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Effects of elevated ozone concentration and nitrogen addition on ammonia stomatal compensation point in a poplar clone[☆]

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The stomatal compensation point of ammonia (χ_s) is a key factor controlling plant-atmosphere NH_3 exchange, which is dependent on the nitrogen (N) supply and varies among plant species. However, knowledge gaps remain concerning the effects of elevated atmospheric N deposition and ozone (O_3) on χ_s for forest species, resulting in large uncertainties in the parameterizations of NH_3 incorporated into atmospheric chemistry and transport models (CTMs). Here, we present leaf-scale measurements of χ_s for hybrid poplar clone '546' (*Populusdeltoides cv. 55/56 x P. deltoides cv. Imperial*) growing in two N treatments (N0, no N added; N50, 50 kg N ha^{-1} yr^{-1} urea fertilizer added) and two O_3 treatments (CF, charcoal-filtered air; E-O_3, non-filtered air plus 40 ppb) for 105 days. Our results showed that χ_s was significantly reduced by E-O_3 (41%) and elevated N (19%). The interaction of N and O_3 was significant, and N can mitigate the negative effects of O_3 on χ_s. Elevated O_3 significantly reduced the light-saturated photosynthetic rate (A_{sat}) and chlorophyll (Chl) content and significantly increased intercellular CO_2 concentrations (Ci), but had no significant effect on stomatal conductance (g_s). By contrast, elevated N did not significantly affect all measured photosynthetic parameters. Overall, χ_s was significantly and positively correlated with A_{sat}, g_s and Chl, whereas a significant and negative relationship was observed between χ_s and *Ci*. Our results suggest that O_3-induced changes in A_{sat}, *Ci* and Chl may affect χ_s. Our findings provide a scientific basis for optimizing parameterizations of χ_s in CTMs in response to environmental change factors (i.e., elevated N deposition and/or O_3) in the future.

1. Introduction

Atmospheric ammonia (NH_3) is the primary alkaline trace gas in the atmosphere and plays a vital role in many biogeochemical and atmospheric processes (Behera et al., 2013). It neutralizes atmospheric acids to yield ammonium (NH_4^+) aerosols, which results in increased mass loadings of fine atmospheric particulate matter ($PM_{2.5}$, aerodynamic diameter ≤ 2.5) (Xu et al., 2015, 2016, 2017), thereby reducing visibility and adversely impacting ecosystem and human health (Gu et al., 2014). By contrast, atmospheric deposition of reduced N (NH_3 and NH_4^+) can cause soil acidification (Du et al., 2015), eutrophication (Pakeman et al., 2016) and loss of biodiversity (Erisman et al., 2007) in sensitive ecosystems.

Plants can be either a source or a sink of atmospheric NH_3, depending on the difference between atmospheric NH_3 concentration and the so-called canopy NH_3 compensation point (Massad et al., 2010). As a major component of canopy NH_3 compensation point, ammonia stomatal compensation point (χ_s) is defined as the atmospheric NH_3 concentration for which there is no exchange between the leaf and the atmosphere under dry conditions

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(Flechard et al., 2013). Theoretically, χ_s is also the gaseous NH_3 concentration in the leaf sub-stomatal cavity that is in equilibrium with ammonium concentration in the apoplast (Husted and Schjoerring, 1995). It plays a vital role in controlling the magnitude and the direction of NH_3 exchange between the canopy and the atmosphere (Sutton et al., 1995). Specifically, if atmospheric NH_3 concentrations exceed χ_s then NH_3 deposition from the atmosphere to vegetation will occur, while with atmospheric NH_3 concentrations below χ_s, there will be a net emission of NH_3 by plants. χ_s depends directly on the plant nitrogen (N) status, developmental stage, and environmental conditions (e.g., N fertilization), with larger values generally observed under conditions of high N supply to the soil-plant system and at senescence (Massad et al., 2009; Schjoerring et al., 1998).

χ_s can be derived from simultaneous measurement of vertical fluxes and concentrations of NH_3 by using micrometeorological flux techniques over large fields (Hansen et al., 2017; Nemitz et al., 2001; Personne et al., 2015), or in chambers by finding the concentration at which the total flux is zero (Hill et al., 2001; Massad et al., 2009; Wang et al., 2011). In addition, the bioassay approach has also been developed for assessing χ_s and it is based on the determination of the leaf apoplastic NH_4^+ concentration and pH by mean of apoplast extraction (Husted and Schjoerring, 1995). These two methods are complementary. Apoplast extraction is more appropriate for leaf and cell scale processes whereas chamber/micrometeorological measurements tend to be more appropriate for flux measurements at an entire plant/canopy scale (Massad et al., 2009; Sutton et al., 2009).

Forests represent a major uncertainty in quantification of regional NH_3 fluxes and parameterization of bi-directional NH_3 exchange in atmospheric chemistry and transport models (CTMs) such as AURAMS (A Unified Regional Air-quality Modeling System, Zhang et al., 2010) and CMAQ (Community Multiscale Air-Quality Modeling System, Fu et al., 2015). This is not only due to the large land area of forests but also because of the wide range of forest types and management practices. In conditions of bi-directional NH_3 exchange, forests are of particular interest. For example, temperate deciduous forests are potentially a natural source of NH_3 (Hansen et al., 2013, 2017; Neirynck and Ceulemans, 2008), leading to impact of forests on the atmospheric NH_3 level. In contrast, tropical humid forest and temperate coniferous forest can acts as net NH_3 sinks (Bertolini et al., 2016; Duyzer et al., 2005), resulting in the impact of atmospheric NH_3 on the ecological functioning of forests.

χ_s is one of the key parameters for parameterizations of NH_3 incorporated into CTMs (Massad et al., 2010). Based on published data on χ_s in relation to different plant species, growth stages, N supply etc., Massad et al. (2010) derived a new operational parameterization for integrating bi-directional NH_3 exchange into CTMs, However, uncertainties still exist for its parameterization, partially due to the following two drawbacks: 1) measurement of χ_s for different ecosystems, specific to forests, is very sparse and is only considered for a single growth stage of plants; 2) the relationships established between N fertilizer application and χ_s remain uncertain due to a lack of co-measurement of χ_s with different organic fertilizer (manure, slurry and urea) application rates. In addition, the actual parameterization of NH_3 exchange models requires large databases accounting for the variability of χ_s. To our knowledge, there is only one process-based model developed by Riedo et al. (2002) for grasslands which accounts for the plants N nutrition and growth stage in calculating χ_s. However, as χ_s is not only driven by N input to the ecosystem and plant growth stage, it may be a strongly regulated process that depends on environmental changes such as elevated ground-level O_3.

Ground-level O_3 can be considered as the most phytotoxic air pollutant due to visible injury to a variety of plants and the rising concentrations in different regions of the world (Cooper et al., 2014; Feng et al., 2014). It affects photosynthetic parameters (e.g., stomatal conductance (g_s), light-saturated CO_2 assimilation rate (A_{sat}), intercellular CO_2 concentration (Ci) and chlorophyll (Chl) content) of forest species to a varying extent (Li et al., 2017). In contrast, atmospheric N deposition represents an important nutrient from the environment for plants (Liu et al., 2010). In N-limited ecosystems (e.g., forest) N deposition might enhance photosynthetic activity (i.e. photosynthetic enzyme activity) and net primary productivity (N fertilization effect) (Liu et al., 2011). In the context of an N-saturation ecosystem, however, N deposition may render plants more susceptible to pollutants and natural environmental stressors (Cardoso-Vilhena and Barnes, 2001). That ozone and N addition induced changes in the growth and metabolism of plants may affect the χ_s of plants due to a clear link between χ_s and photosynthetic parameters. For example, Mattsson and Schjoerring (1996) showed that leaf NH_3 emission from *Hordeum vulgare L. cv. Golf* plants showed a consistent diurnal pattern with photosynthesis but the opposite trend with g_s. Furthermore, Schjoerring et al. (1998) found that NH_3 emission from leaves of *Brassica napus L.* plants increased with Chl degradation. Such results demonstrate that there are corresponding influences of those parameters on χ_s, which positively impacts leaf NH_3 emission (Massad et al., 2010). In this context, understanding the effects of elevated O_3 and N as well as their influence on the plant physiological parameters controlling χ_s is important for prediction of χ_s. Unfortunately, the relevant information for different forest species is still unknown, significantly restricting the optimization of the χ_s parameter in CTMs.

Poplars are widespread deciduous plants in temperate and boreal forests. In China, poplar is a native species, with a cultivated area of more than 10 million ha (Yuan et al., 2016). We designed an experiment to investigate for the first time the individual effects of N addition (with controlled application of urea) and elevated O_3 and their interactions on χ_s of hybrid poplar clone '546' (*Populusdeltoides cv. 55/56 x P. deltoides cv. Imperial*). In addition, we estimated the relationships between photosynthetic parameters (g_s, A_{sat}, Ci and Chl) and χ_s, and discuss how N and O_3, as well as their-driven modifications in the aforementioned photosynthetic parameters, respectively affect χ_s.

2. Materials and methods

2.1. Experimental site and plant materials

The study was conducted in Yanqing Field and Experimental Basin, Tangjiapu village, Yanqing District (40°29′N, 115°59′E, 500 m.a.s.l.), about 74 km northwest of Beijing city centre. When the winds come from the north or northwest, this basin is located upwind of the Beijing urban area. The site is characterized by a continental monsoon climate, with mean annual temperature of 9 °C and mean annual precipitation of 400–500 mm.

Rooted cuttings of hybrid poplar clone '546' (*Populusdeltoides cv. 55/56 x P. deltoides cv. Imperial*) were planted on 7 May 2017 and cultivated in individual 20 L circular plastic pots when they were about 31 days old. The plots were filled with local light loamy farmland soil, which was excavated at 0–10 cm depth, sieved out by a 0.3 mm pore mesh and then thoroughly mixed for homogeneity. Plants with similar height (ca. 27 cm) and basal stem diameter (ca. 4.5 mm) were selected and pre-adapted to open-top chambers (OTCs, octagonal base, 12.5 m^2 of growth space and 3.0 m height, covered with toughened glass) for 10 days before O_3 fumigation. All seedlings were manually irrigated at 1–2 day intervals in order to keep moisture at a similar level to that in farm fields.