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Meeting Report

Soil respiration across scales: towards an integration of patterns and processes

European Science Foundation Exploratory Workshop ‘Diurnal- to century-scale controls on soil respiratory fluxes. Towards a new generation of integrated experimental and modelling approaches’, Innsbruck, Austria, September 2009

In view of a rapidly changing climate system there has been a growing interest in the role of ecosystems in the global C cycle. Considerable uncertainties still exist concerning the factors determining the largest source of CO₂ from terrestrial ecosystems, i.e. soil respiration (SR) and how it will respond and feed back to climate change. SR includes a component derived from carbon recently assimilated by plants, i.e. the respiration of roots, mycorrhizae and rhizosphere microorganisms, and a component derived from the C respired during decomposition of dead plant litter, microbial debris and destabilized soil organic matter (Fig. 1). Thanks to a range of observational and manipulative studies, and the advances in technology, progress has been made in our understanding of biotic and abiotic effects on soil carbon fluxes (Kutsch *et al.*, 2009; Norby, 2009; Paterson *et al.*, 2009). The ESF Exploratory Workshop addressed the need to synthesize recent insights on diurnal to century scale controls of soil respiratory fluxes and incorporate them into a new generation of process-based models, for developing a larger framework with an improved capacity for predicting SR in changing environments.

Short-term links between photosynthesis and soil respiration

In recent years there has been increasing evidence that plant activity is a key determinant of SR (e.g. Högberg & Read, 2006). Besides producing litter as a major substrate for heterotrophic activity in the soil, plants directly influence soil respiratory processes *via* root respiration and by providing photo-assimilates that fuel the metabolic processes of mycorrhizae, endophytes and microbial populations in the rhizosphere (Fig. 1). Easily degradable compounds, including root exudates, may also provide energy for stimulating an increased microbial breakdown of more complex SOM compounds, so-called priming effects of SOM decomposition (Kuzyakov, 2002) (Fig. 1).

While effects of photosynthesis on SR have been well documented at annual and seasonal timescales, a consistent picture of their short term coupling is only just beginning to emerge. Yakov Kuzyakov (University of Bayreuth, Germany) presented a synthesis of a range of short-term studies indicating that a photosynthetic signal appears in soil-respired CO₂ within hours (herbaceous vegetation) to a few days (trees) (Kuzyakov & Gavrichkova, 2010). While isotope tracer studies track the time for transfer of individual C atoms from the canopy to the rhizosphere, photosynthetic signals may be transmitted much more rapidly to the soil by pressure-concentration waves (Mencuccini & Hölttä, 2010). Jorge Curiel Yuste (University of Barcelona, Spain) and Rodrigo Vargas (University of California, Berkeley, USA) provided two synthetic studies that explored relationships between canopy photosynthesis (as derived from eddy covariance measurements) and SR based on continuous measurements in different vegetation types across the growing season. These larger-scale studies only partly confirm a strong and rapid coupling between photosynthesis and SR. They suggest that there might be a fast link between these processes at the timescale of hours and a slower one at the timescale of a few days, while there may also be extended periods in the season without any clear correlation between photosynthesis and SR.

Short-term relationships between photosynthesis and SR may be obscured by changing soil diffusivity, which affects the transfer rates from CO₂ produced in the soil to the soil surface (Stoy *et al.*, 2007) (Fig. 1). Furthermore, as suggested by isotopic labelling and shading experiments, the involvement of different substrate pools within the plant may lead to a temporary decoupling between photosynthesis and SR, with storage pools buffering short-term changes in photosynthetic C uptake (Carbone & Trumbore, 2007; Bahn *et al.*, 2009). Susan Trumbore (University of California, Irvine, USA) and Mariah Carbone (University of California, Santa Barbara, USA) presented further evidence based on radiocarbon analyses that CO₂ from root respiration is only partly derived from very recently fixed C pools. Moreover, Arthur Gessler (University of Freiburg, Germany) demonstrated that a re-fixation of root respired CO₂ and its upward export to aboveground plant tissues (Aubrey & Teskey, 2009) can cause a mixing of different substrate pools e.g. in the trunks of trees (Kodama *et al.*, 2008), and may potentially also lead to an underestimation of the amount of CO₂ respired belowground by soil surface CO₂ efflux measurements (Fig. 1). Finally, irrespective of the size and age of plant C pools, during periods of increased nutrient demand by plants rhizodeposition is often increased, stimulating SOM decomposition in the rhizosphere (Frank & Groffman, 2009; Jones *et al.*, 2009).

C fluxes in the plant-soil system: differential responses and effects of different biota

Different components of the soil system may access and use fresh photoassimilates to different degrees. Peter Högberg (Swedish University of Agricultural Sciences, Sweden) demonstrated for a boreal forest that fresh plant-derived C entering the soil is mainly transferred to fungal and less to bacterial components, and is taken up to very different degrees by different faunal groups. Andreas Heinemeyer (University of York, UK) showed

that excess C from photosynthesis may affect mycorrhizal respiration more immediately and strongly than root respiration. Sébastien Fontaine (INRA, France) provided further evidence for the hypothesis that two distinct microbial functional groups respond differently to priming by fresh plant C inputs versus increased nitrogen availability. Slow growing, “mining” microbes are more responsive to fresh plant C inputs, while fast growing, “storing” microbes are more affected by changes in nitrogen availability (Fontaine & Barot, 2005). He suggested that their interactions exert a major control on SOM dynamics. Furthermore, biotic interactions involving different trophic levels, such as above- and belowground herbivory, may alter source-sink relations and thus C fluxes in the plant-soil system, thereby substantially affecting soil C dynamics in changing environments (Ayres *et al.*, 2009).

Modelling soil respiration and soil C turnover

To be able to account for multiple processes operating at diurnal to annual timescales, process-based models of SR should take into account more than simple soil temperature and moisture relationships. Markus Reichstein (Max Planck Institute for Biogeochemistry, Germany) showed that ignorance of plant-soil coupling leads to erroneous interpretations of respiration in relation to abiotic drivers in models, e.g. to an overestimation of the temperature sensitivity (Reichstein & Beer, 2008). Data analysis (and modelling) on explicitly distinct time-scales offers new perspectives for inferring processes and disentangling confounded responses to abiotic and the above-mentioned abiotic drivers (Mahecha *et al.*, 2010). The ultimate goal for model development must be to overcome “dead-soil-box paradigm” models, i.e. to consider key processes and properties governing soil carbon dynamics including vertical differentiation and transport mediated by roots and soil biota, and root-microbial as well as microbial-mineral interactions with respective effects on carbon dynamics (e.g. priming).

Eric Davidson (Woods Hole Research Center, USA) pointed out that most available soil carbon turnover models have been successful in describing effects of land use, but may be less suitable for assessing impacts of climate change. Developing further the perspective outlined by Davidson & Janssens (2006), he suggested that this limitation could be overcome by separating physico-chemical (aggregation, sorption-desorption, hydrophobicity) from enzymatic processes. He furthermore emphasized that SOM pools should not be based on age, but on process. Such a new generation of models would ideally be structured in a modular way, including modules on plant C inputs, microbiology, SOM quality (distinguishing assimilable versus higher molecular weight compounds), and soil physics. Pete Smith (University of Aberdeen, UK) highlighted recent developments in soil C fractionation schemes that allow measurable and modelled pools to be reconciled (Zimmermann *et al.*, 2007), which could help bridging the gap between experimentalists and modellers, and contribute to improved model validation schemes.

Conclusion and Outlook: Towards a new generation of integrated experimental and modelling approaches

In the presentations and many discussions at the workshop a number of issues emerged that need to be addressed in more detail in the future: 1) the plant-to-soil C transfer, as related to plant C allocation and belowground C partitioning, focusing on the interactions with the nitrogen cycle, soil and vegetation types, and phenology, and as affected by changing environmental conditions; 2) soil C turnover, with particular reference to effects of substrate quality and quantity on decomposition rates, and the mechanisms of soil C stabilization and destabilization (aggregates, priming) across soil and vegetation types as affected by quantity and quality of soil C inputs (litter, exudates, DOC, DIC); 3) the role of biota for SOM pools and fluxes, considering effects of different functional groups (e.g. fungi, bacteria, soil fauna);

4) development of soil C models, particularly for improving suitability for climate change scenarios, separating physico-chemical from enzymatic processes and improving the representation of different SOM pools. Such models should advance the description of physico-chemical stabilization and the interface between ecophysiology (C allocation) and soil modules and account for vertical soil heterogeneity and biotic interactions. The explicit incorporation of ^{13}C and ^{14}C will permit the use of isotopic datasets for model testing and validation.

From the insights outlined above it is clear that future research efforts on soil C dynamics would profit substantially from an increased collaboration between plant ecophysiologicals, microbiologists and soil scientists. Linking experimental and advanced model-data integration approaches will help develop, refine and test a consistent framework for understanding and predicting soil respiratory fluxes across spatial and temporal scales.

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Figure Legend:

Fig. 1: Major C pools (boxes) and fluxes (arrows) in the plant-soil system, including plant, mycorrhizal, rhizosphere and bulk soil microbial communities. Gaseous fluxes are indicated by broken lines. **P** refers to potential priming effects, **R** indicates the transport of re-fixed root-respired CO₂ to above-ground plant parts. Σ symbolizes effects of gas diffusivity in the soil pore space on the transfer of respired CO₂ to the soil surface. Shades in the soil organic matter (SOM) box indicate a gradient of complexity and molecular weight of organic C compounds. For simplicity, faunal components grazing on all above- and below-ground C pools and feeding into the litter and the SOM pools have not been included. For more detailed depictions see e.g. Kutsch *et al.* (2009) and Paterson *et al.* (2009).

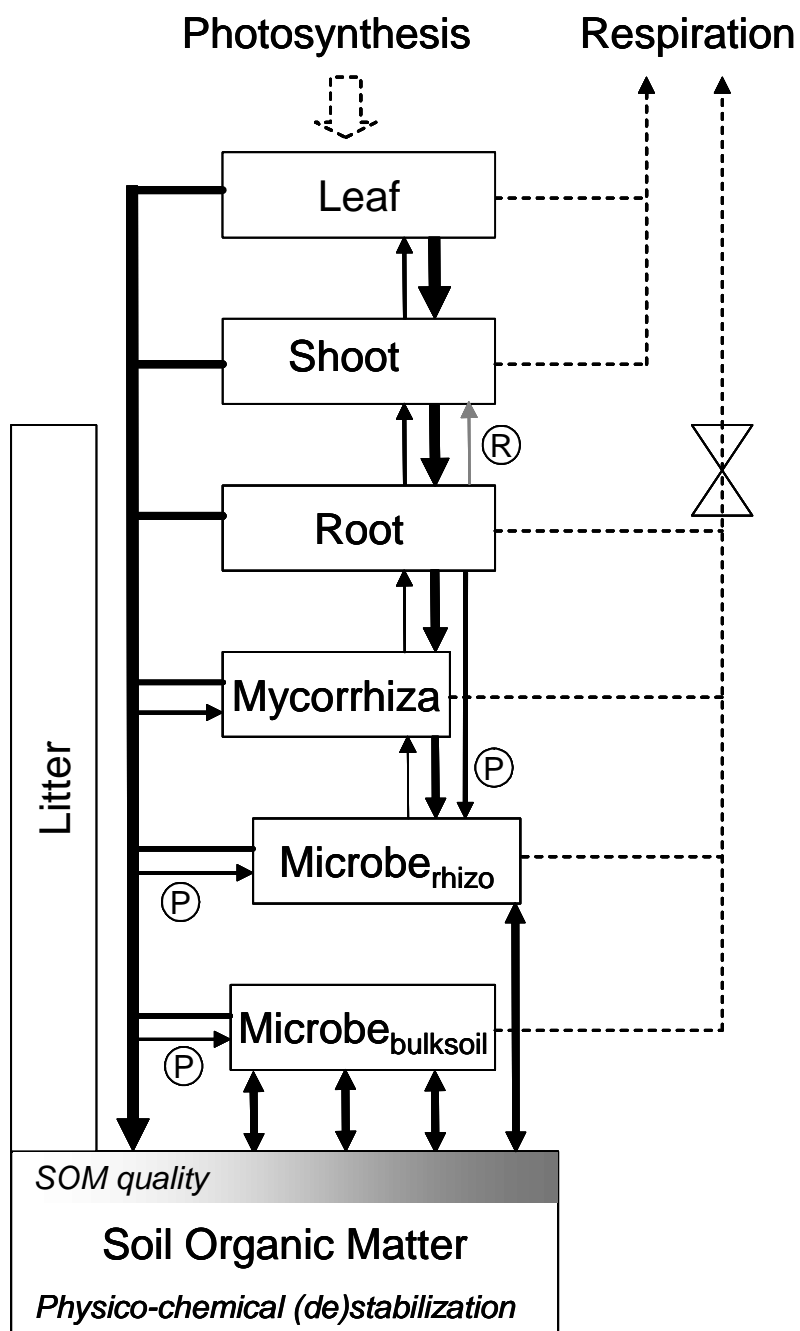


Fig. 1