



Soil pores and their contributions to soil carbon processes



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ABSTRACT

It has been generally recognized that micro-scale heterogeneity in soil environments can have a substantial effect on many soil physical, chemical, and biological processes driving physical protection of soil carbon (C). However, only recently the development of tools for micro-scale soil analyses, including X-ray computed micro-tomography (μ CT), enabled quantitative analyses of these effects. X-ray μ CT application to soil science is arguably one of the newest and fastest growing areas of soil science research; and its methodology is still being actively developed. The large amount of spatially explicit data that μ -CT scanning generates coupled with specially designed experiments can open new avenues for improved understanding of soil functioning and soil-plant interactions. Pores are both drivers and products of a variety of soil processes that ultimately determine physical protection of organic matter in soil by influencing its accessibility to microorganisms. The μ CT tools are well suited for providing information on characteristics of soil physical micro-environments, a.k.a. soil pores. Here we review the experimental approaches currently employed by research groups around the world in exploring the role of pore characteristics in soil C processes, with specific focus on soil C decomposition and protection at 5–1000 μ m spatial scale. We discuss pore/C/microbe relationships with emphasis 1) on direct and indirect effects of pore characteristics on soil microorganisms and subsequent microbial effects on decomposition of organic inputs; 2) on presence of feed-back effects of microorganisms on soil pore architecture; and 3) on importance of pore characteristics for decomposition of freshly added organic inputs/plant residues. The pore-oriented perspective will contribute to better structuring of the research efforts in deciphering the mechanisms of soil C protection/sequestration by soils.

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1. Introduction

Carbon (C) stored in soils plays a crucial role in providing a broad range of ecosystem services including production of food and fiber, nutrient supply, flood and erosion controls. By judicious land use and agricultural management soil C can be increased, thus reducing atmospheric CO₂ levels and mitigating climate change (Davidson and Janssens, 2006; Falkowski et al., 2000). While empirical evidence of importance of different soil management strategies in sequestering/loosing soil C is overwhelming, physical processes driving soil C protection are not well understood, particularly at the micro-scale, thus knowledge of mechanisms driving managements' contribution to soil C cycling is still lacking. Relying only on empirical observations without understanding the underlying mechanisms cripples our ability to model ecosystem processes, to predict how the ecosystems will respond to changing climate, and to develop effective management strategies to maximize soil C sequestration.

Physical protection, i.e., when soil C eludes decomposition by being inaccessible to microorganisms, has been long recognized as one of

the pathways of soil C protection (Adu and Oades, 1978; Kilbertus, 1980; Oades, 1988). Yet, recently it became apparent that physical protection plays a greater role in C sequestration than previously believed (Dungait et al., 2012; Schmidt et al., 2011). Realizing the importance of physical protection renewed awareness of the broad range of scales, micro- to global-, relevant soil C cycling; and particularly emphasized the significance of the micro-scale. In order to understand, quantify, and model a process it is crucial to look at it at the scale at which it takes place (O'Donnell et al., 2007; Young and Crawford, 2004), and it is at the <1–1000 μ m scale the physical protection of soil C occurs. Inability to quantify and model what transpires at the micro-scale diminishes the ability for up-scaling. Indeed, when underlying processes are not fully understood, the up-scaling capabilities are reduced to solely empirical approaches, which may or may not work under changing climate.

What enables physical protection of C at the <1–1000 μ m scale is the presence of diverse micro-environments generating a wide range of conditions for C accessibility to microbial decomposers and for microbial functioning (Kuzyakov and Blagodatskaya, 2015). By scale here we refer to the physical size of a micro-environment at which the process in question dominates. At a scale of a few microns (<5 μ m) properties of micro-environments are determined by mineralogical and surface

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characteristics of soil particles. Physical protection of C there is driven by adsorption of organic compounds on the surfaces of soil minerals; the adsorption that is sufficiently strong to override activities of microbial enzymes (Marschner et al., 2008; von Lutzow et al., 2006).

At a 5–1000 μm scale properties of micro-environments are defined by the presence and characteristics of soil pores. Our choice of 5 μm as an approximate lower boundary for this scale is based on accounting for fungal hyphae diameters ($\sim 10 \mu\text{m}$) and for the notion that bacteria exist in soil primarily in pores that are >3 times of their diameter (Kilbertus, 1980) ($\sim 2\text{--}3 \mu\text{m}$). At this scale soil C protection becomes largely a function of physical barriers between the decomposers and organic substances and/or a function of local micro-conditions incapacitating the decomposers (Ekschmitt et al., 2008; Ekschmitt et al., 2005). Soil pores are the key drivers for both of these phenomena (De Gryze et al., 2006; Negassa et al., 2015; Young and Crawford, 2004). In this manuscript we specifically focus on the processes taking place at 5–1000 μm scale.

Conceptually, the importance of pores as contributors to physical protection of soil C is well recognized. However, quantification of their specific impacts is yet to be developed (Moyano et al., 2013). In order to become quantitatively predictable, current understanding of the chemical and biological processes involved in C protection needs to be combined with an understanding of the routes for transports and fluxes, which enable these processes (Or et al., 2007). Such quantification is an important prerequisite for the emerging efforts to model soil C protection while explicitly representing the contribution of soil structure to microbial activity and functioning (Falconer et al., 2015; Monga et al., 2014; Vogel et al., 2015). The need for models that reflect micro-scale soil heterogeneity cannot be overstated. Ignoring such heterogeneity produces a great oversimplification of the actual belowground processes and can potentially seriously undermine reliability of model predictions under future climate changes (Crawford et al., 2005).

What appears to be a deterrent in quantifying and modeling the mechanisms of soil C physical protection is a persistent disconnect between research efforts of soil physicists, who focus on soil flow and transport phenomena, and research efforts of the soil scientists studying C sequestration. The majority of C physical protection research operates via a notion of C occlusion and protection within soil aggregates. The amount of experimental evidence of C protection within the aggregates, especially within aggregates of $<250 \mu\text{m}$ size range, is enormous. The evidence convincingly proved the concept of protection via “occlusion within aggregates” (Six et al., 2000) and this concept provided effective diagnostic tools for comparing management and land use effects on soil C storage (Six and Paustian, 2014). However, despite its scientific consistency and experimentally supported validity, the “occlusion within aggregates” concept does not easily lend itself to process-based modeling.

In order to model the presence/absence/magnitude of physical accessibility of a C substrate to decomposers one has to be able to quantify the routes by which the substrate can be accessed. Pores are the physical entities within/between aggregates that provide such routes. It is implied that aggregate-size distributions reflect the presence and characteristics of surrounding pores (Ashman et al., 2003; Dexter, 1988; Elliott and Cambardella, 1991; Young et al., 2001; Young and Ritz, 2000) and it is intuitively understood that the occlusion of C substrate within an aggregate minimizes the routes by which it can be reached. However, neither quantitative description of such routes nor assessment of their effectiveness can be obtained from information on size distributions and C contents of soil aggregates, which at present serve as key tools in soil C protection research.

Thus, success in process-based modeling of the mechanisms of C protection requires switching from a general focus on “occlusion within aggregates” to the specific direct quantification of what makes the intra-aggregate occlusion protect C, that is, to the presence of pores and their abilities to accommodate flow and transport. Luckily, more and more of such modeling efforts start to emerge (Kuka et al., 2007; Moyano et al.,

2013; Vogel et al., 2015) and success in bringing together soil physics and microbiology (Or et al., 2007) demonstrates that there is hope for successful quantitative bridges between soil physics and C sequestration research.

Quantification of the roles of pores in soil processes is assisted by rapid advances in the use of X-ray computed micro-tomography ($\mu\text{-CT}$) and other imaging tools in soil studies. Until very recently extreme complexity of soil matrix has created many technical difficulties that limited quantitative analysis of soil processes at micro-scale levels. Over last few decades advances in X-ray $\mu\text{-CT}$ led to the development of state-of-the-art soil analysis approaches that permit acquisition of 3-dimensional images of soil interiors with micron resolutions, e.g., (Kravchenko et al., 2011; Pridmore et al., 2012; Nunan et al., 2003; Peth et al., 2008; Vogel et al., 2010; Wang et al., 2012; Young and Crawford, 2004). This is a significant step for quantifying heterogeneity of soil environments at micro-scales, creating tools particularly effective for identification and description of soil pores.

While tools for physical characterization of soil micro-environments are ready, their implementation for understanding mechanisms of C protection lags behind. Such implementation requires that experimental procedures for C measurements, including but not limited to soil organic C levels, CO_2 emissions, decomposition of added organic substrates, were compatible with $\mu\text{-CT}$ measurements. Building such compatibility is currently at a stage of active development.

Despite rapidly growing interest in quantitative characterization of the role of pores in soil C processes a comprehensive understanding of the various avenues by which pore characteristics can influence soil C has yet to emerge. Lack of such general concept limits progress and diminishes research opportunities. Our objectives are (i) to review current experimental methods used for quantifying roles of pores on soil C processes with specific emphasis of the opportunities offered by X-ray $\mu\text{-CT}$, (ii) to address relationships of soil pore characteristics with protection/decomposition of soil organic C at 5–1000 μm scale within a unified conceptual framework, and (iii) to review experimental evidence of such relationships.

2. Experimental approaches for studying roles of pores in C processes

Quantifying the role of pores in the chemical and biological processes taking place at micro-scales is experimentally challenging. What is needed for a successful experiment is that pores are kept intact and are functioning in a manner consistent with what transpires in the actual soil. Creating such conditions in the lab is not trivial and requires judicious use of either intact soil samples or artificially created samples with certain pore characteristics. But then even a greater challenge is to obtain within-sample information on pore functioning and to relate it in a meaningful fashion to relevant chemical, physical, and biological soil observations associated with specific pores.

Several experimental approaches were explored by the research community in order to match pore information with C processes. The approaches can be broadly classified into three groups: (1) experiments where water and C substrates are placed in pores of certain sizes, (2) experiments with artificially created contrasting pore architectures, and (3) experiments with intact soil samples subjected to X-ray $\mu\text{-CT}$ measurements followed by procuring information on other soil characteristics either from “geo-referenced” dissection or from other high resolution sensing sources.

X-ray $\mu\text{-CT}$ scanning is a valuable tool that can greatly complement such experiments. It enables examining pore presence and determining pore characteristics in soil samples without disturbing them. The X-ray $\mu\text{-CT}$ is based on the differences in attenuation of the X-rays by materials with different densities and different atomic numbers (Ketcham, 2005; Peth, 2010). Pores are identified by classifying them based on their gray scale values, while accounting for a variety of other features including gray scale values of surrounding voxels, positions within an image, and histograms of the image's gray scale values (Iassonov et al., 2009;

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