Soil Micropore Development and Contributions to Soluble Carbon Transport within Macroaggregates

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Soil biophysical transport mechanisms promoting biogeochemical sorption of soluble organic carbon (SOC) compounds within macroaggregates control the retention and release of most soil nutrients, C- and N-based polysaccharides, and contaminants. Ecosystems containing continuous supplies of soluble root exudates and particulate organic matter (POM) provide a constant supply of mobile SOC compounds to surfaces and internal pore networks of soil aggregates. Intra-aggregate pores, especially the ultrafine pores, appear to be developed, interconnected, and blocked or disconnected by repeated drying and wetting (DW) cycling with direct but unknown contributions to movement and retention of SOC compounds. There is evidence that the severity (e.g., range of soil water potential) and frequency of severe DW cycles control intra-aggregate micro- and nanopore formation and function. Heterogeneously distributed microsites within aggregates contain microbial communities that readily mineralize available C and N compounds, producing mobile SOC that can be tightly sorbed to additional mineral surfaces made available within micro- and nanosized fissures during repeated DW cycling. Mechanical removal of concentric soil layers of aggregates, synchrotron imaging and computer microtomographic (CMT) image processing software of three-dimensional pore networks and connectivities, coupled with synchrotron X-ray small angle scattering to measure pore sizes. Natural isotopes of ^{13}C and ^{15}N to quantify C and N sorption and CO_2 respiration provide new and integrated approaches for quantifying spatially heterogeneous changes of pore diameters, connectivities, and organo-ion-mineral sorption within intra-aggregate pore networks. Net C and N alterations at surfaces and within aggregates appear to modify both the microbial activities and bacterial community structures, producing integrated feedback and feed-forward processes between the soil biological and physical components of soil aggregates.

ABBREVIATIONS: CMT, computer microtomography; CT, conventionally tilled; DW, drying and wetting; EPS, extracellular polymeric substances; NT, no-till; POM, particulate organic matter; SAE, soil aggregate erosion; SOC, soluble organic carbon; SOM, soil organic matter.

Spatial distributions and physical connectivities of soil pores contribute to both the heterogeneous distribution of soluble organic compounds and the establishment of gradients that maintain microbial communities within and among soil aggregates. Spatial variability of soil C content arises from multiple management events and management intensities applied at different times and multiple locations across the landscape (Kravchenko et al., 2005, 2007). Cumulative nonuniform climate events frequently cross the same landscape, producing various biophysical conditions controlling the two-way diffusion of solutions, gases, and ions among the macropores surrounding soil aggregates. These heterogeneities are amplified by nonuniform soil responses at scales ranging from the landscape to pore-accessed microsites within aggregates of each soil profile. The development and disruption of soil pores alter solution conductivity and SOC sorptive surfaces that control the distribution, retention, and losses of soil C. Soil pores control flux rates of plant-based SOC originating from root exudates and the decomposition products of particulate organic mater (POM) distributed within the soil profile. Published rates for SOC compound diffusions into aggregate interiors range from 1 mm h^{-1} for laboratory saturated aggregates (Chenu et al., 2001) to as slow as 7×10^{-4} mm h^{-1} for aggregates in field measurements (Smucker and Park, 2006). Although solution diffusivities, conductivities, and flux rates for saturated and unsaturated soil pores are well known, more information relating soil biophysical pore control of the diffusion and flux rates of SOCs into the interconnected microsite porosities within soil aggregates is needed (Peth et al., 2006, 2007). Microbial mineralization of POM provides a continuous supply of SOC compounds that are distributed via the soil porosity. A continuous supply of SOC, distributed through soil micropores, is key to the sustainability of terrestrial ecosystems (Collins et al., 2000). Microbial communities governing these processes also respond to environmental conditions, including oxygen, temperature, moisture, nutrient supply, and the quality and quantity of the organic matter (Sextone et al., 1985; Camberdella and Elliott, 1993). Briefly, soil pore conductivity and associated biogeochemistry have substantial control over the gains and losses of soil C in most ecosystems. Therefore, it is imperative that additional process-level mechanisms of the dynamic biogeochemical and biophysical processes within soil pore structures be understood, especially at the micropore level.

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Soil macroaggregates are among the most cost-effective natural reservoirs of soil C (Mikha et al., 2005). High C soils develop feed-forward combinations of stable soil structures that retain more nutrients and water and more favorable environments for root growth and plant biomass production, returning additional SOC to the soil. A greater understanding of these feed-forward and feedback cycling mechanisms that lead to the best interrelationships between photosynthetic fixation of CO_2 and concomitant long-term soil retention of SOC offer tremendous opportunities for doubling or tripling current soil C contents for longer periods of time (Fig. 1). Doubling and tripling soil C levels will require a much greater understanding of soil C solution diffusivities and flux rates into intra-aggregate pore networks and associated biogeochemistries of C sorption at the molecular scale. Although the general mechanisms of management and tillage modifications of C sequestration have been reported for decades (Lal et al., 1997), discovery of microtomographic imaging of single aggregate interiors has led researchers to the discovery of new biophysical mechanisms within soil-aggregate microsites.

Soil aggregate complexes are among the most active biogeochemical structures known, primarily because of the complex assemblages of microniches at their surfaces and within (Young and Crawford, 2004). The complex soil biophysical nature of soil aggregates includes interconnected networks of macro- and micropores that control the flux rates and establish dynamic gradients of soil solutions, gases, and thermoviscous sorptivities forming organo-mineral complexes (Calamai et al., 2000; Kaiser and Guggenberger, 2003; Masaphy et al., 1996) in a manner similar to that briefly outlined in Fig. 2. The heterogeneous array of these physical-chemical interactions is further modified by myriads of microbial communities located in microniches distributed within each aggregated structure (Horn et al., 1995; Santos et al., 1997; Paul and Clark, 1996; Scow and Alexander, 1992; Sextone et al., 1985; Blackwood et al., 2005).

Delivery of Soil Organic Carbon to Aggregate Surfaces

Although the exact pathways of mobile SOC compounds within the soil matrix remain unclear, most aggregate surfaces are bathed by the preferential flow of SOC compounds via soil macropores surrounding aggregates and diffuse into aggregate interiors, forming organo-mineral complexes (Priesack and Kisser-Priesack, 1993; Calamai et al., 2000; Kaiser and Guggenberger, 2003; Masaphy et al., 1996). Solute and water movements into aggregates are also related to the entrapment of air within aggregates (Zaher et al., 2005) and liquid phase sintering (Or, 1996). Evapotranspiration combined with precipitation and irrigation events contribute to hysteretic water retention patterns addressed, in part, by the Richards equation relating hydraulic conductivity $[-K(\theta)]$ of SOC solutions to the soil water retention relationship between water potential and water content ($d\psi/d\theta$). Conductance capacities can be calculated for specific water content ($C\theta$) as determined by the slope of the water retention curve. Consequently, during natural DW cycling, the repeated sorption and desorption of soil water contents experienced by most aggregates near the soil surface generate surges of enriched and labile SOC solutions to aggregate surfaces within the rhizosphere (Denef et al., 2002), where they are easily respired by the myriad of microbes (Park et al., 2007).
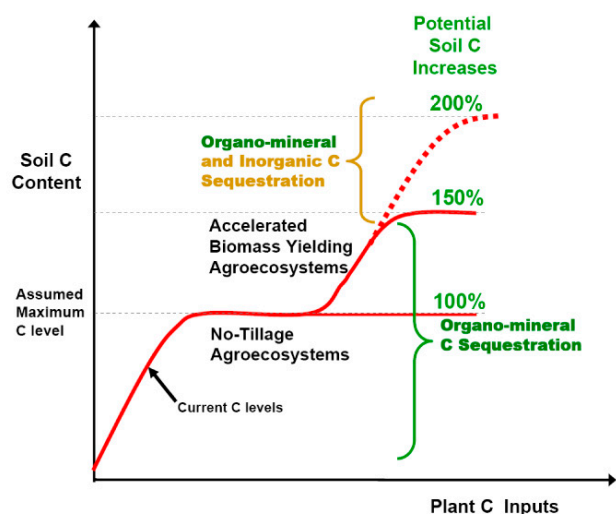

FIG. 1. Projected possibilities for augmenting C sequestration in soils through a greater understanding of biogeochemical mechanisms within micropores of soil aggregates that could be realized in management operations. Greater knowledge of the relationships among flux rates, surface adsorption, hysteretic water capacities, pore blockage, and the bioavailability of organic compounds provide additional long-term soil C sequestration potentials within structured soils. These projected 150 and 200% increases could be realized with augmented biomass resources for increased soil organic matter accompanied by more stable soil aggregates containing greater microporosities that sequester higher quantities of C protected from microbial mineralization.
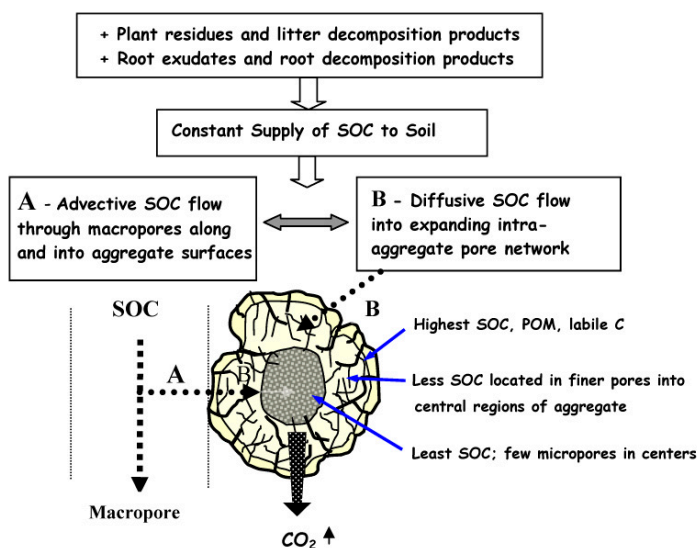

FIG. 2. This outline of the sources and pathways of soluble organic C (SOC) flowing among interaggregate macropores depicts pathways for SOC diffusion into myriads of newly formed intra-aggregate micropore networks produced by frequent drying and wetting cycles. Many of these new micropores are dead-end pores that store additional immobile water, as defined by DeSmedt and Wierenga (1979), within aggregate centers. A continuous flux of SOC into these newly exposed mineral surfaces contributes to the further stabilization of aggregates and appears to protect C from microbial mineralization (Park and Smucker, 2007).

Specific intra-aggregate porosities controlling soil water flux rates and CO_2 respiration are complicated by soil aggregation processes (Schjønning et al., 2003). Our studies demonstrated long-term conventionally tilled agriculture reduced the K_s velocities through macroaggregates, 6.3 to 9.5 mm across, by 16-fold compared with the same aggregate size fraction sampled from nearby wood lot soils of a Wooster silt loam. Comparing K_s values through aggregate size fractions ranging from 2 to 9.5 mm for the same forest soils, we identified K_s reductions through individual aggregates from conventionally tilled (CT) soils to be 50% lower among the 2- to 4-mm size fractions and as much as 80-fold greater through individual aggregates 6.3 to 9.5 mm from native forest soils (Park and Smucker, 2005c). Using these measured soil parameters, we modeled K_s velocities through macroaggregates 7.9 mm in diameter. The unsaturated soil hydraulic properties in the HYDRUS-2D code were described by a set of closed-form equations. The original van Genuchten equations were modified to add extra flexibility in the description of the hydraulic properties near saturation (Vogel and Cislerova, 1988). A uniform hydraulic head of 50 cm was applied to 25% of one edge of the idealized soil aggregate to generate water flow across the whole aggregate. Moist aggregates at −40 hPa were subjected to these uniform hydrostatic head pressures and K_s in whole, −1/3, and central regions of aggregates using K_s values ranging from 0.0042 to 430×10^{-4} mm s^{-1}. Soil bulk density, porosity, texture, $K\theta$, tensile strength, and C data for each of two hypothetical concentric surface layers: external (M1) and transitional (M2) mechanically peeled from the interior region (M3) of the macroaggregates were reported earlier (Park and Smucker, 2005b). The remaining soil parameters, listed in Table 1, were inserted into or generated by the model. Homogeneous aggregates conducted uniform water flow through aggregates having continuous pore geometries between adjacent concentric layers and regions within soil aggregates (Fig. 3A). These simulations demonstrate intra-aggregate pore continuities and discontinuities control water flow rates and distributions within aggregates, influencing the water–air relationships at this scale. However, as porosity and K_s parameters were adjusted across aggregate regions (Park and Smucker, 2005c) most water flow through these "more natural" aggregates was limited to exterior regions,
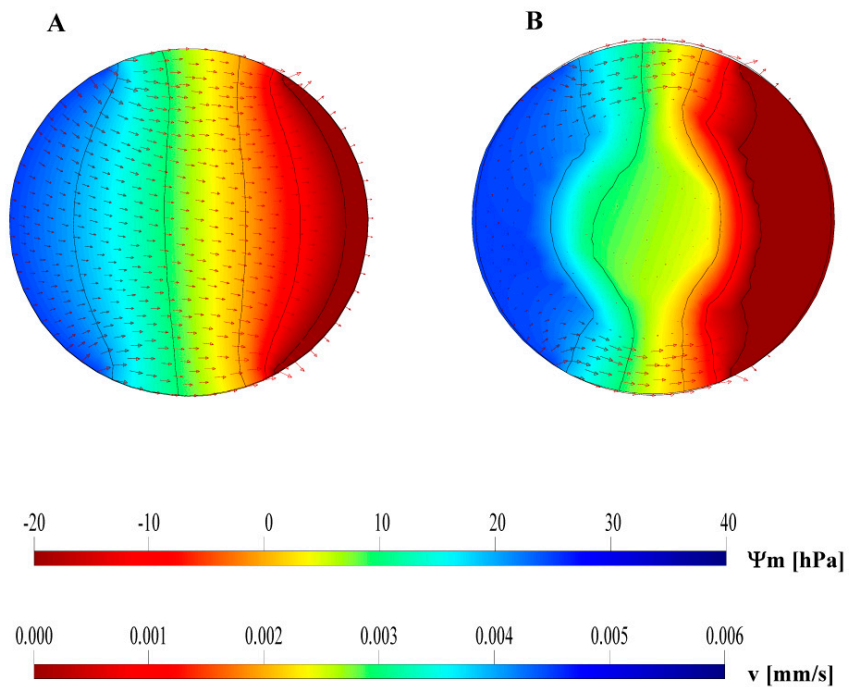

FIG. 3. HYDRUS 2D models of water flow: (A) uniform water flow through homogeneous aggregates with similar interior regions, (B) water flow limited to exterior layers due to heterogeneous regions within aggregate interiors. To model the water movement inside the aggregates, the van Genuchten parameters were defined for each aggregate layer (Table 1). The values of *f* were used to define θ_S. The parameters θ_R, α, and *n* were taken from Rosetta v. 1.0 (1999). To compare the water movement in different aggregate configurations, the water flow was modeled with the same and different texture distributions, implying different values for the van Genuchten parameters and K_s. A constant hydraulic gradient of 50 hPa was applied across the soil aggregate to generate the water flow (left to right).

bypassing internal regions (Fig. 3B). For the sake of brevity, we do not show all modeled water flux patterns, but these various modeling exercises clearly identified how the spatial distribution of water throughout individual aggregates becomes more heterogeneous as the discontinuities among the layers and interior regions increase. Although models are not always conclusive, this exercise suggests that the higher concentrations of soil C sequestered within micro and mesoaggregates (Six et al., 2000b) may be more recalcitrant with longer residence times primarily because little water flows across the discontinuous regions of these adjacent smaller aggregates contained within macroaggregates. Consequently, soil solutions containing SOC compounds that continuously bathe macroaggregates surfaces may not be able to connect with microaggregates nor their intra-aggregate pore volumes buried within macroaggregates.

Lower C contents in CT aggregates appear to be the result of both lower diffusion of SOC (e.g., the C most labile to microbial respiration) into aggregate interiors and lower quantities of labile C stored within interiors of aggregates from the same Hoytville clay loam soil managed for 42 yr as no-till (NT). Continuous conventional tillage reduced intra-aggregate porosities by 17% (Park and Smucker, 2005c). Rapidly respired C, during the first 5 d, from interior regions of CT aggregates was three times less than C respired from NT aggregate interiors (Fig. 4a). Additionally, the ratios of labile C respired from interiors to that from whole aggregates, an index of recent SOC

TABLE 1. van Genuchten parameters used in the modeling of water flow in Fig. 3.†

Concentric layer	Homogeneous aggregate						Heterogeneous aggregate					
	T	θ_S	θ_R	α	N	K_s	T	θ_S	θ_R	α	N	K_s
M1	cl	42.3	9.5	0.19	1.31	0.44	scl	42.3	8.9	0.001	1.23	0.44
M2	cl	34.6	9.5	0.19	1.31	0.42	cl	34.6	9.5	0.0019	1.31	0.0042
M3	cl	29.3	9.5	0.19	1.31	0.43	c	29.3	6.8	0.0008	1.09	0.043

† T, texture; cl, clay loam; scl, silty clay loam; K_s, saturated hydraulic conductivity ($K_s \times 10^{-4}$) (mm/s).

influx into aggregate interiors, was approximately 50% lower in the CT than NT aggregates (Fig. 4b). These data suggest less labile soil C was sequestered by CT aggregates and at least twice as much labile C was retained by NT aggregates. The diffusion of fewer labile SOC compounds into interior regions of CT aggregates suggests lower porosities reduced pore connectivities, reducing flux rates of SOC to interior regions of CT aggregates. Dell et al. (2001) reported accumulations of SOC compounds on aggregate exteriors are more rapidly respired. Consequently, aggregates from CT soils, containing lower internal porosities, loose more SOC because of their inability to conduct these labile C compounds into their interiors and away from microbial metabolism, as defined by Denef et al. (2001a, 2001b).

Development of Intra-Aggregate Micro- and Nanopores

Repeated DW cycling promotes the accumulation of SOC compounds within aggregates (Mikha et al., 2005; Park et al., 2007). More SOC compounds are transported into macroaggregate interiors by solution diffusivities influenced by changing water contents, continuous supplies of SOC compounds, and greater soil aggregate stability (Kaiser and Guggenberger, 2003, Denef et al., 2002). When more POM is occluded within macroaggregates (>250 μm) and microaggregates (20–250 μm), higher concentrations of soluble C are produced and diffuse into newly established microsites adding to the stabilization of macroaggregates (Jastrow, 1996; Golchin et al., 1997; Six et al., 2000a, Denef et al., 2002). Soil aggregates from CT soil are subjected to more DW cycles per growing season (~54). In contrast, aggregates from NT soils are subjected to fewer (~37) DW cycles per growing season (unpublished SALUS modeling of changing soil water contents in 0–5 cm soil depths for a Kalamazoo loam soil in SW Michigan, 1994–1996). Conventional tillage incorporates surface plant residues, continuously exposing soil surface aggregates to DW cycles. In contrast, plant residue covers associated with NT diminish the energies of rainfall impact and rapid hydration, preserving more aggregates (Beare et al., 1994; Paustian et al., 1997). Our field time domain reflectometry observations also recorded 50% greater drying rates of surface soils by CT than NT soils (Huang, 1995). Reports by Hussein and Adey (1998) support the DW cycling promotion of C sequestration by aggregates, by comparing the effects of different irrigation wetting rates on soil structures, and suggest fast capillary wetting promoted greater internal porosity and higher tensile strength for soil aggregates.

Microbial communities and higher microbial populations accumulating at soil aggregate surfaces are altered by tillage and current cropping sequences (Blackwood et al., 2005). Although the direct contributions of these higher microbial populations to long-term C storage remain uncertain, it is known they mineralize POM into SOC compounds. Furthermore, DW cycling promotes the diffusion of SOC compounds into aggregate interiors when aggregates are subjected to DW cycling (Mikha et al., 2005; Park et al., 2007). Greater C within aggregates also stabilizes aggregate pore structures, improving internal porosity and hydraulic conductivity (Park and Smucker, 2005c). Using newly designed soil aggregate erosion (SAE) chambers, Park and Smucker (2005b) mechanically removed multiple concentric layers from different regions within air-dry soil aggregates. Briefly, each aggregate is weighed initially and at frequent intervals during the mechanical removal process. Each concentric layer can be identified and analyzed for soil C following the mechanical removal process. The SAE approach separates surface regions from aggregates that contain different textures, pH, bulk densities, porosities, C and N compounds, and bacteria community structures (Santos et al., 1997; Smucker et al., 1998; Blackwood et al., 2005; Horn and Smucker, 2005; Kavdir and Smucker, 2005; Park and Smucker, 2005a; Smucker and Park, 2006; Park et al., 2007).

Discontinuous pore geometries within macroaggregates often limit the distribution of substrates, enzymes, and microbial cells (Chenu and Stotzky, 2002; Smucker et al., 1998). Chenu and Stotzky (2002) estimated that 15% of pores in sandy soils and 52% of pores in clay soils are not accessible to microorganisms. Some of these pores are connected by extremely small (2–10 nm diam.) micropores (Mayer et al., 2004; Zimmerman et al., 2004) or terminate throughout aggregates as "dead end" pores that may serve as anaerobic C reservoirs (DeSmedt and Wierenga, 1979; Sextone et al., 1985; Smucker and Park, 2006) (Fig. 2).

We believe that considerable quantities of C could be stored in these ultra-small fissures with very large surface areas. Furthermore, these microstorage regions would separate C from microbes and their enzymes. Since the majority of soil sorptive surfaces are located among the meso- and micropores of
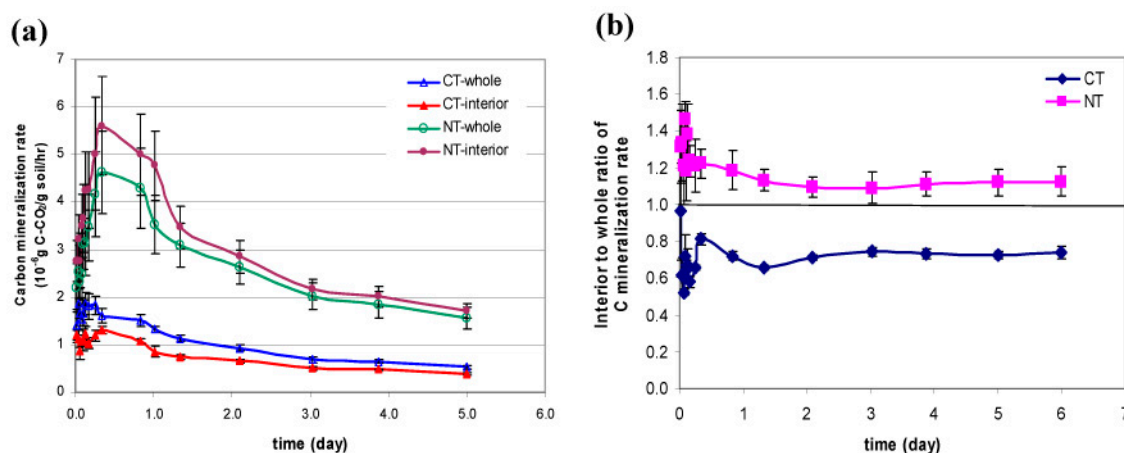

FIG. 4. (a) Carbon mineralization rates by whole and interior regions of aggregates 4.0 to 6.3 mm in diameter, from a Hoytville clay loam soil managed as conventionally tilled (CT) and no-till (NT). (b) Differential ratios of C mineralization rates between interior and whole aggregates. Bars are the standard errors of three field replicates, n = 45.

aggregate interiors (Kaiser and Guggenberger, 2003), we are confident that if intra-aggregate pore connectivities and associated pore networks are expanded, greater quantities of C will be retained by the best managed soils, as outlined in Fig. 1.

There appears to be a range of intra-aggregate pore diameters—from 0.2 to 1000 nm—that could transport SOC compounds yet prohibit on-site mineralization of C by bacteria and their associated enzymes (Mayer et al., 2004; Zimmerman et al., 2004). Many of these nanosized pores appear to be connected and could receive supplies of SOC from micro- and mesopores in both micro and macroaggregates as suggested by Marschner and Kalbitz (2003). Current evidence suggests that rapidly changing internal pore geometries contributing to the well-known hysteretic changes in the sorbed and desorbed soil water retention relationship during changing soil water potentials and the associated migration of microcolloids during intensive DW cycling (Golchin et al., 1994) can present physical barriers to microbes and their associated enzymes (Baldock and Skjemstad, 2000).

Carbon isotopic techniques, using stable tracers (^{13}C/^{12}C), provide highly accurate approaches for tracing C transfer from plant roots to soil C pools associated with previous soil organic matter (SOM) dynamics (Leavitt et al., 1996; Paul et al., 2001). We have reported C and N compounds transported from plant roots contribute up to 66% of the total C content retained by exterior regions of field aggregates (Smucker and Park, 2006). Additionally, most rhizosphere aggregates are more stable than bulk soil aggregates, which leads to the accumulation of additional C sequestration by aggregates adjacent to plant roots. We planted C$_3$ alfalfa (*Medicago sativa* L.) into field soil planted predominately to C$_4$ maize (*Zea mays* L.). The isotopic composition of soil organic C depends on the plant materials grown previously. When soil, planted historically to predominately C$_4$ plants is planted to C$_3$ plants, the ^{13}C/^{12}C ratio of the SOM will be altered by the modified ^{13}C/^{12}C ratio from the C$_3$ alfalfa plant. Exterior regions of soil macroaggregates, removed from the rhizospheres of 20-month-old alfalfa plants in a Kalamazoo loam field study, contained the most new C$_3$ from alfalfa roots. Sixty-six percent of the total C within the surface layer (0–24 mm deep) contained new C$_3$. Forty-eight percent of the total C in the second concentric layer (24–38 mm deep) contained new C$_3$ (Smucker and Park, 2006). Although the diffusion rate for these studies was approximately 7×10^{-4} mm h^{-1} for field aggregates, no new C was deposited in the central regions of these macroaggregates during the 20-mo exposure to the soluble root exudates of alfalfa. However, when similar-sized aggregates were subjected to repeated DW cycling in the laboratory, ^{13}C-glucose was sorbed throughout the aggregates, suggesting that both DW cycling and repeated saturation promoted C flux into aggregates. Repeated additions of glucose ^{13}C, following each rehydration, resulted in the establishment of ^{13}C gradients with the greatest concentrations along aggregate surfaces and lowest concentrations within aggregate centers (Park et al., 2007). Continuous additions of C reduced the mineralization of pre-existing soil C in the DW plus ^{13}C-glucose treatments by an average of 45%. The ^{13}CO$_2$–C efflux, derived from glucose added during each DW cycle period, decreased from 96 μg C g^{-1} soil at the first DW cycle to 42 μg C g^{-1} soil at the fifth DW cycle. These decreases of ^{13}CO$_2$–C efflux with increased concentrations of ^{13}C-glucose within aggregates suggest that

newly added glucose C was transported further into aggregate interiors, where they were chemically and physically protected, reducing the respiration of the original soil C (Park et al., 2007). Following typical accelerated respiration peaks associated with additions of new C, successive additions of ^{13}C-glucose retarded microbial respiration, suggesting newly added C was retained by aggregates subjected to multiple DW cycling. These studies identify the potential for augmenting SOC diffusion throughout aggregates, subjected to extremes of DW cycling (i.e., from air dry to saturated conditions) during the first three cycles, and the C storage capacity of macroaggregates continued to expand during the remaining two cycles of that study. In contrast, new C$_3$ root exudates from alfalfa roots, reported for the field study mentioned above, did not diffuse into the central regions of aggregates, which undoubtedly remained fully saturated.

Soluble C compounds bathing surfaces of macroaggregates establish rather large concentration gradients from aggregate surfaces toward their interiors. Mineralization of nonuniformly distributed POM materials throughout the macroaggregate matrix also generates high C concentrations at surfaces of micro- and mesoaggregates encapsulated within macroaggregates (Denef et al., 2001a, 2001b; Smucker and Park, 2006). Although these SOC compounds represent a small proportion of the total SOM in soils, SOC and N compounds are the primary energy sources for microbial communities that mineralize both the labile and more recalcitrant pools of soil C adsorbed to the mineral surfaces along interior orifices of macropores. In contrast, C stored within micro- and nanopore-sized fissures is inaccessible to microorganisms and is retained for longer periods of time (Sollins et al., 1996; Kaiser and Guggenberger, 2003; Zimmerman et al., 2004).

Soil Macroaggregate Stabilization and Carbon Sequestration

Natural soil DW cycles physically modify the formation and function of soil structure, aggregate stability, C flux, and C mineralization. Disruption of dry aggregates by rapid rewetting appears to be the result of differential swelling and internal pressure buildup by the compression of entrapped air (Or, 1996; Tessier et al., 1990; Zaher et al., 2005). However, nondestructive slow wetting of moist aggregates by soil solutions containing SOC and N compounds generated by decomposing plant residues and root exudates strengthens soil aggregates (Degraff et al., 2006; Zaher et al., 2005). Horn and Dexter (1989) reported tensile strengths of aggregates adjacent to roots were increased by the intense and periodic drying of soil due to plant root absorption of soil water. Czarnes et al. (2000) suggested root exudates combined with DW cycles stabilize soil structure by increasing the strength of bonds between particles and buffering the destructive features of rapid rewetting rates. Therefore, the effects of DW cycles on aggregate formation and stabilization appear to depend on their rates of wetting; the chemical composition of wetting solutions generated by root exudates; C and N compounds originating from POM, fungal hyphae, and bacterial communities; the number and severity of DW cycles; and clay mineralogy (Hussein and Adey, 1998; Mullins et al., 1990; Czarnes et al., 2000; Denef et al., 2001b; Degraff et al., 2006; Denef and Six, 2005). Rapid re-wetting of dry soils

may also accelerate the release and decomposition of SOM protected within micropores (Utomo and Dexter, 1982). Denef et al. (2001a, 2001b) reported that extreme DW cycles disrupted macroaggregates, inhibiting microaggregate formation in the short term, but eventually induced a more rapid reformation of macroaggregates that incorporate new POM. Plante and McGill (2002) also suggested intermediate physical disturbance is necessary to increase the occlusion of POM within aggregates. Therefore, the net effects of long-term DW on C mineralization are dependent on the frequency (i.e., cycles per season) and the intensity (i.e., range of soil water potentials), which appears to have cumulative and stabilizing contributions of macroaggregates for most soil types. Kaiser and Guggenberger (2003) emphasized the importance of micropores at aggregate surfaces for maximizing DOC compounds and suggested increased DOC inputs into subsoil horizons will increase soil recalcitrant C pools. Therefore, it appears that C sequestration within aggregates could be augmented at all depths within soil profiles, when the majority of stable aggregates are predisposed with maximum quantities of micropores that rapidly absorb and transport DOC compounds into the aggregate fissures and micropores beyond contact with microbial communities.

Calculations by Or et al. (2007, this issue) demonstrate that for typical values of soil matric potentials found in field soils mass diffusion through liquid films and crevices connecting bacterial colonies is severely limited. Therefore, microbial survival cannot rely on the maintenance of functional and hydrated microenvironments of pore geometry and surface roughness alone. He further suggests that microbial aggregation in colonies and their production of extracellular polymeric substances (EPS) provides advantages for anchoring and a protective matrix; EPS alters microbial surroundings by improving diffusion pathways via the maintenance of higher hydration states relative to soil. Quantifying the complexity of interactive and often competing processes is critical for optimal management of microbiological processes in the vadose zone. Continuous production of EPS by microbes in drying aggregates, which glues surrounding soil regions together, combined with the formation of new fissures and micropores in soil regions with fewer microbial communities during aggregate rewetting pose an interesting possibility for bypass flow of these "enveloped microbial communities" by SOC compounds during subsequent DW cycles. This "SOC bypass flow" option is one possible mechanism to explain the reduced soil respiration of newly added SOC during subsequent DW cycles reported by Park et al. (2007).

Pore Transport of Soil Organic Carbon and Microbial Community Metagenomics within Soil Aggregates

Pores within soil aggregates offer numerous microhabitats for various microbial communities and thus control many microorganism-based biogeochemical processes. Microbial communities in well-aerated surfaces of aggregates metabolize large quantities of SOM, while less aerobic environments within aggregates (Sextone et al., 1985) appear to modify microbes for specific functions (e.g., hydrogen consumption, enzyme production, denitrification; Loeffler et al., 1999). Soluble organic C indirectly contributes a plethora of cementing compounds processed by microbial communities, which form cation bridges with mineral surfaces or are transported within individual aggregates. Microbial communities convert these high molecular weight and C-rich energy compounds into SOC compounds that become tightly sorbed to mineral surfaces. Many of these microbial metabolites and their associative enzymes (Zimmerman et al., 2004) diffuse and conceivably become diluted during long-distance transport through soil pore networks. As C and N compounds are broken down into soluble and more mobile compounds they could easily diffuse within aggregates during the further development of micro- and nanofissures with each natural DW cycle. We believe these ever-changing mineral-cation-organo compounds within soil aggregates are continuously providing substrates to the metagenomic communities of microbes described by Liles et al. (2003) and Stein et al. (1996). They contend specific microbial communities appear to assemble for specific environmental purposes and communicate in a manner that refines their function. New information about multiple pore flow velocities controlling the suspension or deposition of colloidal sized particles (Gao and Saiers, 2006) will undoubtedly lead to the identification of specific channels that regulate enzyme diffusivities and other communication pathways influencing metagenomic communities.

Knowledge of the biophysical modifications of the constantly changing pore storage capacities, pore connectivities, and pore blockage of these heterogeneously distributed pore pathways (Fig. 5) should contribute to our understanding of the microbial processes at the interfaces within soil aggregates.
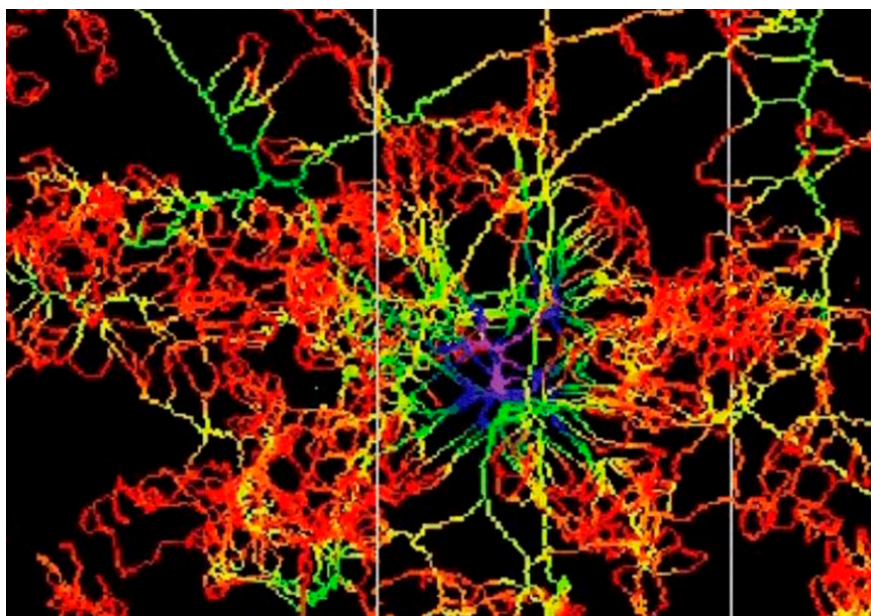

FIG. 5. Synchrotron microtomographic image processed by Linux Red Hat software from Lindquist (2002). Blue and green colors indicate larger diameter macropores (>100 μm). These are connected to surrounding smaller fragmented and highly interconnected micropores. Red and yellow indicates diameters ranging between 8 and 100 μm (Peth et al., 2007).

Distances between microbial communities, combined with protected reservoirs of C, effectively limit signaling among different microbial communities within macroaggregates. Thus, newly deposited SOC should be sequestered for longer periods of time.

Analyzing bacterial community structures using terminal restriction fragment length polymorphism (T-RFLP) of soil microbial samples from microhabitats, Blackwood et al. (2005) reported contrasting microbial community structures on both surfaces and interior regions of macroaggregates subjected to contrasting tillage and crop rotations. These metagenomes may have resulted from the contrasting quality of SOC compounds produced by different plants and aggregate transport of these SOC compounds by the tillage-altered internal porosity reported by Park and Smucker (2005c).

Increasing soil porosity within the numerous soil aggregate storage units of most highly structured soils offers continuous expansion of C reservoir capacities for storing more C beyond the metabolic catabolism of most soil biology. Changes in the total porosities of macroaggregates to DW cycling of soils from specific management systems (Mikha et al., 2005; Park and Smucker, 2005c: Park et al., 2007) indirectly suggest the expansion of pore networks, connectivities, and microfissures. Network models of pores typically use a rather simple cubic lattice, meaning that pores have coordination numbers no greater than six—they have at most six throats linking them to neighboring pores. On the basis of recent evidence of geometrical–topological correlation in sandstones (Lindquist et al., 2000), a growing number of soil scientists are applying image processing of microtomographic pore images that assist with both the visualization and development of mathematical pore-scale networks. Once these models are established, then solute diffusion, as a function of water content, can be geometrically correlated with specific pore networks.

Identification of three-dimensional reconstructions and pore diameters within soil aggregate images, Albee et al. (2000) suggested that pore pressures in dead-end pores expand internal pore networks within aggregates subjected to multiple DW cycles. Zaher et al. (2005) reported greater quantities of SOM decreased pore pressures and swelling during rapid rewetting and contributed to the destruction of unstable aggregates subjected to disintegration forces. Computer microtomography offers high resolution images, as small as 2.7 µm, for repeated non-destructive quantifications of micropore networks within the same aggregate subjected to multiple DW cycles (Fig. 5). Pore diameters, connectivity, throat constrictions, and tortuosities of intra-aggregate networks of pores are quantified by the 3DMA Rock software (Lindquist and Venkatarangan, 1999; Lindquist et al., 2000; Lindquist, 2001, 2002). Image processing of CMT images offers high resolution images for repeated quantifications of micropores within the same aggregate subjected to multiple DW cycles and associated swelling and shrinking forces (Albee et al., 2000). Typical algorithms required include segmentation to identify the material type of each voxel in the image and medial axis reduction of objects in the image to provide a skeleton, enabling efficient searching and geometrical characterization of specific networks of connected and tortuous pores (Peth et al., 2007). Specific applications of these imaging tools include the extraction of specific features; measurement of pore lengths,

cross-sectional areas and volume; and stochastic characterization of pore properties portrayed in Fig. 5, which can be precisely quantified.

Feedback Theory

Microbial hotspots are heterogeneously distributed within macroaggregates along with interconnected pores containing sufficient C and N compounds, water, and O_2 gradients (Sextone et al., 1985). They are protected from predation and desiccation stresses by very fine pores within aggregates (Six et al., 2000a; Zimmerman et al., 2004). Larger pores, located in the outer regions of aggregates, retain SOC compounds and provide microorganisms with unlimited O_2 and exposure to predation and frequent DW cycles (Hattori and Hattori, 1976; Harris, 1994). Chenu et al. (2001) found contrasting microbial habitats in aggregates with clayey and sandy soils, indicating that spatial variations in porosity and nutrient availability control many microhabitats. Frequent additions of new SOC further stabilize aggregates (Park et al., 2007), which we believe enables the formation of DW cycling–induced microfissures that sequester additional C. Continuous DW cycles combined with frequent additions of SOC solutions appear to be interactively controlling feedback mechanisms that enhance C sequestration and aggregate stabilization. Stable macroaggregates produce more microfissures during subsequent DW cycling. Greater efflux of SOC compounds into aggregate micropores, protected from microbes reduce respiratory losses, increasing aggregate stability of shrinking and swelling clay responses to large gradients of soil water potential and frequent wetting and drying cycles reported by Horn and Dexter (1989). If intra-aggregate pore networks of macroaggregates could be expanded without disrupting the whole aggregate, then additional organo-mineral compounds would strengthen aggregates, producing an aggregate stabilizing feedback mechanism (Jasinska et al., 2006). Further investigation of this mechanism is needed.

Conclusions

This report describes numerous literature contributions in an effort to provide an integrated summary of soil biophysical approaches to controlling the augmentation of intra-aggregate pore geometries from aggregate surfaces to their interiors. These pores are responsible for developing gradients of soil C that promote the diffusion into micropores and adsorb to their mineral surfaces, protecting C from microbial respiration. We suggest process-level biogeochemical and biophysical mechanisms that form micro- and nanosized fissures that promote the transfer of SOC compounds into the innermost regions of soil aggregates and may also be responsible for closing C-filled pores, sequestering C for longer periods of time. Discovery of these and other biophysical processes controlling organo-cation-clay mineral triages are necessary before additional C accumulating in NT management systems can be sequestered for longer periods of time (Lal et al., 1997). We hypothesize naturally constructed soil pore networks, exposing highly sorptive mineral surfaces, are eventually blocked by subsequent DW cycling, separating labile C substrates from microbial invasion. Further sorption of SOC compounds facilitates cation-organic-mineral bond-

ing, which strengthens aggregate structures. Understanding the extent, mechanisms, and dynamic alterations of microfissure formation and closure processes within soil aggregates will provide new knowledge applicable to bioremediation processes, convective–dispersive flow, C sequestration, nutrient availability, metagenomics of soil microbial communities, and soil aggregate stabilization processes.

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