

Exemplifying whole-plant ozone uptake in adult forest trees of contrasting species and site conditions

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Received 16 January 2006; received in revised form 15 June 2006; accepted 24 June 2006

Sap flow-based assessment of whole-tree O₃ uptake reflects similar responsiveness of canopy conductance and O₃ uptake across contrasting tree species and site conditions.

Abstract

Whole-tree O₃ uptake was exemplified for *Picea abies*, *Fagus sylvatica* and *Larix decidua* in stands at high and low altitude and contrasting water availability through sap flow measurement in tree trunks, intrinsically accounting for drought and boundary layer effects on O₃ flux. O₃ uptake of evergreen spruce per unit foliage area was enhanced by 100% at high relative to low elevation, whereas deciduous beech and larch showed similar uptake regardless of altitude. The responsiveness of the canopy conductance to water vapor and, as a consequence, O₃ uptake to soil moisture and air humidity did not differ between species. Unifying findings at the whole-tree level will promote cause–effect based O₃ risk assessment and modeling.

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Keywords: *Picea abies*; *Fagus sylvatica*; *Larix decidua*; Altitude; Timberline; Drought; Xylem sap flow; Foliage transpiration; Canopy conductance; O₃ uptake; Boundary layer

1. Introduction

The analysis of ozone (O₃) impact on forest trees requires knowledge on the O₃ transport towards the canopy and on the stomatal and non-stomatal fluxes to the leaves (Stockwell et al., 1997; Emberson et al., 2000; Grünhage et al., 2004), which are the primary sites of O₃ uptake. Stomatal O₃ uptake denotes, therefore, the physiologically meaningful O₃ dose of plants. Quantification of stomatal O₃ uptake is crucial for understanding potentially toxic O₃ effects on forest trees, because it is widely acknowledged that O₃ impact is more

closely related to O₃ uptake than external O₃ concentration (Wieser, 1997; Fuhrer and Achermann, 1999; Musselman and Massman, 1999; Massman et al., 2000; Wieser et al., 2000, 2002; Matyssek and Sandermann, 2003; Matyssek et al., 2004; Musselman et al., 2006).

Quantification of O₃ uptake may be based on gas exchange measurements of leaves enclosed in cuvettes (Wieser and Havranek, 1993, 1995; Wieser et al., 2000) or eddy covariance techniques (Duyzer et al., 1995; Pilegaard et al., 1995; Mikelsen et al., 2000; Zeller and Nikolov, 2000) at the canopy level. Although gas exchange measurements in cuvettes allow the assessment of the O₃ flux into leaves, boundary layers are neglected that typically impede O₃ uptake (Matyssek et al., 1995; von Willert et al., 1995). Eddy covariance approaches, in contrast, measure total O₃ deposition, but stomatal O₃

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Nomenclature

O_3	ozone
$[O_3]$	O_3 concentration of the ambient air [$nl\ l^{-1}$]
SUM0	total sum of hourly O_3 concentrations
AOT40	accumulated O_3 dose over a threshold of $40\ nl\ l^{-1}$ at daylight hours
F_{O_3}	foliage area-related whole-tree O_3 flux or uptake rate [$nmol\ m^{-2}\ s^{-1}$]
COU	cumulative O_3 uptake
E_C	whole-tree transpiration [$ml\ min^{-1}$]
G_C	crown conductance for water vapor [$mmol\ m^{-2}\ s^{-1}$]
P	air pressure [kPa]
VPD	water vapor pressure deficit of air [Pa]
Δw	leaf/air mole fraction difference of water vapor at canopy height
PPFD	photosynthetic photon flux density [$\mu mol\ m^{-2}\ s^{-1}$]
DBH	diameter at breast height
LAI	leaf area index [m^2 foliage m^{-2} ground]

uptake can hardly be separated from O_3 adsorption onto external tree surfaces (Zeller and Nikolov, 2000).

Whole-tree transpiration can be obtained quantitatively from sap flow measurements in tree trunks (Schulze et al., 1985; Köstner et al., 1998). Since transpiration and O_3 flux into leaves are coupled through stomatal regulation, sap flow assessment can be used to determine the O_3 flux into the whole-tree foliage, i.e. at the canopy level (Wieser et al., 2003a; Matyssek et al., 2004). Advantages of this latter approach are (1) the assessment of the crown gas exchange (i.e. transpiration and O_3 uptake) under prevailing boundary layer conditions, and (2) the potential use in heterogeneous and mountainous landscapes, where eddy covariance methods may fail.

The present study examined the capacity of sap flow measurement in tree trunks for assessing whole-tree O_3 uptake of adult forest trees. This task was to be exemplified for contrasting tree species in terms of foliage habit (deciduousness versus evergreenness), autecology and contrasting environmental conditions regarding site altitude and water availability in summer. The sap flow-based assessment of O_3 uptake represents (as opposed to modeling) an empirical whole-tree approach that intrinsically integrates the time courses of weather conditions and ambient O_3 levels at the forest site under the actually prevailing boundary layer effects on O_3 uptake (Wieser et al., 2003a; Matyssek et al., 2004). Evergreen Norway spruce (*Picea abies*), deciduous European beech (*Fagus sylvatica*) and European larch (*Larix decidua*) were chosen as study objects to warrant a maximum range in foliage differentiation and autecology within the tree flora of Central Europe (Tranquillini, 1979; Matyssek, 1986; Ellenberg, 1996). This autecological perspective was combined with a site-ecological one, warranting a maximum range of altitudes above sea level (including the timberline ecotone of the

Alps) and water availability (including 2003 with exceptional summer drought in Central Europe, cf. Ciaia et al., 2005; Löw et al., in press) in examining the applicability of the sap flow approach. Hence, the rationale of this study was to quantitatively demonstrate the performance of whole-tree O_3 flux assessment under contrasting ecological perspectives in Central Europe. The O_3 uptake of spruce was exemplified at two altitudes and under the influence of water availability, while the latter factor was highlighted in its effect on the O_3 uptake of beech at low, and of larch at high elevation.

2. Materials and methods

2.1. Study sites and plants

The study site at high elevation was located at the timberline ecotone (1950 m a.s.l.) near the Klimahaus Research Station on Mt. Patscherkofel ($47^\circ 12' N$, $11^\circ 27' E$) south of Innsbruck, Austria. The timberline site was characterized by open stands of Norway spruce (*P. abies*), European larch (*L. decidua*) and Cembra pine (*Pinus cembra*). Stand density was 148 trees ha^{-1} , basal stem area $47.6\ m^2\ ha^{-1}$ and projected leaf area index (LAI) $3.9\ m^2\ m^{-2}$ (Wieser and Stöhr, 2005). Two 80–100-year-old, dominant individuals of spruce and larch each were selected as study trees. The trees grew in a podsol on an SW-exposed slope of 20–30% inclination. Measurements were made from April 28 through October 6, 1998. The high-altitudinal site is characterized by a cool sub-alpine climate with low soil temperatures and the possibility of frost during the entire year, with the growing season extending from May through October (Benecke et al., 1981; Wieser and Havranek, 1995).

The low-altitudinal study site was located at Kranzberger Forst near Freising, Germany ($48^\circ 25' N$, $11^\circ 39' E$, elevation 485 m a.s.l.) in a mixed stand of 53–60-year-old Norway spruce (*P. abies*) and European beech (*F. sylvatica*). Given common planting practice in managed forests, beech formed dense groups of up to 50 individuals within the spruce-dominated stand that had developed a closed canopy. Stand density was 829 trees ha^{-1} , basal stem area $46.4\ m^2\ ha^{-1}$ and projected leaf area index (LAI) $5.6\ m^2\ m^{-2}$ (Wipfler et al., 2005; Grote and Reiter, 2004). Five trees of each species were investigated in August each of three consecutive growing seasons (2002–2004). Long-term averages of annual air temperature and precipitation were 7.0 – $7.5\ ^\circ C$ and 730–790 mm, respectively (Pretzsch et al., 1998). The growing season extends from mid-April through the end of October.

2.2. Assessments of environmental conditions and xylem sap flow

Given the open stand conditions at Mt. Patscherkofel, environmental parameters were monitored by a meteorological station at 2 m aboveground (shielded Skye SKH 2013 temperature/humidity sensors, Skye Instruments, Powys, U.K.; Li-190PAR quantum sensor, LiCor, Inc., Lincoln, NE; A100R switching anemometer, Vector Instruments, Rhyll, U.K.; ARG100 tipping bucket rain gauge, Campbell Scientific Ltd., Shepshed, U.K.). Trees were foliated along the entire stem length. In the absence of vertical O_3 gradients within the open stand, ambient O_3 levels were monitored at 20 m aboveground at the top of the canopy with an O_3 analyzer (Model ML8810, Monitor Labs, San Diego, CA, USA).

In the closed-canopy stand of Kranzberger Forst, temperature, relative humidity (RH), pressure and O_3 levels of the ambient air were monitored at 24 m aboveground at the top of the canopy (psychro- and baro-transmitter, ThiesClima, Göttingen, Germany; O_3 analyzer: ML8811, Monitor Labs, USA). A total of eight O_3 analyzers was operated across the site, checked each day for consistency across zero lines and spans, and were recalibrated as necessary (on an average once per month) or after repair (on an average once per month). Stand foliage was concentrated between 17 and 24 m aboveground (Reiter et al., 2005). At Kranzberger Forst, only minor vertical O_3 gradients were found within the foliated canopy (Nunn et al., 2002). Wind velocity was measured above the canopy (at 32 m height; wind-transmitter,

ThiesClima, Germany). Precipitation was assessed in a clearing at about 1 km distance (data by courtesy of LWF, G. Gietl).

At both sites, sap flow was measured with 2 cm long continuously heated sap flow gauges according to Granier (1987) at 0–2 cm sapwood depth. Sensors were inserted into the tree xylem at breast height (NW exposure at Mt. Patscherkofel; one sensor each S and N-exposed at Kranzberger Forst). At Kranzberger Forst, additional sensors at 4 and 6 cm depth determined the variation in sap flow across the cross-sectional sapwood area of two trees per species. The sapwood area-related flow density at depths beyond 6 cm was linearly extrapolated towards the heartwood area on the basis of the assessments at 2, 4 and 6 cm depth. The proportional reductions in sap flow with increasing depths were used to express the sap flow density across the entire cross-sectional sapwood area in relation to the sensor readings at 2 cm depth. The relationship was adapted to all study trees in each species. The cross-sectional sapwood area of the trees was derived from increment cores taken in late spring of 1999 at Mt. Patscherkofel. At Kranzberger Forst, this area was derived from increment cores of neighboring trees with DBH similar to that of the study trees. The product of sap flow density and cross-sectional sapwood area at breast height rendered whole-tree transpiration (E_C ; expressed as ml min^{-1}). At Mt. Patscherkofel, micro-climatic and sap flow data were recorded as 15-min means (Campbell CR10 data logger, Campbell Scientific Ltd., Shepshed, U.K.), and 10-min means were recorded at Kranzberger Forst (DL2e data logger, Delta-T-Devices, Burwell, Cambridge, U.K.).

2.3. Assessment of crown conductance for water vapor and whole-tree O_3 uptake

Crown conductance (G_C) for water vapor was derived from measured E_C (ml min^{-1}) according to Köstner et al. (1992) and Wieser et al. (2003a):

$$G_C = E_C / \Delta w; \quad \Delta w = \text{VPD} / P$$

where P is the air pressure [kPa], VPD is the water vapor pressure deficit of the air [Pa] and Δw is the leaf/air mole fraction difference of water vapor at canopy height (cf. Cowan, 1977). In expressing Δw , leaf temperature at the canopy level was assumed, on average, to equal air temperature, given the major part of the foliage to be shaded at canopy closure. Since VPD was assessed at canopy height, boundary layer and aerodynamic conductances were accounted for by G_C . G_C was scaled to the foliage area of each tree. Foliage area was calculated on the basis of DBH and allometric equations by Burger (1950) for beech and Patzner (2004) for spruce. In the case of beech projected foliage area and in the case of spruce and larch total foliage surface area were used as reference to base comparisons between the hypostomatic beech leaves and amphistomatic spruce and larch needles (Geburek, 2002) on the actually O_3 -absorbing surfaces each (Wieser et al., 2002, 2003b; Matyssek et al., 2005; Nunn et al., in press).

At Kranzberger Forst, a minimum G_C ($G_{C \text{ min}}$) was employed when Δw was $< 1 \text{ Pa kPa}^{-1}$, owing to the fact that stomata were not fully closed at any time, even during night (Nunn et al., 2005). $G_{C \text{ min}}$ was 10% of the mean maximum stomatal conductance during the daylight hours (Musselman and Minnick, 2000; Grulke et al., 2004; Nunn et al., 2005) in 2002 and 2004, i.e. in beech $19.5 \text{ mmol m}^{-2} \text{ s}^{-1}$ and in spruce $4 \text{ mmol m}^{-2} \text{ s}^{-1}$. In the dry year of 2003, $G_{C \text{ min}}$ was about 50% of the level in 2002 and 2004 in both species. As G_C tended to reach unrealistically high levels at high air humidity due to limitations of Δw assessment (von Willert et al., 1995), maximum G_C ($G_{C \text{ max}}$) was confined in beech to $250 \text{ mmol m}^{-2} \text{ s}^{-1}$ (Nunn et al., 2005) and in spruce to $60 \text{ mmol m}^{-2} \text{ s}^{-1}$ (Nunn, unpubl. data) at Kranzberger Forst.

As previously shown, the range and daily course of G_C as derived from sap flow measurements agreed with G_C as calculated by a three-dimensional canopy gas exchange model or with the surface conductance derived from eddy covariance measurements (when accounting for soil evaporation and understory transpiration; Köstner et al., 2001). Assuming zero O_3 concentration at the mesophyll surface (cf. Laisk et al., 1989; Moldau et al., 1990), the whole-tree O_3 uptake was then calculated according to:

$$F_{O_3} = [O_3] G_C 0.613$$

where F_{O_3} is the foliage area-related whole-tree O_3 flux or uptake rate [$\text{nmol m}^{-2} \text{ s}^{-1}$], $[O_3]$ is the O_3 concentration of the ambient air [nl l^{-1}],

G_C is the foliage conductance for water vapor [$\text{mmol m}^{-2} \text{ s}^{-1}$; cf. Cowan, 1977], and 0.613 is the conversion factor accounting for the lower diffusivity of O_3 relative to water vapor in air (Nobel, 1983). Data analysis was based on daily, half-hour or 10-min means. At Kranzberger Forst, sap flow at breast height was initiated at approximately 2 h after sunrise (when stomata open in the foliage), indicating temporary use of the tree-internal water storage capacitance in crown transpiration (Schulze et al., 1985). This time shift relative to the onset of crown transpiration at sunrise was accounted for according to Matyssek et al. (2004) when calculating G_C . At Mt. Patscherkofel no such time delay in sap flow at breast height was observed, as tree foliation was present along the entire stem length (see above), and hence, water storage was drained at each stem position beginning at sunrise.

2.4. Statistics

Statistically significant differences ($p < 0.05$) between means were calculated using a univariate analysis (General Linear Model, SPSS 13.0, SPSS Inc., Chicago, USA). Response functions of G_C were derived from boundary line analysis, using $G_{C \text{ max}}$ of five trees per species for different Δw classes (step width: 1 Pa kPa^{-1}). Regressions in Figs. 3 and 4 were calculated with Sigma-Plot 9 (Systat Software, Erkrath, Germany). Differences between linear regressions in Figs. 3 and 4 were tested using an analysis of covariance (General Linear Model, SPSS 13.0).

3. Results

3.1. Whole-tree O_3 uptake at high water supply but different altitude

Quantification of whole-tree O_3 uptake will be demonstrated first for similarly humid conditions during August, i.e. of 1998 at Mt. Patscherkofel, and of 2002 and 2004 at Kranzberger Forst. Means of air temperature, VPD, Δw and PPFD_{sum} were considerably lower at Mt. Patscherkofel than at Kranzberger Forst, whereas precipitation at low elevation was variable relative to the timberline site (Table 1). At Mt. Patscherkofel, maximum and mean monthly O_3 concentrations were higher than at Kranzberger Forst. O_3 levels resulted in SUM0 (total sum of hourly O_3 concentrations) to be higher at Mt. Patscherkofel by 18–37% relative to those at Kranzberger Forst, whereas AOT40 at Kranzberg (accumulated O_3 dose over a threshold of $40 \mu\text{l l}^{-1}$ at daylight hours; global radiation $> 50 \text{ W m}^{-2}$) at the latter site could exceed the level assessed at high elevation (Table 1).

In spruce, mean G_C was about 3–5 times higher at the high than at the low altitude site (Table 2) so that the cumulative O_3 uptake (COU) was enhanced by a factor of about 2–3 at the timberline (Table 2). Regarding the deciduous tree species, larch at Mt. Patscherkofel displayed a mean G_C (foliage surface area-based) similar to that in beech at Kranzberger Forst (projected foliage area-based). Nevertheless, COU tended to be similar in both species or to be enhanced in beech at low altitude. In evergreen spruce, COU was about twice as high at the timberline as at low elevation.

3.2. Wind velocity and implications for boundary layers

The distinct difference in G_C and COU of spruce between the two sites may have resulted from the open stand structure

Table 1
Environmental data, including O₃ regimes, of August 2002, 2003 and 2004, respectively, at Kranzberger Forst and of August 1998 at Mt. Patscherkofel

	Year	Kranzberger Forst	Year	Mt. Patscherkofel
Mean air temperature at canopy height (24 m) [°C]	2002	17.3	1998	11.3
	2003	22.8		
	2004	19.0		
Mean VPD (at 24 m) [h Pa]	2002	4.2	1998	3.1
	2003	14.1		
	2004	5.0		
Mean Δw (at 24 m) [Pa kPa ⁻¹]	2002	4.4	1998	3.6
	2003	14.6		
	2004	5.2		
PPFD _{sum} [mol m ⁻²]	2002	779	1998	603
	2003	1194		
	2004	1121		
Precipitation [mm]	2002	165	1998	127
	2003	30		
	2004	84		
Soil moisture [vol.%] (Löw et al., in press)	2002	30	1998	>30
	2003	16		
	2004	20		
[O ₃] _{mean} [nl l ⁻¹]	2002	35	1998	47
	2003	59		
	2004	40		
[O ₃] _{max} [nl l ⁻¹]	2002	82	1998	120
	2003	183		
	2004	117		
SUM0 (at 24 m) [μl l ⁻¹ h]	2002	25.4	1998	34.9
	2003	43.0		
	2004	29.5		
AOT40 (at 24 m) [μl l ⁻¹ h]	2002	2.5	1998	3.2
	2003	10.3		
	2004	5.3		

VPD, water vapor pressure deficit of the air; Δw, leaf/air mole fraction difference of water vapor; PPFD_{sum}, sum of photosynthetic photon flux density; SUM0, total sum of hourly O₃ concentrations; AOT40, accumulated O₃ dose over a threshold of 40 nl l⁻¹ at daylight hours.

at the timberline so that the trees were exposed to higher wind velocities (up to 14 m s⁻¹) relative to the closed-canopy situation at Kranzberger Forst (about 2 m s⁻¹ on an average; Fig. 1). At the low elevation, wind velocity was ≤2 m s⁻¹ during 65% of the recorded time intervals, but >2 m s⁻¹ during 70% of the covered time period at Mt. Patscherkofel. Such latter conditions promote crown transpiration through shrinkage of boundary layers. Overall, soil moisture (being close to field capacity throughout summer at the timberline, Table 1; Wieser, 2004) appeared to govern G_C and COU in spruce. In contrast, the deciduous tree species (although one being a conifer) displayed similar G_C and COU at both sites, irrespective of the stand structure. As sap flow assessment inherently accounts for wind, and hence, boundary layer effects in reflecting transpiration and Δw within the canopy, COU is comparable between the two sites without further correction.

3.3. Whole-tree O₃ uptake at low elevation and variable water supply

August 2003 was driest (precipitation: 30 mm; soil moisture: 16 vol.%) and warmest (mean air temperature: 22.8 °C) at Kranzberger Forst relative to the corresponding months of 2002 or 2004 (Table 1). In August 2002, precipitation and soil moisture were highest and insolation lowest across the three years. August 2004 displayed moderate rainfall and lower soil moisture compared to 2002 and insolation similar to 2003. Consequently, SUM0 and AOT40 (both parameters representing external O₃ exposure) were highest in August 2003, whereas lowest SUM0 and AOT40 occurred in August 2002 (Table 1: SUM0 increased in 2003 by 69% and 46% relative to levels in 2002 and 2004, respectively).

Despite maximum SUM0 and AOT40 in August 2003, COU in spruce was highest in 2004 (Table 2). Spruce showed statistically significant reductions in COU in response to the extraordinary drought in 2003 (Table 1; cf. Löw et al., in press), resulting from reductions in xylem sap flow and G_C (Table 2). G_C was significantly lowered in 2003 by 70–80% compared to the levels in 2002 and 2004, respectively. Consequently, COU was significantly reduced in 2003 by 53% compared to the level in 2002, and by 71% relative to the uptake in 2004. In beech, however, COU during August did not differ statistically across the three years (Table 2). Although G_C was significantly reduced by about 50% in 2003, COU was lowered by only 20% and 36% relative to the levels in 2002 and 2004, respectively. Additionally, E_C was slightly enhanced in 2003 compared to the humid years (not statistically significant). This latter effect was incited by mean Δw being about three times higher than in 2002 and 2004 (Table 2). Beech did not reduce E_C under drought to the same extent as did spruce (Table 2; statistically significant for spruce).

O₃ flux in beech and spruce trees significantly depended on PPFD, Δw and the external O₃ concentration (see Fig. 2 for August 2003; *p* < 0.01; Spearman correlation). Radiation and Δw governed G_C and, hence, the O₃ influx into leaves. In 2003, O₃ influx was reduced, in addition, by restricted water availability (cf. Löw et al., in press) and high Δw during early August, but did not recover as Δw decreased during mid-August (Fig. 2). The decrease in Δw was caused by thunderstorms through a distinct drop in air temperature (from daily maxima of 35 °C to 22.5 °C). As Δw dropped, G_C max was reached in parallel, causing peak levels in O₃ flux (Fig. 2). Spruce had 10 times lower O₃ influx as compared to beech when based on the stomata-bearing leaf area each. In both species, O₃ influx was highest during the morning hours, even though O₃ exposure peaked during early afternoon, as G_C became limited under the restricted soil moisture and high Δw during the second half of the day.

3.4. Dependence of E_C and G_C on Δw at both altitudes

At Kranzberger Forst, the relationship between E_C and Δw differed in August between dry (2003) and humid conditions (2002, 2004; Fig. 3). Maximum E_C occurred across a broader

Table 2

Mean daily foliage area-related crown transpiration (E_C) and conductance (G_C) for water vapor in beech (*Fagus sylvatica*), spruce (*Picea abies*) and larch (*Larix decidua*) together with monthly cumulative O_3 uptake (COU) in August 2002, 2003 and 2004, respectively, at Kranzberger Forst and in August 1998 at Mt. Patscherkofel

	Year	Kranzberger Forst	Year	Mt. Patscherkofel	
<i>Beech</i> : mean daily E_C based on projected foliage area [$l\ m^{-2}$]	2002	11.6 ± 1.7^a			
	2003	14.0 ± 2.2^a			
	2004	12.7 ± 1.5^a			
<i>Spruce</i> : mean daily E_C based on total foliage surface area [$l\ m^{-2}$]	2002	2.7 ± 0.3^b			
	2003	2.0 ± 0.3^c			
	2004	3.9 ± 0.5^b			
<i>Beech</i> : mean daily G_C based on projected foliage area [$mmol\ m^{-2}\ s^{-1}$]	2002	46.7 ± 4.5^a	1998	52.0 ± 3.3	<i>Larch</i> *
	2003	24.6 ± 3.9^b			
	2004	49.0 ± 5.1^a			
<i>Spruce</i> : mean daily G_C based on total foliage surface area [$mmol\ m^{-2}\ s^{-1}$]	2002	10.1 ± 1.1^c	1998	51.5 ± 4.6	<i>Spruce</i> *
	2003	3.3 ± 0.5^d			
	2004	14.3 ± 1.8^c			
<i>Beech</i> : monthly COU based on projected foliage area [$mmol\ m^{-2}$]	2002	4.7 ± 0.5^a	1998	4.2	<i>Larch</i> *
	2003	3.7 ± 0.6^a			
	2004	5.8 ± 0.6^a			
<i>Spruce</i> : monthly COU based on total foliage surface area [$mmol\ m^{-2}$]	2002	1.1 ± 0.1^b	1998	3.5	<i>Spruce</i> *
	2003	0.5 ± 0.1^c			
	2004	1.7 ± 0.2^d			

Means \pm SE: $n = 4-5$ at Kranzberger Forst and $n = 2$ at Mt. Patscherkofel. Different letters denote statistically significant differences at $p < 0.05$ of E_C , G_C and COU between beech and spruce, and between August 2002, 2003 and 2004 at Kranzberger Forst (Univariate analysis, General Linear Model, SPSS 13.0).

* Based on total foliage surface area.

range of Δw in 2003 than in 2002 or 2004, both in beech and spruce. In both species, E_C reached its maximum during the humid years at around $\Delta w = 10\ Pa\ kPa^{-1}$ and declined with rising Δw . In 2003, maximum E_C was reached at around $\Delta w = 25\ Pa\ kPa^{-1}$, although E_C was high across nearly the entire range of Δw encountered during August (Fig. 3). Stomatal regulation reduced E_C at $\Delta w \leq 25\ Pa\ kPa^{-1}$ to below the levels of the humid years and kept E_C constant at $\Delta w > 25\ Pa\ kPa^{-1}$. Beech lowered the mean maximum E_C by about 20% in 2003, although the variation was large amongst trees (Fig. 3). In contrast, spruce responded more distinctly to drought, reducing mean maximum E_C by 50% and 75% compared to the levels in 2004 and 2002, respectively. Remarkably, the relationship between G_C and Δw did not differ in beech of Kranzberger Forst between the dry and humid conditions of 2003 and 2004, when comparing G_C across the same ranges of Δw between 2004 and 2003 ($p = 0.713$; Fig. 4A; Table 3A). Spruce, however, lowered G_C more sensitively in response to Δw under drought (2003) relative to humid conditions (2004, $p < 0.01$; Fig. 4A; Table 3A).

The responsiveness of G_C to Δw was similar, under humid conditions, in the spruce trees of Mt. Patscherkofel and Kranzberger Forst (in 2004, $p = 0.367$; Fig. 4A; Table 3A). Regarding the deciduous tree species, larch at the timberline responded to Δw less sensitively than did beech at low elevation, but more sensitively than did spruce ($p < 0.01$; Fig. 4A; Table 3A). Stomata of beech and spruce were somewhat less responsive to Δw at $> 15\ Pa\ kPa^{-1}$ under drought as compared to humid conditions (Fig. 4B). When normalizing G_C of the three tree species across the two sites (setting $G_C = 1$ at

$\Delta w = 10\ Pa\ kPa^{-1}$), the dependence on Δw did not differ amongst species, altitudes and years, including contrasting conditions of water availability ($p = 0.699$; Fig. 4C; Table 3B). Under severe drought, correlation between G_C and Δw was highest as expressed by a mono-exponential regression, whereas a linear fit resulted in higher R^2 under moist conditions (Table 3). Under such latter conditions, high Δw as occurring in 2003 was not reached at any time, preventing comparison of mono-exponential fits. Except for the minor differences addressed above, G_C and Δw followed, in total, a common relationship across the investigated tree species, altitudes and moisture conditions.

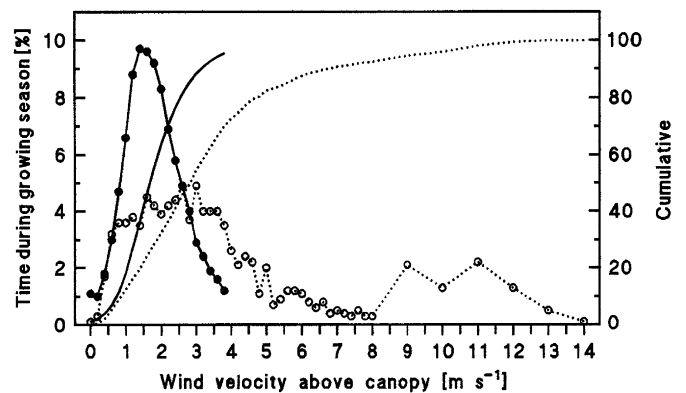


Fig. 1. Frequency distribution of above-canopy wind velocity and its accumulation during growing seasons at Kranzberger Forst (solid lines and closed symbols; means across 2001 and 2002) and Mt. Patscherkofel (open symbols and dotted lines, data of 1998).

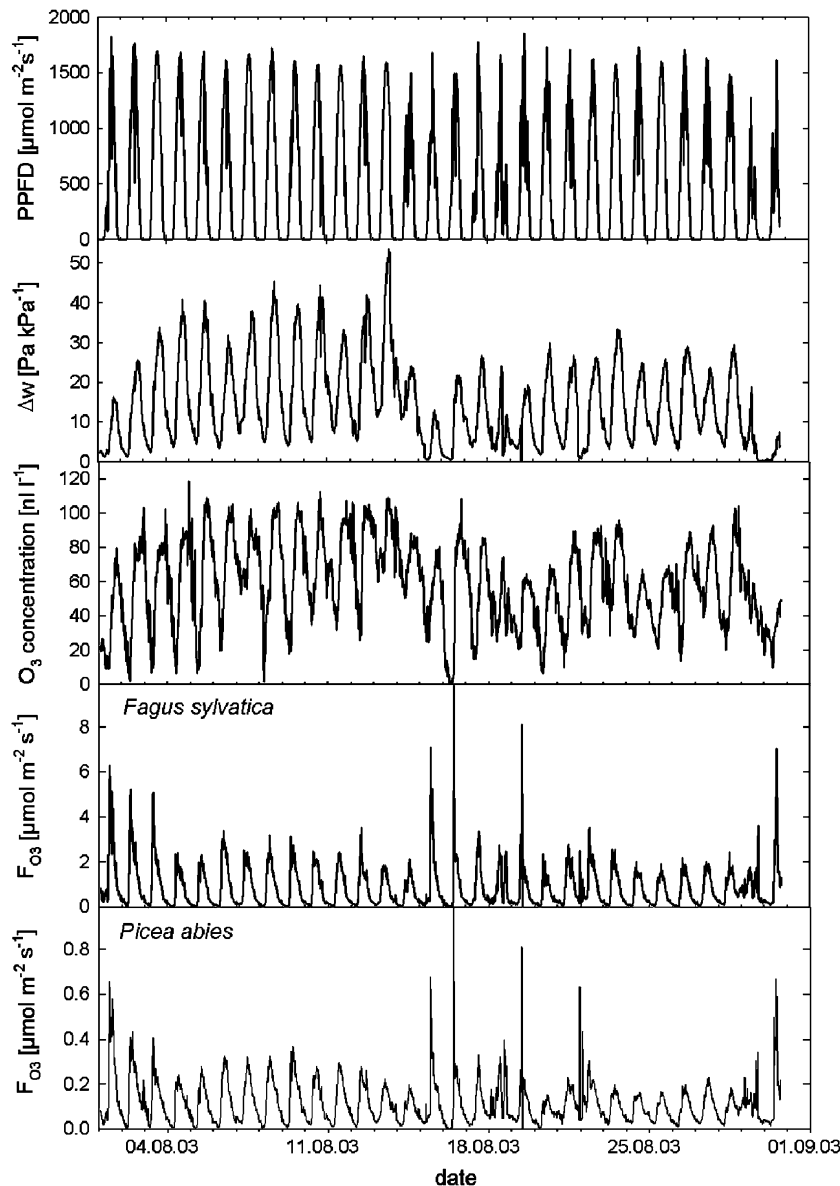


Fig. 2. Time courses for photosynthetic photon flux density (PPFD), leaf/air mole fraction difference of water vapor (Δw), O_3 concentration and whole-tree O_3 flux (F_{O_3}) of *Fagus sylvatica* and *Picea abies* in August 2003 at Kranzberger Forst. Note that the highest O_3 uptake rates (F_{O_3}) coincide with high O_3 concentrations and low Δw levels.

4. Discussion

4.1. Whole-tree O_3 uptake at different altitudes and water availability

COU was enhanced in spruce at high elevation (Mt. Patscherkofel), due to enhanced O_3 exposure, wind velocity, soil moisture and G_C at the timberline. G_C and COU of larch and beech were similar at both elevations. At the timberline, mean monthly Δw was considerably lower, while higher wind velocities prevailed than at low altitude (Fig. 1). At the same Δw , the reduced boundary layers (at high wind velocity) were conducive to enhanced G_C and COU at high elevation as compared to the low-elevation site, as boundary layer effects are inherently accounted for when deriving COU from sap

flow assessment. High G_C appeared to be favored at the timberline also through the open stand structure (enhanced light supply) and permanently high soil water availability (Table 1; Wieser, 2004).

The low-elevation site (Kranzberger Forst) suffered from the exceptional summer drought in 2003 (Ciais et al., 2005), as reflected in decreased annual stem increment in both beech and spruce (Nunn, 2005; Wipfler et al., 2005; Löw et al., in press). The severe drought in August 2003 had forced stomata to close (Löw et al., in press), hence sap flow, E_C and, as a consequence, COU were restricted in beech and spruce in relation to the increases in SUM0 and AOT40. Deriving whole-tree O_3 uptake from sap flow assessment reflected the influence of the reduced water availability in 2003 on crown transpiration and stomata: the drought-induced decline in G_C limited the

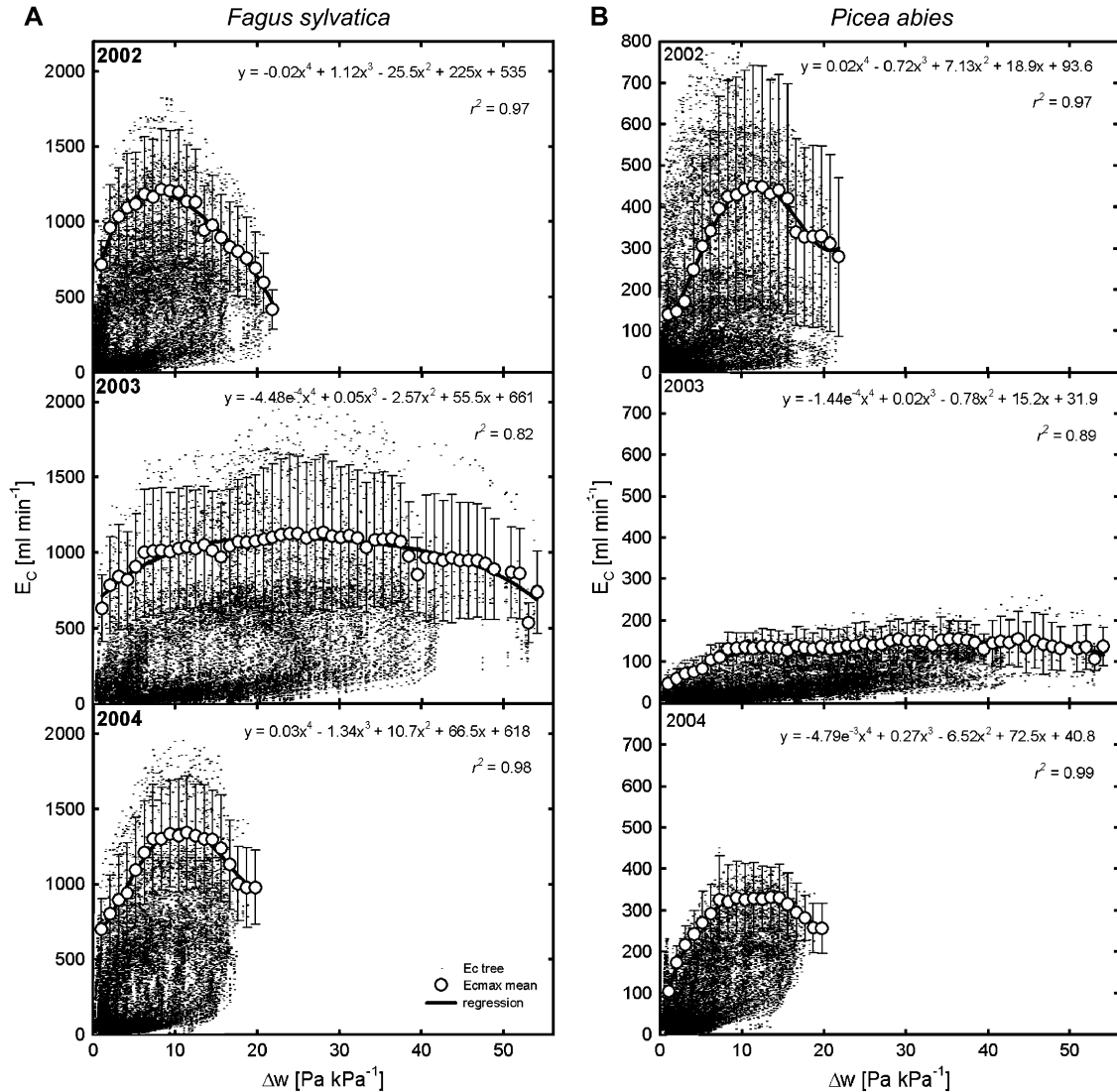


Fig. 3. Dependence of foliage area-related crown transpiration (E_C) on leaf/air mole fraction difference of water vapor (Δw) in (A) *Fagus sylvatica* and (B) *Picea abies* during August 2002, 2003 and 2004, respectively, at Kranzberger Forst. Response functions of $E_{C\max}$ derived from boundary line analysis, using mean $E_{C\max}$ of five trees per species for different Δw classes (step width: 1 Pa kPa⁻¹). Dots represent actual measurements, white circles display mean $E_{C\max} \pm SE$ for each Δw class ($n = 4-5$). Regressions calculated with SigmaPlot 9.

whole-tree COU of spruce and beech to levels lower than in 2002 and 2004, although O₃ exposure (SUM0) was enhanced in 2003. Sap flow assessment reflected impacts of soil moisture and Δw on COU across the three study years, while different extents of responsiveness to drought became evident in beech and spruce. No further data correction of boundary resistance or parameterization of soil moisture effects on COU were required, using the demonstrated empirical approach, as opposed to modeling stomatal conductance for COU assessment (Nunn et al., 2005; Emberson et al., 2000).

4.2. Dependence of E_C and G_C on Δw

The relationship between E_C and Δw differed at Kranzberger Forst between humid and dry conditions (Fig. 3), with spruce reducing maximum E_C by about 75%, and beech by 20% under drought. Leuzinger et al. (2005) did not find

severe drought effects in beech during the summer of 2003, either. Beech trees, in their study, reached maximum E_C between $\Delta w = 15-20$ Pa kPa⁻¹ and reduced E_C by stomatal closure at $\Delta w > 22$ Pa kPa⁻¹. In the present study, beech maintained high E_C up to $\Delta w = 35$ Pa kPa⁻¹ (Fig. 3A). Similar to beech and spruce at Kranzberger Forst, trees of *Quercus petraea*, *Carpinus betulus* and *F. sylvatica* investigated by Leuzinger et al. (2005) followed a polynomial dependence of E_C on Δw . The relationship between E_C and Δw appears to be similar across species, even in the presence of drought (including the study by Hölscher et al., 2005 on beech). Similar conclusions were reported from conifers in the Austrian Alps (Wieser, 1999, 2002).

Spruce at Kranzberger Forst showed a greater decline of G_C in relation to Δw under drought (Fig. 4A; Table 3A), whereas beech did not change its G_C response across variable water availability (Fig. 4A; Table 3A). In *Vitis vinifera*, Lu et al.

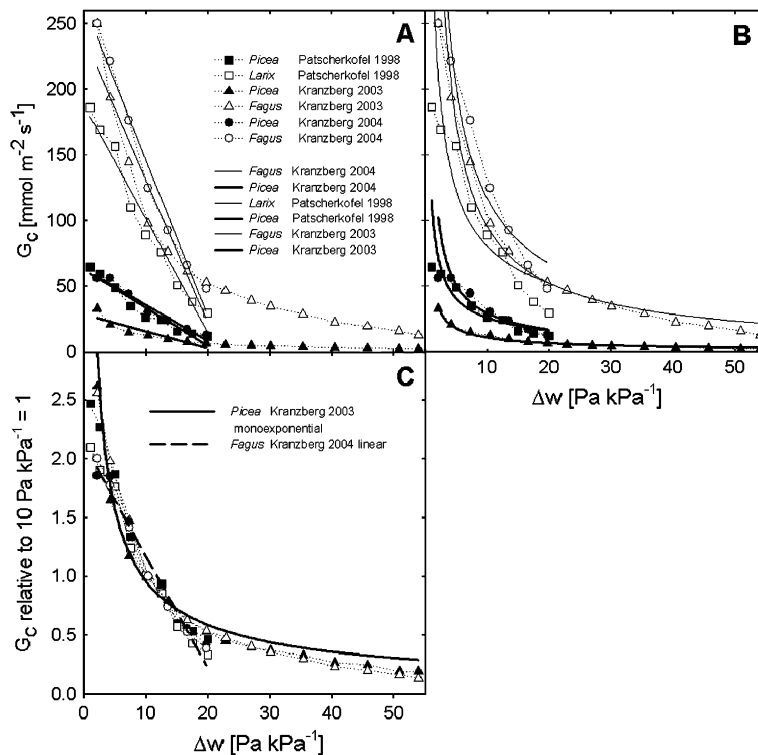


Fig. 4. (A) Dependence of foliage area-related crown conductance (G_C) on leaf/air mole fraction difference of water vapor (Δw) in *Fagus sylvatica* and *Picea abies* during August 2003 and 2004, respectively, at Kranzberger Forst and in *Larix decidua* and *Picea abies* during August 1989 at Mt. Patscherkofel. Response functions of G_C derived from boundary line analysis, using $G_{C \max}$ of 2–5 trees per species for different Δw classes (step width: 1 Pa kPa⁻¹). Symbols represent mean maximum G_C for each Δw class ($n = 2–5$). Regressions calculated with a linear response curve for the Δw range of 2004. (B) Regressions calculated with a mono-exponential response curve for the whole Δw range available from the different years, otherwise as (A). (C) Dependence of normalized G_C (foliage area-related crown conductance) on Δw (leaf/air mole fraction difference of water vapor) of the three investigated tree species and site conditions ($G_C = 1$ at $\Delta w = 10$ Pa kPa⁻¹). Only regression lines for *Picea abies* Kranzberger Forst 2003 and *Fagus sylvatica* Kranzberger Forst 2004 are exemplified. Regressions calculated with SigmaPlot 9.

(2003) found a negative exponential correlation between G_C and Δw , which was similar to the responses reported from the present study. Martinez-Vilalta et al. (2003) used a logarithmic regression for the relation between G_C and Δw in *Arbutus unedo*, *Phillyrea latifolia* and *Quercus ilex*. They reported on a greater decline of G_C in relation to Δw in drought-stressed *A. unedo* during early to late summer as compared to control trees, even though maximum E_C was similar across treatments. In the present study, only the stomatal responsiveness of spruce was consistent, under drought, with that of drought-stressed *A. unedo* (Fig. 4A). A common relationship between G_C and Δw became evident, in the present study, across different species, altitudes and moisture conditions (Fig. 4B; Table 3B), rendering the sap flow-based determination of O_3 uptake an attractive tool in mechanistic O_3 risk assessment both at the tree and – in combination with stand density data – at the stand level (cf. Matyssek et al., 2007; Wieser et al., 2006).

4.3. Applicability of the sap flow-based approach of whole-tree O_3 flux assessment

The present study demonstrated the empirical sap flow-based COU assessment to be independent of specific corrections under drought as compared to modeling O_3 uptake for

the same study trees (see Nunn et al., 2005). As boundary layers within the canopy are intrinsically accounted for by the empirical approach, crown-level COU is valid under the prevailing stand conditions (i.e. no need for considering non-stomatal O_3 deposition). Lu et al. (2003) found G_C to reach only about one-third of the levels of stomatal conductance as assessed by porometry on sunlit leaves, and Kurpius and Goldstein (2003) reported stomatal O_3 uptake to make up only 25–35% of the total O_3 deposition, when comparing sap flow with eddy covariance measurements.

Typically, an offset occurs between the time courses of E_C and xylem sap flow in the trunk, as the sap flow at breast height is initiated with some delay: about 0.5–3 h after sunrise on sunny days (Lu et al., 2003; Matyssek et al., 2004; Patzner, 2004; Ewers et al., 2005; 30–40 min after total solar eclipse, Häberle et al., 2001), depending on the capacitance for water storage in the tree (Jarvis, 1976; Schulze et al., 1985; Tyree and Zimmermann, 2002). At the timberline ecotone of Mt. Patscherkofel, no such time lag was observed (Wieser et al., 2003a), which perhaps is a consequence of the open canopy structure that allows branching and foliation down to the forest floor and, by this, an immediate drain of water reserves in the trunk at sunrise. Matyssek et al. (2004) suggested to account for time lags in sap flow-derived E_C assessment by correcting the diurnal course of sap flow by the offset in time between the

Table 3

Regressions for (A) dependence of foliage area-related crown conductance (G_C) on leaf/air mole fraction difference of water vapor (Δw) in *Fagus sylvatica* and *Picea abies* during August 2003 and 2004, respectively, at Kranzberger Forst (KF) and in *Larix decidua* and *Picea abies* during August 1989 at Mt. Patscherkofel and (B) dependence of normalized G_C (foliage area-related crown conductance) of the three investigated tree species on Δw (leaf/air mole fraction difference of water vapor) and on site conditions ($G_C = 1$ at $\Delta w = 10 \text{ Pa kPa}^{-1}$)

		Linear	Mono-exponential
(A) Absolute G_C			
<i>Picea abies</i>	Mt. Patscherkofel	$-2.89x + 62.6^a$ $R^2 = 0.98$	$115.6x^{-0.65}$ $R^2 = 0.98$
	KF 2003	$-1.28x + 28.5^b$ $R^2 = 0.94$	$56.4x^{-0.71}$ $R^2 = 0.99$
	KF 2004	$-2.74x + 63.3^a$ $R^2 = 0.99$	$183.2x^{-0.79}$ $R^2 = 0.98$
<i>Larix decidua</i>	Mt. Patscherkofel	$-8.65x + 188.0^c$ $R^2 = 0.99$	$329.7x^{-0.61}$ $R^2 = 0.96$
<i>Fagus sylvatica</i>	KF 2003	$-10.80x + 239.5^{cd}$ $R^2 = 0.97$	$704.7x^{-0.87}$ $R^2 = 0.99$
	KF 2004	$-11.85x + 264.8^d$ $R^2 = 0.99$	$724.1x^{-0.79}$ $R^2 = 0.98$
(B) Normalized G_C ($G_C = 1$ at $\Delta w = 10 \text{ Pa kPa}^{-1}$)			
<i>Picea abies</i>	Mt. Patscherkofel	$-0.11x + 2.39^a$ $R^2 = 0.98$	$2.77x^{-0.42}$ $R^2 = 0.95$
	KF 2003	$-0.10x + 2.26^a$ $R^2 = 0.94$	$4.47x^{-0.71}$ $R^2 = 0.99$
	KF 2004	$-0.09x + 2.08^a$ $R^2 = 0.99$	$3.00x^{-0.49}$ $R^2 = 0.95$
<i>Larix decidua</i>	Mt. Patscherkofel	$-0.10x + 2.12^a$ $R^2 = 0.99$	$2.37x^{-0.40}$ $R^2 = 0.94$
<i>Fagus sylvatica</i>	KF 2003	$-0.11x + 2.45^a$ $R^2 = 0.97$	$4.60x^{-0.69}$ $R^2 = 0.98$
	KF 2004	$-0.09x + 2.12^a$ $R^2 = 0.99$	$3.24x^{-0.53}$ $R^2 = 0.96$

Regressions calculated with SigmaPlot 9. Different letters denote statistically significant differences at $p < 0.01$ of absolute and normalized G_C each across species, sites and years (analysis of covariance, General Linear Model, SPSS 13.0).

onsets of E_C in the crown (at sunrise) and of sap flow at breast height. Such a time correction of E_C (and hence, G_C and COU) was readily employed to the trees at the low-elevation site and needs to be performed whenever time lags occur between sunrise and the onset of sap flow through the stem basis.

Attention is also required when assessing G_C at $\Delta w < 1 \text{ Pa kPa}^{-1}$, which is a common situation at night and on rainy days. Here, $G_{C \text{ min}}$ was determined as 10% of the mean maximum G_C . Ewers et al. (2005) calculated G_C only at $\Delta w > 0.6 \text{ Pa kPa}^{-1}$ to keep measurement errors below 10%. Martinez-Vilalta et al. (2003) excluded measurements at low Δw and used daily means of E_C and Δw to calculate G_C . Lu et al. (2003) reported G_C to linearly depend in the morning on irradiance rather than Δw at global radiation $< 200 \text{ W m}^{-2}$ so that within this latter range a response function of G_C to radiation was implemented.

In conclusion, whole-tree O_3 uptake can readily be assessed on the basis of sap flow measurement without requiring

specific correction of drought or boundary layer effects, while database requirements are low, as only Δw (derived from VPD and air pressure) needs to be considered as input variable along with O_3 and sap flow data. This empirical approach represents a promising tool for the validation of modeling O_3 uptake and O_3 risk for forest trees and ecosystems (Tuovinen et al., 2001). Remarkably, forest trees of contrasting foliage type, autecology and site altitude above sea level followed similar relationships between whole-tree transpiration, canopy conductance and COU. Unifying findings on functional relationships (as shown in this paper for Central Europe) will promote the cause–effect based O_3 risk assessment (Matyssek et al., in this volume) and the practicability of related mechanistic modeling.

Acknowledgments

We are grateful to Dr. H. Werner, C. Heerd, Prof. P. Fabian (Bioclimatology, TUM) for providing environmental background and O_3 data. We gratefully acknowledge the skilful technical assistance of Dipl. Ing. T. Feuerbach and I. Süß. The investigations were funded by “Deutsche Forschungsgemeinschaft” (DFG) through SFB 607 “Growth and Parasite Defence – Competition for Resources in Economic Plants from Agronomy and Forestry”. Dr. A.J. Nunn was supported by an HWP II fellowship “Chancengleichheit für Frauen in Forschung und Lehre”.

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