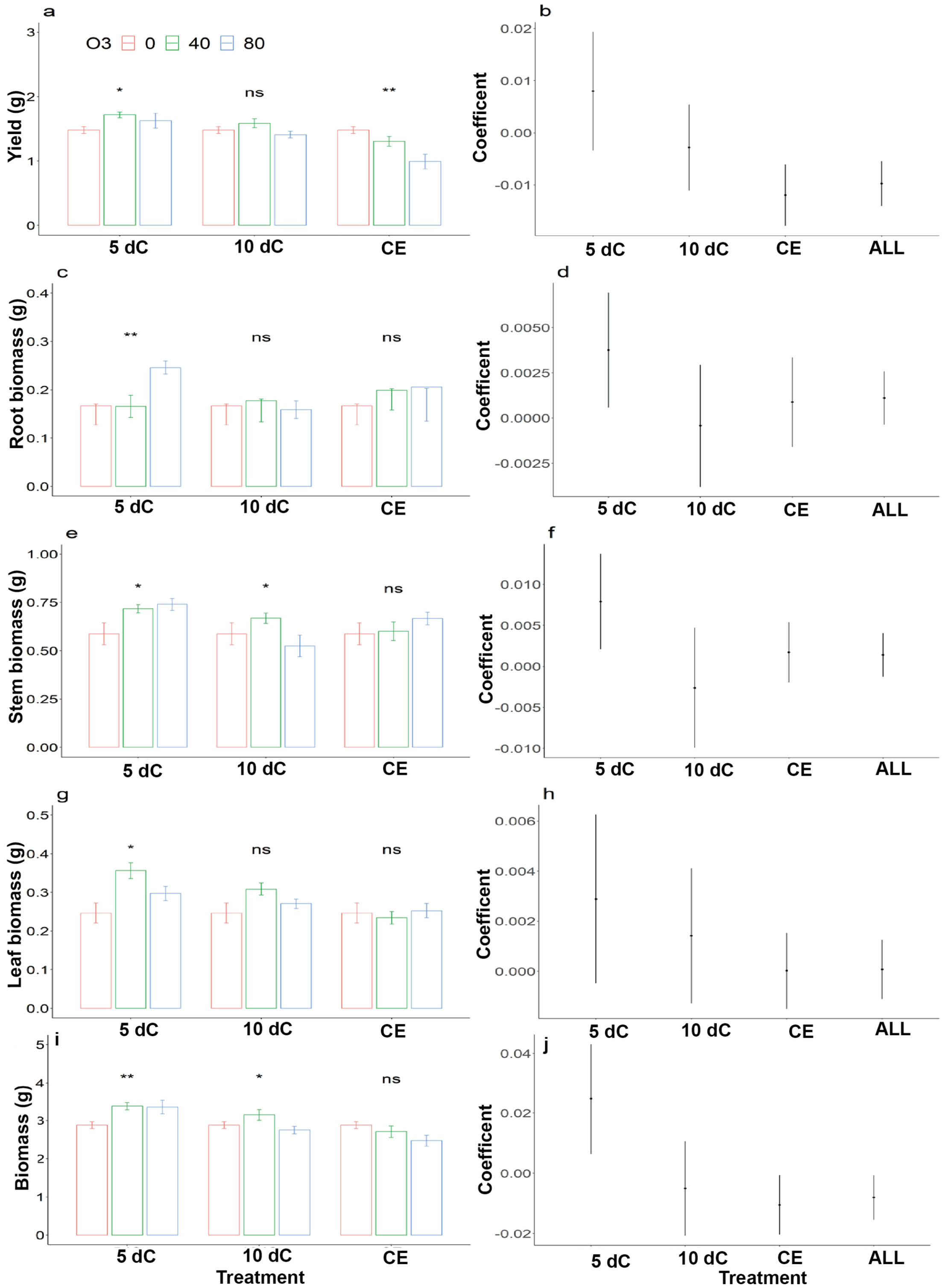

Figure 1. The winter wheat yield (**a**) and root (**c**), stem (**e**), leaf (**g**), and total biomass (**i**) under different ozone concentrations and their responses (the 95% confidential interval of the slope of the regression relation between the crop biomass or yield to O_3 exposure dose AOT40.slopes of the regression relation of yield or biomass of winter wheat yield (**b**), and root (**d**), stem (**f**), leaf (**h**), and total biomass (**j**) to ozone exposure dose AOT40) under different intermittent elevated ozone exposures (5 dC and 10 dC: crops were sequentially exposed for 5 and 10 days of elevated ozone concentration and then interrupted for 5 and 10 days, respectively. CE: crops were exposed continuously to an elevated ozone concentration). The significance levels: ** ($p < 0.01$), * ($p < 0.05$), ns ($p \geq 0.05$).

3.2. Soybean

An elevated O_3 concentration significantly reduced the yield (grain weight) of soybean plants under CE ($p < 0.001$) and 10 dC ($p < 0.01$) but did not significantly influence the yield under the 5 dC treatment (Figure 2a). However, the 95% CI of the regression slopes of the crop yield to AOT40 overlapped among the different treatments (Figure 2b), suggesting that intermittent exposure did not change the response of soybean yield to O_3 exposure. There were significant linear regressions between the relative yield and AOT40 for all the treatments as follows:

$$RY = 0.985 - 0.012\ AOT40\ (r2 = 0.34,\ p = 0.007) \tag{2}$$

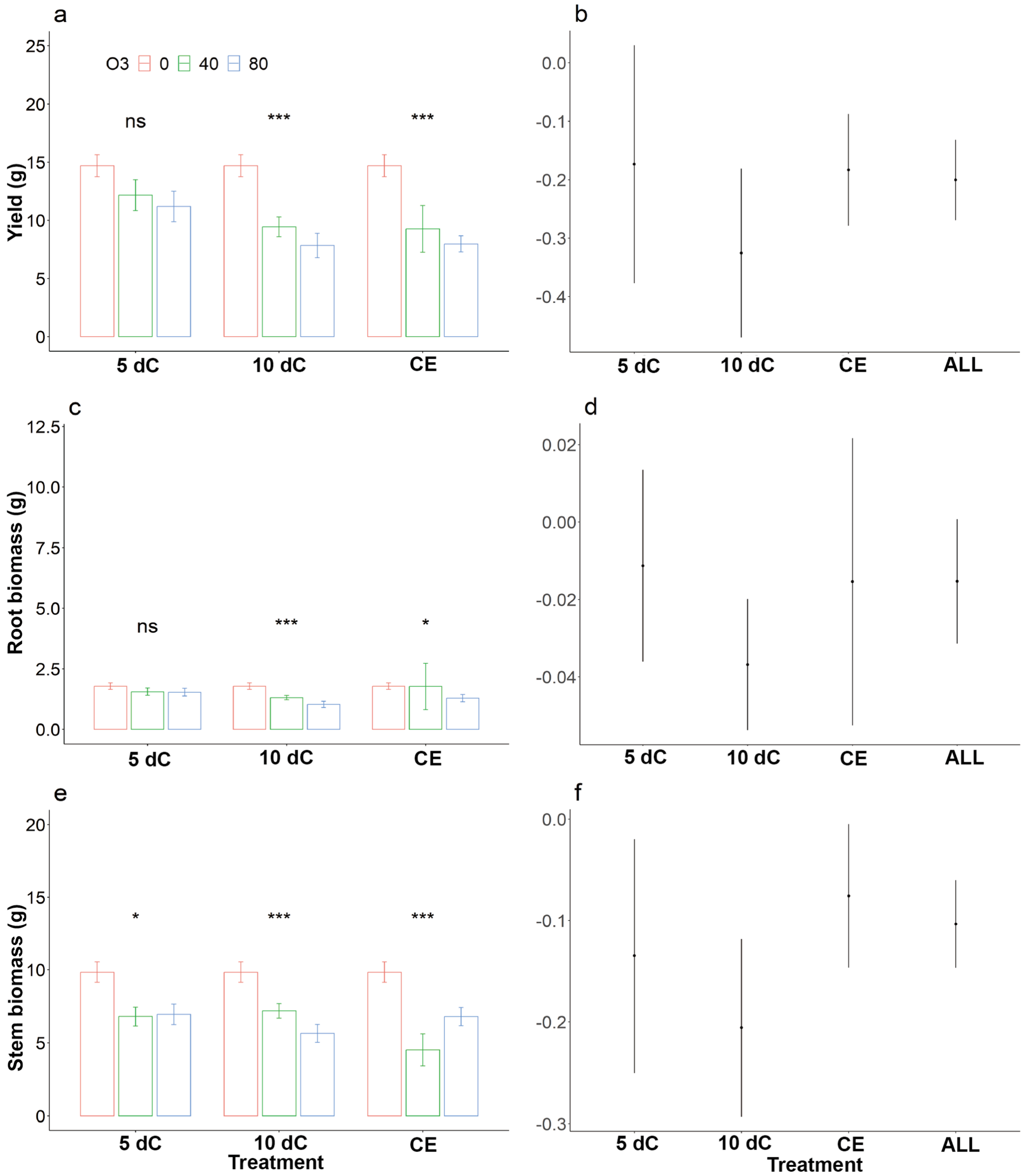

Figure 2. The soybean yield (**a**) and root (**c**) and stem (**e**) under different ozone concentrations and their responses (the 95% confidential interval of the slopes of the regression relation between the crop biomass or yield of soybean yield (**b**) and the root (**d**) and stem (**f**) to ozone exposure dose AOT40) under different intermittent elevated ozone exposures (5 dC and 10 dC: crops were sequentially exposed for 5 and 10 days of elevated ozone concentration and then interrupted for 5 and 10 days, respectively. CE: crop was exposed continuously to elevated ozone concentration). The significance levels: *** ($p < 0.001$), * ($p < 0.05$), ns ($p \geq 0.05$).

Elevated O_3 concentrations significantly reduced the root ($p < 0.01$ and $p < 0.1$), stem ($p < 0.01$ and $p < 0.05$), and total biomass ($p < 0.01$ and $p < 0.01$) of soybean plants under CE and 10 dC treatment and the stem biomass ($p < 0.1$) under 5 dC treatment but did not significantly influence the root or total biomass (Figure 2c,e). However, the 95% CI of the regression slopes of the crop biomass to AOT40 overlapped among the different treatments, indicating that there was no significant difference in the responses of biomass to O_3 exposure among the different exposure regimes (Figure 2d,f) and suggesting that intermittent exposure (5 dC and 10 dC treatments) did not change the response of the soybean biomass to O_3 exposure.

4. Discussion

Our experiments clearly showed that elevated O_3 concentrations could significantly reduce the crop yield for both winter wheat and soybean plants, which is consistent with the findings of previous studies conducted in China [36,37], as well as throughout the world, including countries such as the USA, the UK, France, Italy, India, and Japan [38,39]. This study revealed that the effects of O_3 on crop yield and biomass were dose-dependent, as shown by the significant linear regressions between the relative yield and AOT40 for all treatments (Equations (1) and (2)) [40,41]. A significant reduction in crop yield only occurred when the O_3 exposure dose exceeded a certain threshold value. Under high O_3 exposure doses, such as that during continuous exposure to O_3 (in the CE treatment in this study, AOT40 = 43.6 and 38.68 ppm for wheat and soybean, respectively), the crop yield significantly decreased for both wheat and soybean. Under low O_3 exposure, such as that during intermittent exposure to O_3 (5 dC and 10 dC treatments in this study, AOT40 = 23.42–23.43 ppm for wheat and 21.77–23.65 ppm for soybean), the crop yield did not decrease significantly ($p > 0.1$). Interestingly, under the 5 dC treatment, the wheat yield increased significantly under O_3 exposure (40 ppb plus fumigation), which is generally referred to as the hermetic effect [28]. Although elevated O_3 concentrations are undoubtedly toxic, there is increasing evidence that low O_3 concentrations might have beneficial effects. Similar results have been reported in experiments in which pretreatment with trace metallic elements was used to stimulate defense mechanisms and induce tolerance of other stress factors, such as osmotic stress, salinity, drought, low temperature, and pathogen attacks, increasing plant production [42,43]. Additionally, cabbage plants (*Brassica oleracea* var. capitata f, alba) that were subjected to 70 ppb O_3 treatment had an increased diameter of rosettes and number of leaves after 3 and 7 weeks [44]. Under these conditions, O_3 exposure ceased to cause compensatory growth, and subsequently, the plant growth not only recovered but also improved. To confirm the universality of the compensatory growth effect, further research is needed to investigate plant growth under different O_3 exposure intensities, durations, recovery times, etc.

The effects of elevated O_3 concentrations on biomass varies with crop type and O_3 dose. In the present study, the root, stem, leaf and total biomass of wheat did not significantly decrease under the 10 dC treatment or CE treatment at elevated O_3 concentrations but increased under the 5 dC treatment. The root, stem, and total biomass of soybean plants significantly decreased under the 10 dC and CE treatments at elevated O_3 concentrations but did not significantly decrease under the 5 dC treatment. Taken together, these findings imply that, under elevated O_3 concentrations, the crop biomass decreases less than the crop yield, and this inconsistency in the magnitude of decline may correspond to a growth strategy for plants under O_3 stress.

In previous studies, crops were often exposed to a constant concentration of O_3. However, in fields, O_3 concentrations vary on a diurnal scale, with O_3 levels peaking after noon and over multiple days, with alterations occurring between sunny days with high O_3 concentrations and cloudy or rainy days with low O_3 concentrations. Wang et al. [24] reported that under the same O_3 exposure dose, O_3 caused more crop yield losses under a diurnal fluctuating O_3 regime than under exposure to a constant O_3 concentration, suggesting that crops are damaged more by short durations of very high O_3 concentrations than by constant, moderate O_3 concentrations. Over multiple days, periods of high O_3 concentration are often separated by periods of low O_3 concentration. Crops are exposed to cycles of high and low O_3 concentrations. Even if the O_3 concentration or cumulative dose is the same, the stomatal absorption flux may be different, which can cause different plant responses. The damage of O_3 to plants is influenced by the actual absorption flux of stomata, and many studies have shown a good correlation between O_3 flux and photosynthetic or yield losses [37,45]. When the O_3 concentration exceeds a certain threshold, the stomatal ozone flux increases as the O_3 concentration rises [37], leading to photosynthesis and growth loss. But under certain conditions, O_3 exposure can reduce stomatal conductance, leading to a lower stomatal O_3 flux [46], which helps reduce the oxidative damage of O_3 to plants. Simultaneously, stomatal closure can lead to the diffusion of carbon dioxide in the stomatal intercellular cavities, thus limiting photosynthesis [47]. Unfortunately, in our study, the O_3 flux is not estimated for assessing crop yield and biomass losses because of a lack of measurements of the air temperature, humidity, as well as leaf conductance parameter within each OTC, which are essential to calculate the O_3 flux within the OTCs. Furthermore, a series of processes, such as detoxification, elimination, and recovery, occur within organisms or populations after the stress on the crops is relieved [48], and these processes could even mitigate crop damage during periods of high O_3 exposure. However, more investigations are required into this topic.

Unlike traditional experiments in which crops are continuously exposed to elevated O_3 concentrations over an entire growing season, we applied different frequencies of high and low O_3 exposure. The effects of the temporal regime of O_3 exposure on crops were assessed by comparing the linear relationships of the crop yield and biomass with the O_3 exposure dose AOT40. The 95% confidence intervals of the regression slopes of the crop yield and biomass to AOT40 overlapped among the different treatments, indicating that the responses of crop yield and biomass to O_3 exposure were similar, regardless of whether the continuous or intermittent O_3 regime was applied. This finding implies that crops' response to O_3 is related to the exposure dose but not to the exposure regime.

Other studies have shown that short-duration and acute O_3 exposure does not necessarily lead to a reduction in crop yield or grain weight [49]. For some species or genotypes, plants grown under chronic O_3 exposure can exhibit altered antioxidant capacity [50]. Researchers have reported differences in the sensitivity and tolerance of crop cultivars and the responses of different traits in plants to elevated O_3 levels [51]. In the present study, crops' responses to elevated O_3 concentrations under intermittent exposure were the same as those under continual exposure for the same cumulative dose. The reason for this might be the damage of O_3 to the crop being influenced by the actual O_3 flux absorbed by stomata and the detoxification and recovery ability of crops. To confirm this explanation, it is necessary to measure the changes in stomatal O_3 flux and crops' morphological and physiological parameters during and after O_3 exposure, especially to investigate how the timing, duration, and sequence of multiple periods of O_3 episodes affect biological systems.

5. Conclusions

Crops' exposure to ambient O_3 often occurs over numerous days with periods of high concentrations interrupted by periods of low O_3 concentrations. In this study, we assessed the impact of O_3 exposure on the crop yield and biomass under two different intermittent exposure regimes. Our results showed that there were significant relationships between winter wheat and soybean yields and the O_3 exposure dose (AOT40). However, these relationships were not significantly altered by continuous or intermittent exposure, suggesting that the temporal distribution of elevated O_3 concentrations was less important than the exposure dose for assessing the effects of elevated O_3 concentrations. This is the first study to investigate the effects of intermittent O_3 exposure on crops. In these preliminary results, we measured the crop yield and biomass at harvest, but several important indicators and processes that are pertinent to intermittent exposures were not measured, such as the crop recovery when the O_3 exposure ceased and crop resistance or tolerance when pre-exposure occurred. Therefore, additional studies are needed to investigate physiological, morphological, and ecological responses during and after O_3 exposure under different frequencies and amplitudes of high-O_3 episodes.

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