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Effects of elevated CO_2 and O_3 concentrations on isoprenoid emissions from Pinus tabulaeformis

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Abstract. Isoprene and monoterpenes have indirect effects on ozone concentration, methane lifetime and aerosol formation. At the same time, the atmospheric composition change (reflected in elevated CO_2 and O_3 concentrations) can affect the speciation of monoterpenes / isoprenoids and magnitude of isoprene and monoterpenes fluxes. Ambient concentrations of CO_2 and O_3 were 342 μmol•mol^{-1} and 40 nmol•mol^{-1}, respectively. The effects of elevated CO_2 (700 μmol•mol^{-1}) and O_3 (80 nmol•mol^{-1}) concentrations on isoprenoid emission rates and patterns from *Pinus tabulaeformis* were studied in open top chambers (OTCs). The released volatiles were quantified by thermal desorption and gas chromatography with flame ionization detector (GC-FID). The study showed that α-pinene was the main compound emitted from P *tabulaeformis*, accounting for more 51.5 - 72.6% of the detected volatile compounds. The emissions of isoprene and monoterpenes were reduced in response to elevated CO_2 concentrations. Exposure to elevated O_3 for 3 years significantly promoted the isoprene and monoterpenes emissions ($p<0.05$). Compared with ambient, elevated O_3 concentration increased isoprene emission from P *tabulaeformis* by about 270.5 ± 13.5%. The response of monoterpene emission to elevated O_3 may vary during the course of exposure to the pollutant. The patterns of monoterpene and isoprene emissions under combined elevated CO_2 and O_3 concentrations were similar to those under elevated CO_2 concentration alone.

Introduction

Isoprenoids, such as isoprene and monoterpenes are estimated to comprise half of the global biogenic volatile organic compound (BVOC) emissions [1]. Isoprene and monoterpenes are rapidly oxidized in the atmosphere leading to the formation of ozone and other secondary pollutants when anthropogenic nitrogen oxides and sunlight are present, thus affecting the atmospheric composition. The isoprenoids increase the atmospheric lifetime of greenhouse gas methane by competing for OH radicals, the principal atmospheric oxidizing agent of methane, and thus have an indirect impact on global changes [2]. The emission of isoprenoids from vegetation exerts the dominant control over regional oxidative chemistry of the atmosphere in many terrestrial ecosystems [3]. In the case of coniferous forests, isoprenoids, which are used primarily for herbivore defense, represent the dominant BVOC.

Urban vegetation is often characterized by the presence of exotic species interspersed with natural vegetation. The different management and the stressful conditions to which urban trees are subjected may affect isoprenoid emission rates [4]. Urban tree canopies in some parts of the world may influence urban ozone chemistry in a significant way. Global atmospheric CO_2 concentration has risen by nearly 30% since pre-industrial times, largely because of the industrial emissions, which also have a significant effect on the urban atmospheric environment. Similarly, background concentration of tropospheric ozone concentration has increased from 10 to over 40 nmol•mol^{-1}. Such changes of the tropospheric atmospheric environment are expected to affect the capacity of plants to emit isoprenoids.

It has generally been assumed that isoprenoid emissions will increase in response to elevated CO_2 and O_3. In the case of control by carbon allocation, it has been hypothesized that carbon in excess of that required for immediate growth should be used in the production of carbon-based defensive compounds (e.g. monoterpenes). Using this hypothesis, one might predict higher rates of monoterpene production and emission from plants growing at elevated CO_2 and limited nitrogen availability. Sallas et al. [5] estimated that α-pinene in needles of Pinus *sylvestris* seedlings, increased about 50% in response to elevated CO_2. Conversely Francesco et al. [6] reported that the monoterpenes emission rates and the enzyme activities of the monoterpene synthases were inhibited at elevated atmospheric CO_2 concentration (to 700 μmol•mol^{-1}). Based on chemistry/climate modeling studies, the CO_2-isoprene effect has possible ramifications for projected tropospheric ozone and OH levels, as both are sensitive to the magnitude and spatial distribution of isoprene emission [7].

Studies investigating the individual effects of elevated CO_2 or O_3 concentration on the isoprenoid emission of plants are common, but there are few about the interactions of CO_2 and O_3 in terms of their effect on isoprenoid emissions from plants, especially for urban trees. Vuorinen et al. [8] reported the interactive effects of elevated CO_2 and O_3 concentrations on Betula pendula clones. They found that elevated CO_2 and O_3 in combination did not have any effect on BVOC emissions in an open top chamber.

Pinus *tabulaeformis* is one of the most popular trees in the north region of China. Zhao et al. [9] reported the effects of elevated CO_2 and O_3 concentration on photosynthetic responses of P *tabulaeformis* grown in an urban area. Elevated CO_2 concentration significantly increase ascorbate content in needles, and reduce accumulation of reactive oxygen species (ROS) caused by elevated O_3 concentration, thus protecting P *tabulaeformis* from oxidative damage caused by elevated O_3 exposure [10]. But there is little experimental data available concerning the effects of environmentally relevant CO_2 and O_3 concentrations on isoprenoid emissions from P *tabulaeformis*. Here, we analyze the isoprene and monoterpene emission rates and emission patterns of P *tabulaeformis* in open top chambers. The aim of this paper is to understand the long term effects of elevated tropospheric CO_2 and O_3 concentrations on isoprenoid emissions.

Materials and Method

Measurement site and plant material. The measurements were made in the Arboretum of the Chinese Academy of Sciences in Shenyang (41˚46′31.29″N, 123˚26′27.51″E) in northeastern China. In the Shenyang urban area, where the total area of forest is 147 km^2, the vegetation cover ratio is 35%. P *tabulaeformis* is one of the dominant native conifer species. 4-year-old P *tabulaeformis* trees were planted in the ground (loamy soil, no extra fertilizer) of twelve open top chambers (OTCs), at a density of 10 trees per chamber in May 2006. The open-top chambers were 4 m in diameter and 3 m in height. The trees were irrigated if the soil water content was below 10%, which was regarded as the threshold for no limiting water uptake.

Experimental design. Three OTCs were designated randomly for each of ambient air (CK), elevated CO_2 (EC), elevated O_3 (EO) and elevated CO_2+O_3 (EC+EO) treatments. During consecutive active growing seasons the trees were exposed to high CO_2 (700 μmol•mol^{-1}) for 24 hours day^{-1} in EC and EC+EO chambers, and exposed to high O_3 (80 nmol•mol^{-1}) for 9 hours (08:00~17:00) day^{-1} in EO and EC+EO chambers. The CO_2 and O_3 concentrations in OTCs were determined by ES-D infrared CO_2 sensor and S-900 O_3 analyzer respectively, with a variance ± 4% for CO_2 and ± 9% for O_3. Ambient air was ~ 342 μmol CO_2 mol^{-1} and ~ 40 nmol O_3 mol^{-1}.

Volatile collection. The samples were collected by drawing air inside the sampling bags through 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 200 mL min^{-1} and the sampling time was 5 min. Before sampling, the adsorbent tubes were purged by ultra-pure N_2 (99.9999 %) at 280 ºC for 1 h, at a flow rate of 35 mL min-1. Samples were sealed and stored at 4 °C until analysis in the laboratory. Samples were collected between 08:30 and 10:00 am on sampling days

Analysis of volatiles. Sample analysis was carried out using a thermal desorber 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 flame ionization detector. The pre-concentrated samples were thermally desorbed at 250 °C for 5 min at 30 ml min^{-1}, and secondary desorption was at 275 °C for 2 min. A fused silica capillary (60 m x 0.32 mm x 0.25 μm) DM-1 column was used to separate isoprene and the monoterpenes [11].

Biomass. After emission sampling, the leaves enclosed in the bags were removed from the trees, weighed and placed in a drying oven at 60 °C for 48 h. The dry weights were used for normalization of isoprene and monoterpenes emission rates to unit leaf mass.

Emission rate calculation. Emission rate ($\mu g \cdot g^{-1} dw \cdot h)^{-1}$) was defined as $M \times V \times \Delta C \times 10^{-3} / (V_i \times \Delta t \times W)$, where *V* is the gas volume in the sampling bag (m^3); *M* is the molecular weight of species *i* (eg. M=68 for isoprene); ΔC is the concentration (ppb C) increment of *VOC* emitted by the plant in the sampling bag; V_i is the gas volume of species *i* inside the sample bag; *W* is the dry weight of the leaves enclosed; and Δt is the sampling time (h).

Data analysis. The effects of elevated atmospheric CO_2 and / or O_3 concentrations on *P tabulaeformis* were analysed using ANOVA in the SPSS statistical package (IBM, Chicago, USA). Treatment effects were also analyzed using a graphical vector analysis of the isoprenoid data by plotting the relative value of isoprenoid content (x-axis), isoprenoid concentration (y-axis) and leaf dry weight (diagonals) on a graph. The values for the CK treatment were used as the reference value for the calculation of the relative values [12]. The vectors representing the different treatments were drawn from the CK treatment (reference point: 1,1,1) and their direction and magnitude were used to interpret the treatment effects (Table 1).

Table 1 Interpretations of shifts in the isoprenoid content (x-axis) and concentration (y-axis) and leaf dry weight (diagonals) in a graphical vector analysis

Emission capacity	Emission rate	Dry weight	Interpretation
+	0	+	Steady increase
+/0	-	+/0/-	Dilution effect
-	-	+	Reduced emission
-	0	-	Steady decrease
-/0	+	-	Concentration effect
+	+	+/0/-	Increased emission

Results

Table 2 Effects of elevated CO_2 and O_3 concentrations on the relative abundances (%) of isoprenoids emitted by *Pinus tabulaeformis* in OTCs. Abbreviations: CK= chamber control, EC=elevated CO_2, EO=elevated O_3, EC+EO=elevated CO_2 and O_3 in combination.

	isoprene	α-pinene	β-pinene	⊿3-carene	camphene	limonene	ocimene	α-terpinene
CK	7.3	72.6	3.3	1.9	5.2	8.3	0.8	0.5
EC	10.8	71.5	2.7	1.1	4.7	7.7	0.8	0.7
EO	27.1	51.5	4.0	1.7	11.2	2.0	1.7	0.8
EC+EO	14.5	64.6	4.9	1.5	5.5	7.0	1.3	0.6

Table 2 shows that in CK, EC, EO and EC+EO treatments, α-pinene was the main compound emitted from *P tabulaeformis,* and accounted for 51.5 - 72.6% of the detected volatile compounds. The total isoprenoid emission was very low in 2007. The emission rates of the isoprene and monoterpenes from *P tabulaeformis* showed strong seasonality trends, for 2007 and 2008, the isoprenoid emission rates increased from June, and reached its maximum at July, then decreased quickly (Fig. 1). The mean emissions of isoprene and monoterpene under ambient, elevated CO_2,

elevated O_3 and elevated CO_2+O_3 concentrations in the growing season were on average 39.04, 23.29, 45.67 and 24.16 $\mu g \cdot g^{-1} dw \cdot h^{-1}$, respectively.

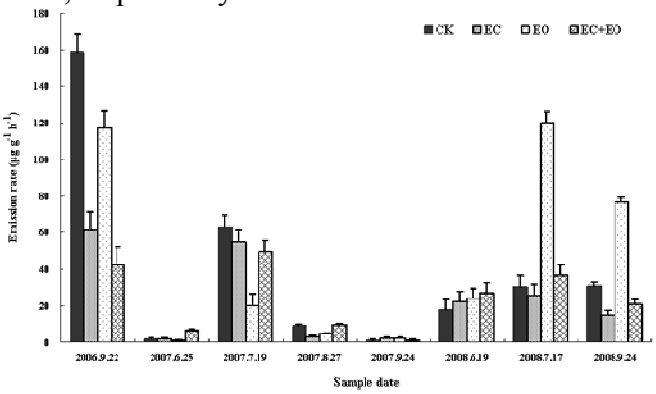
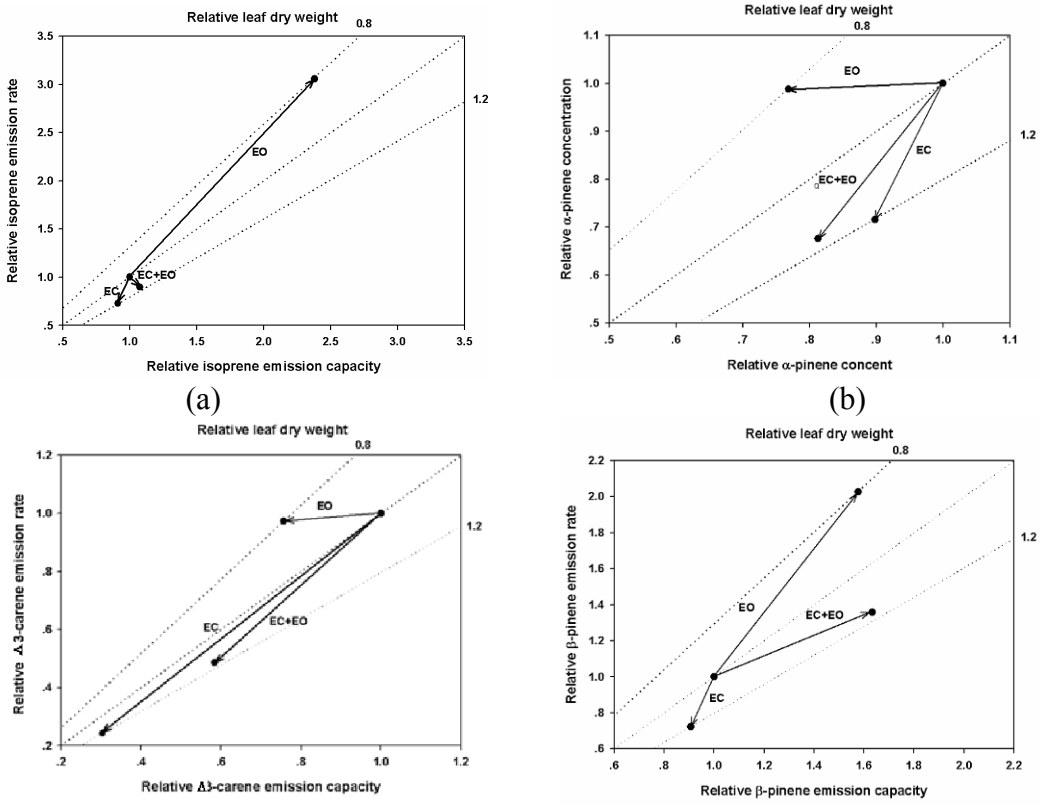


Fig. 1 Emission rates of isoprenoids from *Pinus tabulaeformis* grown at ambient air (CK), elevated CO_2 (EC), elevated O_3 (EO) or at elevated CO_2+O_3 (EC+EO). Error bars indicate SE (n=9).

In all of the three years the emission at ambient CO_2 was higher than the emission at elevated CO_2, but not significantly. The emission rates at elevated CO_2 of all 8 detected compounds were reduced by 22.6 - 71.5%. Isoprene emission were increased under elevated CO_2 concentration (Table 3), and the mean emission rate of isoprene was 2.65 $\mu g \cdot g^{-1} dw \cdot h^{-1}$. Vector analysis confirmed that the emissions of isoprene and monoterpenes were reduced in response to elevated CO_2 concentrations (Fig. 2a-i).



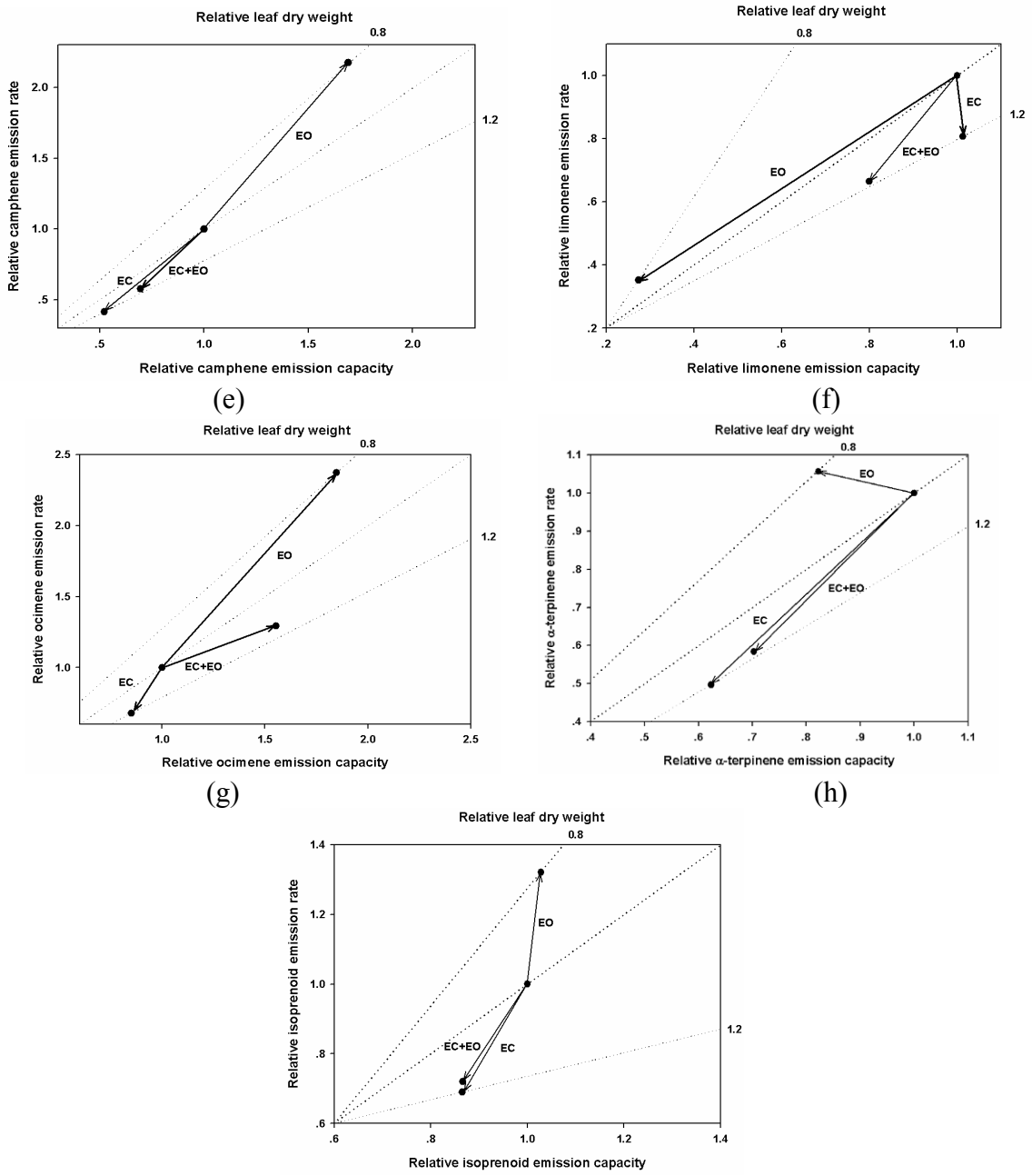


Fig. 2 Effects of treatments on the relative concentration and content of isoprene and monoterpenes, and the relative leaf dry weight of *Pinus tabulaeformis* needles.

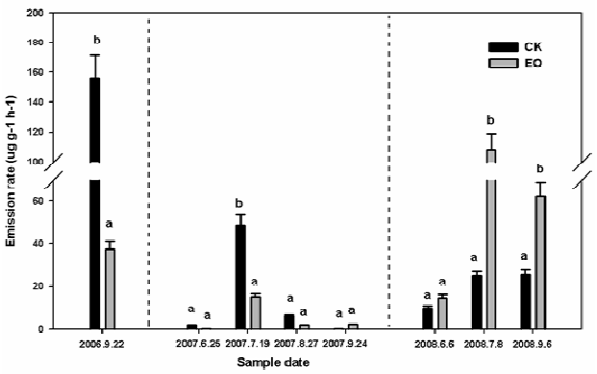


Fig. 3 Emission rates of α-pinene emitted from *Pinus tabulaeformis* needles grown at ambient or elevated O_3 concentration in three different years.

In 2008, daily exposure to elevated O_3 for the previous 3 years significantly promoted the isoprene and monoterpene emissions ($p<0.05$) (Fig. 3). Compared with the control, elevated O_3 concentration resulted in increased isoprene emissions from *P tabulaeformis* of about 270.5 ± 13.5%. The isoprene emission rate in the CK and EO treatments were 3.43 μg $g^{-1}h^{-1}$ and 12.75 μg $g^{-1}h^{-1}$, respectively. Elevated O_3 concentration resulted in a decreased α-pinene emission in 2006 and 2007, where the exposure had been for only 1 or 2 years respectively. According to the vector analysis, elevated O_3 induced the isoprene, β-pinene, camphene, ocimene and total isoprenoid compound emissions, but reduced the α-pinene, Δ3-carene and limonene emissions (Fig. 2a-i).

The patterns of monoterpene and isoprene emissions under combination of elevated CO_2 and O_3 concentrations were similar to under elevated CO_2 concentration alone (Fig 2a-i). The results of this study indicated that the combination of elevated CO_2 and O_3 had compound-specific effects on isoprenoid emissions (Table 3). Vector analysis indicated that the EC+EO treatment diluted the isoprene emission, and induced β-pinene and ocimene emission, but reduced emissions of the other compounds examined (Fig. 2a-i). The combination of elevated CO_2 and O_3 concentrations resulted in a strong decrease (-49.5 ± 2.5%) of monoterepene emission, however, there was not a significant difference between EC+EO and CK treatments on the total isoprenoid emission, except in 2006 (Fig. 1).

Discussion

Our experiment demonstrates that the monoterpene emission is generally inhibited in *P tabulaeformis* needles grown under elevated CO_2 with respect to the emission of needles grown at ambient CO_2. However, according to Zhao et al [9] the main photo-physiological characteristics of *P tabulaeformis*, such as photosynthetic rates ($p<0.05$), Hill activity, soluble sugar and starch contents are all increased if CO_2 concentrations are elevated for the whole growing season. Thus there seems to be no relationship between monoterpene emission and photosynthesis, and Francesco et al. [13] determined that the percentage of carbon re-emitted as monoterpenes actually decreased dramatically at elevated CO_2.

According to the hypothesis of Honkanen et al. [14] based on source-sink balance theory, growth at elevated CO_2 would not necessarily have an enhancing effect on BVOC emission. Under conditions of elevated CO_2 concentration, terpenoid substances biochemical inter-conversion pathways are probably different in different plant species and at different developmental stages. Moreover, the storage capacity of terpene-storing organs may restrict the incorporation of excess carbon into terpenoids at elevated CO_2 concentrations, and leave the constitutive terpene emission unaffected [8]. Snow [15] found that increased atmospheric CO_2 concentration reduced the monoterpene content in *Douglas fir* needles, which may be due to competition within the carbon pool, altering the distribution of carbon in plant tissues, including synthesis of other secondary metabolites and the increase carbon in plant roots [16]. In a parallel study of the needles of *P tabulaeformis* analysed in this study, growth at elevated CO_2 levels was found to increase the concentration of condensed tannins and the overall sum of phenolics indicating enhanced partitioning of carbon to secondary compounds. However, the emission of monoterpene seems to be never limited by enzyme activity, and is likely controlled by substrate availability. Moreover, isoprene can be synthesized from a number of alternative C sources [17].

The Free-Air CO_2 Enrichment (FACE experiment) by Centritto et al. [18] showed that elevated the atmospheric CO_2 concentration only had a very limited role on isoprene emission. However, the estimations at large scale may differ from those at the leaf level, because of the indirect effects of global climate change on leaf area index, canopy temperature, water and nutrient availability and length of growing season [19]. It should be remembered that low emissions on a leaf dry weight basis may not result in low emissions on a canopy basis if plant growth is enhanced at elevated CO_2 [13]. Moreover, *P tabulaeformis* growing in the OTCs at elevated CO_2 has been shown to have a significantly increased leaf weight per needle with respect to trees growing in OTCs at ambient CO_2 [20].

The results from our experiment were different to those of the aspen FACE experiment, in which isoprene emission was decreased significantly by elevated O_3 concentration (at 1.5-fold the ambient levels) for several years [21]. Similarly, Velikova et al. [22] reported that exposure to high O_3 caused a significant increase of BVOC emission from reed. At the same time, in laboratory experiments, ozone fumigation was found to stimulate emission of monoterpenes in *Q ilex* [23]. O_3 exposure may cause oxidative stress, and allocation of resources to synthesis of defence proteins could lead to increases in monoterpenes emissions, but the presence of O_3 in the gas phase would lead to atmospheric degradation reactions and to a net decrease in detectable volatile compounds [24]. In our study, vector analysis showed that elevated O_3 concentration led to induced isoprenoid emissions, hence our result are consistent with the hypothesis that BVOCs function as antioxidants to decrease damage by O_3 stress. Moreover, our results indicate that the response of monoterpene emissions to elevated O_3 may vary depending on the length of exposure to the pollutant.

The effect of elevated O_3 on isoprenoid emission is influenced by plant species, growing seasons, O_3 concentration and other factors. In our experiment, O_3 concentrations were constant at 80 $nmol \cdot mol^{-1}$, whilst in a real-world situation the O_3 concentration would be increased gradually, so we would recommend that O_3 concentration be elevated gradually in future experiments. In urban regions with high nitrogen oxide ($NOx = NO + NO_2$) concentration, isoprenoid oxidation products react with NOx and increase the tropospheric O_3 levels, which then have a further impact on the urban atmospheric environment. The effect would be amplified by further warming and urbanization [25].

The joint effect of elevated CO_2 and O_3 on the rates and patterns of BVOC emission by plants has not been well studied, especially for urban trees. Our results indicate that growing under elevated CO_2 and O_3 together does not result in major effects on the emissions of *P tabulaeformis*. This has been observed in other species, for example, where elevated CO_2 or O_3 concentration singly had considerable effect on BVOC emissions of *Ginkgo biloba*, the effect of elevated CO_2 and O_3 in combination did not change the BVOC emission rates significantly [26]. A similar observation was made by Vuorinen et al. [8], who found that growing under CO_2+O_3 fumigation did not have any significant effect on emissions of total monoterpenes, sesquiterpenes, or individual quantified VOCs of silver birch (*Betula pubescens*) clones in an open top chamber.

Some researches concerning interactions in plants' secondary metabolism has found that elevated CO_2 can mitigate the effects of elevated O_3. However, Calfapietra et al. [19] reported that elevated CO_2 could not alter the effect of elevated O_3 on isoprene synthase transcript levels, isoprene synthase protein levels and isoprene emission rate of aspen trees. Therefore, the decline of isoprene emission observed when elevated CO_2 and elevated O_3 co-occur may be exacerbated by a combination of substrate limitation and enzyme limitation [21]. The terpenes in pine needles were not affected significantly by the combination of elevated CO_2 and O_3 concentrations, except for α-pinene and limonene [5]. More research is needed to understand the complicated biosynthesis and emission mechanisms.

In conclusion, the isoprene and monoterpenes emissions from *P tabulaeformis* were found to have significant seasonal changes. The α-pinene was the main constituent of the BVOCs. Elevated O_3 concentration had considerable effect on isoprenoid emissions of *P tabulaeformis*, but elevated CO_2 and the elevated CO_2 and O_3 in combination had no significant impact on isoprenoid emissions, confirming that increasing the amount of available CO_2 can counteract the effects of elevated O_3. Some isoprenoids are believed to have antioxidant activity, which could protect plants from ozone damage, but the mechanisms are unclear yet.

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