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# REPORTS FROM THE 2009 ESA ANNUAL MEETING

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## Missing Links in the Root–Soil Organic Matter Continuum

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The 2009 ESA Organized Oral Session 3 was organized by Colleen M. Iversen and Sarah L. O'Brien, and held during the Ecological Society of America 94th Annual Meeting in Albuquerque, New Mexico, on 3 August 2009.

### Spanning the Continuum from Living Roots to Soil Organic Matter

#### Introduction

Plant–soil interactions control important processes that are crucial for ecosystem stability, including ecosystem water use, nutrient cycling, and long-term C storage (van der Putten et al. 2009). However, belowground processes are notoriously difficult to study, because most measurements dramatically disturb the soil system, and critical processes occur across a wide range of spatial and temporal scales (Ettema and Wardle 2002). In addition, belowground dynamics span ecological disciplines (Young and Crawford 2004), ranging from microbial activity in the rhizosphere, to the diffusion of water and gases throughout the soil matrix, to physical soil structure and porosity. This necessitates interdisciplinary communication and collaboration in order to develop a complete understanding of belowground ecosystems.

Plant root inputs and the cycling of soil organic matter (SOM) are important drivers of belowground processes. The relationship between roots and SOM can be characterized as a continuum, with fresh root detritus on one end, and highly processed SOM at the other (Fig. 1). Organic matter is transferred along the root–SOM continuum as it is decomposed, comminuted, and complexed with minerals by

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the activities of microbial communities and larger soil fauna, as well as mycorrhizae (Coleman 2008, Talbot et al. 2008). The concept of a root–SOM continuum is not new (Melillo et al. 1989, Olk and Gregorich 2006), and recent special issues on “Rhizosphere: achievements and challenges” (*Plant and Soil*, Volume 321, 2009) and ‘Plant-Soil interactions and the carbon cycle’ (*Journal of Ecology*, Volume 97, 2009), indicate that the root–SOM continuum remains an important focus in ecosystem research. However, while much work has been done to investigate root decomposition (Parton et al. 2007), and soil C and nutrient cycling (Sollins et al. 1996, Bais et al. 2006, Frank and Groffman 2009), few studies have explicitly linked root dynamics with SOM cycling (e.g., Personeni and Loiseau 2004). This has led to a knowledge gap between the turnover of roots and the subsequent fate of root-derived C and N in SOM pools.

To continue the dialogue on the root–SOM continuum, we organized a session at the ESA Annual Meeting in Albuquerque, New Mexico, USA in August 2009. Our goal was to facilitate a discussion across ecological subdisciplines by gathering a docket of speakers whose efforts were complementary—all were studying critical processes that drive the transformation of root detritus into SOM—but represented distinct portions of the root-SOM continuum (Fig. 1). By encouraging a holistic view of the root–soil ecosystem, we hoped to synthesize disconnected pieces of knowledge from whole-system, root- and soil-centric studies into a more comprehensive understanding of important belowground ecosystem processes, particularly soil C and N cycling. The collaborations and discussions resulting from this session will help shed light on poorly understood, yet fundamental, ecosystem processes operating in all terrestrial ecosystems.

We asked the participants to address two key questions: (1) Can we use current studies to synthesize an overarching framework for understanding the continuum from plant root inputs to long-term SOM pools? (2) What new studies or tools are needed to facilitate our understanding of how plant dynamics drive belowground processes such as SOM formation and ecosystem C and N cycling? The speakers addressed these questions in a series of talks that ranged from the influence of living roots on the soil and microbial environment to the transfer of C and N from decaying roots into different soil fractions, and spanned from microscale microbial activity to large-scale ecosystem modeling.

### The importance of root inputs

Roots, which are the direct interface between plants and the soil environment, are an important source of organic matter inputs to the soil (Aerts et al. 1992, Jackson et al. 1997). Ann Russell (Iowa State University, USA) opened the session by discussing the relative importance of root inputs compared with surface litter to the formation of SOM within the context of ecosystem-level C cycling. She demonstrated that root inputs were more important than aboveground litter inputs in determining the amount of organic matter in the soil in three separate sets of long-term experiments across a diverse range of ecosystems, from tropical plantation forests (Russell et al. 2004, 2007) to agricultural fields (Russell et al. 2009). The quantity and chemistry of the root inputs varied among species within an ecosystem, which could lead to altered root decomposition rates (Raich et al. 2009), and affect long-term soil C storage. Others have demonstrated a disconnect between above- and belowground litter cycling (Garten 2009), indicating that both above- and belowground litter inputs should be explicitly represented in conceptual and ecosystem models (van der Putten et al. 2009).

## Rooting distribution and root-mediated biogeochemical cycling

Root activity is typically inferred from estimates of root biomass distribution throughout the soil profile. However, direct measurements of root activity (i.e., water and nutrient uptake), which are critical for understanding biogeochemical cycling between roots and the soil, are relatively rare. Andrew Kulmatiski (University of Alaska, Anchorage, Alaska, USA), along with coauthors Richard Verweij, Edmund February, and Karen Beard, measured root activity using a depth-controlled tracer study in a mesic savanna in Kruger Park, South Africa. Kulmatiski and co-authors found that water uptake throughout the soil profile by grasses and trees could not be extrapolated from measurements of root distribution alone. This highlights the need for better understanding of the relationship between root abundance and important soil processes such as water and nutrient fluxes that impact the transfer of root detritus to SOM pools.

The conditioning of the soil system by living root activity is an important link in the root–SOM continuum. Zoe Cardon (Ecosystems Center, Marine Biological Laboratory, Massachusetts, USA) emphasized a long-standing but seldom-tested idea, namely, that the fate of organic C deposited from active roots (cf. Cardon and Gage 2006) is likely strongly influenced by daily fluctuations in rhizosphere soil water driven by the transpiration stream and the hydraulic redistribution of water from wetter soils to drier soils via root systems (Caldwell et al. 1998). Cardon described a recent experiment conducted with John Stark and Patrick Herron in a sagebrush ecosystem in northern Utah exploring the potential for localized wet–dry cycles to stimulate or depress the decomposition of rhizosphere organic matter through measurements of soil respiration, nitrogen cycling, and provision of nitrogen to inflorescences. A recently published experiment in a similar sagebrush system found that greater root density, coupled with a threefold increase in the magnitude of hydraulic redistribution, led to increased microbial decomposition rates despite lower absolute soil moisture in zones of high root density (Aanderud and Richards 2009). Thus, water fluxes in the rhizosphere of living roots could potentially increase the rate at which root-associated organic matter is transferred along the root–SOM continuum.

## Microbial activity

Microbial activity is an integral driver of the root–SOM continuum (Bais et al. 2006, Schimel et al. 2007, Lambers et al. 2009). Claudia Boot (University of California, Santa Barbara, USA), continued the focus on soil moisture by presenting results from a study conducted with coauthors Sean Schaeffer, Allen Doyle, and Joshua Schimel on the effects of drought on microbial stress responses and ecosystem C cycling (i.e., Schimel et al. 2007). Boot and coauthors found increased concentrations of microbial biomass in response to drought in a Mediterranean ecosystem in California, USA. This material was likely from osmolyte accumulation and is rapidly turned over at the onset of rain. The turnover of relatively labile microbial populations in response to drought–rewetting cycles may have direct implications for the long-term storage of root-derived C in SOM, as much of the C available for microbial synthesis comes from root exudation or turnover (Bais et al. 2006).

Fluxes of water, C, and N in the rhizosphere provide an ideal environment for organic matter decomposition, and most microbial activity takes place in this zone of root influence (Lambers et al. 2009). David Nelson (University of Maryland Center for Environmental Science, Appalachian Laboratory,

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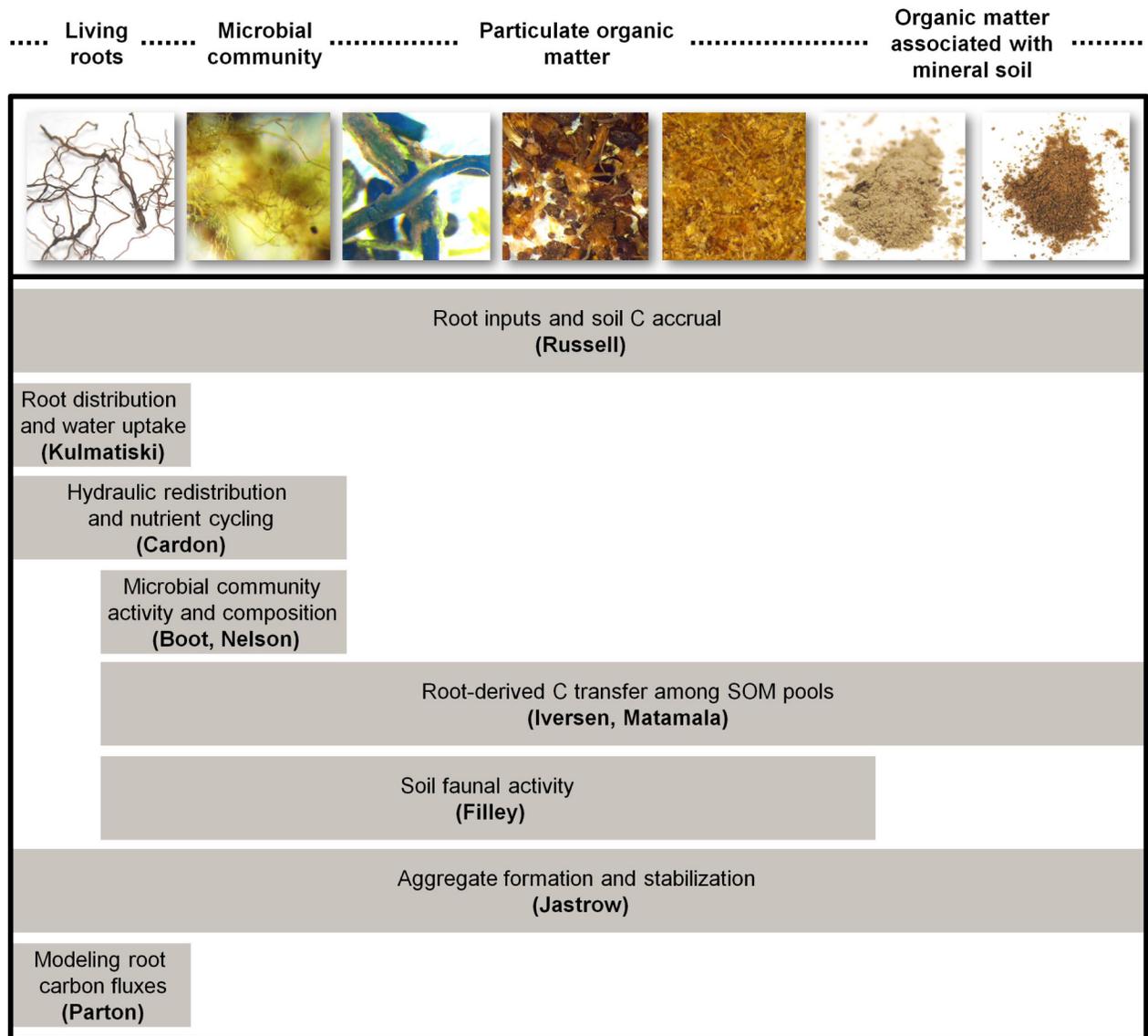


Fig.1. The interdisciplinary docket of speakers in the organized oral session “Missing links in the root–soil organic matter continuum” covered a diverse array of topics that spanned a continuum from living roots to organic matter associated with mineral soil (described at the top of the figure). The images are as follows (from left to right): fine roots (<2 mm diameter); fungal colonization of organic detritus; root-like coarse particulate organic matter (light fraction, >250  $\mu\text{m}$ , <1.4  $\text{g}/\text{cm}^3$ ); more degraded coarse particulate organic matter (heavy fraction, >250  $\mu\text{m}$ , >1.4  $\text{g}/\text{cm}^3$ ); fine particulate organic matter (53–250  $\mu\text{m}$ ); silt-associated organic matter (2–53  $\mu\text{m}$ ); clay-associated organic matter (<2  $\mu\text{m}$ ). Images (photo credits: Colleen Iversen) are from a root decomposition experiment where fine roots were allowed to decompose in soil; image resolutions differ along the continuum. Speakers are listed in the order in which they were featured in the session, and the shaded bars indicate the portion of the continuum covered in each of the speakers’ talks. The pictures represent relatively distinct SOM pools, whereas the shaded bars represent portions of the conceptual continuum that do not necessarily correspond to distinct pools.

USA) discussed N cycling by microbial communities in the rhizosphere of CO<sub>2</sub>-enriched agricultural systems. Nelson, along with co-authors Isaac Cann and Roderick Mackie, found that archaea are likely important nitrifiers in the rhizosphere, and that elevated [CO<sub>2</sub>] induced a change in archaeal community composition in the rhizosphere of at least one crop plant. The interplay between rhizosphere inputs and microbial community composition and activity, especially under changing environmental conditions, can have an important impact on the processing of organic matter in the soil (de Graaff et al. 2007).

### Bridging the gap between roots and SOM

While fine roots are an overwhelming source of organic matter inputs to the soil, the question remains whether these inputs will be stabilized in long-lived SOM pools, or be quickly decomposed and respired back to the atmosphere (Iversen et al. 2008). Long-term C storage in the soil is governed by the interplay among plant root inputs (Dijkstra and Cheng 2007), microbial dynamics (Balser et al. 2006), and the soil environment (Schimel et al. 1994, Jobbagy and Jackson 2000). Colleen Iversen (Oak Ridge National Laboratory, USA), along with coauthors Julie Jastrow and Richard Norby, used a <sup>13</sup>C label- and mass-based approach to trace root-derived C and N into a series of SOM pools. The experimental design of Iversen and her coauthors specifically investigated the interacting effects of root inputs and soil conditioning under elevated [CO<sub>2</sub>] on the appearance of root-derived C in SOM pools. Using a similar design and a radiocarbon tracer, Roser Matamala (Argonne National Laboratory, USA), examined the effect of soil edaphic properties and climate variables on root decomposition. Preliminary data shown by both scientists indicated that root-derived C is an important starting point in fueling organic matter transfer among soil pools, and that the soil environment can play a large role in the rate at which root-derived residues move into and along the root–SOM continuum.

### Soil organisms

Microbes are not the only soil organisms that break down plant-derived detritus and contribute to SOM pools; there is an abundance of soil macrofauna that each play an important role in the transformation of root-derived C along the continuum (i.e., Coleman 2008). Tim Filley (Purdue University, USA) discussed the importance of different species of earthworm and scarab beetle larvae to the processing of plant biopolymers and the incorporation of root- and litter-derived C into different soil fractions. He found selective losses of specific C compounds from decomposing plant litter, and his analyses indicated that worms and beetles specialized on different components of the root–SOM continuum. Soil faunal communities, and the trophic dynamics that control their abundance and activity (Coleman 2008), may be as important as plant inputs for C stabilization in SOM (Rawlins et al. 2007, Filley et al. 2008b).

### Soil characteristics

In addition to climatic controls, inherent soil characteristics such as texture and aggregate structure are also important to long-term C storage in SOM. Root-derived C can be stabilized (protected from decomposition) in SOM pools in a variety of ways (Six et al. 2002), and previous work has shown that physical protection of SOM in aggregates is critically important for C stabilization in many soils (Jastrow et al. 1996, Six et al. 2002). Roots may play an important role in aggregate formation, as they can serve as a nucleus for the formation of stable soil aggregates (Gale et al. 2000), and root activities such as

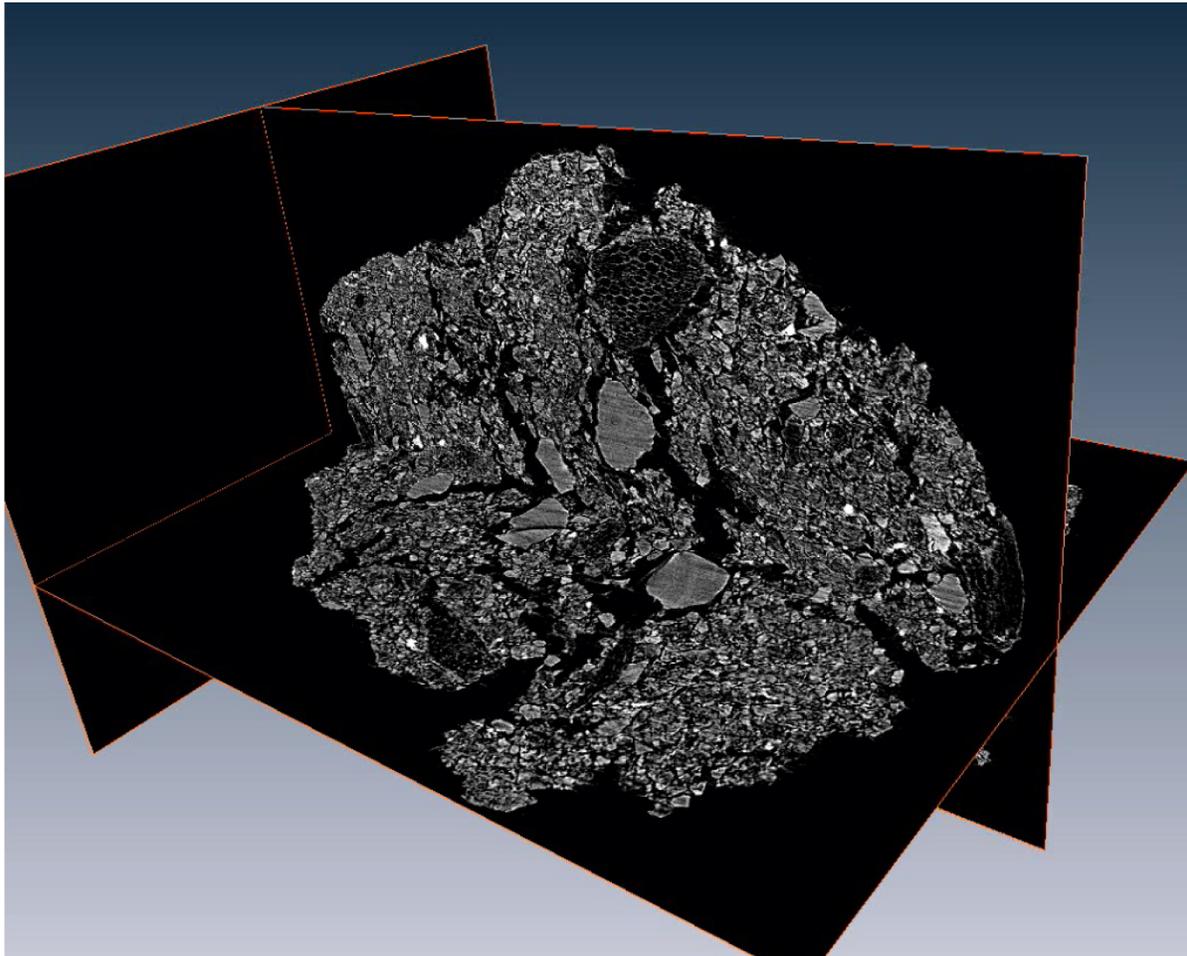


Fig. 2. Perpendicular two-dimensional slices through a three-dimensional reconstructed image of a water-stable macroaggregate (1–1.5 mm in diameter; image pixel size = 1.4  $\mu\text{m}$ ) obtained by high resolution X-ray microtomography at the Advanced Photon Source, Argonne National Laboratory, USA. The macroaggregate is composed of mineral soil, organic matter, microbial residues, and pore spaces. The gray-scale of the image corresponds to X-ray absorption, with the gradient from black to white indicating increasing density. The fine-root piece coming directly through the top center of the aggregate completes a stunning visual representation of the root–SOM continuum. (Image credit: M.I. Boyanov, F. De Carlo, J.D. Jastrow, K.M. Kemner, K.K. Moran, S.L. O’Brien, and the Advanced Photon Source beamline 2-BM staff. Use of the Advanced Photon Source was supported by the U.S. Department of Energy, Office of Science, Office of Basic Energy Sciences, under Contract No. DE-AC02-06CH11357.)

soil moisture depletion, physical entanglement, and support of rhizosphere microbial communities can positively influence soil aggregation (Allison 1968, Oades and Waters 1991). Julie Jastrow (Argonne National Laboratory, USA) presented a path analysis from her research in restored prairie ecosystems in Illinois, USA that linked root inputs with C stabilization in macroaggregates (Jastrow et al. 1998). She then showed via a new path analysis how macroaggregates mediate the effects of roots on microbial biomass and contribute to C accrual in mineral soil. To further explore the mechanisms behind aggregate-facilitated SOM accrual, Jastrow used ultra-small-angle X-ray scattering to quantify the filling of fine-scale porosity with organic matter in microaggregates (McCarthy et al. 2008), and high-resolution X-ray microtomography to construct three-dimensional images aimed at investigating organic matter protected in the larger pore spaces of soil macroaggregates. These images provided an excellent example of the intimate relationships between plant roots, SOM, and soil mineral particles, which exist as a continuum of organomineral associations (Fig. 2).

### Synthesizing an overarching framework

The main focus of the organized session was to use data derived from multiple experiments along the root–SOM continuum to develop a broader understanding of important ecosystem-scale process. A larger perspective, such as that of an ecosystem model, is useful for validating the information gleaned from multiple experiments. Data–model interaction can help empirical scientists to determine whether results are realistic, constrain assumptions in both models and experiments, and confirm whether findings from a single study system broadly represent ecosystem processes. However, the lack of a model that can be rigorously tested is one of the main impediments to synthesizing experiments along the root–SOM continuum into an overarching framework. In effect, there is often a disconnect between what is “measured” and what is “modeled” in belowground research (reviewed in Six et al. 2002).

Bill Parton (Natural Resource Ecology Laboratory, Colorado State University, USA), along with coauthors Robin Kelly, Christopher Swanston, and Paul Hanson, attempted to improve the representation of roots in an ecosystem model that was parameterized with data from a deciduous forest subjected to a whole-ecosystem  $^{14}\text{C}$  tracer (i.e., Gaudinski et al. 2009). Parton found that partitioning roots into two pools of differing ages and turnover rates was the key to accurately capturing the C fluxes of the entire ecosystem. However, more work is needed to standardize the quantification and characterization of root characteristics (Guo et al. 2008) and rhizosphere C fluxes (Cardon and Gage 2006), and also to isolate meaningful SOM pools (Olk and Gregorich 2006).

### New approaches

More creativity in methods development will greatly advance our understanding of the root–SOM interface. There were two overarching questions that emerged from this session that demand novel methodology: (1) What are the effects of living roots on the transformation of root detritus to SOM? (2) How are plant-derived C inputs cycled through SOM pools? Most of the speakers employed sophisticated analytical techniques in their work, and a combination of advanced analytical approaches with standard methodologies may offer the most promise for uncovering mechanisms important to the root–SOM continuum. The advanced pyrosequencing techniques used by David Nelson and co-authors (e.g., Ronaghi 2001) are revolutionizing soil microbiology and providing information related to the

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multitude of belowground processes mediated by microbes (Edwards et al. 2006). The application of stable and radioisotopes, discussed by Kulmatiski, Iversen, and Matamala, are well known but provide endless opportunities for tracing biogeochemical cycling throughout the SOM continuum (e.g., Paterson et al. 2009). Filley's microscale measurements of biopolymers in invertebrate residues (Filley et al. 2008a) demonstrated the unique roles of different organisms in biogeochemical processes. Likewise, Jastrow's use of X-ray techniques on soil aggregates sheds new light on how soil structure facilitates SOM stabilization. However, each methodology, whether novel or standard, has inherent strengths and weaknesses that introduce uncertainty into estimates of ecosystem pools and fluxes. Thus, the key to new technology may be to apply it in a way that is grounded in ecological theory, while integrating the new information with new conceptual frameworks. The most realistic approaches will assimilate information garnered from multiple smaller-scale studies, while incorporating constraints imposed at the ecosystem level by an over-arching model framework. In this way, belowground research can span ecological disciplines, and also span the continuum from living roots to long-lived SOM.

*... no one discipline will be able to understand the most complex biomaterial on the planet. There is mounting evidence that the essential features of soil will emerge only when the relevant physical and biochemical approaches are integrated. Some progress has been made, but there remains much to be done" (Young and Crawford 2004).*

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