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Elevated CO_2 and O_3 Levels Influence the Uptake and Leaf Concentration of Mineral N, P, K in *Phyllostachys edulis* (Carrière) J.Houz. and *Oligostachyum lubricum* (wen) King f.

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Abstract: Rising CO_2 and O_3 concentrations significantly affect plant growth and can alter nutrient cycles. However, the effects of elevated CO_2 and O_3 concentrations on the nutrient dynamics of bamboo species are not well understood. In this study, using open top chambers (OTCs), we examined the effects of elevated CO_2 and O_3 concentrations on leaf biomass and nutrient (N, P, and K) dynamics in two bamboo species, *Phyllostachys edulis* (Carrière) J.Houz. and *Oligostachyum lubricum* (wen) King f. Elevated O_3 significantly decreased leaf biomass and nutrient uptake of both bamboo species, with the exception of no observed change in K uptake by *O. lubricum*. Elevated CO_2 increased leaf biomass, N and K uptake of both bamboo species. Elevated CO_2 and O_3 simultaneously had no significant influence on leaf biomass of either species but decreased P and N uptake in *P. edulis* and *O. lubricum*, respectively, and increased K uptake in *O. lubricum*. The results indicate that elevated CO_2 alleviated the damage caused by elevated O_3 in the two bamboo species by altering the uptake of certain nutrients, which further highlights the potential interactive effects between the two gases on nutrient uptake. In addition, we found differential responses of nutrient dynamics in the two bamboo species to the two elevated gases, alone or in combination. These findings will facilitate the development of effective nutrient management strategies for sustainable management of *P. edulis* and *O. lubricum* under global change scenarios.

Keywords: elevated CO_2; elevated O_3; *Phyllostachys edulis*; *Oligostachyum lubricum*; biomass; N; P; K

1. Introduction

Nitrogen (N), phosphorus (P), and potassium (K) are considered essential elements for plant growth [1], but are also the most limiting elements for terrestrial vegetation, especially under environmental change [2,3]. Two important drivers of environmental change, concentrations of atmospheric CO_2 and tropospheric O_3, have been increasing substantially as a result of human activities since the industrial revolution and will continue to increase in the future [4]. These changes have affected growth and N, P, and K concentrations and uptake in plants, which may influence nutrient cycles in ecosystems [5–7].

Most previous studies that have considered the effects of elevated CO_2 and O_3 on N, P, and K concentrations and uptake in plants, have mainly focused on the response of plant N and P to elevated CO_2, while other nutrients, especially K, have rarely been investigated [7–9] Studies have shown that elevated CO_2 generally reduces plant N concentration and increases plant N uptake [10–12]. This is partly explained by the dilution hypothesis [13,14], reduction in soil N availability [15,16], nitrate assimilation restriction [17–19], and a change in leaf physiological characteristics (e.g., a decrease in leaf protein and the photosynthetic enzyme RuBisCO) [14]. Compared to plant N, the effects of elevated CO_2 on plant P concentration and uptake are more variable (Gifford et al., 2000). Elevated CO_2 has been associated with increased [20,21], neutral [22,23] and decreased plant P concentration and uptake [24,25]. Similar results have been found in the response of plant K to elevated CO_2, although relevant studies are rare [7]. Consequently, the response mechanisms of N, P, and K uptake in plants to elevated CO_2 remain unclear [7,21] and warrant further study, especially regarding the complexity of the response of P and K to elevated CO_2.

In comparison, a few studies have investigated nutrient concentration and uptake in plants under elevated O_3 [26–29]. These studies have shown that the responses of plant N, P, and K concentrations and uptake to elevated O_3 are more complicated than responses to elevated CO_2 [28,30]. For example, several studies have demonstrated that elevated O_3 decreases N, P, and K concentrations and uptake to some extent due to a reduction in nutrient demand by the plants, caused by O_3-induced inhibition of plant growth [5,31]. However, other studies have shown either an increase [29] or no change in nutrient concentration and uptake [32–34], which have been partly attributed to a defense mechanism against elevated O_3 and an adaptive strategy for plants. Due to the complexity of nutrient response to elevated O_3, and the lack of information available, it remains unclear how N, P, and K concentrations and uptake respond to elevated O_3.

In view of the contrasting effects of elevated CO_2 and O_3 on plant growth [35], some studies have concluded that elevated CO_2 and O_3 might drive plant nutrient dynamics in opposite directions [36–38]. However, to our knowledge, there is little evidence to support this hypothesis due to the complexity of nutrient responses to elevated CO_2 and O_3 described above. Moreover, limited information is available on the combined effect of elevated CO_2 and O_3 on plant nutrient dynamics, which may potentially limit our ability to further understand nutrient cycles [30,39]. It is important to understand how increases in CO_2 and O_3 concentrations will affect the concentrations and uptake of N, P, and K in plants, in order to understand nutrient cycle dynamics and predict potential nutrient limitation under future regional climate change [40,41].

Bamboo is the main important non-timber sub-tropical and tropical forest product in China, and is widely distributed in Zhejiang, Fujian, Jiangxi, Hunan, Guangxi, and Yunnan [42]. It also plays important roles in regional water and soil conservation efforts, carbon sequestration, oxygen emission, and climate regulation, making it an important element of terrestrial ecosystems [42]. Among bamboo species, *Phyllostachys edulis* (Carrière) J.Houz. and *Oligostachyum lubricum* (wen) King f. are the two dominant bamboo species in the subtropical zone of China, and are characterized by fast growth rates (60 days), hollow stems and complicated rhizome-connecting stems (ramets). Previous studies have demonstrated that elevated CO_2 enhances the growth of these two bamboo species [43,44], while elevated O_3 inhibits their growth [45]. Moreover, the growth of both bamboo species under climate change is related to nutrient availability [46]. However, it remains unclear how elevated CO_2 and O_3 independently, and interactively, affect leaf N, P, and K uptake and leaf concentrations. Therefore, the objective of this study was to reveal the dynamics of N, P, and K uptake and leaf concentrations in *P. edulis* and *O. lubricum* under conditions of elevated CO_2 and O_3. We attempt to answer the two following questions: (1) Do elevated CO_2 and O_3 independently, and interactively, affect leaf N, P, and K uptake and leaf concentrations? (2) Do the responses of N, P and K dynamics to elevated CO_2 and O_3 differ between *P. edulis* and *O. lubricum*?

2. Materials and Methods

2.1. Research Site and Experimental Design

The experiment was carried out at the Taihuyuan Ornamental Bamboo Planting Garden in Zhejiang, China (29°56′–30°23′ N, 118°51′–119°72′ E). The region has a subtropical monsoon climate. Average annual precipitation is 1450 mm, and average annual temperature is 15.4 °C.

Open-top chambers (OTCs) that were used in the experiments were built using steel tubes and colorless clear glass, including a filtered air system, vent system and gas distribution system. The details of the OTCs are described in Zhuang [46]. O_3 and CO_2 concentrations were obtained from CFG-20 O_3 generator (Sankang Environmental Technology Co., Ltd., Jinan, China) and steel cylinders of pure CO_2 and from, respectively. The microclimatic (temperature, relative humidity) conditions were measured. We designed four treatments based on a 2 × 2 factorial design based on the local average and observed the peak O_3 and CO_2 concentrations in the field of the study site. (Table 1). Specific treatments were as follows: ambient air (O_3 concentration of 40 ± 5 nmol mL^{-1}, CO_2 concentration of 360 ± 20 μmol mL^{-1}); elevated O_3 (O_3 concentration of 100 ± 10 nmol mL^{-1}, CO_2 concentration of 360 ± 20 μmol mL^{-1}); elevated CO_2 (O_3 concentration of 40 ± 5 nmol mL^{-1}, CO_2 concentration of 700 ± 35 μmol mL^{-1}); and combined elevated CO_2 and O_3 (O_3 concentration of 100 ± 10 nmol mL^{-1}, CO_2 concentration of 700 ± 35 μmol mL^{-1}). Each treatment was replicated threefold.

Table 1. 2 × 2 factorial design.

O_3 (nmol mL^{-1})	CO_2 (μmol mol^{-1})	
	360~380	685~730
40~45	Ambient air	Elevated CO_2
92~106	Elevated O_3	Combined elevated CO_2 and O_3

Experiments were conducted from 10 July to 30 October 2011. During the experimental period, CO_2 was released all day (24 h) and O_3 was released from 07:00 a.m. to 17:00 p.m..

2.2. Plant Materials

Two-year-old bamboo plants of two species *Phyllostachys edulis* (diameter: 18.2 ± 1.8 mm; height: 2.75 ± 0.25) and *Oligostachyum lubricum* (diameter: 12.2 ± 1.3 mm; height: 2.70 ± 0.30 m) were planted in plastic pots in October 2010. The detailed information was described in our previous study [46].

2.3. Biomass and N, P, and K Measurements

At harvest, three plants of *P. edulis* and *O. lubricum* were randomly selected from each OTC and the only green leaves were collected for biomass and N, P, and K measurements. Leaves were oven dried at 75 °C to a constant weight. To evaluate N, P, and K concentrations, the samples were first digested in a solution of H_2SO_4–$HClO_4$, and the N, P, and K concentrations were determined using Kjeldahl, molybdovanadate, and atomic absorption spectrometry methods respectively [47]. All nutrient measurements were replicated three times within the same treatment.

2.4. Statistical Analysis

The N, P, and K content of leaves was obtained by multiplying the leaf N, P, and K concentrations by leaf biomass. We used one-way analysis of variance (ANOVA) in SPSS ver. 17.0 statistical software (SPSS Inc., Chicago, IL, USA) to analyze the differences among treatments. p values < 0.05 indicated a significant difference among treatments.

3. Results and Discussion

3.1. Leaf N, P, and K Concentrations

Different responses of plant N, K, and P concentrations to elevated CO_2 were observed in our study in both *P. edulis* and *O. lubricum* (Table 2). Elevated CO_2, in comparison with ambient air, decreased leaf P concentration in both *P. edulis* and *O. lubricum* by 19.1% and 23.6%, respectively, which may be ascribed to a dilution effect resulting from an increase in biomass [14]. Compared with ambient CO_2, elevated CO_2 significantly decreased leaf N concentration (−14.5%) in *O. lubricum*, which is consistent with extensive previous studies [14,48], and can be largely explained by the carbohydrate dilution effect [12,48,49]. However, the observed increase in leaf N concentration (+18.5%) in *P. edulis* under elevated CO_2 is in contrast with most studies on elevated CO_2. This difference may be associated with higher N uptake with increasing leaf biomass growth resulting from an adequate supply of soil N in the present study, and an acceleration of nitrate assimilation [7,12,16]. Elevated CO_2 significantly increased leaf K concentration (+31.1%) in *O. lubricum*, but decreased K concentration (−30.1%) in *P. edulis* (Table 2), suggesting a complex response of leaf K concentration to elevated CO_2, as reported in numerous previous studies [11,50,51]. The possible explain was that elevated CO_2 enhances the activity of stomata/guard cells, the operation of which is driven by the availability of K; therefore, the potential difference between leaf stomata and the lower plant parts results in active absorption of K [52]. However, the response mechanism of K concentration to elevated CO_2 remains unclear and warrants further research [53,54].

Table 2. Leaf nutrient concentrations (g/kg DM) (mean ± s.d., kg DM) of *Phyllostachys edulis* and *Oligostachyum lubricum* in response to ambient air, elevated O_3, CO_2 and combined elevated O_3 and CO_2. Different letters indicate significant differences among treatments ($p < 0.05$).

Bamboo Species	Determination Index	Treatments			
		Ambient Air	Elevated CO_2	Elevated O_3	Combined Elevated CO_2 and O_3
Phyllostachys edulis (Carrière) J.Houz.	N	19.37 ± 0.46b	22.96 ± 0.41a	21.20 ± 0.58ab	20.50 ± 0.61b
	P	1.27 ± 0.04a	0.97 ± 0.02b	1.35 ± 0.04a	1.01 ± 0.05b
	K	8.41 ± 0.10ab	5.88 ± 0.82c	9.17 ± 0.89a	7.34 ± 0.96bc
Oligostachyum lubricum (wen) King f.	N	17.97 ± 1.07a	15.37 ± 0.45b	18.30 ± 0.40a	15.90 ± 0.89b
	P	1.05 ± 0.08a	0.81 ± 0.05b	1.07 ± 0.42a	1.06 ± 0.16a
	K	4.25 ± 0.45b	5.62 ± 0.20a	6.35 ± 0.39a	5.60 ± 0.63a

Elevated O_3 had a minor effect on N and P concentrations in both bamboo species (Table 2), which is consistent with several previous studies [32–34], but is inconsistent with others [5,55]. The inconsistency in these results could be related to a difference in ozone-resistance level among plants [56], as evergreen species (e.g., bamboos) are more tolerant to elevated O_3 than deciduous species [57]. The possible mechanism affecting the response of N and P in plants warrants further study. Elevated O_3, compared with ambient O_3, significantly increased K concentration (+49.4%) in *O. lubricum* but did not change the K concentration in *P. edulis*. This result indicates a difference between the two bamboo species in the response of K to elevated O_3. These results suggest that increasing K concentration can be regarded as an adaptive strategy of *O. lubricum* that could enhance the plant defensive capability against elevated O_3 [5,21]. Moreover, these results may also explain the higher tolerance of *O. lubricum* to elevated O_3 relative to *P. edulis* [45].

The combination of elevated CO_2 and O_3, in comparison with ambient air, significantly decreased the leaf P concentration (−20.5%) in *P. edulis* and the N concentration (−11.5%) in *O. lubricum*, but increased the leaf K concentration (+31.8%) in *O. lubricum* (Table 2). In addition, elevated O_3 significantly increased leaf P concentration in *P. edulis* under ambient CO_2 conditions, but reduced P concentration under elevated CO_2, indicating a significant interactive effect of combined elevated CO_2 and O_3 on leaf P concentration. Similar results were found for leaf N and K concentrations in *O. lubricum* under combined elevated CO_2 and O_3. These results demonstrate that the nutrient concentrations

of both bamboo species under elevated CO_2 may offset the O_3-induced change, although some differences exist between *P. edulis* and *O. lubricum* in nutrient-type response to combined elevated CO_2 and O_3 [36,37].

3.2. Leaf Biomass

Previous studies have reported that elevated O_3 significantly decreased plant biomass by reducing photosynthesis [58,59], while elevated CO_2 acted as a fertilizer to increase plant biomass [16,60]. A similar phenomenon was found in our study. Compared to ambient air, elevated O_3 significantly decreased leaf biomass of *P. edulis* and *O. lubricum* by 35.1% and 26.7%, respectively (Table 3), while elevated CO_2 significantly increased leaf biomass of the two bamboo species by 24.9% and 20.9%, respectively. Some studies have demonstrated that combined elevated CO_2 and O_3 does not change leaf biomass as elevated CO_2 alleviates the negative effects induced in plants by elevated O_3 [35,61,62]. A similar result was found in the present study (Table 3).

Table 3. The leaf biomass (kg DM) (mean ± s.d., kg DM) of Phyllostachys edulis and Oligostachyum lubricum in response to ambient air, elevated O_3, CO_2 and combined elevated O_3 and CO_2. Different letters indicate significant differences among treatments ($p < 0.05$).

Bamboo Species	Treatments			
	Ambient Air	Elevated CO_2	Elevated O_3	Combined Elevated CO_2 and O_3
Phyllostachys edulis	73.17 ± 6.01b	91.39 ± 7.14a	47.54 ± 3.53c	80.34 ± 4.84b
Oligostachyum lubricum	62.67 ± 2.28b	75.77 ± 1.87a	45.97 ± 2.79c	58.07 ± 2.24b

3.3. N, P, and K Uptake

We found that elevated CO_2, compared to ambient air, increased leaf N uptake (+47.9%) in *P. edulis* and K uptake (+59.6%) in *O. lubricum* (Figure 1). This is consistent with previous findings that elevated CO_2 promotes nutrient uptake in plants to satisfy the demands of plant growth [7,11,12]. In addition, it is likely that elevated CO_2 could have various implications on nutrient dynamics between bamboo requirement and supplement among different bamboo species, which have proved in other plants [63]. However, the mechanisms underlying the observed discrepancy in nutrient demand of *P. edulis* and *O. lubricum* under elevated CO_2 remain unclear and need further research. Compared to ambient air, elevated O_3 decreased significantly leaf N (−28.9%), P (−31.6%), and K (−29.6%) uptake in *P. edulis* and N (−25.7%) and P (−25.8%) uptake in *O. lubricum* (Figure 1), which can be attributed to nutrient-uptake limitation in the plants (including *P. edulis* and *O. lubricum*) caused by O_3-induced plant growth inhibition [5,31]. In addition, the combination of elevated CO_2 and O_3, in comparison with ambient air, significantly decreased P uptake in *P. edulis* (−13.0%) and N uptake in *O. lubricum* (−18.3%) (Figure 1). This result implies that: (1) leaf nutrient uptake under a combination of elevated CO_2 and O_3 was used to repair O_3-induced plant damage and maintain regular growth [27,38]; (2) the difference in nutrient uptake in *P. edulis* and *O. lubricum* further revealed that there are species-dependent physiological mechanisms and adaptive mechanisms affecting nutrient uptake under elevated CO_2 and O_3 conditions. Nonetheless, it should be noted that the combination of elevated CO_2 and O_3 significantly increased K uptake in *O. lubricum* (+22.1%), which is likely related to properties of K that enhance plant resistance to environmental stress [39,64] and could also explain the higher tolerance of *O. lubricum* under elevated CO_2 and O_3 as reported by Zhuang et al. from the nutrient perspective [43–45].

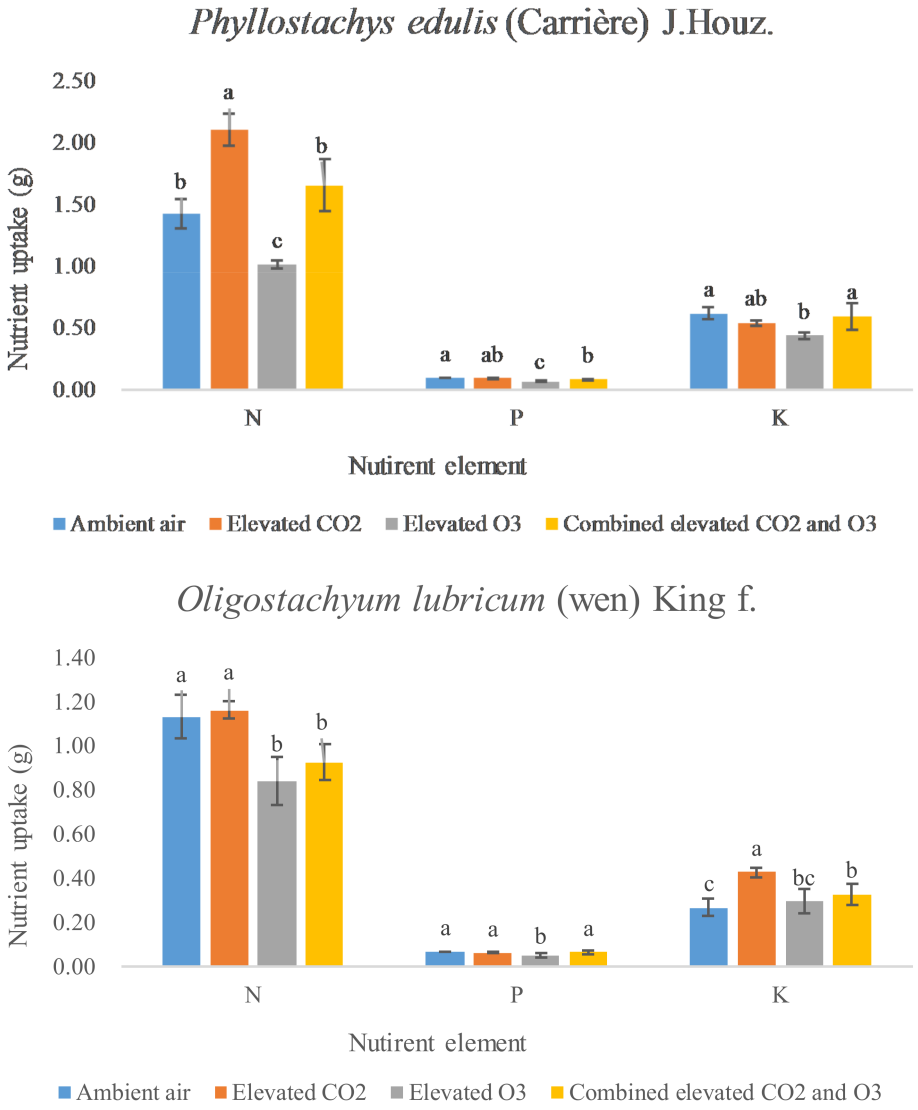

Figure 1. Leaf nutrient uptake (g) (mean ± s.d.) of *Phyllostachys edulis* and *Oligostachyum lubricum* in response to ambient air, elevated O_3, CO_2 and combined elevated O_3 and CO_2. Different letters indicate significant differences among treatments ($p < 0.05$).

4. Conclusions

Elevated O_3 decreased leaf biomass and nutrient uptake in both *P. edulis* and *O. lubricum* to some extent, while elevated CO_2 increased leaf biomass and uptake of some nutrients in both bamboo species. The combination of elevated CO_2 and O_3 did not change leaf biomass but altered certain nutrients in the two bamboo species. The differential response of *P. edulis* and *O. lubricum* to elevated CO_2 and O_3 or combined in terms of nutrient uptake indicated that nutrient management in bamboo forests under further climate change should consider differences between bamboo species (Figure 2). In addition, the nutrient (N, P, and K) supply in our experimental soil was sufficient to either maintain or increase nutrient uptake of both bamboo species under elevated CO_2 and O_3; however, the utilization of leaf nutrients was still relatively low, especially under elevated O_3. Therefore, further research on enhanced utilization of nutrients in bamboo is required for the development of effective strategies in nutrient (N, P, and K) management for sustainable management of bamboo ecosystems under climate change (e.g., elevated CO_2 and O_3).

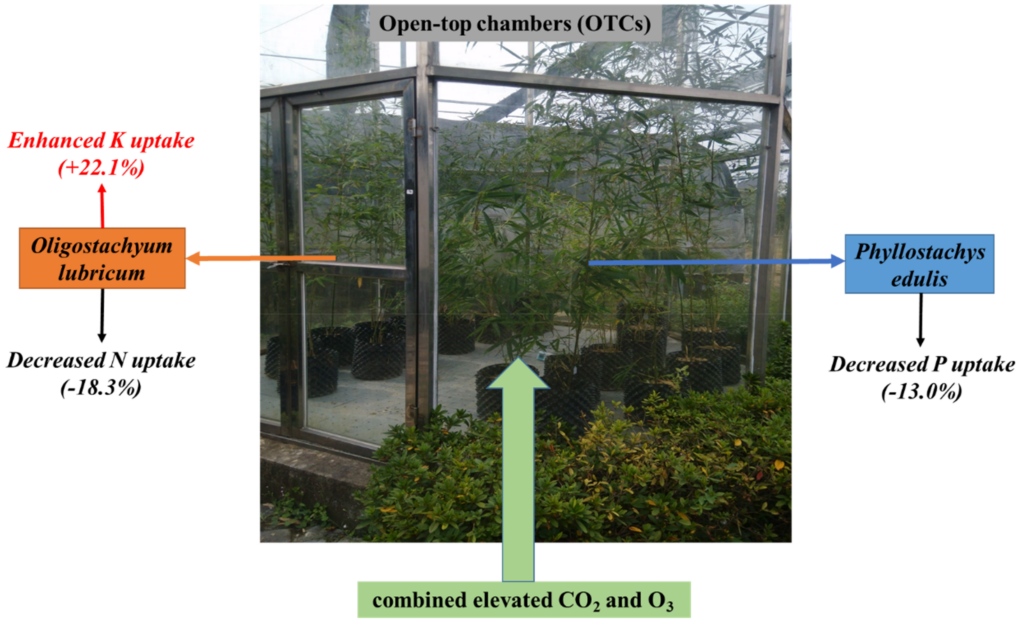

Figure 2. Significant change in P uptake of *Phyllostachys edulis* and N and K uptake of *Oligostachyum lubricum* under combined elevated O_3 and CO_2.

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Conflicts of Interest: The authors declare no competing financial interest.

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