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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 Beijng, 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