

Upscaling Ozone Flux in Forests from Leaf to Landscape

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Summary

Although stomatal conductance for ozone (O_3) correlates with leaf to air water vapor difference (VPD_{LA}) at the leaf level, uncertainty in up-scaling to the whole tree level can be overcome by means of sap flow measurements at the tree trunk. Further up-scaling to the stand level is possible by relating whole tree O_3 flux to silvicultural and/or tree-allometric data. In such a way, canopy conductance and O_3 uptake can be related to ground surface area. When normalized, canopy conductance is demonstrated to follow a functional relationship to VPD_{LA} across several forest ecosystems thus allowing a generalization of model approaches. Further up-scaling to the landscape level, however, needs further investigations due to differences in the response of canopy conductance to environmental drivers in forest stands and grassland ecosystems, respectively.

Key-words: Ozone uptake, trees, forest, stand, grassland, up-scaling.

1. Introduction

Analysis of ozone (O_3) impact on vegetation requires knowledge of site-specific O_3 formation, transport, and uptake by the foliage. Crucial O_3 fluxes are non stomatal deposition, including deposition on external surfaces (soil, bark and leaf), reactions with air volatiles (Cieslik, 2004), and, in particular, stomatal deposition, i.e. absorption or uptake through the stomata into the leaf mesophyll (Wieser, 2002; Matyssek et al., 2007).

Foliage is the primary site of O_3 uptake (Wittmann et al., 2007), as stomata represent the interface of this uptake with the atmosphere. Assessment of O_3 uptake by plants is important because only the amount of O_3 absorbed

through the stomata into the leaf mesophyll represents the “phytomedically” relevant O_3 dose, which may affect molecular/biochemical, (eco-) physiological and, eventually, growth processes (Matyssek and Sandermann, 2003; Wieser and Tausz, 2006; Wieser and Matyssek, 2007; Matyssek et al., 2007). Duyzer et al. (1995) and Munger et al. (1996) demonstrated O_3 deposition in forest ecosystems to relate to stomatal conductance, indicating the stomatal pathway to govern O_3 uptake also at the stand level (Bortier et al., 2000). The degree of stomatal opening, however, is controlled by physiological processes, predominantly imposed by irradiance, evaporative demand of the atmosphere and soil water availability (Wieser, 2002; Matyssek et al.,

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2004; Nunn et al., 2005; Löw et al., 2006). In total, the apparent O₃ uptake of stands is determined, apart from stomatal regulation, by the foliage area at a specific site, as expressed, e.g., by the leaf area index (LAI; Nunn et al., 2007).

Given the dependence of O₃ risk of vegetation on the amount of O₃ taken up by the foliage it is the aim of this paper to examine recent progress in up-scaling O₃ uptake from the leaf to the stand and landscape level, respectively.

2. Scaling from the leaf to the tree and stand levels

The traditional focus of plant ecophysiology, i.e. understanding how plants cope with often stressful habitats (incl. exposure to O₃), is organism centred. Predicting and analysing the structure and function of ecological systems on larger spatial and temporal scales are research challenges of high importance, but of great difficulty. Estimating O₃ flux via the stomata into intact leaves by gas exchange measurements (section 2a.) is the primary stage for further up-scaling to the tree, stand and landscape level. Then we will bring in the use of the sap flow technique as a tool for up-scaling to the whole tree and the stand level. We will also focus on the combination of the eddy covariance technique with the sap flow approach for validating non-stomatal O₃ deposition (section 2b). Finally, possible differences in the O₃ flux between forests and grassland ecosystems will be highlighted (section 2c).

2.1 Assessment of ozone uptake at the leaf level

The stomatal O₃ flux as a proportion to the total flux into stands (Wang et al., 1995; Winner, 1994) can quantitatively be related to the leaf level and derived from cuvette or fumigation chamber studies, using a mass-balance approach (Havranek and Wieser, 1989, 1994; Skärby et al., 1987; Wang et al., 1995). Total O₃ flux is calculated from the difference between the O₃ concentration at chamber inlet and outlet, as multiplied by the air flow rate. As this approach provides O₃ deposition both on leaves and chamber walls, O₃ fumigations with empty chambers need to be operated as a control to assess the chamber sink strength for O₃ deposi-

tion (Matyssek et al., 1995; Wieser, 2002). Still, by adopting this approach, the stomatal O₃ influx cannot be distinguished from the non-stomatal O₃ deposition at the leaf level, unless measurements are also carried out after stomatal closure (Grulke et al., 2007).

The stomatal O₃ influx is typically derived from leaf-level gas exchange measurements, employing the *water vapour surrogate method* (e.g. Matyssek et al., 1995). This method makes use of stomatal conductance for water vapour (G_{H₂O}), which is calculated from the leaf transpiration rate and the gradient of vapour pressure inside the intercellular spaces to that of the ambient air surrounding the leaf. Once G_{H₂O} is known, stomatal O₃ flux into the leaf mesophyll results as:

$$FO_3 = (O_a - O_i) * G_{O_3},$$

upon exchanging, in stomatal conductance, the diffusion coefficient of water vapour (cf. Cowan, 1977; Nobel, 1983) against that of ozone (i.e. G_{O₃} = G_{H₂O} * 0.613; Laisk et al., 1989). FO₃ is the flux or uptake rate of O₃ into the leaves; O_a and O_i are the mole fractions of ozone in air outside the leaf and within the leaf-intercellular space, respectively. As O_i approaches nil in the leaf-intercellular space (Laisk et al., 1989; Moldau et al., 1990), given the rapid decomposition of O₃ into oxidative derivatives in the intercellular air space and apoplast (cf. low mesophyll resistance to O₃, Runeckles, 1992), FO₃ is governed by G_{O₃} and O_a. Passage of O₃ across the cuticle is negligible, as the cuticle's high diffusion resistance to O₃ is high relative to that of open stomata (Kerstiens and Lenzian, 1989).

In general, O₃ uptake derived from gas exchange measurement is in good agreement with assessments based on the chamber inlet/outlet approach of differential O₃ concentrations (see above), as shown for *Fagus sylvatica* in figure 1. Similar results were obtained for *Larix decidua* (Wieser, 2002), *Picea abies* (Dobson et al., 1990; Polle et al., 1995; Wieser and Havranek, 1993) and *Populus spp.* (Wang et al., 1995). However, O₃ uptake rates based on the chamber approach tend to be higher than those derived from leaf-level gas exchange, in Figure 1 by about 0.8 nmol m⁻² s⁻¹. This difference is attributable to non-stomatal O₃ deposition on external leaf and

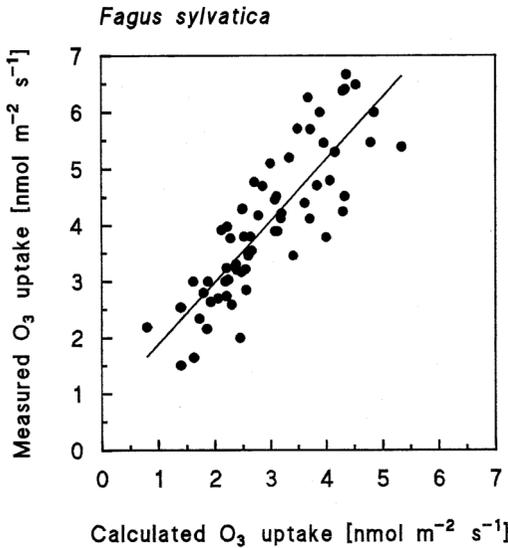


Figure 1. Correlation between calculated and measured ozone uptake rates in leaves of *Fagus sylvatica*. Each point represents a daily mean value taken from 65 diurnal courses of shoot gas exchange measured continuously during the growing season 2004 at Kranzberg Forest. The points were fitted by the linear regression: $y = 1.096x + 0.78$; $r^2 = 0.71$; $p < 0.001$.

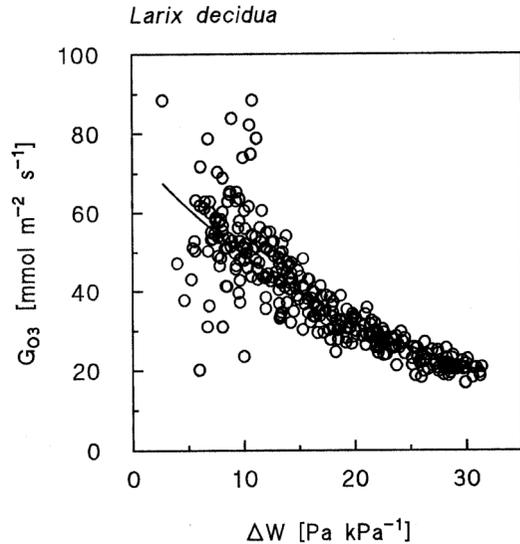


Figure 2. Stomatal conductance for ozone (G_{O_3}) of *Larix decidua* needles in relation to leaf to air vapour pressure difference (Δw). Data are half hour means obtained at Mt. Patscherkofel (1950 m a.s.l.) at a photosynthetic photon flux density $< 600 \mu\text{mol m}^{-2}\text{s}^{-1}$. Points were fit by exponential regression: $y = 79 \cdot \exp(-0.045x)$; $r^2 = 0.71$ (Wieser unpublished).

twig surfaces, which cannot be resolved by the chamber approach (see above). Conversely, boundary layers are destroyed by leaf-level gas exchange assessments, which typically affect O_3 uptake (Wieser et al., 2003), tending to overestimate stomatal O_3 deposition. Nevertheless, as at the leaf level the influence of environmental factors on stomatal aperture, and hence also on FO_3 , became evident (Fig. 2; Wieser and Havranek, 1993, 1995; Wieser et al., 2000), this approach provided the basis for modelling O_3 flux as a tool in risk assessment (e.g. Emberson et al., 2000; Tuovinen et al., 2007). Such models, however, need a species- and site-specific parameterisation, especially with respect to maximum stomatal conductance, evaporative demand and soil water availability (Wieser and Emberson, 2004; Nunn et al., 2005)

2.2 Upscaling o_3 flux from trees to forest stands

Since transpiration and O_3 flux into the foliage are coupled through stomatal regulation, sap flow techniques (cf. Cermak et al., 1973; Sakuratani, 1981; Granier et al., 1985) that determine crown transpiration can be used to assess stomatal O_3 flux at the tree level (Wieser et al., 2003;

Matyssek et al., 2004; Nunn et al., 2007). Whole-tree O_3 uptake rates combined with stand density data (cf. Cermak et al., 2004) so that stomatal stand-level O_3 uptake can be expressed per unit of ground area (Wieser et al., 2006a; Matyssek et al., 2007). As an example, the seasonal course of environmental parameters, daily mean canopy conductance for O_3 and FO_3 of a subalpine *Pinus cembra* forest are shown in figure 3. Cumulative O_3 uptake (COU) during the growing season was 140 mmol m^{-2} ground area, which corresponds to COU of 13.8 mmol m^{-2} on a total needle surface area basis (leaf area index, LAI, 10.1 m^2 total surface area per m^2 ground surface area). As only minor boundary layer effects prevailed under the open-canopy conditions of this timberline forest, the leaf-level COU is in good agreement with that of 14 mmol m^{-2} obtained in the same forest at the needle level by the cuvette technique (Wieser et al., 2000). Quantitative clarification, however, is needed for closed-canopy forest conditions. Nevertheless, as $\text{COU}_{\text{leaf}} = \text{COU}_{\text{stand}} / \text{LAI}$, data as shown in figure 3 will enable the validation of models which are currently used in risk assessment, where $\text{COU}_{\text{leaf}} = \text{cumulative}$

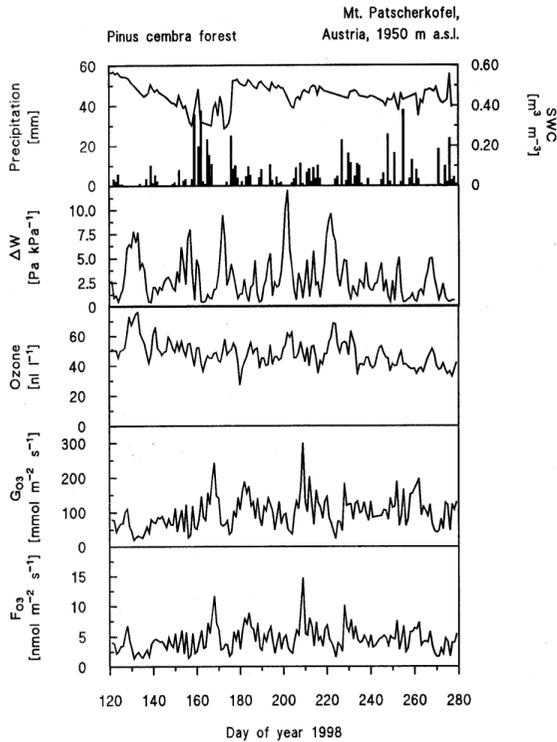


Figure 3. Time course of daily sum of precipitation, daily mean soil water content (SWC), mean leaf to air vapour pressure difference (Δw), mean ambient ozone concentration [O_3], ground-area scaled daily mean canopy conductance for ozone [G_{O_3}], and ground-area scaled daily ozone uptake rate [F_{O_3}] in a subalpine *Pinus cembra* forest (stand density 1038 trees ha⁻¹, stand basal area 47.6 m² ha⁻¹, LAI 10.1 m² total surface area per m² ground surface area) during 28 April through 6 October 1998 (Wieser unpublished).

ozone uptake at the leaf level and $COU_{\text{stand}} =$ cumulative ozone uptake at the stand level

The acceptance of sap-flow derived whole-tree O_3 uptake for risk assessment on a routine basis will depend on model applications, which should preferably not become too complex for practical use (Matyssek et al., 2007; Emberson et al., 2000). One step towards simplification is the finding, that the dependence of canopy conductance (G_C) on leaf to air vapour pressure difference (VPD_{LA}) obeys a similar relationship across a wide range of contrasting tree species and site conditions (Nunn et al., 2007; cf. also Schulze and Hall, 1982) and even entire forest stands (Fig. 4). Furthermore, normalizing the relationship between canopy conductance and VPD_{LA} by setting G_c in each stand to 100 % at a VPD_{LA} of 10 Pa kPa⁻¹ allows to derive one

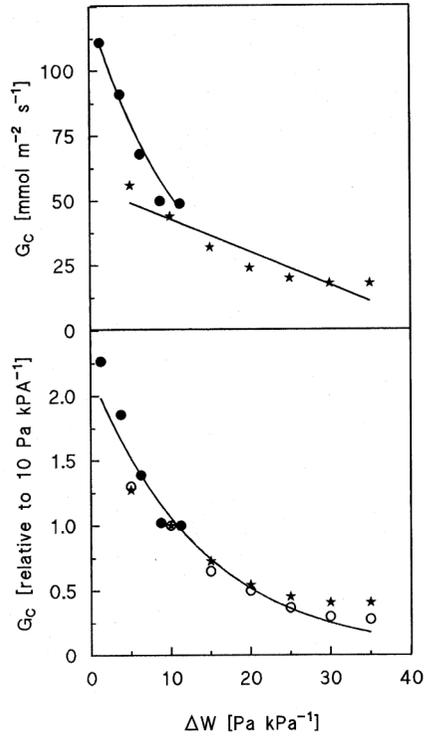


Figure 4. Absolute and relative canopy conductance of a *Pinus cembra* forest (●) at Mt. Patscherkofel, south of Innsbruck, Austria (1950 m a.s.l.), a *Pinus canariensis* (★) forest in the Mountains of La Victoria, Tenerife (1650 m a.s.l.), and *Populus tremuloides* (○) forest in Prince Albert National Park, central Saskatchewan, Canada in relation to leaf to air vapour pressure difference (Δw). Relative data were fit by the mono-exponential equation $y = 2.19 \cdot \exp(-0.073x)$; $r^2 = 0.94$. Redrawn after data from Wieser et al., 2006b (*P. cembra* and *P. canariensis*), and Hogg and Hurdle, 1997 (*P. tremuloides*).

common underlying, exponential function (Fig. 4) also obtained at the entire tree (Nunn et al., 2007) and the leaf level (Wieser, 2002).

The sapflow-based O_3 flux assessment may be combined with eddy covariance techniques (Duyzer et al., 1995; Mikkelsen et al., 2000; Zeller and Nikolov, 2000). These latter techniques in combination with measuring profiles of O_3 levels in stands inherently assess the total O_3 flux, i.e. the sum of stomatal and non-stomatal O_3 deposition at the stand level (Zeller and Nikolov, 2000). Then, the resistance analogy is used to calculate stomatal O_3 fluxes (Cieslik, 2004). In addition, when combining eddy covariance and sapflow approaches (the latter upon upscaling stomatal O_3 flux to the stand level, see above), the non-stomatal O_3 deposition at the stand level, which is crucial for validating

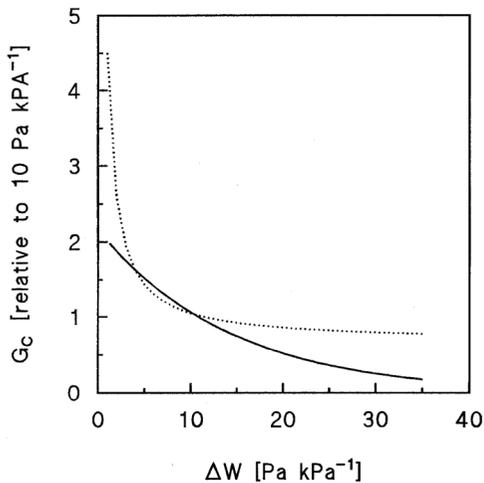


Figure 5. Relative conductance of forests (solid line; from Fig. 4) and grasslands (dotted line; after data from Wieser 1983) in relation to leaf to air vapour pressure difference (Δw).

current flux-based O_3 risk models, can be derived empirically as the difference between the respective outcomes of the two approaches.

2.3 From forests to landscape

The eddy covariance technique (Wohlfahrt, 2004; Hammerle et al., 2007) as well as weighing lysimeters (Wieser, 1983; Scott et al., 2002) can also be used for short or annual vegetations, such as grassland ecosystems, to assess stand-level transpiration and hence derive canopy conductance and FO_3 . However, as depicted in figure 5, forests and grasslands may differ in their dependence of G_c on VPD_{LA} . Such differences may be attributed to contrasting canopy structure and roughness of tall forests versus low-stature grasslands, and hence, coupling of transpiration with the atmosphere. In addition, differences in leaf mass ratio (LMR) (forests having more unfavourable LMR than grasslands) may also influence uptake and loss of water, and hence, stomatal response in particular to VPD_{LA} (Fig. 5) and soil water availability. Therefore, differential uptake characteristics of ozone are likely to exist in forests and grasslands, although this issue still demands for clarification.

3. Conclusions

The sap-flow based estimation of O_3 flux represents a novel tool for estimating the actual O_3

dose taken up by the foliage of entire trees and forest stands under actual site conditions. In addition, common underlying relationships between G_c and environmental parameters may foster plain, process-based model development of O_3 uptake with respect to risk assessment in forests and grassland ecosystems. Furthermore, such data can be used for the parameterisation and the validation of O_3 uptake models (Wieser and Emberson, 2004; Deckmyn et al., 2007). However, further research is needed to clarify the differences in the response of G_c to environmental factors between forests and grasslands in order to merge O_3 flux measurements in forest, semi-natural and crop ecosystems as at the landscape level each of these vegetation types has to be integrated into one common modelling approach.

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