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Drought Alleviated the Negative Effects of Elevated O_3 on *Lonicera maackii* in Urban Area

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Abstract Open top chambers were used to study the changes in photosynthesis, physiology and stomata characteristics in 1-year-old *Lonicera maackii* seedlings exposed to drought (DT, 30%–35% soil saturated water content) or/and elevated ozone (EO, 80 ppb). The results showed that DT or/and EO significantly decreased net photosynthetic rate (Pn), stomatal conductance (gs), maximum photochemical efficiency (Fv/Fm), but increased the activity of superoxide dismutase (SOD), and malondialdehyde content ($p < 0.05$). Compared with EO alone, the combination of EO and DT caused higher values in Pn, Fv/Fm, SOD activity ($p < 0.05$), and smaller stomata size and lower visible injury rate. DT alleviated the adverse impact of EO on the shrub by increasing enzyme activity and decreasing stomatal size, particularly stomatal width. The study provided increasing evidence that moderate drought might exert a beneficial effect on the tested plants to adapt to the future climate change, particularly in high ozone regions.

Keywords *Lonicera maackii* · Drought · Elevated O_3 · Photosynthesis · Stomata response

Tropospheric ozone (O_3) is one of the most important phytotoxic air pollutants, formed from photochemical reactions of its precursors such as VOCs and NOx due to the increased consumption of fossil fuels (IPCC 2014). Ground-level O_3 concentration has increased from less than 10 ppb to currently between 20 and 45 ppb since pre-industrial times in the Northern Hemisphere (Derwent et al. 2015), having a potentially detrimental impact on forest trees in temperate and boreal regions (Fares et al. 2013). In particular, O_3 pollution in many cities around the world is becoming more and more serious, as has been shown by Wang et al. (2017). High O_3 concentration at ground level has been constantly detected in many cities of China, especially in summer (Zhang et al. 2014b; Xu et al. 2015). Many studies showed that elevated O_3 concentrations cause negative impacts to trees such as visible foliar injury (Calatayud et al. 2011; Feng et al. 2014), decreased photosynthesis (Xu et al. 2015), accelerated tissue aging and reduced growth of trees (Kitao et al. 2016). The negative impacts greatly depend on the amount of O_3 entering tree leaves (Gao et al. 2017) through stomata and the efficiency of the defense system, including a variety of antioxidant enzymes.

Meanwhile, as a result of climate change, particularly changes in precipitation patterns, the frequency and severity of drought are expected to increase in the northern hemisphere (IPCC 2014). Drought is probably the most important stress factor in determining tree growth and productivity world-wide (Peng et al. 2011). In China, forest trees, including urban trees, are subject to periodic drought during summer (Li et al. 2015; Xie et al. 2016; Gao et al. 2017) which can coincide with episodes of O_3 pollution severe enough to cause foliar injury and decreased growth. Many studies have been carried out to determine possible ways in which drought would interact with elevated O_3 to affect plants (Grünehage and Jäger 2003; Low et al. 2006; Pollastrini et al. 2014; Hayes et al. 2015), but there were controversies about whether drought alleviated the negative effect of O_3 on trees or not. The interaction of the two factors may be antagonistic resulting from reducing stomata aperture, synergistic or additive due to the double stresses (Li et al. 2015).

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Lonicera maackii is widely used as a landscape ornamental plant and for forestation in urban areas of northeast China (Zhang et al. 2016). Extensive physiological studies on *L. maackii* have been reported (Wang et al. 2010), but little information about its response to drought has been published, especially when combined with elevated O_3. In this study, we assessed the effects of drought and elevated O_3 alone and in combination on photosynthesis and other physiological parameters in leaves of *L. maackii*. Our hypotheses in this experiment are that: (1) both drought and O_3 will exert some adverse effects on *L. maackii*; and (2) drought may alleviate the adverse effects of elevated O_3 by closing the stomata and/or increasing the inherent antioxidant level of plants.

Materials and Methods

The experiment was conducted at Shenyang Arboretum with an area of 5 km^2, located in the populated central area of Shenyang City, China (41°46′N, 123°26′E). This urban area is in a region belonging to the temperate continental monsoon climate. Average annual precipitation is 755 mm and average annual temperature is 7.4 °C. One-year-old seedlings of *L. maackii* were obtained from a local nursery in Shenyang, and were transplanted into 25 cm diameter and 20 cm depth pots filled with 2 kg of soil composed of sand, peat, and clay (2:3:1, v:v:v). Organic carbon and pH of the soil were 32.7 and 6.5 g kg^{-1}, respectively. Two seedlings were planted in each pot. All the seedlings were grown for 60 days in a growth chamber with temperatures of 26/22°C day/night, 65%–85% relative humidity (RH), and a 12-h photoperiod under 500 µmol m^{-2} s^{-1} of photosynthetically active radiation (PAR). At the end of the 60 days period, the pots grown plants with or without drought treatment were divided into the two identical parts, respectively. One of them was exposed to O_3 fumigation.

Drought and high O_3 treatments were performed in open top chambers (OTCs). The OTCs were 4 m in diameter, 3 m in height and equipped with a 45° sloping frustum (Xu et al. 2015). The O_3 concentration in the OTCs was monitored by an automatic controller (SDM-CD16AC, Beijing) connected to an O_3 analyzer (S-900 Aeroqual, New Zealand). All the data were stored using a data logger (CR800, Campbell Scientific Inc., Logan, UT, USA). Target O_3 concentration was generated from pure medical oxygen using the high-voltage discharge method (XH-2000, Xinghang Industry & Trade Co. Ltd., Shenyang, China). Drought was imposed by adjusting the quantity of watering. After the drought treatment started, the water moisture contents in the drought pots were reduced to ~30%–35% saturated water content (SWC). Well-watered treatments were provided about 1.5 L of water weekly per pot while drought stress treatments were provided nearly 0.5 L Irrigation frequencies and volume of water varied a small amount during the hottest summer time depending on soil moisture. Four treatments were set: (1) Control (CK, 40 ppb O_3): ambient air and well-watered pots with 75%–80% SWC. (2) Drought: 30%–35% SWC (DT). (3) Elevated O_3 concentration (EO, 80 ppb). (4) The combination of drought and ozone: DT + EO. Each treatment was designed with three replicates (OTCs). The treatments lasted 30 days from June 25 to July 25 in 2013. The plants were fumigated with elevated O_3 for 9 h daily in the daytime (8:00–17:00). The O_3 concentrations and microclimatic conditions in the OTCs are shown in Table 1. During the experiment, the recorded average day time concentration of O_3 in the EO–OTCs was 85.3 ppb. After the 30-day treatment period, six healthy seedlings from each treatment set were used for the measurements of photosynthetic gas-exchange, chlorophyll fluorescence and physiological parameters including total chlorophyll, malondialdehyde (MDA) contents and superoxide dismutase (SOD) activity. The fully expanded leaves of the second youngest node from the top of main stem were used for these analyses.

Chlorophyll (Chla and Chlb) content was measured and calculated according to the specific absorption coefficients provided by Lichtenthaler (1987). Lipid peroxidation was estimated by MDA content according to the method of Buege and Aust (1978). The assay of SOD activity was based on the method described by Beyer and Fridovich (1987) with

Table 1 Concentrations of O_3, AOT40 and microclimatic conditions in OTCs during the experiment

Treatments	$[O_3]_{mean}$	$[O_3]_{max}$	$[O_3]_{min}$	$AOT40^{(30)}$	T_{mean}	SWC
CK	41.5	58.3	1.2	165.3	25.9	65.9
DT	39.8	62.1	0.9	170.9	26.7	35.6
EO	85.3	125.0	75.4	12,073.5	27.1	62.5
DT + EO	84.9	119.0	68.9	11,685.2	26.4	38.4

CK control, *DT* drought, *EO* elevated O_3, *DT + EO* the combination of DT and EO. $[O_3]_{mean}$, average daily (07:−16:00) concentrations of O_3 (ppb); $[O_3]_{max}$ and $[O_3]_{min}$ average maximum and minimum daily concentrations of O_3 (ppb), respectively; *AOT40* cumulative the sum of the differences between the hourly mean ozone concentration in ppb and 40 ppb for each hour of gas exposure; $AOT40^{(30)}$ indicates the accumulated values of AOT40 for 30 days from the beginning gas fumigation to the end of this experiment (ppb·h); T_{mean} average daily air temperature (°C); *SWC* soil water content in the experimental pots (%)

a slight change. These physiological parameters were measured in leaves detached at 5, 15 and 30 days after imposition of the treatments. Leaf gas-exchange parameters were measured at the end of experiment using a portable photosynthesis system (Li-6400, Li-Cor Inc., Lincoln, NE, USA). Net photosynthetic rate (Pn), stomatal conductance (gs), intercellular CO_2 concentration (Ci), and transpiration rate (Tr) were determined at light-saturation (about 1000 μmol m^{-2} s^{-1}). Water use efficiency (WUE) was calculated by the ratio of Pn and Tr. Chlorophyll fluorescence parameters were measured by a FMS-2 fluorometer (Hansatech Instruments, Ltd, Norfolk, UK) and included minimum dark fluorescence yield (Fo), maximal fluorescence yield (Fm), the maximum quantum efficiency of PSII photochemistry (Fv/Fm), and potential photochemical efficiency of PS II photochemistry (Fv/Fo) (Schreiber and Bilger 1993). Stomatal parameters including stomatal length (SL), width (SW), perimeter (SP) and area (SA) and were measured and calculated using an Environmental Scanning Electron Microscope (Quanta-250, Hongkong, China). Stomatal data were obtained and analyzed by Adobe Photoshop CS3.

One-way ANOVA was carried out using the SPSS computer package (SPSS 12.0, Inc. 1999, Chicago, IL, USA). The values presented are the means of all the measurements at every sampling point, and comparisons of means between control and treatments were determined using the least significant difference test. Differences were considered statistically significant when $p \leq 0.05$.

Results and Discussion

Generally, O_3 can lead to different injury symptoms for different tree species (Skelly et al. 1999; Skelly 2000; Feng et al. 2014). In this study, we found that O_3 stressed *L. maackii* showed the typical visible symptoms induced by elevated O_3 fumigation. The initial chlorotic spots in leaves coalesced into roundish dark-brown necrotic areas (3–5 mm in diameter) located in the interveinal adaxial areas of the older leaves after 2 weeks exposure. The O_3 injured area was about 60% of the total leaf area of plants in well-watered pots by the end of experiment. However, only slightly visible injury symptoms were observed under the combination of the DT + EO treatments. Visible injury in leaves usually indicates a decrease of chlorophyll content under adverse environments (Gottardini et al. 2014; Sicard et al. 2016). In this study, chlorophyll content significantly decreased under both drought and O_3 treatments. Compared with CK, chlorophyll content decreased by 48.6% and 35.1% under elevated O_3 and drought ($p < 0.01$) (Fig. 1a), respectively. However, the extent of decrease in chlorophyll content under the combination of the two stresses was lower than any of the single stresses by the end of experiment. MDA,

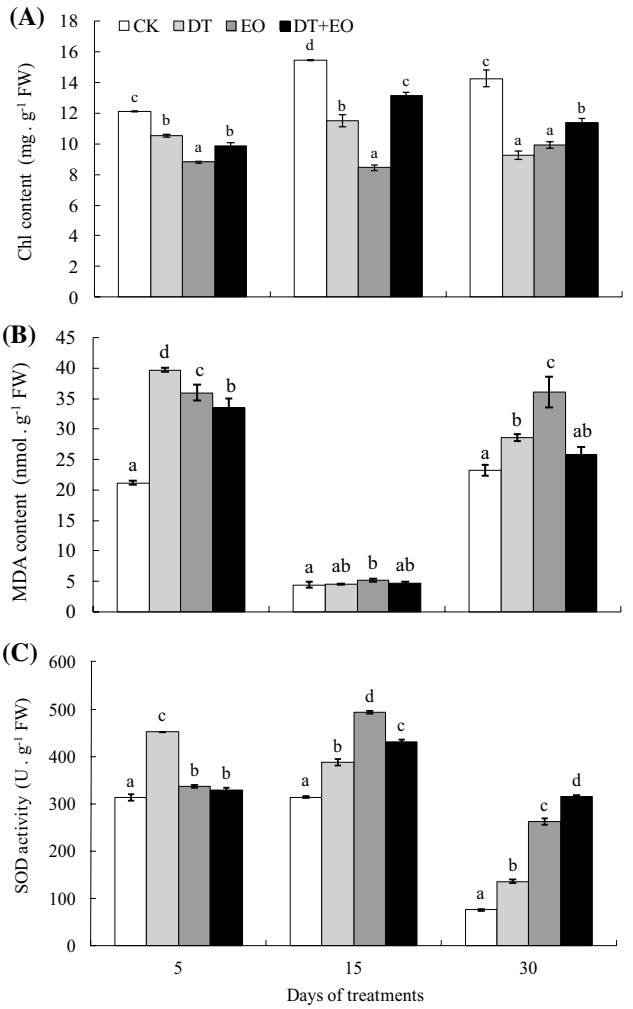

Fig. 1 Effects of drought or/and elevated O_3 on chlorophyll content (**a**), MDA content (**b**) and SOD activity (**c**) in leaves of *L. maackii* (mean ± SD, n = 6). Different letters in the same sampling day represented significant difference at 0.05 level among different treatments. *CK* control, *DT* drought, *EO* elevated O_3

the product of membrane lipid peroxidation in plants, can accumulate under adverse conditions such as drought and O_3 (Xu et al. 2014; Wu et al. 2016) and there was a significant increase of MDA content early in this experiment (after 5 days) for plants subject to either stressor (Fig. 1b). Elevated O_3 increased significantly the MDA content by 55.6% at the end of gas fumigation (Fig. 1b), indicating that severe oxidative stress occurred under O_3 fumigation. No significant change of MDA content was found under DT + EO combination of the CK treatment. In this study, we also found that SOD activity increased by 0.8, 2.5 and 3.2 times under DT, EO and the combination of the two stresses by the end of experiment, respectively (Fig. 1c), which implied that a high antioxidative ability was maintained under stress conditions, especially under the combination of the two stressors.

By the end of this experiment, Pn, gs, and Tr decreased significantly by 51.5%, 29.6% and 60.9% under DT ($p < 0.05$), and 51.5%, 40.7%, 28.8% under EO, respectively, indicating that drought or high O_3 alone had a negative effect on photosynthesis of plant (Table 2). This is in agreement with the result reported by Zhang et al. (2014a) in 1-year-old seedlings of *Metasequoia glyptostroboides*. Under DT + EO treatment, Pn kept a higher level than that of DT or EO alone, suggesting that the adverse effect of O_3 on photosynthesis was alleviated by DT treatment (Table 2). Under EO treatment, plants showed a significant lower WUE (decreased by 31.9%) than CK ($p < 0.05$), which shows that O_3 stress can adversely affect photosynthesis and exacerbate evaporation of water (Gao et al. 2016). In DT and EO treated plants, we found that the maximal efficiency of PSII photochemistry (Fv/Fm) significantly decreased by 7.2% and 10.8%, respectively (Table 2). A similar situation involving the same two stressors was also found to inhibit Fv/Fm in other plants (Gao et al. 2017). The value of Fv/Fm is in the range (from 0.80 to 0.86) reported by Bjorkman and Demming (1987) for healthy plants. Compared with CK, Fv/Fm slightly decreased, but never went below 0.80, indicating that the combination of DT and EO did not impair the efficiency of PSII of *L. maackii* leaves in this study. Pellegrini et al. (2011) suggested that Fv/Fo was a better parameter than Fv/Fm to discriminate small differences in the PSII quantum yield under stress conditions. In this study, we observed that Fv/Fo significantly decreased by 26.4% under EO (Table 2, $p < 0.05$), indicating a partial inhibition at PSII donor side (Pellegrini et al. 2011).

Both drought and high O_3 concentrations can decrease stomatal conductance. In this study, drought and O_3 also affected stomatal anatomy as indicated by decreases in the the size of all the measured parameters (SL, SW, SP and SA) (Table 3). What's more, the decrease in stomatal size was more under drought than that of elevated O_3, especially for SW. This indicates that drought could inhibit the elongation and division of mesophyll cells, which leads to smaller leaf area and stomatal size (Wang et al. 2016). By the end of this experiment, drought decreased SL, SW, SP and SA by 12.4%, 34.9%, 19.6% and 41.9%, respectively (Table 3). A reduction in stomata size under drought will decrease in the amount of CO_2 assimilated into the leaf and this may cause a decline in Pn (Mutava et al. 2015), which is in agreement with our result in this study that Pn shows a significant decrease under drought. However, the combined stresses of drought and ozone may limit the uptake of O_3, which in turn would help the leaves better cope with oxidative stress and permit a higher Pn as a result.

In conclusion, our results showed that drought and elevated O_3 treatments both significantly decreased photosynthetic parameters and stomata size, and induced visible injury symptoms in leaves of *L. maackii*. Drought could

Table 2 Changes in photosynthetic parameters in leaves of *L. maackii* exposed to drought and/or elevated O_3 at the end of the experiment (mean ± SD, n = 6)

Photosynthetic parameters	CK	DT	EO	DT + EO
Pn (μmol m^{-2} s^{-1})	14.94 ± 0.03c	7.24 ± 0.07a	7.25 ± 0.02a	11.47 ± 0.09b
gs (mol m^{-2} s^{-1})	0.27 ± 0.002d	0.19 ± 0.001c	0.16 ± 0.002b	0.11 ± 0.001a
Ci (μmol mol^{-1})	261.43 ± 0.45b	212.30 ± 8.32a	266.03 ± 2.40b	261.17 ± 0.85b
Tr (mmol m^{-2} s^{-1})	6.05 ± 0.02c	2.36 ± 0.12a	4.31 ± 0.10b	6.17 ± 0.10c
WUE (μmol $mmol^{-1}$)	2.47 ± 0.01b	3.07 ± 0.03c	1.68 ± 0.01a	1.85 ± 0.02a
Fv/Fm	0.83 ± 0.01c	0.77 ± 0.04b	0.74 ± 0.02a	0.80 ± 0.01c
Fv/Fo	3.03 ± 0.16b	3.33 ± 0.06c	2.23 ± 0.08a	3.65 ± 0.09d

CK control, *DT* drought, *EO* elevated O_3, *DT + EO* the combination of DT and EO. *Pn* net photosynthetic rate, *gs* stomatal conductance, *Ci* intercellular CO_2 concentration, *Tr* transpiration rate, *WUE* water use efficiency, *Fv/Fm* the maximum quantum efficiency of PSII photochemistry, *Fv/Fo* potential photochemical efficiency of PS II photochemistry. Different letters in the same row represented significant difference at 0.05 level among different treatments

Table 3 Changes in stomata parameters in leaves of *L. maackii* exposed to drought or/and elevated O_3 at the end of the experiment (mean ± SD, n = 15)

Treatments	SL (μm)	SW (μm)	SP (μm)	SA ($μm^2$)
CK	21.71 ± 0.60b	18.05 ± 0.46c	63.98 ± 1.62b	308.14 ± 15.24c
DT	19.02 ± 1.52a	11.76 ± 0.74a	51.45 ± 3.87a	179.01 ± 25.16a
EO	18.53 ± 0.60a	15.36 ± 0.30b	54.58 ± 1.53a	224.07 ± 11.42b
DT + EO	18.05 ± 0.46a	14.14 ± 0.49b	52.21 ± 1.30a	200.71 ± 10.85ab

CK control, *DT* drought, *EO* elevated O_3, *SL* stomatal length, *SW* stomatal width, *SP* stomatal perimeter, *SA* stomatal area. Different letters in the same column represented significant difference at 0.05 level among different treatments

partially ameliorate the adverse effect of O_3 stress on this urban shrub.

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