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Elevated ozone affects C, N and P ecological stoichiometry and nutrient resorption of two poplar clones☆

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ABSTRACT

The effects of elevated ozone on C (carbon), N (nitrogen) and P (phosphorus) ecological stoichiometry and nutrient resorption in different organs including leaves, stems and roots were investigated in poplar clones 546 (*P. deltoides cv. '55/56'* × *P. deltoides* cv. 'Imperial') and 107 (*P. euramericana* cv. '74/76') with a different sensitivity to ozone. Plants were exposed to two ozone treatments, NF (non-filtered ambient air) and NF60 (NF with targeted ozone addition of 60 ppb), for 96 days in open top chambers (OTCs). Significant ozone effects on most variables of C, N and P ecological stoichiometry were found except for the C concentration and the N/P in different organs. Elevated ozone increased both N and P concentrations of individual organs while for C/N and C/P ratios a reduction was observed. On these variables, ozone had a greater effect for clone 546 than for clone 107. N concentrations of different leaf positions ranked in the order upper > middle > lower, showing that N was transferred from the lower senescent leaves to the upper ones. This was also indicative of N resorption processes, which increased under elevated ozone. N resorption of clone 546 was 4 times larger than that of clone 107 under ambient air (NF). However, elevated ozone (NF60) had no significant effect on P resorption for both poplar clones, suggesting that their growth was only limited by N, while available P in the soil was enough to sustain growth. Understanding ecological stoichiometric responses under ozone stress is crucial to predict future effects on ecological processes and biogeochemical cycles.

1. Introduction

Tropospheric ozone (O_3) is a secondary pollutant and a greenhouse gas originated from photochemical reactions of precursor gases, mainly nitrogen oxides and volatile organic compounds (Bytnerowicz et al., 2007; The Royal Society, 2008; Yamaji et al., 2008). In China, fast industrialization and urbanization have led to an increase in the emission of these precursors, and the tropospheric ozone also increased rapidly (Feng et al., 2015; Wang and Mauzerall, 2004). In a cropland area near Beijing, Yuan et al. (2015) found that the mean daily 8 h (9:00–17:00) ozone concentration was very high, approximately 71.3 ppb, and AOT40 (accumulated ozone concentration over an hourly threshold of 40 ppb) was 29.0 ppm h from June to September 2014. Elevated ozone concentrations cause a series of physiological and biochemical effects on trees, such as foliar visible injury (e.g., Feng et al., 2014), reduced photosynthesis (e.g., Feng et al., 2008; Wittig et al., 2007; Zhang et al., 2012), changed antioxidant capacity (e.g., Dai et al., 2017; Gao et al., 2016) and decreased biomass (e.g., Hu et al., 2015; Shang et al., 2017; Wittig et al., 2009). This decline in photosynthesis affects the carbon (C) acquisition and accumulation of plants (Matyssek and Sandermann, 2003; Nunn et al., 2006). Likewise, ozone affects the roots of plants and soil processes (e.g., Nikolova et al., 2010; Pregitzer et al., 2008), which could have indirectly effect on the uptake and allocation of nutrients such as nitrogen (N) and phosphorus (P) (Inclán et al., 2005; Piikki et al., 2007; Weigt et al., 2012; Zheng et al., 2013).

Ecological stoichiometry deals with the balance of multiple chemical elements under ecological interactions (Elser et al., 2000). Ecological stoichiometry, especially for key elements such as C, N

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and P, is used to analyze vegetation composition, ecosystem function, and nutrient limitation (Allen and Gillooly, 2009; Hessen et al., 2004). Carbon plays an important role in the plant, providing its structural basis and accounting for about 50% of a plant's dry mass (Ågren, 2008). N is the main component of proteins, chlorophylls, nucleic acids and many secondary plant metabolites (Luo et al., 2013). Further, leaf N content is related to plant photosynthetic performance, as it is an important component of Rubisco enzyme (LeBauer and Treseder, 2008), which catalyzes the initial step of photosynthesis by combining CO_2 with ribulose-1,5-bisphosphate (RuBP) and changes inorganic carbon to organic matter (Mizohata et al., 2002; Kroth, 2015). On the other hand, P is critical element in the production of phosphorus-rich ribosomes and rRNA to support the synthesis of N-rich proteins (Ågren, 2008). Therefore, these three macronutrients are very important to the plant, and are associated with each other. Understanding stoichiometric responses to environmental changes is essential for predicting the future biogeochemical cycles in terrestrial ecosystems (Yang et al., 2011). Over the past several decades, a large number of studies have been conducted on the C, N and P ecological stoichiometry changes of the plant due to global changes, such as elevated CO_2 concentrations, N deposition, warming, drought and their interaction (e.g., Huang et al., 2012; Jiroušek et al., 2011; Lü et al., 2012; Liu et al., 2013; Yuan and Chen, 2015). However, little research has been done so far on the effect of elevated ozone on C, N and P ecological stoichiometry (Broberg et al., 2015; Cao et al., 2016). Therefore, to study the effects of ozone on plants from an ecological stoichiometric perspective is highly relevant, in order to be able to predict ozone impacts on plant productivity, nutrient utilization of ecosystems, decomposition of litter and several other ecosystem processes under future global change scenarios (Elser et al., 2007; Güsewell and Gessner, 2009; Vitousek, 1982).

Nutrient resorption from senescing plant tissues is a critical strategy and ecological process on nutrient conservation (Lü et al., 2013). Elevated ozone accelerates senescence processes and leads eventually to leaf abscission. Leaf injury appears first in older leaves which suffered from a higher ozone dose (Gao et al., 2017). Depending on the cell injury, nutrient translocation from older to younger leaves is changed by elevated ozone, so ozone can affect the nutrient resorption of mobile nutrients. There are some studies on the effects of ozone on nutrient resorption, but their results are inconsistent (Gyu et al., 2015; Lindroth et al., 2001; Temple and Riechers, 1995). Therefore, this study can provide evidence for the effect of ozone on nutrient resorption, and it is necessary to better understand the impact of ozone on plant nutrient use.

There are more than 7.0 million km^2 of poplar plantation in China, ranking top one in the world (Fang, 2008). These plants grow under different soil conditions, N deposition and ozone pollution levels. Based on an inventory data set of 2384 soil profiles, the mean C/N, C/P and N/P ratios for the entire soil depth in China were 11.9, 61 and 5.2, respectively (Tian et al., 2010), and the total deposition fluxes of atmospheric N species were 2.9–83.3 kg N ha^{-1} yr^{-1} across the 43 monitoring sites in China (Xu et al., 2015). On the other hand, ozone levels are known to be high in some parts of China, especially in the North China Plain and Central/Western area (Feng et al., 2015) and previous studies have shown that sensitivity to this pollutant differs among different poplar clones (e.g., Shang et al., 2017). In order to meet the needs of a growing world for social-economic development and environmental protection, it is necessary to study the effects of environmental changes on poplar, including factors such as the increasing ozone levels. The present paper is oriented to address the latter question from the point of view of the ecological stoichiometry in this economically relevant tree.

The objectives of this study are (1) to determine C, N and P concentrations and ecological stoichiometry of the different leaf positions or the different organs under the elevated ozone for two poplar clones; (2) to investigate nutrients resorption under the elevated ozone for two poplar clones; (3) to compare the response of nutrients' variables (all indicators mentioned above) in the two different sensitive poplar clones to ozone.

2. Materials and methods

2.1. Ozone treatments and plant materials

The experiment was conducted in open-top chambers (OTCs) located at Yanqing (40°30′N, 116°E), northwest of Beijing, China. The region has a continental monsoon climate. Each OTC had octagonal base, 12.5 m^2 of growth space and 3.0 m of height, and was covered with toughened glass. Ozone was generated from pure oxygen by an ozone generator (HY003, Chuangcheng Co. Jinan, China), and mixed with air and blown into the OTC by a fan (1.1 kW, 1080 Pa, 19 m^3 min^{-1}, CZR, Fengda, China). Ozone concentrations inside the OTCs were continuously monitored using an ultraviolet (UV) absorption ozone analyzer (Model 49i; Thermo Scientific, Franklin, MA, USA).

The experiment had two ozone treatments: non-filtered ambient air (NF) and NF with targeted ozone addition of 60 ppb (NF60). The ozone fumigation experiment lasted 96 days from 26 June to 30 September 2016. The daily fumigation time was 10 h (from 08:00 to 18:00) except on rainy days. During the experiment, the plants were fully watered according to need to avoid drought stress. Each treatment had three replicated chambers. Based on our previous studies (Shang et al., 2017; Hu et al., 2015), two widely-planted hybrid poplar clones with similar leaf morphology and phenology but different sensitivity to ozone were selected: clones '546' (P. deltoides cv. '55/56' × P. deltoides cv. 'Imperial') and '107' (P. euramericana cv. '74/76'). There were 6 plants of each clone in each chamber. Rooted cuttings were cultivated into 20L circular plastic pots on April 10, 2016. Pots were filled with the soil that was taken from farmland at 0–10 cm depth, sieved out by a 0.3 mm pore mesh and then carefully mixed for homogeneity. Plants with the same height and base diameter were selected to move into the OTCs to adapt the condition of chambers before ozone fumigation.

The values of mean daytime ozone concentrations during the experiment in NF and NF60 treatments were 45.2 ppb and 89.9 ppb, respectively, and AOT40 (accumulated ozone exposure over an hourly threshold of 40 ppb) were 11.7 ppm h and 50.8 ppm h, respectively. The mean daytime ozone concentration of NF60 was 1.9 times that of NF, and AOT40 of NF60 was 4.4 times that of NF.

2.2. Sample collection and measurement

Plants were harvested when growth stopped, on 30 September. Two plants of each clone were randomly selected in each chamber for biomass determinations. They were separated into stems, roots, and leaves from different positions (upper, middle and lower). These organ materials were oven dried at 80 °C to constant mass, and weighed and ground using a ball mill. Total C and N concentrations of the plant components were measured with an elemental analyzer (Vario EL III, Elementar, Germany). To measure total P content, samples were first digested with nitric acid and hydrogen peroxide, and then the extracted solutions were analyzed by Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES, Prodigy, Leeman, USA).

2.3. Calculation

Nutrient resorption efficiency (NRE) was defined as the

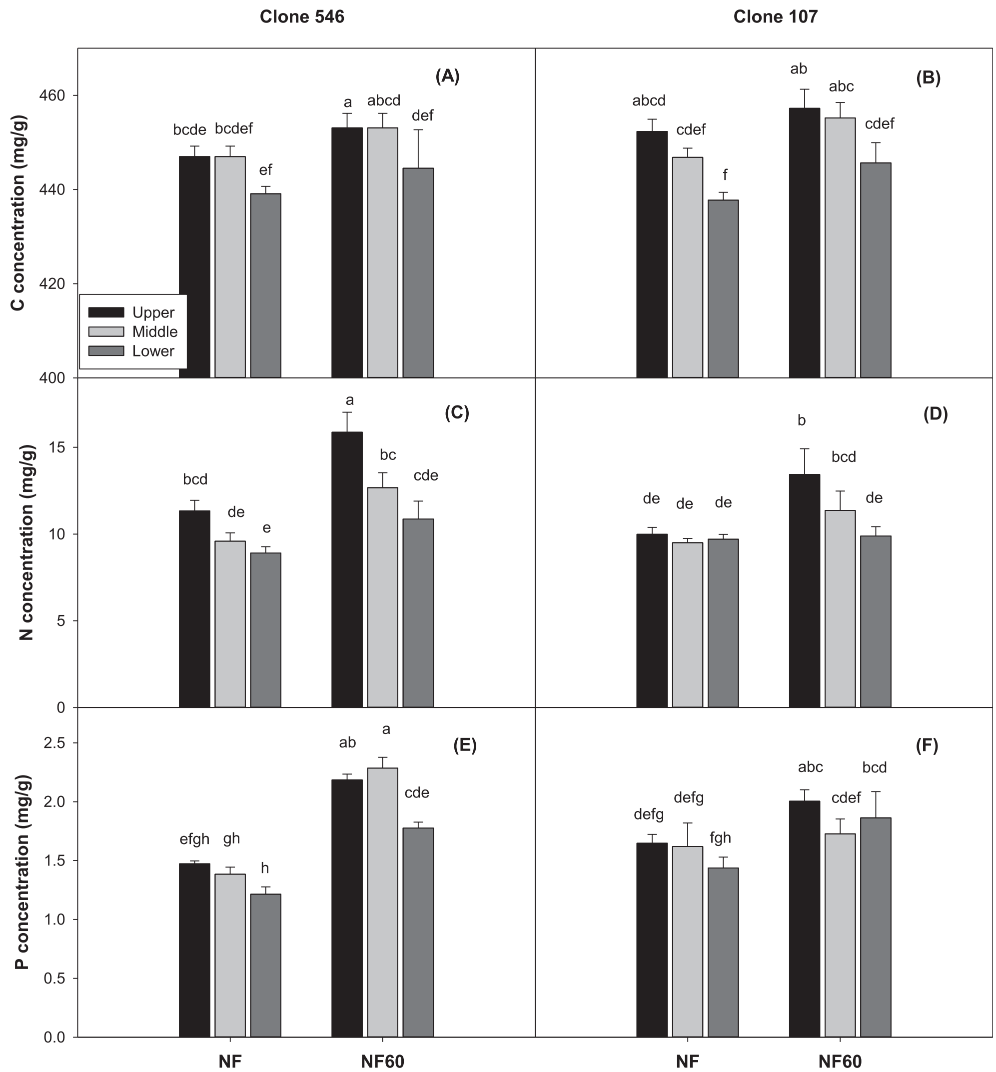

Fig. 1. Effects of ozone (NF and NF60), poplar clone (clone 546 and clone 107) and leaf position (upper, middle and lower) on carbon concentration, nitrogen concentration and phosphorus concentration. Different letters indicate significant differences among bars within each variable (mean ± SD, Tukey test, $P < 0.05$, n = 3).

proportion of the mature leaf nutrient pool that was resorbed (Lü et al., 2013; Zeng et al., 2016):

$NRE = (1 - Nutrient_{senesced}/Nutrient_{green}) \times 100\%$, where $Nutrient_{green}$ and $Nutrient_{senesced}$ are N or P concentrations of the upper leaves and the lower leaves, respectively. At the sampling time, the lower leaves of the plants were yellow and senescent, while their upper leaves were green and active.

2.4. Statistical analysis

Statistical analyses were performed using the JMP software (SAS Institute, Cary, NC, USA). Data from the two plants of each OTC were averaged. The statistical unit was the single OTC (n = 3 OTCs). The data of each dependent variable (C concentration, N concentration, P concentration, C/N, C/P and N/P) were subjected to three-way analysis of variance (ANOVA) with mixed linear model to test the effects of ozone, clone, organ (leaf position) and their interactions on all variables. The variables (N resorption, P resorption) were subjected to two-way analysis of variance (ANOVA) to test the effects of ozone, clone and their interactions. The Tukey's Honestly Significant Difference (HSD) test was applied to identify significant differences. Results were considered significant when $P < 0.05$. Data shown in figures are means ± SD.

3. Result

3.1. C, N and P concentrations and ecological stoichiometric ratios in different leaf positions

When comparing leaves of the same position, ozone tended to increase leaf C concentration, but differences were only significant for upper leaves of clone 546, in which NF60 significantly increased C concentration by 2.5% relative to NF (Fig. 1A and B). C concentrations of different leaf positions were not significantly different for clone 546. However, for clone 107, the C concentration of the upper leaf position was significantly higher than that of the lower leaf position in both ozone treatments (3.3% and 2.6% higher for NF and NF60, respectively) (Fig. 1A and B). There was no significant difference in C concentration between different clones, and interactions among ozone, clone and leaf position (Table 1).

When comparing leaves of the same position, in clone 546, ozone significantly increased the leaf N concentration in upper and middle positions, while in clone 107, it significantly increased only in the upper leaves. (Fig. 1C and D). N concentration of the leaf

Table 1
ANOVA results (*P* values) for main effects and interactions of ozone (NF and NF60), poplar clone (clone 546 and clone 107) and leaf position (upper, middle and lower) on carbon concentration (C), nitrogen concentration (N), phosphorus concentration (P), carbon to nitrogen ratio (C/N), carbon to phosphorus ratio (C/P) and nitrogen to phosphorus ratio (N/P).

	C	N	P	C/N	C/P	N/P
Ozone	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0045**
Clone	0.6627	**0.003**	0.9341	**0.0055**	0.1836	**0.0045**
Leaf position	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0001**	**0.0246**
Ozone × Clone	0.8105	**0.0194**	**<0.0001**	**0.0236**	**<0.0001**	**0.0109**
Ozone × Leaf position	0.8711	**0.0008**	0.8956	**0.0096**	0.396	**0.0146**
Ozone × Clone × Leaf position	0.2187	0.8626	**0.0049**	0.1116	0.1079	0.0601

Statistically significant effects are marked in bold ($P < 0.05$).

Table 2
ANOVA results (*P* values) for main effects and interactions of ozone (NF and NF60), poplar clone (clone 546 and clone 107) and organ (leaf, stem and root) on carbon concentration (C), nitrogen concentration (N), phosphorus concentration (P), carbon to nitrogen ratio (C/N), carbon to phosphorus ratio (C/P) and nitrogen to phosphorus ratio (N/P).

	C	N	P	C/N	C/P	N/P
Ozone	**0.0342**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.1005
Clone	0.0922	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0037**
Organ	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Ozone × Clone	0.3132	**0.0009**	**<0.0001**	**0.0272**	**0.0002**	**0.0298**
Ozone × Organ	**0.0101**	**0.0129**	0.2469	**0.014**	0.142	0.2371
Ozone × Clone × Organ	0.9769	0.5989	**0.0132**	0.3846	0.0932	**0.0002**

Statistically significant effects are marked in bold ($P < 0.05$).

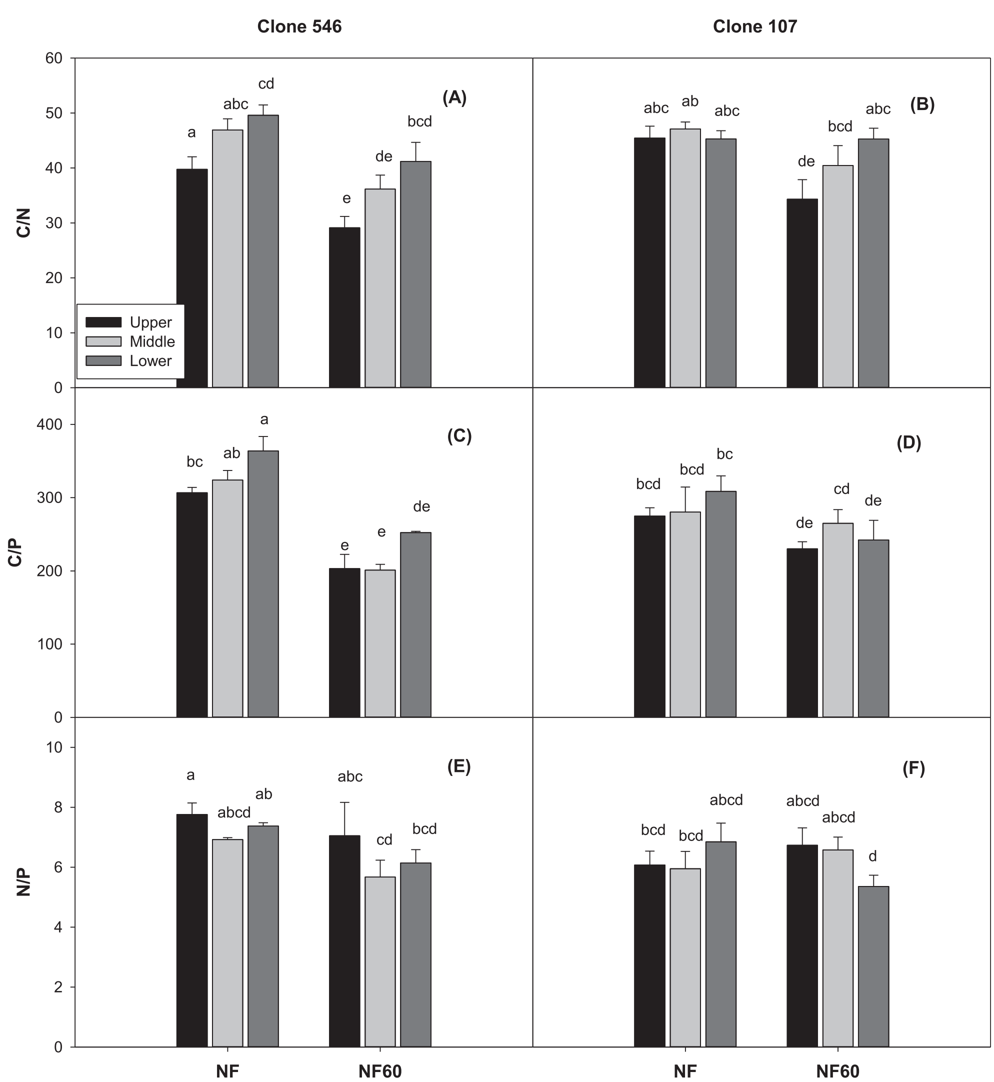

Fig. 2. Effects of ozone (NF and NF60), poplar clone (clone 546 and clone 107) and leaf position (upper, middle and lower) on carbon to nitrogen ratio (C/N), carbon to phosphorus ratio (C/P) and nitrogen to phosphorus ratio (N/P). Different letters indicate significant differences among bars within each variable (mean ± SD, Tukey test, $P < 0.05$, n = 3).

positions ranked in the order upper > middle > lower, with the N concentration of the upper leaves being significantly higher than that of the lower position in all cases except the NF treatment of clone 107 (Fig. 1C and D). The N concentration of clone 546 was 8.4% higher than that of clone 107, when averaged across ozone treatments and leaf positions (Fig. 1C and D and Table 2).

The effect of ozone on P concentration in leaves was similar to that on N concentration, as NF60 increased the P concentration by 53.5% and 18.9% relative to NF (when averaged across leaf positions) for clone 546 and clone 107, respectively. Ozone also had a greater effect on the leaf P concentration in clone 546 than in clone 107 (Fig. 1E and F), and within the same ozone treatment, P concentration of the upper leaf position was higher than that of the lower leaf position.

Ozone significantly affected C/N, C/P and N/P in leaves, and these variables also showed significant differences between the three leaf positions (Table 1). Relative to NF, the C/N and C/P in NF60 were reduced by 21.9% and 33.9% (average across leaf positions) in clone 546, and by 12.9% and 14.6% in clone 107, respectively (Fig. 2A–D). The leaf C/N of different leaf positions ranked in the order of lower > middle > upper, except for the NF treatment of clone 107 (Fig. 2A and B). The C/P of the upper leaves was larger than that of the lower leaves, while this effect was only significant in NF for clone 546. Across all the treatments and clones, leaf N/P varied from 4.9 to 8.0, with an average of 6.5. The leaf N/P for clone 546 showed a decreasing trend when exposed to elevated ozone, although differences among leaf positions were not significant. However, the decreasing trend did not apply to leaf N/P for clone 107 (Fig. 2E and F).

3.2. N and P resorption

Elevated ozone had a positive effect on N resorption, although this positive effect was only significant for clone 107. Compared to NF, N resorption in NF60 increased by 47.9% and 516.1% for clone 546 and clone 107, respectively (Fig. 3A). The N resorption of clone 546 was 4 times larger than that of clone 107 in NF, and interaction between ozone and clones was close to be significant (Fig. 3A). Elevated ozone had no significant effect on P resorption. P resorption of clone 546 was 92.3% higher than that of Poplar 107 when averaged across ozone treatments (Fig. 3B).

3.3. C, N and P concentrations and ecological stoichiometric ratios in different organs

The C concentration of the stems was the highest, and the C concentration of the leaves and roots were similar. There were no significant differences between the C concentrations of the two poplar clones (Fig. 4A and B and Table 2). The separate analysis with the C concentration of each organ showed that ozone had no significant effect on C concentration (Fig. 4A and B). The N concentration of the leaves was 2.1 and 2.0 times that of the stems and roots (average across clones and ozone treatments), respectively (Fig. 4C and D). Elevated ozone had a significantly positive effect on the leaf N concentration, while effects on the N concentration of stems and roots were not significant, except the stems of clone 546. The N concentration of clone 546 was 17.1% larger than that of clone 107 when averaged across ozone treatments and organs (Fig. 4C and D). P concentration in the two poplar clones generally showed an increasing trend in response to elevated ozone, while this positive effect was significant in all organs of clone 546 and in roots of clone 107. The P concentration of different organs ranked in the order leaf > root > stem. Similar to N concentration, the P concentration of clone 546 was 12.6% higher than that of clone 107 when averaged across ozone treatments and organs (Fig. 4E and F).

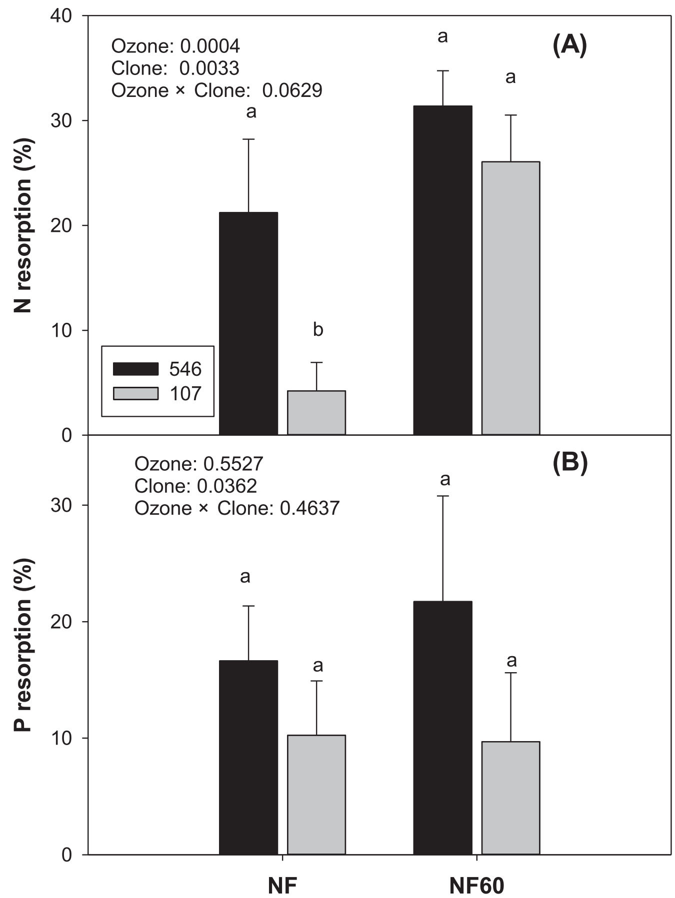

Fig. 3. Effects of ozone (NF and NF60) and poplar clone (clone 546 and clone 107) on nitrogen resorption and phosphorus resorption. Different letters indicate significant differences among bars within each variable (mean ± SD, Tukey test, $P < 0.05$, n = 3).

The C/N in all organs of the two clones showed a decreasing trend in response to elevated ozone, although statistically significant differences were only observed for stems and roots of clone 546. The C/N of stems and roots was higher than that of leaves (Fig. 5A and B). Elevated ozone had a significantly negative effect on the C/P in all organs for clone 546. Although the C/P of clone 107 also exhibited the same trend, differences between both ozone treatments were significant only for the stems (Fig. 5C and D). Elevated ozone had no significant effect on the N/P in any of the organs ($P = 0.1005$, Table 2). The N/P of leaves was 1.8 times and 2.2 times that of the stems and roots (averaged across ozone treatments and clones), respectively (Fig. 5E and F).

4. Discussion

4.1. Effects of elevated ozone on C, N and P ecological stoichiometry

In this study, the ranges of leaf C, N and P concentrations were 436.24–461.78 mg/g, 8.59–16.96 mg/g and 1.17–2.37 mg/g for all poplar plants, respectively. The C concentrations were relatively stable in different treatments. Considering the average values, leaf N concentration (11.09 mg/g) was clearly lower than that of China's (20.2 mg/g) and the global floras (20.6 mg/g), but leaf P concentration (1.72 mg/g) was higher than that of China's flora (1.46 mg/g) and was similar to the global flora (1.77 mg/g) (Han et al., 2005; Reich and Oleksyn, 2004). Leaf N/P ratio could be indicative of plant growth limitations by N or by P, or by both. Koerselman and

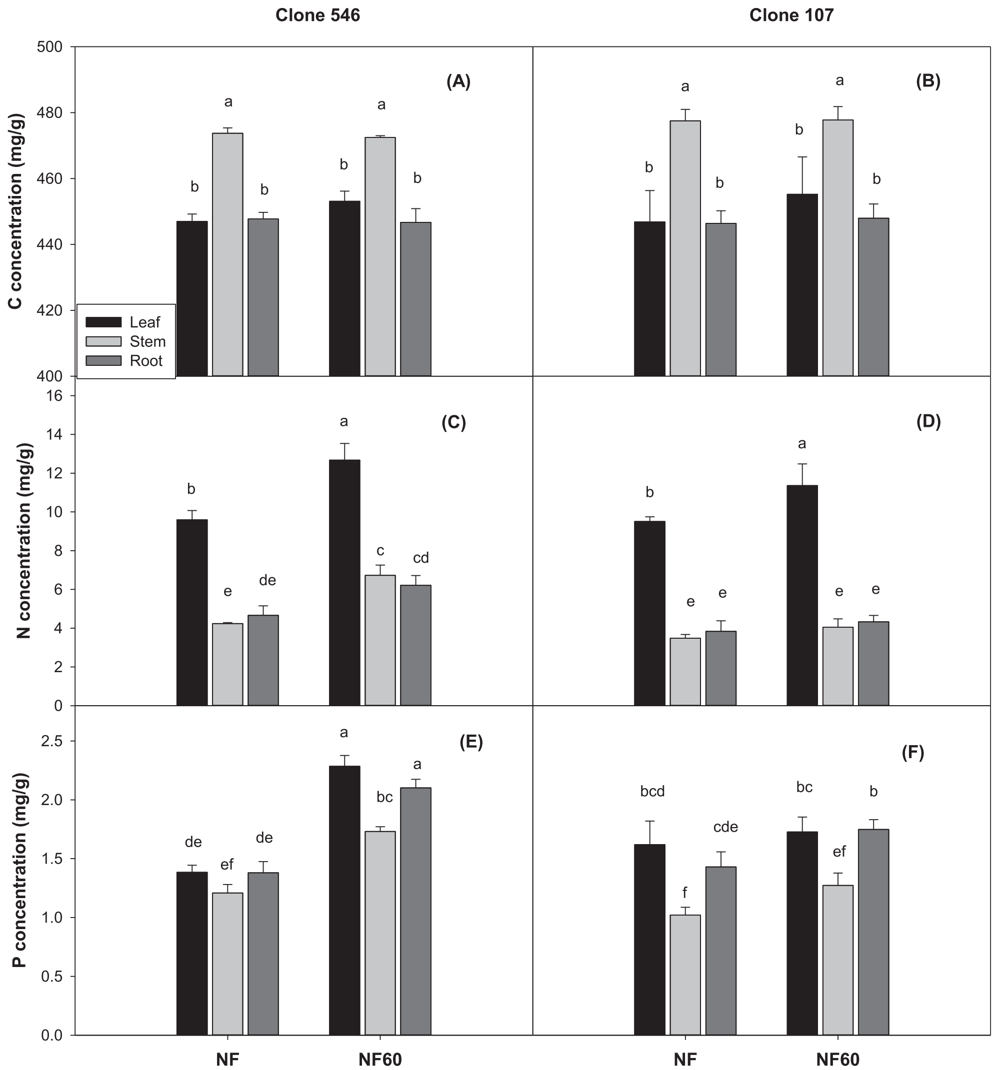

Fig. 4. Effects of ozone (NF and NF60), poplar clone (clone 546 and clone 107) and organ (leaf, stem and root) on carbon concentration, nitrogen concentration and phosphorus concentration. Different letters indicate significant differences among bars within each variable (mean ± SD, Tukey test, $P < 0.05$, n = 3).

Meuleman (1996) showed that the leaf N/P > 16 indicated P limitation, whereas leaf N/P < 14 was indicative of N limitation. When leaf N/P was between 14 and 16, either N or P could be limiting, and plant growth was co-limited by N and P together. In this study, the range of leaf N/P was 4.93–8.02, and the average leaf N/P across all ozone treatments and poplar clones was 6.54, which was far less than 14. Therefore, under our experimental conditions the growth of the two poplar clones was limited by N but not by P, which is consistent with a lower leaf N concentrations and N/P rations in comparison to China's and of the global floras mean values. The fact that poplar is a fast-growing plant and has low N/P ratio is on the other hand consistent with the growth rate hypothesis that faster growing plants would have lower leaf N/P ratios due to a high requirement of P-rich RNA relative to N-rich proteins (Matzek and Vitousek, 2009).

Many studies have reported that the concentrations of the plant elements were increased by ozone (e.g., Cao et al., 2016; Fangmeier et al., 2002; Wang et al., 2014; Zhang et al., 2014; Zheng et al., 2013; Zhuang et al., 2017). In a meta-analysis of 143 independent observations of leaves grown in elevated ozone (61 ppb relative to ambient ozone concentration of 34 ppb), nitrogen concentration was also significantly increased by 5% (Wittig et al., 2009). In the present study, when comparing leaves of the same position, we found that ozone tended to increase leaf C, N and P concentrations for the two poplar clones, and that most of the increases in N and P concentrations were statistically significant (Fig. 1). Increasing N concentration may be a plant response in order to enhance the defense capability against ozone stress and can be an adaptive strategy for plants against this pollutant (Cao et al., 2016). Dumont et al. (2014) suggested an important remobilization of amino acids in response to ozone, in order to provide energy and antioxidants to limit negative effects. N is an important component of the proteins, including functional proteins, structural proteins and photosynthetic proteins, and more N allocation to structural proteins is needed for stronger structural defenses under polluted stress (Guan and Wen, 2011). As P is the main component element of ribosomal RNA, which is used to synthesize N-rich proteins (Ågren, 2008), consistently, P concentration increased at elevated ozone levels in our experiment. On the other hand, a large number of studies have shown that the effect of ozone and carbon dioxide on dry matter and C assimilation of plants is the opposite. Carbon dioxide tends to increase dry matter or carbon assimilation, which may lead to reduce nutrient concentration (dilution effect); while ozone reduces plant biomass and increase the nutrient

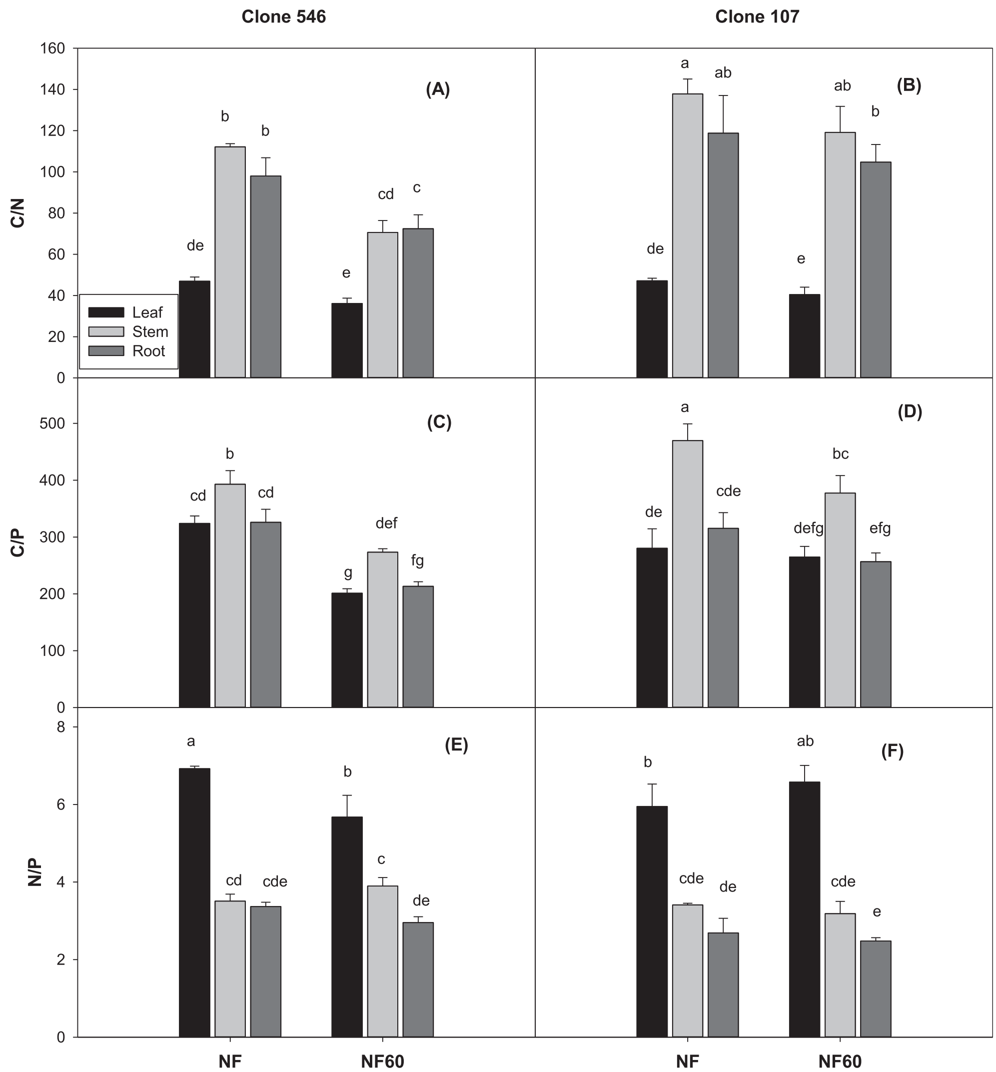

Fig. 5. Effects of ozone (NF and NF60), poplar clone (clone 546 and clone 107) and organ (leaf, stem and root) on carbon to nitrogen ratio (C/N), carbon to phosphorus ratio (C/P) and nitrogen to phosphorus ratio (N/P). Different letters indicate significant differences among bars within each variable (mean ± SD, Tukey test, $P < 0.05$, n = 3).

concentration (enrichment effect) (Wang et al., 2014). At the same time, stems and roots responses to ozone in each clone were consistent with changes observed in leaves, suggesting that leaves, stems and roots were strongly linked in nutrient status. Leaves and roots are the main plant organs responsible for carbon assimilation and nutrient uptake, respectively, while stems are important intermediaries for linking leaves to roots (Zhao et al., 2016). Given that the effect of ozone on the C, N and P concentration in different organs of clone 546 was greater than in clone 107, this result suggests that clone 546 was more sensitive to this pollutant than clone 107.

Ecological stoichiometry ratios (C/N, C/P and N/P) are considered important and sensitive indexes that can be related to ecological processes such as productivity (Elser et al., 2010), rates of herbivory (Pérez-Harguindeguy et al., 2003), litter decomposition (Esmeijer-Liu et al., 2009), or overall ecosystem dynamics (e.g. Sterner and Elser, 2002). Relative to NF, the C/N and C/P in NF60 were reduced in all leaf positions for both poplar clones (Fig. 2A–D), and elevated ozone had a negative effect on the C/N and C/P in all organs for both poplar clones (Fig. 5A–D). The C/N and C/P could reflect the plant N and P use efficiencies, respectively (where the higher C/N and C/P can reflect more C fixation per unit of N and P, respectively) (Dijkstra et al., 2016). Elevated ozone significantly reduced the C/N and C/P of two poplar clones in this study, suggesting that the nutrient use efficiency of plants was reduced by elevated ozone. Furthermore, C/N affects litter decomposition rates (Ågren et al., 2013). Esmeijer-Liu et al. (2009) showed that a lower C/N in *Betula pendula* may increase the litter decomposition rate during early decomposition stages, and it may have the opposite effect during later decomposition stages. Therefore, the effect of ozone on leaf C/N may lead to a change in the decomposition rate of litter, thus indirectly affecting nutrient cycling, primary production, carbon storage, and soil organic matter formation (Hobbie and Vitousek, 2000; Huysen et al., 2016). On the other hand, the N/P provides information on nutrient limitations for plant growth (Koerselman and Meuleman, 1996). In this study, elevated ozone had no significant effect on the N/P for both poplar clones ($P = 0.1005$, Table 2). This is consistent with other observations that N and P were strongly correlated, mainly due to the fact that N-rich proteins are synthesized by P-rich ribosomes RNA (Ågren, 2008), and it is also indicative of homeostasis of plants, i.e. plants try to keep the state of the N/P ratio less variable under environmental stress (Persson et al., 2010). To maintain the poplar N/P ratio homoeostasis under ozone stress and N-limited conditions, the plants could increase the supply of N by increasing N resorption efficiency (Fig. 3).

4.2. Effects of elevated ozone on nutrient resorption

Nutrient resorption from senescent leaves is a process that makes plants to store or to directly use such nutrients, making them less dependent on current soil nutrient availability. Nutrient resorption affects litter chemistry and litter decomposition and therefore has important consequences for nutrient cycling in ecosystems (Aerts and Chapin, 2000; Lü et al., 2013). So far, several studies have investigated the response of plant nutrient resorption in relation to ozone exposure, however, with inconsistent results. It has been reported that exposure to ozone reduced plant nutrient resorption (Gyu et al., 2015; Uddling et al., 2005), had no significant effect on it (Baker and Allen, 1995; Lindroth et al., 2001), or increased it (Temple and Riechers, 1995). The mentioned inconsistencies are probably related to the different nutrient availability in the soil and different ozone treatments used in these experiments, but probably also to plant species-specific differences in their response to ozone. In the present study, we found that the N concentrations of the upper leaf position were significantly higher than those of the lower leaf position under NF60 (Fig. 1). N resorption in the two poplar clones showed an increasing trend in response to elevated ozone (Fig. 3A). Increased N resorption may be due to accelerated senescence of the lower leaves caused by ozone, with more N transferred to the upper and new leaves. This result is fully consistent with Schmutz et al. (1995), who showed that ozone exposure caused a significant increase of N concentration in leaves and that N concentration was lower in the order leaves than in the top leaves under a regime of low soil N, but on the contrary retranslocation of N prior to abscission was very low in a regime of high soil N. This may be explained by a compensatory effect (Brendley and Pell, 1998). For example, Bielenberg et al. (2002) showed N remobilized during ozone-induced accelerated senescence was incorporated into young leaves in hybrid poplar, because older leaves were exposed to higher cumulative ozone effects. In the present experiment, responses differed between the two clones. Under ambient air conditions (NF), the N concentration of the upper leaf position was significantly higher than that of the lower leaf position for clone 546, while no significant differences were observed for clone 107 (Fig. 1C and D). N resorption was also clone-specific: under ambient ozone levels (NF), N resorption in clone 107 was significantly lower than in clone 546. These results further support the previous conclusion that clone 107 was more tolerant to ozone than clone 546 (Shang et al., 2017). It is therefore expected that under moderate ozone pollution conditions N resorption will be more altered in clone 546 than in clone 107. However, under elevated ozone (NF60), N resorption also increased in clone 546, suggesting that under high ozone pollution conditions N resorption effects will be important for both clones. The resorption of nutrients from senescing leaves represents an important source of usable N, which could reduce the N uptake failing to meet the demand for new growth of the plants (Bielenberg et al., 2002). In our study, ozone increased N resorption, hence it is expected that ozone-exposed poplar plants would require less N from the soil for new growth. Unlike N resorption, elevated ozone had no significant effect on P resorption for both poplar clones (Fig. 3B). The responses of N resorption and P resorption to ozone were therefore different. As previously mentioned, the main explanation is that the growth of the two poplar clones was only limited by N and not by P. Landolt et al. (1997) also found the role of fertilization as an important modifier of ozone-induced effects at the plant biochemical level. Therefore, it can be concluded that interaction of ozone with nutrient resorption processes of plants will be importantly modulated not only by the ozone levels but also by the nutrient availability in the soil.

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