

**BELOWGROUND EFFECTS OVER ABOVEGROUND IMPACTS –
FOREST TREE-RHIZOSPHERE RESPONSES TO CHANGING SITE
CONDITIONS**

Rainer Matyssek¹, Reinhard Agerer², Karin Pritsch³

Setting the stage: Soils and their respiration govern carbon (C) pools and fluxes in forest ecosystems, as mycorrhizae substantially drain C gains belowground. Still, response processes belowground to environmental impact as such by climate change are initiated aboveground. This is the case not only for warming and associated drought, but also atmospheric CO₂ accumulation, which upon impacting on foliage becomes effective through altering whole-plant and rhizospheric C relations. Anthropogenic ozone (O₃) with its currently enhanced regimes similarly acts in the lower troposphere, being recognized today as an intrinsic component of climate change, but hardly understood in ecologically meaningful ways for forest sites. Mediated by precursor formation from natural sources, fuel combustion and forest burning, O₃ is climate-effective, spread at hemispheric scales and, if high influx passes stomata, incites toxicity in plants. Although not destroying trees rapidly (as posed by forest decline discussions of the 1980s), enhanced O₃ uptake chronically weakens tree and ecosystem-level C fixation and storage. O₃ only indirectly acts belowground, depending on plant-internal response pathways originating from aboveground impact.

What do we actually know about belowground O₃ effects in forest trees and ecosystems in view of climate change? Knowledge is scarce despite a plethora of indoor and outdoor chamber O₃ fumigation studies since the 1940s, as findings (mostly aboveground and short-term) from well-watered and fertilized juvenile, typically potted and single trees, and inevitably affected by micro-climatic bias, are not transferable to prevalent forest site conditions. Only two prolonged experiments were conducted in tree plantations (AspenFACE, USA) and in a maturing beech/spruce forest (*Fagus sylvatica/Picea abies*, Kranzberg Forest/Germany), both making use of novel free-air O₃ canopy fumigation technology. We will highlight the Kranzberg Forest experiment, referring to O₃/drought interactions also that had occurred during the dry summer of 2003.

O₃ belowground effects: : A conspicuous impact of canopy-level O₃ was an increase in soil respiration around beech and spruce trees under the experimentally enhanced O₃ regime. The effect was associated with stimulated fine-root production (in consistency with findings from AspenFACE) and increased density but altered fungal community structure of ectomycorrhizae (ECM), in particular, on beech. Reduced specific N uptake was attributed to ECM-mediated O₃ influence and corroborated through ¹⁵N soil labelling. Notwithstanding, the number of vital ECM on beech was increased under enhanced aboveground O₃ exposure, and so was the number of ECM types and fungal species richness. In spruce, shifts had occurred from “medium” and “long-distance” towards “short-distance” and “contact” ectomycorrhizal exploration morphotypes after eight years of elevated O₃ treatment. Aboveground O₃ impact led to loss in mycelial soil volume occupation, which represents decline in belowground resource exploration capacity, and hence, in tree competitiveness, if space-related resource turnover is similarly crucial as along aboveground organs.

Largely vague remained potential influences by O₃-stressed trees on soil microbial communities including ECM. Extracellular enzyme activities in mycorrhizosphere soil integrate activities from roots, fungi and associated as well as free-living microorganisms. Indications may be biased, however, by plant age and tree species, as O₃-driven enzyme stimulations in the mycorrhizosphere of adult forest trees was not confirmed in juvenile trees. Given that soil bacteria may promote nutrient mobilization and provide beneficial capacities in general (“helper bacteria”), holobiontic understanding of O₃-incited interference with

¹ Ecophysiology of Plants, Technische Universität München, Freising-Weihenstephan, Germany.

E-mail : matyssek@wzw.tum.de

² Mycology, Ludwig-Maximilians Universität München, Germany.

³ Biochemical Plant Pathology, Helmholtz-Zentrum München, Neuherberg, Germany

belowground tree, fungal and bacterial interactions poses a challenge for research. The challenge implies focus on such mutualistic interaction networks that may turn to parasitic relationships under O₃ stress.

O₃/drought interaction: During the extraordinarily dry summer of 2003, the stimulating O₃ effect on soil respiration rate vanished under spruce, in consistency with decreased fine-root production by a factor of six, reflecting some kind of dormancy, whereas fine root production stayed unchanged in beech. δ¹³C of newly formed fine roots was consistent with stomatal limitation by O₃ in beech. Overall, drought had the capacity of overriding the stimulating O₃ effects on fine-root dynamics and soil respiration in both tree species. Autotrophic soil respiration (SRa) was drought-sensitive, as total SR (SRt) ceased in spruce to follow the seasonal course of soil temperature. SRa rather than heterotrophic SR (SRh) was sensitive to changes in soil temperature and plant-available soil water.

Explanatory model of O₃ belowground effects: O₃-induced stimulations in soil respiration, fine-root growth and mycorrhization were accompanied by a dramatic decline in stem productivity by annually 44 % in beech (spruce with incipient tendency). The effect related to leaf-level phytohormonal disturbance inflicted by O₃, while effects on photosynthesis stayed minor. Leaf-level destruction of cytokinins (CK) incited drain via xylem from roots, where CKs, if accumulating under non-limiting N soil availability (as was the case at Kranzberg Forest), typically impose growth inhibition. The impeded CK accumulation evoked fine root production and created a belowground C sink that outcompeted that posed by the stem. Hence, aboveground O₃ impact pretended belowground N limitation, misguiding fine root response.

Ecological significance: Modelling approaches have shown substantial loss in C fixation of forest ecosystems worldwide since 1900, although parameterization and validation are inadequate and limited, respectively. Kranzberg data are supportive regarding the O₃ response of adult beech. Radiative forcing of the atmosphere appears to lesser extent to be caused by photosynthetic limitation under O₃ stress than by belowground shift in whole-tree C allocation and increase in soil respiration. Belowground O₃ effects in forest ecosystems demand for attention during the post-Kyoto debate.

REFERENCES

- (1) Agerer, R., Hartmann, A., Pritsch, K., Raidl, S. *et al.*, 2012. – Plants and their ectomycorrhizosphere: cost and benefit of symbiotic soil organisms. In: Matyssek R, Schnyder H, Osswald W, Ernst D, Munch J C, Pretzsch H (eds.): Growth and Defence in Plants – Resource Allocation at Multiple Scales. Ecol. Stud. **220**, 213–242
- (2) Grebenc, T., Kraigher, H., 2007. – Changes in the community of ectomycorrhizal fungi and increased fine root number under adult beech trees chronically fumigated with double ambient ozone. Plant Biol. **9**, 279–287.
- (3) Matyssek R, Wieser G, Ceulemans R, Rennenberg H, Pretzsch H, *et al.*, 2010. – Enhanced ozone strongly reduces carbon sink strength of adult beech (*Fagus sylvatica*) - Resume from the free-air fumigation study at Kranzberg Forest. Environmental Pollution **158**, 2527-2532
- (4) Matyssek R, Kozovits AR, Schnitzler J, Pretzsch J *et al.*, 2014. – Forest trees under air pollution as a factor of climate change. In: Tausz M, Grulke N. (Eds.) Trees in a Changing Environment. Springer, Plant Ecophysiology **9**, pp. 117-163
- (5) Nikolova PS, Andersen CP, Blaschke H, Matyssek R, Häberle KH., 2009a.– Belowground effects of enhanced tropospheric ozone and drought in a beech/spruce forest (*Fagus sylvatica* L./*Picea abies* [L.] Karst). Environmental Pollution **158**, 1071-1078.
- (6) Nikolova P., Raspe S., Andersen C., Mainiero R., Blaschke H., Matyssek R., Häberle K.H., 2009b. – Effects of the extreme drought in 2003 on soil respiration in a mixed Forest. Eur J Forest Res **128**, 87-98.
- (7) Pretzsch H, Dieler J, Matyssek R, Wipfler P., 2010. – Tree and stand growth of mature Norway spruce and European beech under long-term ozone fumigation. Environmental Pollution **158**, 1061-1070.
- (8) Pritsch K, Luedemann G, Matyssek R, Hartmann A, Schlöter M, Scherb H, Grams TEE, 2005 – Mycorrhizosphere responsiveness to atmospheric ozone and inoculation with *Phytophthora citricola* in a phytotron experiment with spruce/beech mixed cultures. Plant Biology **7**, 718-727

- (9) Weigt RB, Häberle KH, Millard P, Metzger U, Ritter W, Blaschke H, Göttlein A, Matyssek R., 2012. – Ground-level ozone differentially affects nitrogen acquisition and allocation in mature European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) trees. *Tree Physiol* **32**(10), 1259-1273
- (10) Winwood J, Pate A.E., Price J. Hanke D.E., 2007. – Effects of long-term, free-air ozone fumigation on the cytokinin content of mature beech trees. *Plant Biol.* **9**, 265-278
- (11) zu Castell W, Fleischmann F, Heger T, Matyssek R., 2015. – Shaping theoretic foundations of holobiont-like systems. *Progress in Botany* **77**, in press