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Foliage type specific susceptibility to ozone in *Picea abies*, *Pinus cembra* and *Larix decidua* at treeline: A synthesis

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ABSTRACT

Cumulative ozone uptake (COU, mmol m^{-2}) and O_3 flux (FO_3, nmol m^{-2} s^{-1}) were related to physiological, morphological and biochemical characteristics of field-grown mature evergreen Norway spruce [*Picea abies* (L.) Karst.], Cembran pine [*Pinus cembra* L.], and deciduous European larch [*Larix decidua* Mill.] trees at treeline. The threshold COU causing a statistically significant decline in photosynthetic capacity (A_{max}) ranged between 19.6 mmol m^{-2} in current-year needles of evergreen conifers and 22.0 6 mmol m^{-2} in short-shoot needles of deciduous *L. decidua* subjected to exposure periods of ≥84 and ≥43 days, respectively. The higher O_3 sensitivity of deciduous *L. decidua* than of evergreen *P abies* and *P. cembra* was associated with differences in FO_3 and specific leaf area (SLA), both being significantly higher in *L. decidua*. FO_3 was 5.9 nmol m^{-2} s^{-1} in *L. decidua* and 2.7 nmol m^{-2} s^{-1} in evergreen conifers. Species-dependent differences were also related to detoxification capacity expressed through total surface area based concentrations of reduced ascorbate and α-tocopherol that both increased with SLA. Findings suggest that differences in O_3 sensitivity between evergreen and deciduous conifers can be attributed to foliage type specific differences in SLA, the latter determining physiological and biochemical characteristics of the treeline conifers.

1. Introduction

Tropospheric ozone (O_3) is one of the most detrimental air pollutants known to affect forest trees (Matyssek and Sandermann, 2003). With O_3 concentrations above pre-industrial levels and given the recent decrease in sulphur emissions O_3 is regarded as an air pollutant potentially most determinant to vegetation and an inherent factor of climate change (IPCC, 2007; Giles, 2005; Ashmore, 2005; Matyssek et al., in press). O_3 can reduce the carbon sink strength of forest trees and ecosystems (Sitch et al., 2007; Pretzsch et al., 2009; Matyssek et al., 2010a) and modify metabolic responses under elevated atmospheric carbon dioxide (CO_2) (Karnosky et al., 2007; Witting et al., 2009; Matyssek et al., 2010b). Trees respond to O_3 stress through mechanisms of avoidance and defence (Hogsett and Andersen, 1998; Wieser and Matyssek, 2007) such as the restriction of O_3 uptake by stomatal closure and metabolic detoxification through biochemical reactions within the leaves (Musselman et al., 2006; Matyssek et al., 2008).

Based on the conceptual model of O_3 injury in plants presented by Massman et al. (2000), Wieser et al. (2002a) suggested weighting O_3 influx by area-based antioxidant concentrations in the leaves. This approach was helpful for interpreting within-species differences in the O_3 susceptibility of *Picea abies* L. [Karst.] seedlings and mature forest trees (Wieser et al., 2002a), as well as of *Fagus sylvatica* L. trees under chamber and free-air conditions (Nunn et al., 2005). To date, however, inter-specific assessment awaits clarification.

Ecosystems at alpine and polar treeline ecotones (cf. Tranquillini, 1979; Wieser and Tausz, 2007) are of special interest with respect to environmental changes (Wieser et al., 2009). Evergreen *P. abies* (L.) Karst. and *Pinus cembra* L., and deciduous *Larix decidua* Mill. are subalpine conifer species well adapted to harsh environmental conditions at high altitude (Tranquillini, 1979). The three species differ, however, by foliage type and successional status, with *L. decidua* being an early succession species, and *P. abies* and *P. cembra* being late succession species (Ellenberg and Leuschner, 2010). Hence the performance of these tree species under conditions of elevated O_3 may give insights on O_3-dose response relationships, regarding their leaf-morphological and site-ecological characteristics.

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Our objectives were: (1) to establish sensitivity threshold ranges for O_3 influx and cumulative O_3 uptake of evergreen and deciduous field-grown mature conifers, (2) to determine foliage type specific differences in antioxidative defense capacity; and (3) to link stress avoidance (O_3 exclusion through stomatal regulation) with tolerance (detoxification upon O_3 uptake) across the range of O_3 sensitivity spanned by the exemplified coniferous species.

2. Material and methods

2.1. Experimental design and ozone treatment

For clarifying long-term effects of O_3 impact on the photosynthetic performance of current-year needles of mature Norway spruce [*P. abies* (L.) Karst.] and Cembran pine [*P. cembra* L.], and of short-shoot needles of mature European larch [*L. decidua* Mill.] trees, we evaluated experimental data from four O_3 fumigation experiments carried out within the treeline ecotone at 1950 m a.s.l. on Mt. Patscherkofel (Klimahaus Research Station; 47°12′11″ N, 11°27′05″ E) in the Central Tyrolean Alps south of Innsbruck, Austria (Table 1). At this site O_3 (annual mean 50–60 nl l^{-1}) was the dominant air pollutant, as concentrations of sulphur dioxide (SO_2; annual mean 0.001 $\mu g\,m^{-3}$), nitrogen dioxide (NO_2, annual mean 0.003 $\mu g\,m^{-3}$) and nitrogen oxide (NO; annual 0.001 $\mu g\,m^{-3}$) were negligible. Scaffolding provided access to the upper portion of the canopy of one isolated *P. abies* tree, one isolated *P. cembra* tree and a group of five *L. decidua* trees differing in age (Table 1). The restriction to only one *P. abies* tree and one *P. cembra* tree was necessary due to the fact that the distance between single trees and between groups was at 20 and 30 m and that we could not build scaffoldings covering such distances. In each experiment twigs similar in size and exposure were sealed into transparent fumigation cuvettes (Havranek and Wieser, 1990, 1994; Wieser et al., 2001) for 43–91 days in the growing seasons of 1986, 1987, 1993 and 1996 (Table 1).

The O_3 exposure regimes were charcoal-filtered air (control), ambient air (A), up to two-fold ambient-air O_3 concentration (1986, 1987, 1996), or a constant O_3 concentration that increased stepwise from 150 to 200 nl l^{-1} (1993) (Table 1). The exposure system enabled the control of ambient climatic conditions and O_3 concentrations tracking diurnal and seasonal fluctuations inside the cuvettes. The cuvettes made of thin Perspex were 12 cm in diameter and 32 cm long. Gas tight nylon bags were used for twig enclosure allowing flexibility in order to prevent breakage of the twigs trough high wind movement. Each chamber was provided with 139 cm^3 of forced air s^{-1}, corresponding to two exchanges of the chamber volume per minute. Four inlet ports and fans inside the chambers allowed a throughout mixing of the air, prevented concentration gradients inside the chambers, and minimised the needle boundary layer resistance. The fumigation system was provided with ambient air drawn through charcoal filters which completely removed O_3. In order to remove short-term fluctuations in CO_2-concentration and humidity the air passed a 250 dm^3 puffer vessel. For each O_3 treatment a manifold supplied the corresponding number of exposure chambers (see Table 1) to the same O_3 concentration. Supplemental O_3 was generated from charcoal-filtered air using an ultraviolet lamp (Osram HNS-UOZ 10), diluted in two steps to the demand of ambient and above ambient O_3 concentration, respectively, before continuously (day and night) entering the manifolds of the ambient and above ambient O_3 treatment. Tests indicated that this method did not produce nitrogen oxides (NO_x) at concentrations above the detection limit of 1 nl l^{-1} of a nitrogen analyser (model 8840, Monitor Labs San Diego, USA; Wieser et al., 2001).

Three to six chambers were operated simultaneously in each of the treatments (Table 1). Air temperature and humidity of the air entering and leaving the cuvettes were measured with *EE20*

Table 1
Summary on the experiments on ozone uptake.

Year	Mean annual temperature [°C]	Annual precipitation [mm]	Species	Tree age [years]	Tree height [m]	Exposure duration [days]	Daily mean O_3 concentrations during the exposure period [nl l^{-1}]	Number of trees investigated and twigs per treatment	References
1986	1.9	862	*Picea abies*	60–65	11	84	0^a, 65^b, 120^c	1/6	Havranek et al., 1989
1987	2.2	958	*Picea abies*	60–65	11	84	0^a, 64^b, 102^c	1/6	Havranek et al., 1989
1993	2.1	801	*Larix decidua*	33	5	43	0^a, 52^b, $150/200^d$	5/5	Volger, 1995
1996	1.8	823	*Pinus cembra*	65	12	91	0^a, 44^b, 89^c	1/3	Wieser et al., 2001, 2006

[a] Charcoal-filtered air as control.
[b] Ambient air.
[c] Tracking ambient O_3 concentration.
[d] Constant (day and night) O_3 concentration of 150 nl l^{-1} for 21 days and then increased to 200 nl l^{-1} for further 22 days.