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A review of ozone responses in Scots pine (*Pinus sylvestris*)

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The data on Scots pine responses to elevated ozone (O_3) mainly come from experimental studies with young seedlings and trees. Based on the 38 experiments reviewed here, Scots pine may be considered as an O_3-sensitive conifer species, with mature pines more sensitive than younger trees. This is due to their relatively small proportion of current (c) year needles with the highest photosynthetic capacity. Moreover, young seedlings and trees seem to acclimate to slightly elevated realistic O_3 exposures, and hence do not often exhibit growth and biomass reductions in spite of the visible and microscopic needle injuries and changes in needle chemistry. The O_3 sensitivity in Scots pine is thought to relate to impaired water status due to the malfunction of stomata and subsequent increase in transpiration. This may lead to reduced wood biomass in the long term, if Scots pines try to maximise the biomass of c needles and root biomass to maintain efficient water and nitrogen (N) supply to support the photosynthesis of c needles. Tree water status also contributes to the spring-time recovery of photosynthesis. We call especially for studies on atmosphere–needle surface interaction that would yield novel information on the impact of O_3 on epicuticular waxes and stomatal functioning, which both regulate O_3 flux and tree water status and hence also modify photosynthesis. The need for flux-based field studies is especially important in the light of future climatic change, since the risk presented by O_3 to Scots pine forests in Northern and Central Europe seems to be equal.

1. Introduction

Ozone (O_3) is a secondary pollutant formed by the action of sunlight on nitrogen oxides (NO_x) in the presence of volatile organic compounds (VOCs). While NO_x emissions are mainly produced from burning fossil fuels for energy production, automobiles and biomass burning, VOCs originate from both natural (including biogenic, i.e. BVOCs) and anthropogenic sources (Fowler et al., 1999a; Atkinson and Arey, 2003). The current mean day-time ambient O_3 concentration (40 ppb) during spring and summer over forested land in the Northern Hemisphere (Fowler et al., 1999b), is more than 4-fold that of the pre-industrial ground-level O_3 concentration (10 ppb) (Volz and Kley, 1988). If current NO_x emission trends continue, background O_3 concentration may rise 20–25% between 2015 and 2050 and a further 40–60% by 2100. This is due to increasing precursor concentrations and climatic conditions becoming more favourable to O_3 formation (Meehl et al., 2007).

The current O_3 levels in the Northern Hemisphere are already high enough to negatively affect trees, especially fast-growing deciduous trees, resulting in growth reductions (reviews by Karnosky et al., 2007; Chappelka and Samuelson, 1998; Skärby et al., 1998; Matyssek and Sandermann, 2003; Percy et al., 2007; Wittig et al., 2007, 2009). In the field, O_3 potentially damages conifers mainly through carry-over or memory effects (abiotic pathway) or by confering a predisposition to pathogen attack (biotic pathway), both of which can be described as chronic effects. Carry-over or memory effects are delayed responses in conifers, which follow detectable initial biochemical stress reactions and occur during known phases of endogenous stress (Langebartels et al., 1990, 1998). Trees respond to O_3-induced stress by mechanisms of avoidance (restriction of O_3 uptake by stomatal closure) and defense (i.e. tolerance through biochemical detoxification). This means that the main parameters determining whole-tree O_3 sensitivity are stomatal conductance (g_s), detoxification capacity, ratio between carboxylases and antioxidant regeneration (Matyssek et al., 2012). In the long term, energy costs for defense mechanisms might exceed the photosynthetic output under chronic O_3 exposure (Langebartels et al., 1997; Wieser and Matyssek, 2007).

The European Scots pine (*Pinus sylvestris* L.) is considered to be more O_3-tolerant than the Californian ponderosa pine (*P. ponderosa* Dougl. ex Laws.) and jeffrey pine (*P. jeffreyi* Grev. and Balf) (Langebartels et al., 1998; and references therein). Among European pine species, Scots pine has been classified as O_3-sensitive

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based on the growth of young trees in fumigation experiments (Karlsson et al., 2003). Scots pine is an ecologically and economically important species in boreal forests in Europe, but the studies on young Scots pine are even fewer than those on young Norway spruce (*Picea abies* (L.) Karst.), and above all, we lack information on the effects of O_3 on mature Scot pines in the field. Although Scots pine occurs in regions with strongly differentiated climatic and edaphic conditions, and may hence be characterised by a great ecological amplitude (Bialobok, 1976), Wang et al. (1991) reported low levels of alloenzyme differentation among Scots pine populations between samples from Sweden and eastern Siberia. This may suggest a relatively low intra-specific variation in O_3 sensitivity.

Generalisations of sensitivity of forest trees to O_3 are complicated by tree developmental stage, microclimate, leaf phenology, compensatory processes, within-species variation and other interacting stresses (Chappelka and Samuelson, 1998). Moreover, the low regressions between visible needle O_3 injury and radial growth observed, for example, in an open-top chamber (OTC) experiment with young Southern Californian ponderosa pine suggest that detection of reductions in stem diameter growth in the field could be difficult, except for severely injured pines with fewer than 2 years of needle retention (Temple and Miller, 1994). There is evidence that O_3 injury relates to the ratio between leaf-area based concentrations of antioxidants and O_3 influx (Wieser et al., 2002a,b). The ratio of O_3 uptake to net photosynthesis appears to be of similar bioindicative relevance (Kolb and Matyssek, 2001). This is because photosynthesis is required to maintain antioxidants such as ascorbate – the prominent antioxidant involved in protective scavenging of O_3 – and the reaction products in plants (Conklin and Barth, 2004), in a reduced state (Wingsle et al., 1999).

The negative impact of increasing background O_3 levels may be exacerbated in the future by the changing climate. Although elevated CO_2 provides some protection against O_3 damage by reducing g_s, and a concomitant decrease in plant O_3 uptake, the carbon (C) sink strength of Northern Hemisphere forests will be reduced due to the simultaneous increase in O_3 concentrations, and the subsequent negative effects (Sitch et al., 2007; Wittig et al., 2009). There is some field evidence for drought providing trees protection against rising O_3, as a result of decreased g_s (Matyssek et al., 2006; Wittig et al., 2009). On the other hand, elevated O_3 may disturb stomatal functioning of trees especially under mild drought, resulting in increased water stress (Pearson and Mansfield, 1993; Karlsson et al., 1995; Dueck et al., 1998). Moreover, some studies imply that O_3 exposure exacerbates winter tree damage via increased sensitivity to winter desiccation and/or photoinhibition rather than through reduction in freezing tolerance (Langebartels et al., 1997; Skärby et al., 1998; and references therein).

This paper reviews O_3 effects on Scots pine, and compare its O_3 sensitivity to that of Norway spruce and other pines. Our hypothesis is that water stress and carry-over effects of O_3 on boreal Scots pine, especially in the northernmost areas, will increase. This is beacause in the future, warm spells with temperatures above 0 °C may occur more often, and earlier, concomitantly with the spring-time intrusion of stratospheric O_3, and because elevated background O_3 levels are likely to occur for longer-periods, resulting in a higher accumulated O_3 dose (Karlsson et al., 2007). Therefore, we also discuss O_3 sensitivity of Scots pine in relation to climatic factors.

2. O_3 responses of Scots pine in experiments

2.1. Visible injury and biomass losses

Girgždienė et al. (2009) ranked young saplings of Scots pine as more sensitive than those of Norway spruce – based on O_3 stimulated leaf senescence expressed as discoloration, needle death, necrosis, premature defoliation, and specific O_3-induced symptoms (e.g. mottling). The average sensitivity class for Scots pine was 6 compared to that of 2 for Norway spruce. However, the sensitivity class of Scots pine was lower than those of deciduous species, for example 10 in silver birch (*Betula pendula* Roth) and 12 in European aspen (*Populus tremula* L.). The experiment was performed in Lithuania, in northern Central Europe. Scots pine has also been ranked as more O_3 sensitive than Norway spruce in other Northern and Central European chamber and open-air fumigation experiments based on visible injury or biomass responses (e.g. Rantanen et al., 1994; Schnitzler et al., 1999; Prozherina et al., 2009).

Visible injury (mainly mottling) was found in 11 out of 15 experiments reviewed (Table 1). Occurrence of visible needle injury in Scots pines is mainly attributed to high O_3 concentrations (>65 ppb) – often applied in controlled chamber or greenhouse conditions (Bialobok et al., 1980; Landolt et al., 1989; Mortensen, 1994; Zinser et al., 1998, 2000; Schnitzler et al., 1999) (Table 1), which do not simulate well the responses found in the field (Musselman and Hale, 1997). Moreover, O_3-related visible injuries vary depending on the developmental stage and acclimation of needles, and may appear as late as in August–September of the year following the treatment (Langebartels et al., 1998).

Growth reductions were only scored in four experiments out of 16 and biomass losses were also uncommon in young Scots pines (needles 1/15, wood or shoot 5/15, roots 3/16) (Table 1). Needle, shoot and/or root biomasses have been shown to be reduced both after a high O_3 exposure (average 24-h accumulated exposure over threshold of 40 ppb (AOT40) per growing season 52.7 ppm h) (Broadmeadow and Jackson, 2000) and a relatively low O_3 exposure (growing season average AOT40 during daylight hours 10.9 ppm h) (Prozherina et al., 2009) in 1- to 2-year-old seedlings originating from the UK, Finland and Russia, respectively (Table 1). The differences in O_3 exposures and environmental conditions between the experiments make it difficult to assess the overall O_3 sensitivity of Scots pine. At any rate, and in contrast to findings on deciduous trees, Vanhatalo et al. (2003) reported the slower-growing provenance of Scots pine being more sensitive to O_3 than the faster-growing one in terms of wood dry weight. This is in accordance with the results of Wulff et al. (1996) and Prozherina et al. (2009), who found the smaller (slower-growing in terms of height growth or needle biomass and length) provenances of Scots pine to be more sensitive to elevated O_3 concentration than the seedlings of the larger provenances under Northern European climatic conditions.

Negative effects of realistic O_3 concentrations on roots (i.e. short root number) have only been reported in a Finnish OTC fumigation expriment with 14- to 24-year-old trees growing in a natural stand (Kasurinen et al., 1999). The results of other Finnish studies with boreal Scots pines show mainly positive or no effects in terms of mycorrhizal development and number (Rantanen et al., 1994; Kainulainen et al., 2000a; Manninen et al., 2000; Utriainen et al., 2000). Pérez-Soba et al. (1995) attributed the reduction in mycorrhizal infection to an O_3-induced quantitative and qualitative modification of root exudates (Lefohn, 1992), rather than to a decrease in C allocation to the roots (Adams et al., 1990; Gorissen et al., 1991). Reductions for example, in root starch concentration of young Scots pines have been reported though (Anttonen and Kärenlampi, 1995; Holopainen et al., 1996). These observations contradict the general assumption that O_3 exposure markedly decreaseas C allocation to roots in tree species such as Norway spruce, Scots pine and sessile oak (*Quercus petraea*) (Grantz et al., 2006), and hence to mycorrhizal symbionts.

To conclude, young Scots pines seem to maintain their root-to-shoot ratio under O_3 stress. Although decreases in spring root growth have been observed in ponderosa pine (Andersen et al., 1991, 1997), Andersen et al. (1997) also only found minor or