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Responses of Growth, Photosynthesis and VOC Emissions of *Pinus tabulaeformis* Carr. Exposure to Elevated CO_2 and/or Elevated O_3 in an Urban Area

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Abstract Responses of growth, photosynthesis and emission of volatile organic compounds of *Pinus tabulaeformis* exposed to elevated CO_2 (700 ppm) and O_3 (80 ppb) were studied in open top chambers. Elevated CO_2 increased growth, but it did not significantly ($p > 0.05$) affect net photosynthetic rate, stomatal conductance, chlorophyll content, the maximum quantum yield of photosystem II, or the effective quantum yield of photosystem II electron transport after 90 d of gas exposure. Elevated O_3 decreased growth (by 42.2% in needle weight and 25.8% in plant height), net photosynthetic rate and stomatal conductance after 90 d of exposure, but its negative effects were alleviated by elevated CO_2. Elevated O_3 significantly ($p < 0.05$) increased the emission rate of volatile organic compounds, which may be a helpful response to protect photosynthetic apparatus against O_3 damage.

Keywords Elevated CO_2 · Elevated O_3 · Photosynthesis · *Pinus tabulaeformis*

As the two most important greenhouse gases, levels of atmospheric CO_2 and O_3 have increased rapidly in the last five decades, and are expected to continue to climb well into the future (Eastburn et al. 2010). CO_2 is expected to double the preindustrial levels by 2050, while O_3 is increasing by as much as 2.5% annually. Furthermore, it is predicted that at the end of this century, the average levels of CO_2 and O_3 in the Earth's atmosphere are going to reach 700 ppm and 80 ppb, respectively (IPCC 2007).

Approximately half of the world's forests are expected to experience increased co-exposure of CO_2 and O_3 by 2100 (Kopper and Lindroth 2003). The two gases affect trees physiologically in diametrically opposite ways. There have been many discussions as to the physiological responses of trees to elevated CO_2 and/or O_3 following long-term exposure. In general, elevated CO_2 stimulates tree growth through increased photosynthetic rates, biomass and leaf area, but the CO_2-induced stimulation of photosynthesis has often been found to decrease over a longer time (Liberloo et al. 2007).

As a phytotoxic secondary air pollutant, O_3 is formed from photochemical reactions involving NO*x* and volatile organic compounds (VOCs), and it usually decreases the growth, damages the photosynthetic apparatus, and disturbs the physiological and biochemical processes of trees. This often results in the reduction of chlorophyll content, decrease of net photosynthetic rate and stomatal conductance, decline of the activities of photosynthetic enzymes, the inhibition of photosynthetic electron transport rates and the inhibition of photochemical reactions in photosystem II (PSII) (Wang et al. 2009).

The combined effects of elevated CO_2 and elevated O_3 on growth and photosynthesis of trees have been investigated by some authors but the results are often contradictory, even for the same species. There have been contradictory reports that elevated CO_2 ameliorated the negative effects of elevated O_3 on trees (Wang et al. 2009), or did not ameliorate them (McDonald et al. 2002), but even sometimes exacerbated the detrimental impacts of elevated O_3 (Niewiadomska et al. 1999).

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Pinus tabulaeformis Carr. (Chinese pine) is an endemic and dominant species of coniferous tree used for timber and soil conservation in northern China (Xia et al. 2009). It is also a typical tree species for forestation in urban areas of northeast China (Lu et al. 2009). Despite its cultural and ecological importance, little is known about the growth, physiological and biochemical responses of *P. tabulaeformis* to elevated CO_2 and/or O_3. It is known that tropospheric O_3 levels are increasing parallel to CO_2 concentrations around urban areas with development of urbanization (Eichelmann et al. 2004). Therefore, urban trees are simultaneously experiencing elevated CO_2 and O_3 levels. We have reported responses of the anti-oxidative system in needles of *P. tabulaeformis* to elevated CO_2 or O_3 concentrations in the urban area (Lu et al. 2009). However, the responses of photosynthesis and VOCs emission of the urban tree species have not been tested, particularly under the combined fumigation of the two gases. As one of the precursors of ozone, VOCs can have direct or indirect effects on the carbon cycle at the terrestrial level. Trees emit VOCs, which may scavenge O_3 and help provide protection of the photosynthetic apparatus against oxidative stress (Loreto and Velikova 2001). Given the importance of VOCs in the interactions between the biosphere and atmosphere, it is essential to understand whether current and future environmental changes, which include increased CO_2 and O_3 (IPCC 2007), will affect VOC emissions by plants.

To further investigate the controversial changes of photosynthesis and VOCs emission of plants under elevated CO_2 and O_3, we here studied the responses of growth, photosynthesis and VOC emissions of *P. tabulaeformis* to elevated CO_2 and O_3 in an urban area. This study may serve as a scientific reference for the management and sustainable development of urban forests under the background of global climate change.

Materials and Methods

The study was conducted at Shenyang Arboretum, Chinese Academy Science, located in the populated central area of Shenyang city (41°46′31.29″ N, 123°26′27.51″ E) in northeastern China. Four-year-old Chinese pine (*P. tabulaeformis*) trees were planted in loamy soil with no extra fertilizer in twelve open top chambers (OTCs) in May 2006. The OTCs have a diameter of 4 m, a height of 3 m, and distance between neighbors of 4 m. Three OTCs each were used for ambient air (CK, about 400 ppm for ambient CO_2 and 40 ppb for ambient O_3), elevated CO_2 (700 ± 80 ppm), elevated O_3 (80 ppb ± 10 ppb) and elevated $CO_2 + O_3$ (700 ± 80 ppm CO_2 + 80 ± 10 ppb O_3), respectively. CO_2 was injected into the chambers from cylinders 24 h daily and the concentrations were monitored with a CO_2 infrared transducer (SenseAir, Sweden). O_3 was generated from pure compressed oxygen by electric discharge (GP-5 J, China), and then added to the OTCs 9 h daily (08:00–17:00). The concentrations of O_3 in the chambers were continuously monitored with an O_3 analyzer (S-900 Aeroqual, New Zealand).

The trees were randomly planted, 12 trees per chamber. The trees were fumigated by elevated CO_2 (24 h day^{-1}), and elevated O_3 (08:00–17:00 h) from 2006 to 2008. The fumigation periods were June 17–October 10 in 2006, June 18–October 10 in 2007, and June 13–September 28 in 2008. All the data in this study were obtained from 2008 (the third growing-season of gas fumigation). One-year-old needles from the middle canopy of six-year-old *P. tabulaeformis* were sampled in each chamber at 9:00–10:00 a.m after 0 (June 12, the day before gas fumigation beginning), 30 (July 13), and 90 (September 11) days of gas fumigation in 2008. During the growing season in 2008, mean daily temperature and relative humidity in the OTCs were 22.3 ± 3.5°C and 64.3 ± 15.3%, respectively. The mean daily CO_2 concentration in the elevated CO_2 treatment was 608.7 ± 155.9 ppm. The mean daily O_3 concentration in the elevated O_3 treatment was 66.1 ± 2.4 ppb.

Growth parameters were evaluated by fresh and dry weight per needle (48 h at 70°C), tree height and stem diameter at ground level. Gas exchange measurements were made periodically on the healthy needles on sunny days from 20 June to the end of September, 2008. Measurements were taken on eight intact, sun-exposed needles per plant selected from the middle canopy. All photosynthetic parameters including net photosynthesis rate (Pn) and stomatal conductance (g_s) were measured by a portable photosynthesis system (LI-6400, Li-Cor Inc., Lincoln NE, USA) with a red/blue LED light source (LI6400-02B) mounted onto a 6 cm^2 clamp-on leaf chamber, and measured in the CO_2 concentration where they were growing (700 ppm for elevated CO_2-plants, and 400 ppm for ambient CO_2-plants). The gas exchange parameters were recorded under saturated light (1,000 μmol photons m^{-2} s^{-1} of PPFD) provided by the red/blue LED light source between 9:00 and 11:00 on one-year-old needles on the middle parts of lateral branches. All measurements were done at a constant air flow rate of 500 μmol s^{-1}.

Chlorophyll fluorescence was measured at ambient temperature in OTCs using a FMS-2 pulse modulated fluorometer (Hansatech, UK). The environmental conditions were similar to gas exchange measurement. The maximum quantum yield of photosystem II (F_v/F_m) was determined in dark-adapted (30 min) samples. The steady-state fluorescence (F_s) and the maximum Chl fluorescence in the light-adapted state (F'_m) were both measured, respectively. The effective quantum yield of PSII electron

transport (ΦPSII) was calculated as $(F'_m - F_s)/F'_m$. The total chlorophyll content was determined using the same needles as used for the Chl fluorescence measurements. The chlorophyll was extracted by 80% acetone from 0.2 g needles samples. The chlorophyll content was determined according to the methods of Lichtenthaler and Wellburn (1983) by the absorbance at wavelengths of 663, 646 and 470 nm measured by a Shimadzu (Japan) UV-1601 spectrophotometer.

Air samples were collected and VOCs content was measured using a method described by Li et al. (2009). Transparent polyethylene bags were used to cover well-lighted plant branches. After 0, 30, 90 days of gases fumigation in 2008, the samples were collected from inside of the bags on glass adsorbent tubes (11.5 cm long and 0.4 cm internal diameter) filled with Tenax-TA, Carboxen 1000 and Carbosieve SIII (Supelco Inc., Bellefonte, PA, USA) using a constant-flow type pump. The flow rates were 100 mL min^{-1} and the sampling time was 5 min. The air samples were kept at 4°C until analysis. After sampling, the needles enclosed in the bags were removed from the trees, and placed in a drying oven at 60°C for 48 h. The dry weights were used for normalization of VOCs emission rate to unit needle mass.

VOCs were separated and detected by a gas chromatograph with flame ionization detection (FID). Desorption and analysis of VOCs was carried out using a thermal disorber sample injection system (ACEM 9300, CDS, USA) connected by a thermal transfer line maintained at 250°C to a gas chromatograph (14B, Shimadzu, Japan) with FID. For details of the experimental procedures see Li et al. (2009).

The emission rate of VOCs was calculated using the following equation.

$$\mathrm{ER} = \frac{M \cdot V}{22.4 \cdot \Delta t \cdot W}(c_2 - c_1) \times 10^{-3}$$

Where ER is the emission rate of VOCs ($\mu g \bullet g^{-1} DW \bullet h^{-1}$, mainly consisting of isoprene), c_1 is the isoprene concentration (ppb) over the branches before the sampling bag was closed, c_2 is the isoprene concentration inside the bag after the sampling bag closed, V is the effective volume of the bag, Δt is time of closing bag for the sample collection, W is dry weight of all the needles in the closed bag (g), and M is the molecular weight of isoprene.

Chambers corresponding to the same treatment were considered statistical replicates. There were three repicates for each OTC. ANOVA was carried out using the SPSS computer package (SPSS Inc. 1999, Chicago, IL, USA) for all sets of data. The values presented are the means of all measurements, and the significance of the differences of means were evaluated by the least significance differences (LSD) test at the 95% confidence level.

Results and Discussion

At the end of the growing season in 2008, elevated CO_2 and its combination with elevated O_3 significantly increased the weight of needles ($p < 0.05$), plant height and stem diameter at ground level under elevated CO_2 (Table 1). Compared with the CK, elevated O_3 alone significantly decreased the fresh weight per needle, dry weight per needle and plant height by 42.2, 38.6 and 25.8%, respectively (Table 1). According to Kubiske et al. (2006), elevated CO_2 increased the height and diameter of *Populus tremuloides* by 11 and 16%, respectively, whereas elevated O_3 decreased these endpoints by 11, 8%, respectively. In our previous study, elevated CO_2 increased the leaf dry weight by 26% in leaves of *Ginkgo biloba*, while elevated O_3 decreased leaf dry weight by 22%. In this study, elevated CO_2 increased dry weight per needle of *P. tabulaeformis* by 17.7%, while elevated O_3 decreased needle weight by 42.2% (Table 1). Elevated CO_2 did not significantly increase plant height of *P. tabulaeformis* ($p > 0.05$), but elevated O_3 significantly decreased plant height by 25.8% compared with the CK (Table 1). This is not in agreement with the recent study by Nikula et al. (2009) who reported that elevated O_3 did not have an effect on tree height of European aspen (*P. tremula*), but rather tended to slightly increase it by 10%. This different result may have been due to a lower O_3 exposure concentration and a shorter exposure period

Table 1 Growth parameters of *P. tabulaeformis* exposed to ambient air (CK), elevated CO_2, elevated O_3 and elevated CO_2 + elevated O_3 at the end of growing season in 2008

Treatments	Fresh weight per needle (mg)	Dry weight per needle (mg)	Plant height (cm)	Stem diameter at ground level (mm)
CK	106.2 (30.3)^{b}	45.6 (9.3)^{b}	141.1 (27.3)^{a}	32.6 (6.6)^{ab}
CO_2	127.8 (11.9)^{a}	53.7 (7.7)^{a}	141.3 (14.4)^{a}	36.4 (4.4)^{a}
O_3	61.4 (11.8)^{c}	28.0 (3.8)^{c}	104.7 (19.5)^{b}	30.5 (5.0)^{b}
$CO_2 + O_3$	141.8 (22.7)^{a}	60.0 (10.5)^{a}	137.4 (14.8)^{a}	32.5 (4.6)^{ab}

Data shown are means with standard deviations (SD) in parentheses. For comparison of means, variance analysis (ANOVA) followed by the least significance differences (LSD) test, calculated at 95% confidence level, was performed. Values followed by the same letter indicate no significant differences

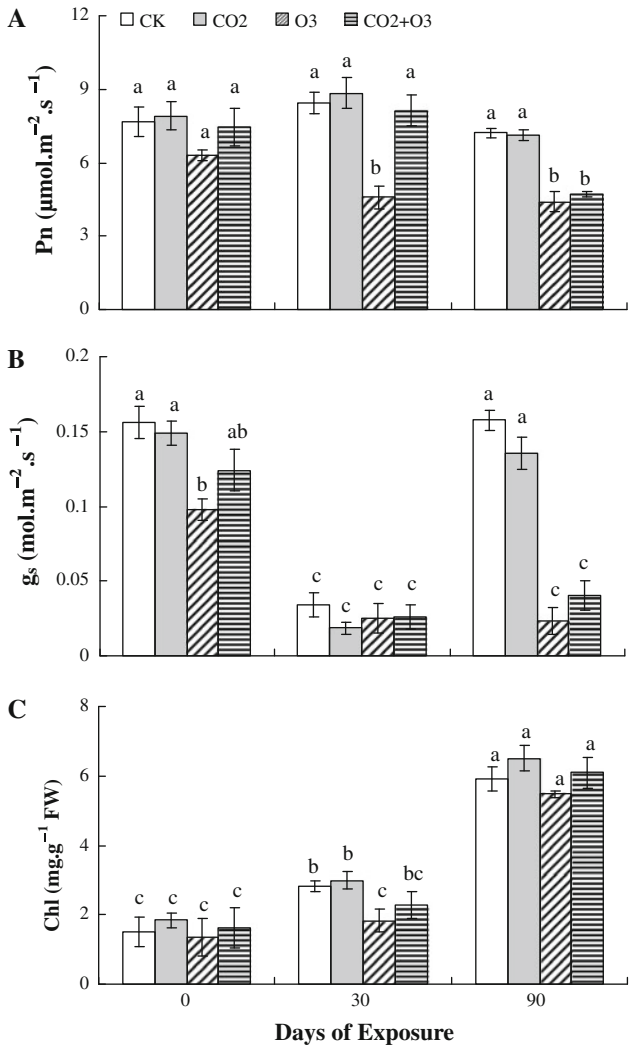

Fig. 1 Net photosynthetic rate (P_n, **A**), stomatal conductance (g_s, **B**), and chlorophyll content (Chl, **C**) in needles of *P. tabulaeformis* exposed to ambient air (CK), elevated CO_2, elevated O_3 and elevated CO_2 + elevated O_3 during the growing season in 2008. Data shown are means with standard deviations (SD) of three replicates. Different *lower case letters* indicate significant difference at $p < 0.05$

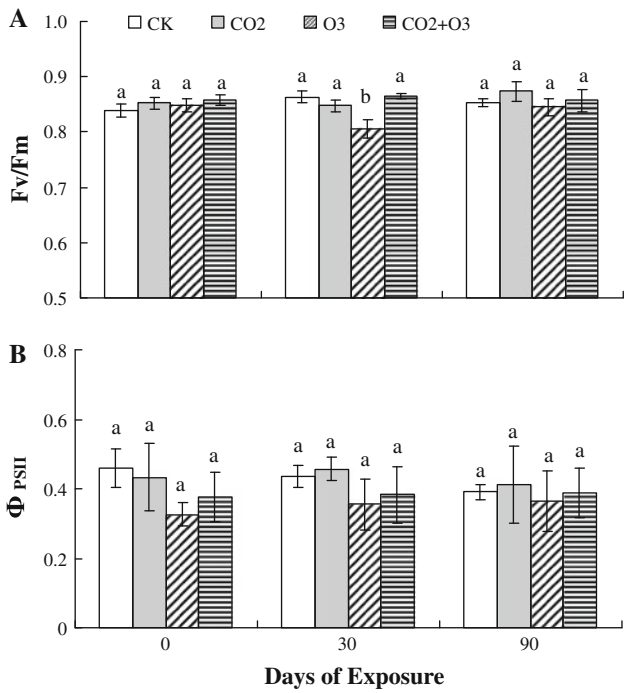

Fig. 2 Maximal photochemical efficiency of PSII in dark-adapted state (F_v/F_m, **A**) and effective quantum yield of PSII electron transport (ΦPSII, **B**) in needles of *P. tabulaeformis* exposed to ambient air (CK), elevated CO_2, elevated O_3 and elevated CO_2 + elevated O_3 during the growing season in 2008. Data shown are means with standard deviations (SD) of three replicates. Different *lower case letters* indicate significant difference at $p < 0.05$

(1.5 times ambient O_3) and 76 days, respectively, as compared to those of our study.

As seen in Fig. 1A, elevated CO_2 did not significantly increased net photosynthetic rate (P_n) in needles of *P. tabulaeformis* ($p > 0.05$) after 30 and 90 days of gas exposure in 2008. Elevated CO_2 did not affect stomatal conductance (g_s) at any time, compared to CK (Fig. 1B), but elevated O_3 alone and in combination with elevated CO_2 reduced g_s after 90 d of exposure. No significant differences in chlorophyll content were observed between elevated CO_2 and CK during the growing season except for after 30 days of fumigation (Fig. 1C). Our observation is in agreement with other studies that elevated CO_2 had no significant effect on chlorophyll content in plants (Turnbull et al. 1998; Riikonen et al. 2005; Zhao et al. 2010). Elevated O_3 decreased significantly P_n, especially after 30 days of gas exposure. Much of the decline in g_s occurred after 90 days of exposure to elevated O_3. Elevated O_3 significantly decreased the chlorophyll content ($p < 0.05$). Elevated CO_2 increased photochemical requirements for light-saturated electron flow through Photosystem II (Hymus et al. 2001), whereas elevated CO_2 was also reported to have a depressive effect on plant photochemistry (Scarascia-Mugnozza et al. 1996). In our studies, elevated CO_2 had no significant impact on F_v/F_m and ΦPSII (Fig. 2), as is consistent with a previous study by Kellomaki and Wang (1997) who reported that doubled ambient CO_2 treatment did not lead to a significant change in either the F_v/F_m or ΦPSII. Ozone has the potential to damage the photosynthetic apparatus and to affect the photochemistry of PSII (Riikonen et al. 2005). In this study, elevated O_3 decreased F_v/F_m and ΦPSII, especially for F_v/F_m after 30 days of exposure (Fig. 2A).

For the combined treatment of elevated CO_2 and O_3, no significant changes were observed in F_v/F_m or ΦPSII after 30 and 90 days of gas exposure, compared with 0 day of gas exposure. It can be inferred that elevated CO_2 ameliorated the adverse impact of elevated O_3 on photosynthetic apparatus. Generally, elevated CO_2 reduced g_s and O_3 uptake, and it might therefore decrease the potential risk

from oxidative stress. Our recent studies showed that elevated CO_2 ameliorated the oxidative stress on cell membrane induced by elevated O_3 in *Quercus mongolica* (Yan et al. 2010) and *G. biloba* (Lu et al. 2009). However, our results in this study are not in agreement with some earlier results showing that elevated CO_2 did not alleviate the adverse impact of elevated O_3 on growth and photosynthesis of trees (Manes et al. 1998), but even exacerbated the damaging effects of elevated O_3 (McDonald et al. 2002). Therefore, it is still a controversial issue to evaluate exactly the degree of interaction on trees when simultaneous exposure of elevated levels of CO_2 and O_3 are provided. The outcome may vary with gas concentrations, the time and duration of exposure, the species of tree being exposed, and other experimental conditions.

It has been suggested that the photosynthesis apparatus of plants may be protected against air pollutants by the emission of VOCs (Li et al. 2009). Loreto and Velikova (2001) posited that isoprene (the main VOC emitted from plants) has antioxidant properties and can protect plants from O_3 damage. In our studies, elevated O_3 significantly increased the emission rate of VOCs compared to CK ($p < 0.05$) after 30 and 90 d of gas exposure compared with 0 d of gas exposure (Fig. 3), which may be a helpful response to protect the photosynthetic apparatus against O_3 damage. However, the results in our studies are not in agreement with a study which reported that elevated O_3 had no significant effect on the emission of VOCs in *Q. ilex* (Loreto et al. 2004). In our previous study, elevated CO_2 or O_3 significantly increased the isoprene emission rate from *G. biloba* after 30 d of exposure (Li et al. 2009). However, one study suggested that elevated CO_2 decreased the emission of VOCs (Rosenstiel et al. 2003). Therefore, there is still some controversy. These varing responses in VOC emission rates may vary with the pollutant, exposure concentration and duration, plant species, its nutrition state, and specific environmental factors, such as light, temperature, and water, especially in an urban area (Li et al. 2009).

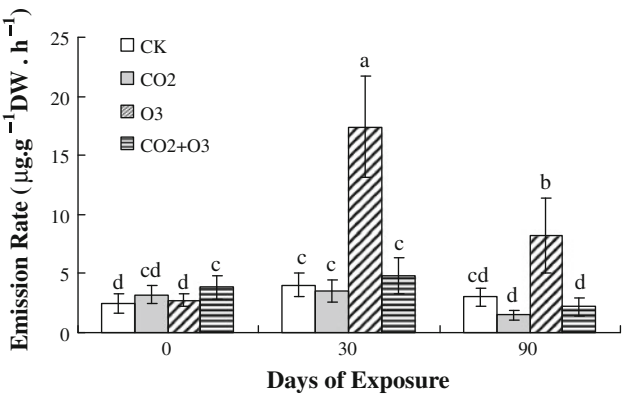

Fig. 3 Emission rates of volatile organic compounds (VOCs) from *P. tabulaeformis* exposed to ambient air (CK), elevated CO_2, elevated O_3 and elevated CO_2 + elevated O_3 during the growing season in 2008. Data shown are means with standard deviations (SD) of three replicates. Different *lower case letters* indicate significant difference at $p < 0.05$

In conclusion, our results showed that elevated CO_2 significantly increased growth of *P. tabulaeformis*, while elevated O_3 decreased growth of this tree species, particularly in needle weight and plant height. Elevated CO_2 alleviated the negative effects of elevated O_3 on growth and photosynthesis. No significant changes between elevated CO_2 and CK were observed in P_n, chlorophyll content, F_v/F_m, ΦPSII, or emission rate of VOCs. Elevated O_3 significantly increased VOC emission rates, which may be a helpful response to protect the photosynthetic apparatus against O_3 damage.

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