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Key words: aerosols, annual growth anomaly, clouds, cosmic rays, ions, time series, tree growth.

Meetings

Missing links in the root–soil organic matter continuum

Organized session at the ecological society of America 94th annual meeting, Albuquerque, NM, USA, August 2009

Finding common ground

The soil environment remains one of the most complex and poorly understood research frontiers in ecology. Soil organic matter (SOM), which spans a continuum from fresh detritus to highly processed, mineral-associated organic matter, is the foundation of sustainable terrestrial ecosystems. Heterogeneous SOM pools are fueled by inputs from living and dead plants, driven by the activity of micro- and mesofauna, and are shaped by a multitude of abiotic factors (Fig. 1). The specialization required to measure unseen processes that occur on a wide range of spatial and temporal scales has led to the partitioning of soil ecology research across several disciplines. In the organized oral session 'Missing links in the root–soil organic matter continuum' at the annual Ecological Society of America meeting in Albuquerque, NM, USA, we joined the call for greater communication and collaboration among ecologists who work at the root–soil interface (e.g. Coleman, 2008). Our goal was to bridge the gap between scientific disciplines and to synthesize disconnected pieces of knowledge from root-centric and soil-centric studies into an integrated understanding of belowground ecosystem processes. We focused this report around three compelling themes that arose from the session: (1) the influence of the rhizosphere on SOM cycling, (2) the role of soil heterotrophs in driving the transformation of root detritus to SOM, and (3) the controlling influence of the soil environment on SOM dynamics. We conclude with a discussion of new approaches for gathering data to bridge gaps in the root–SOM continuum and to inform the next generation of ecosystem models.

> *'…living roots, and organic matter derived from root detritus, are important parts of the continuum of organic matter in the soil.'*

Bottoms up: the importance of the living rhizosphere

Although leaf litter has often been considered to be the main source of organic inputs to soil, Ann Russell (Iowa State University, USA) synthesized a convincing body of

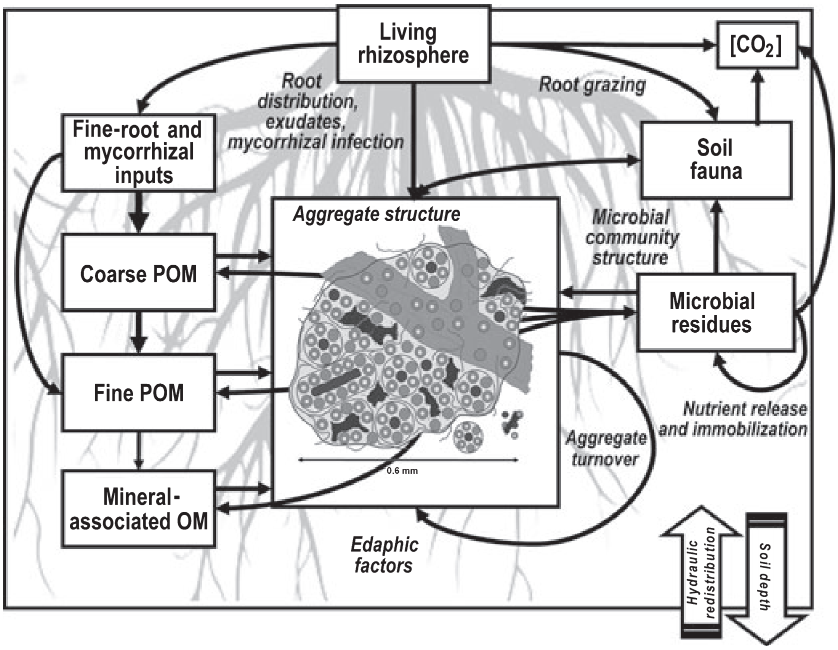

Fig. 1 Conceptual diagram of pools and fluxes occurring on the root–rhizosphere–soil continuum. We have represented the root–soil organic matter (SOM) continuum as ranging from living roots and root inputs, to fresh and more degraded particulate organic matter, to organic matter associated with mineral soil. The pools represented in the continuum are operationally defined; they depend on the methodology used to quantify them. We use this broad perspective to illustrate that the belowground environment is intricately connected; the arrows indicate interactions among pools, such as mass or energy transfer, or physical association. In addition, each box encapsulates its own series of related processes, and the turnover rates of the pools, which range from weeks to millennia, depend on a series of other factors. For example, biotic factors such as plant chemistry, microbial activity, and trophic dynamics interact with the soil environment, including location (i.e. depth, association with the rhizosphere), soil texture, chemistry, bulk density, water content and nutrient availability to control the turnover of organic matter. While difficult to represent in two-dimensions, organic matter processing by the microbial and soil faunal communities is often 'filtered' by soil structure, which protects fresh organic matter from decomposition, but also provides a habitat for microbes. The aggregate represented here (from Jastrow & Miller, 1998), comprises a root nucleus surrounded by organic matter in various stages of decomposition that is protected to various degrees from decomposers by associations with mineral soil components and cemented in place by the deposition of microbial residues and chemical interactions between organic and mineral phases. OM, organic matter; POM, particulate organic matter.

work demonstrating that roots, rather than surface residues, control the accumulation of SOM in a variety of ecosystems (Russell *et al.*, 2004). Living roots, which are chemically diverse and highly dynamic, also influence a wide range of soil processes, from the exudation of labile C compounds to the development of fungal associations (Hodge *et al.*, 2009). For example, Zoe Cardon (Ecosystems Center, Marine Biological Laboratory, USA) demonstrated that the root-mediated redistribution of deep soil water to relatively dry shallower soil (i.e. hydraulic redistribution, cf. Caldwell *et al.*, 1998), increased soil CO_2 efflux and nutrient cycling near the surface in an arid ecosystem. Andrew Kulmatiski (University of Alaska, Anchorage, USA) also discussed the importance of rooting distribution throughout the soil profile for strategies of water uptake by different species in an African savanna. Later, Julie Jastrow (Argonne National Laboratory, USA) demonstrated that living roots shape soil physical structure by promoting the formation of soil aggregates, which facilitated accrual of SOM in restored grasslands. Taken together, the evidence is compelling that living roots, and organic matter derived from root detritus, are important parts of the continuum of organic matter in the soil.

Soil heterotrophs: large and in charge

Larger soil organisms (i.e. 50 μm to many cm in body size) play an important role in the root–SOM continuum by grazing on roots and microbes, comminuting organic matter and aggregating soil in fecal pellets (Coleman, 2008). However, litterbag and soil incubation studies necessarily exclude invertebrates, and research on faunal activity and trophic dynamics tends to be independent from research on the biogeochemistry of SOM cycling. Tim Filley (Purdue University, USA) used plant-derived biomarkers in invertebrate residues to bridge the gap between larger soil organisms, such as earthworms and beetle larvae, and SOM distribution. He found that larger soil organisms help to stabilize root-derived organic matter in soil aggregates. Similar coupling of biogeochemistry with food web studies could prove fruitful for describing mechanisms that underlie critical ecosystem processes.

Despite considerable research efforts, the breadth of the microbial role in the root–SOM continuum remains unresolved (Young *et al.*, 2008). Using advanced pyrosequencing techniques, David Nelson (University of Maryland, Center for Environmental Science Appalachian Laboratory, USA) demonstrated the importance of archea as nitrifiers in agricultural systems exposed to elevated [CO_2]. Rising atmospheric [CO_2] and other changing environmental factors add a layer of complexity to the quest to understand microbial process (Paterson *et al.*, 2008). For example, Claudia Boot (University of California, Santa Barbara, USA) demonstrated that microbially mediated C and N cycling in Mediterranean California grasslands is intricately linked with summer drought. Ongoing research across subdisciplines seeks to uncover the many complex links between soil organisms of all sizes and the root–SOM continuum (Coleman, 2008).

The soil environment: what is the matrix?

While the role that living organisms play in the transformation of root detritus to SOM is disproportionate to their body size, the nonliving soil environment also influences SOM cycling. However, destructive sampling can obscure feedbacks between abiotic and biotic processes, making it difficult to quantify the role of edaphic factors in the root–-SOM continuum. Roser Matamala (Argonne National Laboratory, USA) presented preliminary evidence from a unique, broad-gradient root and soil transplant study which suggested that site-specific soil factors may outweigh climatic controls on the decomposition of roots and their subsequent fate in SOM pools.

In many ecosystems, the soil environment is dominated by aggregate structure (Kay, 1998) and thus many of the processes involved in the transformation of roots to SOM must pass through the 'filter' of soil structure (i.e. Fig. 1). Julie Jastrow (Argonne National Laboratory, USA) used ultra-small-angle X-ray scattering techniques and new, high-resolution microtomographic images to demonstrate the importance of microaggregates as both habitat for microbes and protection for SOM. Three-dimensional scans revealed mineral soil and organic matter clustered around a root nucleus, and a tortuous network of micropores that could harbor microbial films in addition to water and gases. A holistic view of the interactions among the soil environment, aggregate dynamics and the continuum of root transformation into SOM is a needed focus in belowground research.

Bridging the gaps

Ecosystem models can help to link disparate measurements at different scales and fill gaps in process knowledge along the root–SOM continuum. However, models have had variable success at accurately predicting observed processes. There are significant challenges associated with defining meaningful plant and soil pools, incorporating processes that operate at multiple temporal and spatial scales, and integrating empirical data into model frameworks (Ettema & Wardle, 2002; Ostle *et al.*, 2009).

Empirical measurements are needed that span multiple processes and scales, and can be used to parameterize or inform models. Colleen Iversen (Oak Ridge National Laboratory, USA) used a novel variation on the traditional *in situ* decomposition study to link decomposing roots with the SOM continuum by measuring the appearance of ^{13}C-labeled root-derived residues in SOM pools (i.e. Fig. 1). The isotopic approach discussed by Iversen is useful for tracking the incorporation of root-derived C into SOM pools (e.g. Personeni & Loiseau, 2004), and the molecular approaches discussed by Tim Filley (Purdue University, USA) and David Nelson (University of Maryland, Center for Environmental Science Appalachian Laboratory, USA) also offer novel ways to integrate the activity of soil organisms with other processes. Another session at the ESA meeting, 'Advances in Biochemical Methods for Studying Organic Matter Dynamics in an Ecological Context', showcased a number of promising new techniques that, if combined with the more traditional approaches and grounded in ecological theory, could help provide much-needed empirical data to reconfigure current model frameworks.

While recently developed tools can aid in measuring integrated belowground processes (e.g. Paterson *et al.*, 2009), continued conversation and collaboration among empirical scientists and modelers is necessary to characterize ecosystem function. Bill Parton (Natural Resource Ecology Laboratory, Colorado State University, USA) approached the challenge of defining meaningful model pools by using a model parameterized with data from an ecosystem labeled with a ^{14}C tracer (Gaudinski *et al.*, 2009). The unique data from this study allowed him to detect the importance of modeling multiple root pools for accurate projections of ecosystem C budgets; similar data are needed from a variety of ecosystems.

Conclusions

The compelling themes arising from 'Missing links in the root–SOM continuum' emphasized the importance of the rhizosphere, soil heterotrophs and the soil environment for the transformation of root-derived C to long-lived SOM. No single experiment can span the entire root–SOM continuum, but by integrating observations made at several points along the continuum, a more holistic view of belowground ecology will surface (Fig. 1). Collaborative relationships among root physiologists and soil ecologists, molecular biologists and modelers, will push us one step closer towards an all-encompassing view of belowground systems.

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