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Ozone Impact on Photosynthetic Capacity of Mature and Young Norway Spruce (*Picea abies* (L.) Karst.): External Versus Internal Exposure.

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Summary

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The use of data from seedling responses in chambers for predicting mature tree response to ozone is questionable but only a few studies have examined whether seedlings are useful surrogates for understanding mature tree response to ozone (O_3). This study compares effects of ambient and above ambient O_3 concentrations on photosynthetic capacity of mature Norway spruce trees (*Picea abies* (L.) Karst.) obtained under field conditions with data of seedlings from chamber experiments. In mature trees photosynthetic capacity was less affected by ozone exposure than in seedlings. Differences in O_3 uptake may explain observed differences in sensitivity. Results indicate that seedlings in chambers may not reflect the O_3 sensitivity of mature trees in the field.

Introduction

Ozone (O_3) is a widespread air pollutant in industrialised regions and peak concentrations up to 120 ppb have been reported for forests in Austria (SCHNEIDER & al. 1996). The phytotoxicity of O_3 has been demonstrated for some tree species and several exposure-response and dose-response relationships have been established (LEFOHN 1992). One exposure index for forest trees is the AOT40 value (Accumulated dose Over a Threshold of 40 ppb) of 10 ppm-h (UN-ECE 1996). This value has been based on open-top-chamber experiments with young

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trees. O_3 effects were reported at lower O_3 concentrations (SANDERMANN & al. 1997) than those persisting at the alpine timberline, where unambiguous evidence of O_3 injury does not exist.

The specific objective of this study was to calculate critical levels for mature spruce trees and seedlings according to the concept of the UN-ECE 1994, 1996 based on fumigation experiments with mature trees carried out under field conditions (WIESER & HAVRANEK 1996) and on controlled chamber experiments with seedlings. Furthermore, as an alternative approach this paper will also focus on total O_3 uptake and hence also on a critical internally absorbed dose.

Material and Methods

Experimental design: Experimental details were described previously by HAVRANEK & WIESER 1994 and WIESER & HAVRANEK 1996. Briefly, twigs from the upper crowns of 33 to 65-year-old spruce trees at two forest sites in the Tyrol, Austria, in 1000 m a.s.l. and at the alpine timberline (1950 m a.s.l.) were sealed into transparent fumigation cuvettes. During the growing seasons 1986 to 1990 charcoal-filtered air, ambient air, and ambient air plus 30, 60 or 90 ppb O_3, respectively, were applied continuously for 6 to 23 weeks, tracking diurnal and seasonal fluctuations. There were four to eight replicates per treatment. Mean ambient O_3 concentrations during the investigation periods were 65 ppb (1985) and 64 ppb (1986) at the high elevation site and 47 ppb (1988), 37 ppb (1989) and 25 ppb (1990) at the low elevation site.

In 1994 (see KRONFUß 1996) and 1995, 20 seedlings were placed into growth-chambers and exposed to either charcoal-filtered air or up to 100 ppb O_3 under controlled conditions for three and two months, respectively. The photoperiod was 14 hours with an average photon flux density of 340 µmol $m^{-2}s^{-1}$ at the height of the upper whorl. Day and night temperatures were kept at 20 °C and 15, °C respectively. The dew point was kept at 13 °C during day and night. In order to maintain optimum water conditions all seedlings were irrigated up to field capacity of the soil every second or third day.

Gas exchange measurements: The effects of O_3 on photosynthetic capacity and stomatal conductance were determined in situ with a Minicuvette system (Walz, Effeltrich, Germany) under standardised conditions (20 °C needle temperature, 9.2 Pa kPa^{-1} leaf-air vapour pressure difference, 350 ppm CO_2 concentration, photon flux density of 2000 µmol m^{-2} s^{-1}). All gas exchange parameters were calculated according to VON CAEMMERER & FARQUHAR 1981 and related to total needle surface area estimated with glass beads (THOMPSON & LEYTON 1971).

Calculation of exposures: The cumulative 24 hour external O_3 exposure (SUM0) was calculated by summing all hourly mean O_3 concentrations for each treatment of each fumigation period. External O_3 dose was also determined as the accumulated exposure over a threshold of 40 ppb (AOT40). Because stomata of Norway spruce do not close completely during the night (WIESER & HAVRANEK 1993, KRONFUß 1996) the summation of 1-h mean concentrations exceeding the threshold value was based on a 24 h period (UN-ECE 1994). Additionally AOT40 values are also given for daylight hours only, as suggested by the UN-ECE 1996.

Continuous microclimatic, O_3, and gas exchange measurements under field conditions were used to calculate O_3 flux into the needles of mature tress according to the flux equation:

$$F_{O3} = (Co - Ci) * g_{O3} \qquad (1)$$

where F_{O3} is the flux of O_3 into the needles, Co is the O_3 concentration outside the leaf and Ci the internal concentration considered to be zero (LAISK & al. 1989). g_{O3} is the stomatal conductance for O_3, calculated by multiplying the conductance for water vapour by 0.612, the ratio of diffusivities of water vapour and O_3.

As gas exchange measurements tracking ambient conditions were not performed throughout the whole fumigation period, O_3 uptake was also estimated by means of an empirical

multiplicative model for stomatal conductance; based on empirical relationships of stomatal conductance to photon flux density and stomatal conductance to vapour pressure deficit, obtained from extensive field measurements (WIESER & HAVRANEK 1993).

In a first step stomatal conductance for O_3 was simulated as a function of photon flux density (PFD), maximum (g_{max}) and minimum (g_{min}) stomatal conductance for O_3 according to equation 2:

$$g_{PFD(O3)} = a*PFD/SQRT\{1+[a^2*PFD^2/(g_{max}-g_{min})^2]\}+ g_{min} \quad (2).$$

A second step considers the effects of water vapour pressure deficit (VPD) as follows:

$$g_{VPD(O3)} = g_{PFD(O3)}*exp^{(-b*VPD)} \quad (3).$$

As an example, Fig. 1 shows both dependencies as well as the corresponding parameters obtained for current-year needles in the shade crown of Norway spruce. Similar flux-based approaches for calculating pollutant uptake have also been proposed by SIEGWOLF & al. 1994 and KÖRNER & al. 1995. Cumulative O_3 uptake was then estimated by integrating all half-hour mean data obtained from equation 1 over the investigation periods.

O_3 uptake into needles of the seedlings was calculated by daily measurements of stomatal conductance with a porometer (ADC, LCA3, Hoddesdon, England) inside the growth-chamber at 10:00 to 11:00 and 22:00 to 23:00 h. Preliminary measurements of diurnal courses showed that these values of stomatal conductance were representative for the light and dark period in order to calculate daily and cumulative O_3 uptake.

Critical levels were determined as an "acceptable" 10% reduction (CL10) compared to the value of the O_3 free control, using linear regression analysis (UN-ECE 1994). For this purpose datasets of all field measurements and chamber experiments, respectively, were pooled.

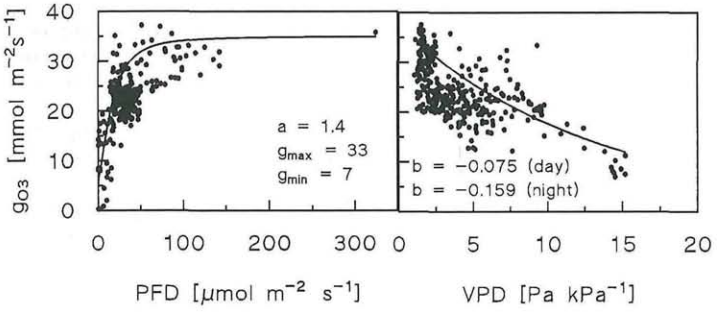

Fig. 1. The influence of (left) photon flux density (PFD) and (right) water vapour pressure deficit (VPD) on stomatal conductance for ozone (g_{O3}) of current-year needles from the shade crown of Norway spruce.

Results and Discussion

To remove age influences (YODER & al. 1994) between photosynthetic capacity and O_3 exposure, photosynthetic rates of mature trees and seedlings were expressed relatively to their respective values in charcoal filtered air. In general, photosynthetic capacity as a function of external exposure indices (SUM0, AOT40) and cumulative O_3 uptake exhibited negative relationships. Evidently, O_3 induced reduction in photosynthesis of the current flush was less pronounced in mature

trees under field conditions as compared to findings from chamber experiments carried out with seedlings (Fig. 2).

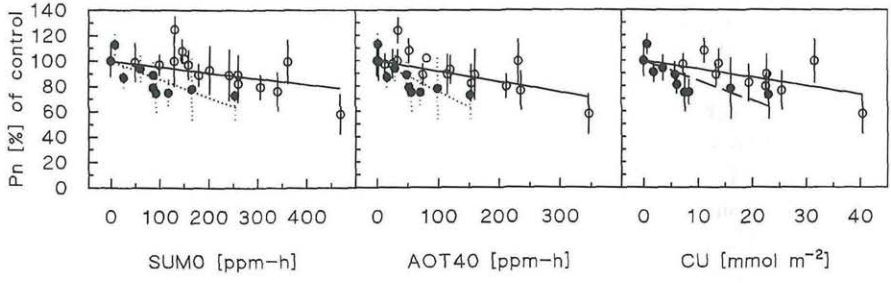

Fig. 2. Photosynthetic capacity (Pn) in percent of charcoal-filtered controls of current-year needles of mature (open symbols) and seedlings (closed symbols) of Norway spruce as a function of total (24-h) cumulative external ozone exposure (left, Sum0), total cumulative exposure over the threshold concentration of 40 ppb (middle, AOT40), and total internal ozone uptake (right, CU). (After WIESER & HAVRANEK 1996, and KRONFUß 1996; n = 4 to 20 ± SD).

As a consequence Critical Levels for a 10% reduction (CL10) of photosynthesis were lower in seedlings than in mature trees (Table 1). Furthermore, in mature trees O_3 induced reductions in photosynthetic capacity declined with increasing needle age and hence CL10 values increased with increasing needle age (Table 1).

As O_3 injury results from biochemical and physiological processes occurring to the leaf interior (TINGEY & TAYLOR 1982), it follows that differences in O_3 uptake might be responsible for observed differences in sensitivity. The lower stomatal conductance of older needles and their lower sensitivity to O_3 exposure support this idea (Table 1). Furthermore, well watered seedlings in the growth chambers were not forced to restrict their water loss, whereas in the field

Table 1. Average stomatal conductance for water vapour (g_{H2O}) during the fumigation period and Critical Levels (CL10) of ozone for photosynthetic capacity in different classes of Norway spruce needles for different exposure indices.

Tree and needle age	g_{H2O} mmol $m^{-2}s^{-1}$	Exposure index external (ppm-h) SUM0 (24-h)	AOT40 (24-h)	AOT40 (daylight only)	internal (mmol m^{-2}) CU (24-h)
seedling 0 yr.	44 ± 11	70	41	23	6.3
mature 0 yr.	31 ± 9	216	120	76	14.9
mature 1 yr.	21 ± 7	500	282	164	-
mature 2 yr.	19 ± 6	9500	3080	1795	-

conductance was often reduced due to increasing leaf/air vapour pressure difference and soil drought (WIESER & HAVRANEK 1993, 1995, HAVRANEK & WIESER 1993). As a consequence average stomatal conductance during the fumigation period of well watered seedlings was at an average 30% higher than conductance found in mature trees under field conditions. This higher stomatal conductance and hence also a higher O_3 uptake rate at a given concentration might help explain the higher O_3 sensitivity of the seedlings. Close correlations between leaf conductance and O_3 sensitivity were also found for giant sequoia (GRULKE & MILLER 1994) and for red oak (HANSON & al. 1994). However, potential differences in antioxidants (OTTER & POLLE 1994) and foliar repair mechanisms between seedlings and trees might also influence O_3 sensitivity.

In conclusion, it appears that seedling net photosynthetic response may not reflect that of mature trees. It might be possible that old spruce trees in the field are better adapted to environmental stress factors including high O_3 concentrations and that they can cope with a higher oxidative stress than young trees. Both, this study with Norway spruce and other studies with Ponderosa pine (MOMEN & al. 1996) and giant sequoia (GRULKE & MILLER 1994) came to the conclusion that mature trees are less sensitive to O_3 than seedlings. However, the opposite pattern has been observed for red oak (HANSON & al. 1994). Therefore, the sensitivity of a species to O_3 may be misinterpreted when extrapolating from seedlings under chamber conditions to mature trees in the field.

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