Upscaling Ozone Flux in Forests from Leaf to Landscape

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Summary
Although stomatal conductance for ozone (O3) 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 O3 flux to silvicultural and/or tree-alometric data. In such a way, canopy conductance and O3 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 (O3) impact on vegetation requires knowledge of site-specific O3 formation, transport, and uptake by the foliage. Crucial O3 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 O3 uptake (Wittmann et al., 2007), as stomata represent the interface of this uptake with the atmosphere. Assessment of O3 uptake by plants is important because only the amount of O3 absorbed through the stomata into the leaf mesophyll represents the “phytomediately” relevant O3 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 O3 deposition in forest ecosystems to relate to stomatal conductance, indicating the stomatal pathway to govern O3 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 O_3 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 O_3 risk of vegetation on the amount of O_3 taken up by the foliage it is the aim of this paper to examine recent progress in up-scaling O_3 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 O_3), 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 O_3 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 O_3 deposition (section 2b). Finally, possible differences in the O_3 flux between forests and grassland ecosystems will be highlighted (section 2c).

2.1 Assessment of ozone uptake at the leaf level

The stomatal O_3 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 O_3 flux is calculated from the difference between the O_3 concentration at chamber inlet and outlet, as multiplied by the air flow rate. As this approach provides O_3 deposition both on leaves and chamber walls, O_3 fumigations with empty chambers need to be operated as a control to assess the chamber sink strength for O_3 deposition (Matyssek et al., 1995; Wieser, 2002). Still, by adopting this approach, the stomatal O_3 influx cannot be distinguished from the non-stomatal O_3 deposition at the leaf level, unless measurements are also carried out after stomatal closure (Grulke et al., 2007).

The stomatal O_3 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 O_3 flux into the leaf mesophyll results as:

\[
F_{O_3} = (O_a - O_i) \times G_{O_3}
\]

upon exchanging, in stomatal conductance, the diffusion coefficient of water vapour (cf. Cowan, 1977; Nobel, 1983) against that of ozone (i.e. G_{O_3} = G_{H2O} \times 0.613; Laisk et al., 1989). F_{O_3} is the flux or uptake rate of O_3 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 O_3 into oxidative derivatives in the intercellular air space and apoplast (cf. low mesophyll resistance to O_3, Runeckles, 1992), F_{O_3} is governed by G_{O_3} and O_a. Passage of O_3 across the cuticle is negligible, as the cuticle’s high diffusion resistance to O_3 is high relative to that of open stomata (Kerstiens and Lendzian, 1989).

In general, O_3 uptake derived from gas exchange measurement is in good agreement with assessments based on the chamber inlet/outlet approach of differential O_3 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, O_3 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 O_3 deposition on external leaf and
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; Sakurataki, 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 COU$_{\text{leaf}}$ = COU$_{\text{stand}}$ /LAI, data as shown in figure 3 will enable the validation of models which are currently used in risk assessment, where COU$_{\text{leaf}}$ = cumulative
ozone uptake at the leaf level and \( \text{COU}_{\text{stand}} = \) cumulative ozone uptake at the stand level

The acceptance of sap-flow derived whole-tree \( \text{O}_3 \) 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 (\( \Delta w \)), mean ambient ozone concentration [\( \text{O}_3 \)], ground-area scaled daily mean canopy conductance for ozone \( [G_{cO_3}] \), and ground-area scaled daily ozone uptake rate \( [F_{\text{O}_3}] \) in a subalpine \( \text{Pinus cembra} \) forest (stand density 1038 trees ha\(^{-1} \), stand basal area 47.6 m\(^2\) ha\(^{-1} \), LAI 10.1 m\(^2\) total surface area per m\(^2\) ground surface area) during 28 April through 6 October 1998 (Wieser unpublished).

The sap-flow-based \( \text{O}_3 \) 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 \( \text{O}_3 \) levels in stands inherently assess the total \( \text{O}_3 \) flux, i.e. the sum of stomatal and non-stomatal \( \text{O}_3 \) deposition at the stand level (Zeller and Nikolov, 2000). Then, the resistance analogy is used to calculate stomatal \( \text{O}_3 \) fluxes (Cieslik, 2004). In addition, when combining eddy covariance and sapflow approaches (the latter upon upscaling stomatal \( \text{O}_3 \) flux to the stand level, see above), the non-stomatal \( \text{O}_3 \) deposition at the stand level, which is crucial for validating
current flux-based O₃ 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 O₃. However, as depicted in figure 5, forests and grasslands may differ in their dependence of Gₑ 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 O₃ flux represents a novel tool for estimating the actual O₃ dose taken up by the foliage of entire trees and forest stands under actual site conditions. In addition, common underlying relationships between Gₑ and environmental parameters may foster plain, process-based model development of O₃ uptake with respect to risk assessment in forests and grassland ecosystems. Furthermore, such data can be used for the parameterisation and the validation of O₃ uptake models (Wieser and Emberson, 2004; Deckmyn et al., 2007). However, further research is needed to clarify the differences in the response of Gₑ to environmental factors between forests and grasslands in order to merge O₃ flux measurements in forest, semi-natural and crop ecosystems at the landscape level each of these vegetation types has to be integrated into one common modelling approach.

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