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Response of gas exchange and yield components of field-grown *Triticum aestivum* L. to elevated ozone in China

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Abstract

To assess photosynthesis and yield components' response of field-grown wheat to increasing ozone (O_3) concentration (based on diurnal pattern of ambient O_3) in China, winter wheat (*Triticum aestivum* L.) cv. Jia 403 was planted in open top chambers and exposed to three different O_3 concentrations: O_3-free air (CF), ambient air (NF), and O_3-free air with additional O_3 (CF+O_3). Diurnal changes of gas exchange and net photosynthetic rate (P_N) in response to photosynthetic photon flux density (PPFD) of flag leaves were measured at the filling grain stage, and yield components were investigated at harvest. High O_3 concentration altered diurnal course of gas exchange [P_N, stomatal conductance (g_s), and intercellular CO_2 concentration (C_i)] and decreased significantly their values except for C_i. Apparent quantum yield (AQY), compensation irradiance (CI), and saturation irradiance (SI) were significantly decreased, suggesting photosynthetic capacity was also altered, characterized as reduced photon-saturated photosynthetic rate (P_{Nmax}). The limit of photosynthetic activity was probably dominated by non-stomatal factors in combination with stomatal closure. The significant reduction in yield was observed in CF+O_3 treatment as a result of a marked decrease in the ear length and the number of grains per ear, and a significant increase in the number of infertile florets per ear. Even though similar responses were also observed in plants exposed to ambient O_3 concentration, no statistical difference was observed at current ambient O_3 concentration in China.

Additional key words: apparent quantum yield; diurnal pattern of O_3; net photosynthetic rate; irradiance; stomatal conductance; yield components.

Introduction

Ozone (O_3) has become one of the most important phytotoxic gaseous pollutants in many parts of the world (Krupa *et al.* 2001). As predicted by IPCC (2002), ambient O_3 concentration at summer would be over 70 mm^3 m^{-3} in Northern Hemisphere at the end of the century if current levels of anthropogenic activity were maintained. O_3 at ambient concentrations in the United States, Europe, and Asia causes a range of effects including reduced photosynthetic activities, altered carbon metabolism, and yield reductions (Soja and Soja 1995, Bosac *et al.* 1998, Heagle *et al.* 1998, Meyer *et al.* 2000, Dizengremel 2001, Fuhrer and Booker 2003, Calatayud *et al.* 2004, 2006a,b, Skotnica *et al.* 2005), but the detrimental effects of O_3 are dependent on the genetic background, development phase of the plants, O_3 doses, and climate (Heath 1994). In China, model simulations and open top chamber (OTC) experiment indicated that O_3 pollution is likely to worsen in the coming decades and ground-level O_3 is sufficiently high to depress yields of winter wheat and rice (Chameides *et al.* 1999, Feng *et al.* 2003).

Ozone enters the plant through open stomata. The phytotoxicity of O_3 inside the leaves is due to its high oxidative capacity (redox potential +2.07 V) and the consequential formation of radicals and reactive oxygen species (ROS) in exposed plants, such as hydrogen peroxide (H_2O_2), superoxide radical anions ($O_2^{-\cdot}$), and hydroxyl radicals ($OH^\cdot$) (Heath 1987, Pell *et al.* 1997).

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Abbreviations: AQY – apparent quantum yield; C_i – intercellular CO_2 concentration; CF – O_3-free air; CF+O_3 – O_3-free air with additional O_3; CI – compensation irradiance; g_s – stomatal conductance; NF – ambient air; OTCs – open top chambers; P_N – net photosynthetic rate; P_{Nmax} – photon-saturated photosynthetic rate; P_{Nmean} – diurnal mean photosynthetic rate; PPFD – photosynthetic photon flux density; SI – saturation irradiance; T – air temperature.

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In the chloroplast, these reactions could directly or indirectly impair the light and dark reactions of photosynthesis (Calatayud *et al.* 2004). Hence, O_3 alters photosynthetic activity through various mechanisms. The direct effect of ozone on stomata is a main role in the impairment of photosynthesis (Płażek *et al.* 2000, Guidi *et al.* 2001, Calatayud *et al.* 2004). Moreover, O_3 can also inhibit the synthesis of photosynthetic pigments, decreasing the electron transport rate between both photosystems (Calatayud *et al.* 2004). Clark *et al.* (2001) indicated that photosynthetic capacity is an ideal physiological activity to monitor when the health and vitality of plants is under scrutiny. Therefore, gas exchange also provides an important source of information about plant growth under O_3-enriched environment.

However, most results mentioned above were mostly based on constant concentration fumigation regimes. Meyer *et al.* (2000) indicated that ozone treatments with comparatively high peak concentration induce more pronounced damage than ozone patterns with moderate peaks under equal dose conditions. Ozone has a typical diurnal profile with peak concentration during the afternoon and low concentrations at night when other pollutants are present. Hence the dynamic fumigation regime according to O_3 diurnal changes can really simulate the response process of the plants to increasing ambient O_3, and scientifically evaluate the yield loss of crops. The diurnal trend in gas exchange is often recognized as one of the best indications in reflecting the ability of plants to maintain their photosynthetic apparatus to readily respond to environment (Geiger and Servaites 1994). Therefore, the objectives of this study were (*1*) to assess responses of photosynthesis and yield components of field-grown wheat to elevated O_3 level with significant diurnal changes under field condition, and (*2*) to clarify potential mechanisms of reduced photosynthesis rate.

Materials and methods

Experimental site was located in Shuangqiao Farm (31°53´N, 121°18´E) at Jiaxing City, Zhejiang Province. The site is about 100 km far from Shanghai (the biggest city in China). In this region, annual average temperature and precipitation are 15.5 ºC and 1 199 mm, respectively. The prevailing cultivation rotations are the rape and rice or wheat and rice. Ozone was the main phytotoxic pollutant present in ambient air reaching a 7-h mean of 46 $mm^3\ m^{-3}$ and a maximum hourly peak of 197 $mm^3\ m^{-3}$ (Zheng *et al.* 2005).

Plants: Winter wheat (*Triticum aestivum* L.) seeds (cv. Jia No. 403) were sown in plots (2×2 m) on 7 November, 2005. In each plot, 60 kg N, 60 kg P_2O_5, and 60 kg K_2O per ha were fertilized into soil surface when wheat was planted, and followed by an additional 69 kg N per ha at the tillering stage. Plants were maintained in the plots until harvest on 16 May 2006. The plants exposed to O_3 fumigation in OTCs started from 13 March 2006, at the jointing stage, and ended on 28 April. The O_3 fumigation was carried out from 09:00 to 17:00 per day, and suspended when it was rainy and cloudy. In fact, there were 30 d for O_3 fumigation during the growth season. No irrigation water was applied to the plots from the germination to harvest of wheat.

OTCs were made of steel frame and polythene plastic film, including charcoal filter system, ventilation and gas distribution system, and framework part. Ozone was generated from pure O_2 by electric discharge (ozone generator, *QHG-1*, Yuyao, China) and then mixed with charcoal filtered air to give different ozone concentrations. The mixed gas was transported to every OTC. Concentrations of ozone within the chambers were measured at plant height continuously on a 5 min interval by a *ML9810B* ozone analyst (*Monitor*, USA). There were three treatments and three replicates of each treatment in this experiment. Three OTCs were ventilated by passing air through activated charcoal filter (CF), three OTCs were ventilated with non-filtered air (NF), and three received additional O_3 ($CF+O_3$) based on diurnal change pattern of ambient O_3 (Fig. 1). Ozone was added to charcoal-filtered air by means of flow controllers linked to a desktop computer programmed with the individual exposure profiles.

Gas exchange: After 25 d of exposure to O_3, at the stage of grain filling, leaf gas exchange rates, *i.e.* net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i), photosynthetic photon flux density (PPFD), and leaf temperature were simultaneously recorded every hour from 08:00 to 16:00 excluding 15:00 on sunny day with a portable photosynthetic system (*CIRAS-1, PP Systems,* UK). The flag leaves for experiment were all fully exposed and oriented to normal irradiation during measurements to find gas exchange at the highest possible PPFD. Five replications were done for each treatment at each time.

P_N-PPFD response curves were also measured by a portable infra-red gas analyzer *CIRAS-1* in the morning when there was no cloud. CO_2 and air temperature in the leaf chamber were maintained at 360 $\mu mol\ mol^{-1}$ and 25 ºC, respectively. PPFD started at 1 400 $\mu mol\ m^{-2}\ s^{-1}$ and decreased stepwise to 40 $\mu mol\ m^{-2}\ s^{-1}$. Apparent quantum yield (AQY) was calculated from the initial slopes by linear regression using PPFD values below 200 $\mu mol\ m^{-2}\ s^{-1}$. Compensation irradiance (CI), saturation irradiance (SI), and photon-saturated photosynthetic rate (P_{Nmax}) were estimated.

Yield components: The ears length and numbers of grains, spikelets, and infertile florets per ear on each plant were recorded. The plants were dried in oven at 80 ºC for 72 h and dry mass (DM) of grains as well as 1 000-grain mass were also recorded.

Statistical analysis: Variance analysis (ANOVA) was performed on experimental data, and the results were analyzed by *SPSS 10.0 for Windows*. The least significant differences (LSD) between the means were estimated at 95 % confidence level. Unless indicated otherwise, significant differences among different treatments are given at $p<0.05$.

Results

Air quality: The data for O_3 concentration and environmental conditions during fumigation period are summarized in Table 1. In CF+O_3 treatment, 8-h mean O_3 concentration inside the chambers was about 1.0-fold higher than that of NF. The mean of high-peak in CF+O_3 treatments during fumigation was approximately 1.3-fold higher than the high-peak mean in NF conditions. The mean O_3 concentration in CF chambers was lower than 10 mm^3 m^{-3}. The environmental conditions were similar in all treatments during the fumigation.

Table 1. Summary of ozone concentrations and environmental conditions in OTCs during the fumigation of wheat plants. $[O_3]_{mean}$, mean O_3 concentration [mm^3 m^{-3}]; $[O_3]_{min}$ and $[O_3]_{max}$, means of the minimum and maximum concentrations during 30 d in 8 h a day [mm^3 m^{-3}], respectively; T_{mean}, mean 24-h air temperature [ºC]; T_{min} and T_{max}, minimum and maximum air temperatures [ºC], and RH [%], air relative humidity.

Treatment	$[O_3]_{mean}$	$[O_3]_{min}$	$[O_3]_{max}$	T_{mean}	T_{min}	T_{max}	RH
CF	9.7	–	–	13.90	8.41	20.10	66.5
NF	52.4	34.9	68.1	13.82	8.59	19.80	65.8
CF+O_3	105.0	59.0	156.0	13.72	8.48	19.50	67.2

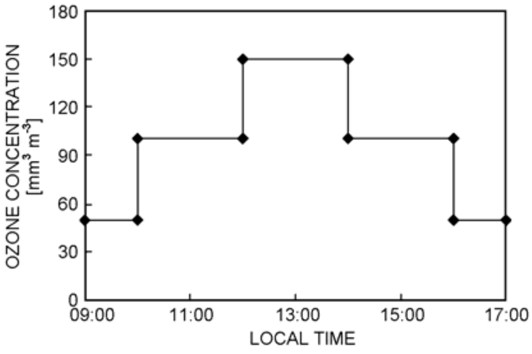

Fig. 1. The profile of O_3 concentration in OTCs in the CF+O_3 treatment.

Gas exchanges: In general, P_N was the highest in CF treatment and the lowest in CF+O_3 treatment (Fig. 2*B*). The diurnal mean photosynthetic rate (P_{Nmean}) in CF+O_3 was significantly lower (about 40 %) than that in CF and NF, but the difference between CF and NF was insignificant (Table 2). P_N displayed a double-peaked diurnal curve at three O_3 treatments (Fig. 2*B*). The midday depressions of wheat occurred at about 12:00 for CF and NF treatments, and at about 11:00 for CF+O_3 treatment. The highest P_N value occurred in 11:00 for CF and NF treatments, whereas its maximum value occurred at 10:00 in CF+O_3 treatment and was 42.4 % lower than that in CF. Ozone altered diurnal course of g_s and decreased significantly its values (Fig. 2*C*). The midday depression of g_s was observed at 12:00 and 14:00 for CF and CF+O_3 treatments, respectively. However, the changes in C_i were just contrary to those of P_N (Fig. 2*D*). A significant positive correlation between P_N and g_s and a negative correlation between g_s and C_i were observed (Fig. 3).

As shown in Fig. 4, all the P_N-PPFD response curves reacted rapidly from 0 to 250 µmol m^{-2} s^{-1}, then the curves were gradually at a plateau. O_3 fumigation induced a significant decrease in AQY (Table 2), indicating that high O_3 concentration led to less efficiency of photon energy use of wheat at the same photon density. In different treatments, CI and SI changed at the range of 27–89 µmol m^{-2} s^{-1} and 906–1 252 µmol m^{-2} s^{-1}, respectively. CI was the highest in CF and was 1.3-fold and 1.7-fold higher than that in NF and CF+O_3, respectively. In CF+O_3 treatments, P_{Nmax} and SI were 27.6 and 40.3 % lower than those in CF, respectively (Table 2). There was no significant difference between CF and NF except for CI and SI.

Yield components: In comparison with CF, O_3 caused a significant reduction (28.6 %) in the number of grains per ear as a result of an O_3-induced reduction in the length per ear (9.5 %) and an increase in the number of infertile florets per ear (128 %), although no significant differences were observed in the number of spikelets per ear (Table 3). Moreover, 1 000-grain mass and grain yield of wheat exposed to CF+O_3 treatment were reduced by 20.6 and 36.0 %, respectively, compared with CF treatment. Even though ambient O_3 concentration also decreased the yields and 1 000-grain mass, no statistical difference was observed between CF and NF.

Discussion

Most studies indicated that O_3 significantly induced a decrease in P_N and crop yields (Bosac *et al.* 1998, Heagle *et al.* 1998, Meyer *et al.* 2000, Feng *et al.* 2003, 2006, Calatayud *et al.* 2004). In our study, O_3 affected the photosynthetic capacity in wheat plants, including changes in diurnal pattern of gas exchanges and P_N-PPFD response parameters, and thus a decrease in yield components was observed.

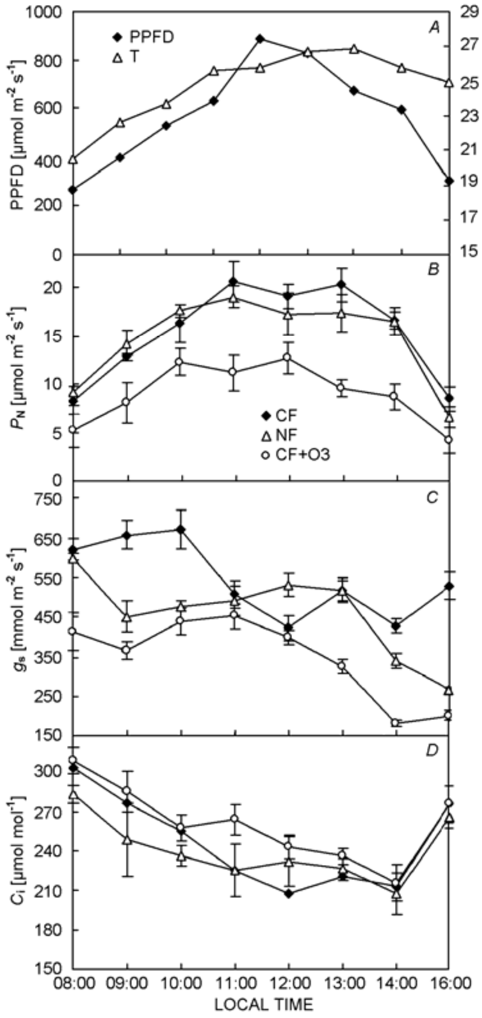

Fig. 2. Diurnal trends of photosynthetic photon flux density (PPFD) and air temperature (T) (*A*), net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) of wheat flag leaf exposed to different O_3 concentrations (*B–D*). SEs are shown ($n = 5$).

Photosynthesis is the primary physiological process by which plants respond to changes in environmental air conditions. Most studies showed stomata closure under stress, and consequent decrease in P_N (Farquhar and Sharkey 1982, Calatayud *et al.* 2004). However, environmental stress may usually act on chloroplast directly with a decrease in P_N, thus becoming non-stomata factors in restricting P_N (Heath 1987, Mackerness 2000, Zheng *et al.* 2000). Therefore, the factors causing a decrease in P_N can be grouped into stomatal and non-stomatal ones (Shangguan *et al.* 1999). The closure of stomata results in the shortage of CO_2 (Boyer 1976). Non-stomatal factors include: (*1*) the increase in diffusive resistance to CO_2 in mesophyll; (*2*) the decrease in activities of photosystem 2, photophosphorylation, and ribulose-1,5-bisphosphate carboxylase; (*3*) the decrease in chlorophyll content and inhibition of electron transport (Wise *et al.* 1992, Heath 1994, Shangguan *et al.* 1999, Mackerness 2000, Hassan 2006), *etc.* If stomatal factors are the main ones, P_N and g_s decrease owing to the decline in C_i. Otherwise, the decrease in P_N is dominated by non-stomatal factors. We found that the close positive correlation between P_N and g_s (Fig. 3*A*) indicated that the midday depression of P_N in wheat might be due to stomatal closure. But the increase in g_s was always accompanied by a decrease in C_i (Fig. 3*B*), suggesting the midday depression of P_N was not caused primarily by the lower g_s, but rather by non-stomatal factors. The results may be related with designed ozone concentration scenario. In this scenario, comparatively high peak of O_3 concentration did not accompany the highest PPFD, thus O_3 went into mesophyll cells through stomata easily. Once O_3 entered into mesophyll, it severely damaged the structure and function of photosynthetic organ (Lütz *et al.* 2000), and was accompanied by a series of physiological and biochemical characters altering in plant, such as an increase of membrane permeability, protein decomposition, and lipid peroxidation (Jin *et al.* 2000, Lütz *et al.* 2000, Płażek *et al.* 2000, Calatayud *et al.* 2004). Therefore, a significant decrease in P_N was found in additional O_3 treatment (CF+O_3), which was also observed by Meyer *et al.* (2000) under two different O_3 concentration peak regimes.

The asymptotic part of the P_N-PPFD curve (PPFD> 400 μmol m^{-2} s^{-1}) is predominantly limited by ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO; *e.g.* Feng *et al.* 2006), hypothesizing a decrease of RuBPCO amount and activity among O_3 treatments (Fig. 4). Also, Eckardt and Pell (1995) demonstrated a decrease of RuBPCO carboxylase efficiency in potato leaves in response to increased O_3. Values of AQY demonstrated a stronger damage of assimilation apparatus by excess photon absorption and photochemical utilization in plants exposed to CF+O_3 treatment (decrease by 28.6 % relative to CF). SI and CI are the important traits for photon energy utilization capability. In comparison with CF, O_3 caused a significant decrease in SI (about 40 %) and CI (70 %), which indicted that lower effective irradiance was utilized by O_3-treated plants (Table 2). Even though saturated photon irradiance was applied, the plants in CF+O_3 treatment had a lower P_{Nmax} ($p<0.05$), suggesting photosynthetic capacity of wheat exposed to additional

Table 2. Comparison of mean net photosynthetic rate (P_{Nmean}), photosynthetic characteristics (P_{Nmax}, photon-saturated photosynthetic rate; AQY, apparent quantum yield; SI, saturation irradiance; CI, compensation irradiance) in wheat leaves under three O_3 treatments. Means ± SE of four replicates. Values in columns followed by the different letters are statistically different at $p<0.05$ (LSD-test).

Treatment	P_{Nmean} [μmol m^{-2} s^{-1}]	P_{Nmax} [μmol m^{-2} s^{-1}]	AQY	SI [μmol m^{-2} s^{-1}]	CI [μmol m^{-2} s^{-1}]
CF	15.10±0.53a	23.10±2.51a	0.063±0.001a	1252±38a	89.44±4.85a
NF	14.90±0.60a	19.10±2.39ab	0.058±0.005a	1095±47b	30.71±5.09b
CF+O_3	8.92±0.68b	13.80±1.34b	0.045±0.003 b	906±42c	27.12±4.56b

Table 3. Yield components of wheat exposed to three O_3 treatments. Means ± SE of three replicates. Values in columns followed by different letters are statistically different at $p<0.05$ (LSD-test).

	Ear length	Spikelets per ear	Grains per ear	Infertile florets per ear	1 000-grain dry mass [g]	Grain yield [g plant^{-1}]
CF	11.00±0.36 a	17.90±0.74 a	46.90±3.93 a	2.50±0.33 a	37.40±1.37 a	1.75±1.01 a
NF	11.00±0.53 a	17.70±0.95 a	46.20±4.25 a	2.60±0.22 a	32.00±0.78 ab	1.31±0.11 ab
CF+100	9.95±0.47 b	16.40±1.06 a	33.50±3.29 b	5.70±1.04 b	29.70±1.20 b	1.12±0.11 b

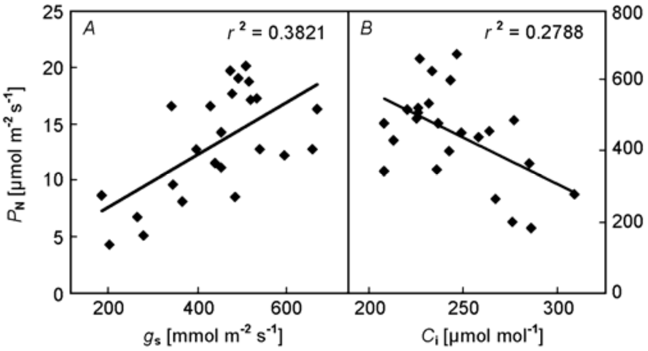

Fig. 3. Relationship between (*A*) net photosynthetic rate (P_N) and stomatal conductance (g_s) or (*B*) between g_s and intercellular CO_2 concentration (C_i) of wheat flag exposed to different O_3 concentrations ($n = 24$).

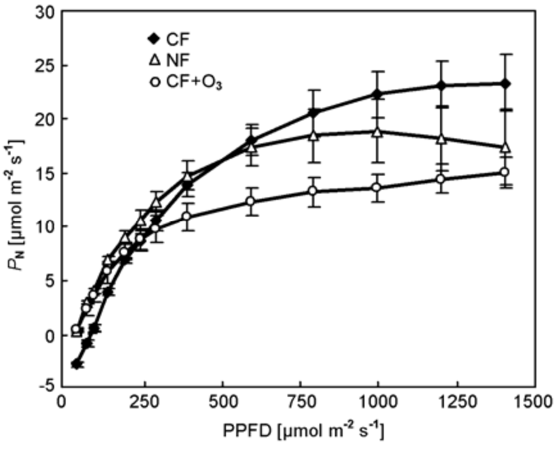

Fig. 4. Photosynthetic photon flux density (PPFD) response curves of net photosynthetic rate (P_N) of field-grown wheat under different O_3 treatments. P_N was measured at CO_2 concentration of 360 μmol mol^{-1}, temperature of 25 °C, and PPFD of 0–1 400 μmol m^{-2} s^{-1}. SEs are shown ($n = 4$).

O_3 had been seriously depressed.

Literature on wheat productivity in response to enhanced O_3 is contradictory. Most studies underlined a reduction in yields (Ojanpera *et al.* 1998, Feng *et al.* 2003), whereas Finnan *et al.* (1996) reported higher biomass and yield of wheat exposed to low O_3 concentration and no significant changes were also observed in spring wheat (Mulholland *et al.* 1997). In our paper, the reduction in yield was observed in CF+O_3 treatment ($p<0.05$), but not in NF in comparison with CF, which were the results of (*1*) a marked decrease in the ear length and the number of grains per ear, and (*2*) a significant increase in the number of infertile florets per ear. Similar results were also observed in spring wheat (Finnan *et al.* 1996). Such reductions in grain yield have been attributed to decreased P_N (Meyer *et al.* 2000, Feng *et al.* 2006) and accelerated flag leaf senescence or alteration in Chl fluorescence (Calatayud *et al.* 2004).

From the above results, ozone episodes (diurnal pattern) as applied in this experiment are capable of reducing significantly the physiological vitality and yields of wheat. Hence setting of thresholds for atmospheric ozone should consider peak concentrations more effectively. For more realistic effects of O_3 on crops, further investigations are important concerning the influence of environmental factors on the actual absorbed ozone dose of plants (O_3 flux).

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