



# Leaf traits and photosynthetic responses of *Betula pendula* saplings to a range of ground-level ozone concentrations at a range of nitrogen loads



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## ABSTRACT

Ground-level ozone ( $O_3$ ) concentrations and atmospheric nitrogen (N) deposition rates have increased strongly since the 1950s. Rising ground-level  $O_3$  concentrations and atmospheric N deposition both affect plant physiology and growth, however, impacts have often been studied in isolation rather than in combination. In addition, studies are often limited to a control treatment and one or two elevated levels of ozone and/or nitrogen supply. In the current study, three-year old *Betula pendula* saplings were exposed to seven different  $O_3$  profiles (24 h mean  $O_3$  concentration of 36–68 ppb in 2013, with peaks up to an average of 105 ppb) in precision-controlled hemispherical glasshouses (solar domes) and four different N loads (10, 30, 50 or 70 kg N ha<sup>-1</sup> y<sup>-1</sup>) in 2012 and 2013. Here we report on the effects of enhanced  $O_3$  concentrations and N load on leaf traits and gas exchange in leaves of varying age and developmental stage in 2013. The response of leaf traits to  $O_3$  (but not N) vary with leaf developmental stage. For example, elevated  $O_3$  did not affect the chlorophyll content of the youngest fully expanded leaf, but it reduced the chlorophyll content and photosynthetic parameters in aging leaves, relatively more so later than earlier in the growing season. Elevated  $O_3$  enhanced the N content of senesced leaves prior to leaf fall, potentially affecting subsequent N cycling in the soil. Enhanced N generally stimulated the chlorophyll content and photosynthetic capacity. Whilst elevated  $O_3$  reduced the light-saturated rate of photosynthesis ( $A_{sat}$ ) in aging leaves, it did not affect stomatal conductance ( $g_s$ ). This suggests that photosynthesis and  $g_s$  are not closely coupled at elevated  $O_3$  under-light saturating conditions. We did not observe any interactions between  $O_3$  and N regarding photosynthetic parameters ( $V_{c,max}$ ,  $J_{max}$ ,  $A_{sat}$ ), chlorophyll content,  $g_s$ , N content in senesced leaves and leaf number. Hence, the sensitivity of these leaf traits to  $O_3$  in young silver birch trees is neither reduced nor enhanced by N load.

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## 1. Introduction

Tropospheric ozone ( $O_3$ ) concentrations have been increasing from a background of ca. 10–15 ppb in the early 20th century, due to increased emissions of  $O_3$  precursors from anthropogenic sources

**Abbreviations:**  $A_{sat}$ , light-saturated rate of photosynthesis at ambient  $CO_2$  (390 ppm); A/Ci curve, plot of net photosynthesis (A) against leaf internal  $CO_2$  concentration (Ci); AICc, Akaike Information Criterion, corrected for small sample size;  $g_s$ , stomatal conductance; ID, identity;  $J_{max}$ , maximum rate of electron transport; LMM, linear mixed model; ppb, parts per billion;  $V_{c,max}$ , maximum rate of carboxylation.

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(Cooper et al., 2014; Royal Society, 2008; Solberg et al., 2005; Volz and Kley, 1988). In Europe, background concentrations have roughly doubled between 1950 and 2000, followed by a decade with no further rise or even a reduction at some sites (Cooper et al., 2014; Parrish et al., 2012). Present day annual average background concentrations are levelling off at ca. 30–40 ppb in Europe and North America, (Cooper et al., 2014; Royal Society, 2008), but are still rising significantly in East Asia (Cooper et al., 2014). In addition, atmospheric concentration and deposition of reactive nitrogen (N) have increased strongly since the 1950s with the application of the Haber-Bosch process to produce N fertilizers on an industrial scale (Sutton et al., 2011). Despite the rise in both ground-level  $O_3$  concentrations and atmospheric N deposition since the 1950s, impacts on vegetation have often been studied in isolation rather than in a combination of both factors. The two pollutants are closely inter-

linked as a major pathway for the formation of tropospheric O<sub>3</sub> is the photochemical reaction with N oxides (Royal Society, 2008).

Generally, O<sub>3</sub> tends to have a negative impact on sensitive plant species, resulting in a decline in photosynthesis, biomass production or crop yield, and accelerated senescence (Ainsworth et al., 2012). A meta-analysis by Wittig et al. (2007) showed that the increase in O<sub>3</sub> since the industrial revolution has been responsible for a reduction in photosynthesis of approximately 11% in trees, which reduced tree productivity by approximately 7% (Wittig et al., 2009). Further reductions were observed with a rise in O<sub>3</sub> concentration above the current ambient level (Wittig et al., 2007, 2009). Partly due to the successful implementation of air pollution abatement policies in Europe, reductions in O<sub>3</sub> precursor emissions have resulted in a decline in peak O<sub>3</sub> concentrations in the summer in recent years at some sites across Europe (Simpson et al., 2014; Tørseth et al., 2012). However, mean annual O<sub>3</sub> concentrations have hardly changed in recent decades (EMEP, 2016) due to a rise in the frequency of low-range O<sub>3</sub> concentrations (Simpson et al., 2014). Background O<sub>3</sub> concentrations are currently at levels where they chronically affect sensitive plant species (Mills et al., 2011a).

In contrast, N tends to have a fertilising effect on plant growth and photosynthesis in areas where N is a limiting nutrient. However, above the critical load or level, the impact of N on sensitive species will become negative in most species (Bobbink and Hettelingh, 2011; Cape et al., 2009). For example, forest observations in Switzerland suggested an increase in phosphorus limitation with increasing N deposition, resulting in a decline in growth in *Fagus sylvatica* (Braun et al., 2010). N pollution is now a major threat to terrestrial biodiversity (Bobbink et al., 2010; Dise et al., 2011).

Relatively few studies have investigated the combined impacts of both O<sub>3</sub> and N on vegetation at realistic ozone concentrations (Mills et al., 2016). Evidence suggests that O<sub>3</sub> and N can have both synergistic and antagonistic effects on tree species. Pääkkönen and Holopainen (1995) and Landolt et al. (1997) showed that high N supply ameliorates the negative impact of O<sub>3</sub> in *Betula pendula*. Similar responses were reported for *Larix kaempferi* (Watanabe et al., 2006), *Populus tremula* × *Populus tremuloides* (Häikiö et al., 2007) and *Quercus kelloggii* (Handley and Grulke, 2008). However, enhanced N supply increased growth sensitivity to O<sub>3</sub> of *Pinus sylvestris* (Utriainen and Holopainen, 2001b) and *Fagus crenata* (Watanabe et al., 2012; Yamaguchi et al., 2007) seedlings. The effect of N supply on the sensitivity to O<sub>3</sub> was not significant for *Picea abies* (Thomas et al., 2005; Utriainen and Holopainen, 2001a) or *Quercus robur* seedlings (Marzuoli et al., 2016). Complex interactions were observed between O<sub>3</sub> and N impacts on growth of young trees of *Fagus sylvatica* (Thomas et al., 2006). In a recent review, Mills et al. (2016) showed that the beneficial effect of N on root development was lost at high O<sub>3</sub> exposure whilst the effects of increasing O<sub>3</sub> on root biomass became more pronounced as N supply increased.

Many previous studies investigating the interactive impacts of O<sub>3</sub> and N on trees have been limited to two to three O<sub>3</sub> and N exposure levels. In the current study, three year old silver birch (*Betula pendula*) seedlings were exposed to seven O<sub>3</sub> regimes (24 h mean of 36–68 ppb) and four levels of N load (10–70 kg N ha<sup>-1</sup> yr<sup>-1</sup>) for two years (2012 and 2013). Silver birch is known to be sensitive to O<sub>3</sub> (LRTAP Convention, 2015; Mills et al., 2011b) and has a widespread distribution in Europe, from northern Finland to Italy and from Ireland to Kazakhstan. We investigated whether O<sub>3</sub> sensitivity of leaf traits was affected by N supply. We report in detail on the impacts of O<sub>3</sub> and N on chlorophyll content, stomatal conductance (g<sub>s</sub>), leaf photosynthetic traits, N concentration in senesced leaves and leaf number during the second year of exposure. Based on the cumulative nature of O<sub>3</sub> impacts on plants (LRTAP Convention, 2015), we hypothesised that negative effects of O<sub>3</sub> on leaf traits will increase with time of exposure, with older leaves being more affected than younger leaves. Based on previously reported results

(Landolt et al., 1997; Pääkkönen and Holopainen, 1995) for silver birch, we hypothesised that enhanced N will reduce negative effects of O<sub>3</sub>.

## 2. Material and methods

### 2.1. Plant material, experimental site and treatments

On 13th April 2012, three-year old trees of silver birch (*Betula pendula*, UK provenance) were planted in 6.5 l pots (diameter 21 cm, height 25 cm) filled with John Innes No. 1 compost (J. Arthur Bowers). Mean height of the trees when planted was 68 cm and they had not branched yet. All plants were inoculated with mycorrhiza (obtained from Buckingham Nurseries, UK). The pots were randomly distributed between seven hemispherical glasshouses (solar domes; 3 m diameter, 2.1 m height) at Abergwyngregyn nr. Bangor, North Wales, United Kingdom. After an acclimation period in the solar domes, treatments were started on 30th April 2012. Plants were exposed to O<sub>3</sub> based on an episodic profile recorded at a rural O<sub>3</sub> monitoring site during July 2006 (Aston Hill, Wales, UK, 52°50'N, 3°03'W). The Aston Hill profile was applied as the highest treatment, and for the other treatments the O<sub>3</sub> concentration was reduced by 10 ppb during the peaks and 3 ppb during periods with background O<sub>3</sub> (Fig. 1; Hewitt et al., 2016). The profiles cover a range of concentrations found in Europe and this is the only facility that has sufficiently sophisticated control of O<sub>3</sub> to be able to deliver O<sub>3</sub> treatments that increase in small increments. The 24 h mean concentration was between 36 and 68 ppb in 2013, with peaks up to on average 105 ppb (Fig. 1). Plants were exposed to O<sub>3</sub> during the growing season, starting on 30th April and finishing on 12th October in 2012, and starting on 17th May and finishing on 16th September in 2013, when the trees were harvested. At harvest, the roots didn't show any signs of being pot-bound. Between 17th October 2012 and 14th May 2013, the trees were kept outside under ambient conditions. The solar domes were ventilated at a rate of two air changes per minute and charcoal-filtered air was injected with controlled amounts of O<sub>3</sub>. O<sub>3</sub> was provided by a G11 O<sub>3</sub> generator (Ozone Industries, UK) equipped with oxygen concentrator (Dryden Aqua, UK). Concentrations were determined by a computer-controlled O<sub>3</sub> injection system (Lab VIEW version 8.6, National Instruments, Texas, US). O<sub>3</sub> was distributed to each solar dome via polytetrafluoroethylene (PTFE) tubing, with the concentration inside each solar dome measured for 5 min every 30 min using two O<sub>3</sub> analyzers (400a, Enviro Technology Services, Stroud, UK) of matched calibration. Four N treatments were applied weekly in each solar dome as ammonium nitrate, in 200 ml water containing other macronutrients (P, K, S, Ca, Mg) and various micronutrients (Fe, Mn, Mo, Cu, Zn, B). N addition rates were 10, 30, 50 and 70 kg N ha<sup>-1</sup> yr<sup>-1</sup>. N and nutrient

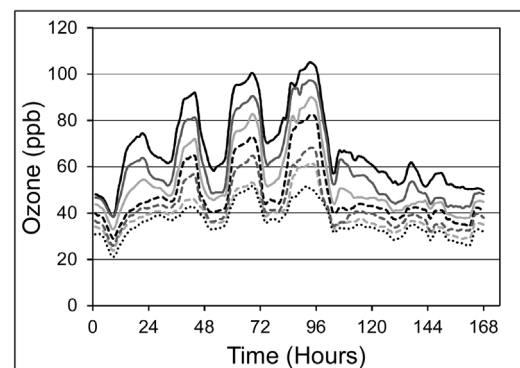


Fig. 1. Weekly ozone profile in seven solar domes at Abergwyngregyn, nr. Bangor, North Wales in 2013.

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