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Review paper

The nature and dynamics of soil organic matter: Plant inputs, microbial transformations, and organic matter stabilization

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ABSTRACT

This review covers historical perspectives, the role of plant inputs, and the nature and dynamics of soil organic matter (SOM), often known as humus. Information on turnover of organic matter components, the role of microbial products, and modeling of SOM, and tracer research should help us to anticipate what future research may answer today's challenges. Our globe's most important natural resource is best studied relative to its chemistry, dynamics, matrix interactions, and microbial transformations. Humus has similar, worldwide characteristics, but varies with abiotic controls, soil type, vegetation inputs and composition, and the soil biota. It contains carbohydrates, proteins, lipids, phenol-aromatics, protein-derived and cyclic nitrogenous compounds, and some still unknown compounds. Protection of transformed plant residues and microbial products occurs through spatial inaccessibility-resource availability, aggregation of mineral and organic constituents, and interactions with sesquioxides, cations, silts, and clays. Tracers that became available in the mid-20th century made the study of SOM dynamics possible. Carbon dating identified resistant, often mineral-associated, materials to be thousands of years old, especially at depth in the profile. The ^{13}C associated with C_3–C_4 plant switches characterized slow turnover pools with ages ranging from dozens to hundreds of years. Added tracers, in conjunction with compound-specific product analysis and incubation, identified active pools with fast turnover rates. Physical fractionations of the intra- and inter-aggregate materials, and those associated with silt and clay, showed that all pools contain both old and young materials. Charcoal is old but not inert. The C:N ratio changes from 25 to 70:1 for plant residues to 6 to 9:1 for soil biota and microbial products associated with soil minerals. Active, slow and passive (resistant) pool concepts have been well used in biogeochemical models. The concepts discussed herein have implications for today's challenges in nutrient cycling, biogeochemistry, soil ecosystem functioning, pollution control, feeding the expanding global population and global change.

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1. Introduction

Soils play a major role in ecosystem dynamics, biotic diversity, water infiltration, erosion control, global food security, biofuels, the control of and response to global change, and the Earth's fresh water quality (Fang et al., 2005; Cheeke et al., 2013; Coleman and Wall, 2014). Decomposition must be slightly lower than plant inputs, on a long-term basis, to produce the soil organic matter (SOM) found in the world's biomes. Our present, industrial society is based on the fossil fuels produced during the Carboniferous and Permian eras. The precursors of the fossil fuels were deposited over millions of years under conditions of high plant productivity with limited decomposition due to high moisture contents and low, fungal lignase activity (Horwath, 2015). These hydrocarbons are now being returned to the atmosphere in excess amounts. Carbon dioxide, the most important plant nutrient, is the major atmospheric component of the global C cycle and a greenhouse gas. The simultaneous advent of agriculture, which occurred 10,000 yr ago on three continents, could be attributable to an increase in atmospheric CO_2 to above 200 ppmv (Sage, 1995). A level below 200 could be too low to allow for domestication of crops. Increased CO_2 levels, rising to today's 400 + ppmv, together with other components of the green revolution such as improved plant genetics and fertilization, have played a part in the three-fold increase in global grain production and associated plant residue inputs since 1950. Future levels of atmospheric CO_2, as well as predicted increased temperatures will also impact SOM dynamics (Batjes, 2014).

A great wealth of information on soil organic carbon (SOC) constituents and dynamics can be found in the literature of the mid-20th century when tracers first became available. Hopefully, this information is not lost, repeated, or disregarded in today's experiments. This review highlights some of the original work, relates it to modern concepts, and will hopefully lead to improved future research. The tables, figures and associated information in this paper are primarily based on the authors' work, but reflect the literature in general. It is not possible to cover all the literature over this extended period. The selected references of both the older and modern literature hopefully can lead interested scientists to the relevant papers.

The composition and global distribution of SOM is a valuable storehouse of information on vegetation, parent materials, climate, and disturbance (Table 1). De Deyn et al. (2008) published a review of plant, functional traits and soil C sequestration in contrasting biomes. Tropical forests constitute 12.2% of the Earth's land area with high net primary productivity (NPP) and annual C inputs of 2.03 kg C m^{-2}. Their soils, long thought to be SOM deficient, are now known to have fairly high SOC contents of 12 kg C m^{-2} or 692 PgC (10^{15} g) on a global basis when analyzed to the depth 3 m.

A useful estimate of gross SOC turnover, at an ecosystem level, can be attained by relating the SOC level to litter inputs (SOC content/annual litter input) on the assumption of steady state conditions. Tropical, forest soils, characterized by high rainfall and temperatures, trees with endotrophic mycorrhiza, lower C:N ratios and abundant soil fauna, have gross turnover times of 5.3 yr in the surface and 22 yr over the 3 m profile depth. Thus, they are major contributors to the annual CO_2 flux. The lower inputs for temperate forests with diverse trees and high litter decomposability, from broad leaved trees, result in lower SOC stocks that however can have reasonable soil ages at the surface (Mathieu et al., 2015). The higher SOC stocks in boreal forests reflect inputs from mostly coniferous trees with ectomycorrhizal fungi, lower temperatures and often wet conditions that result in high C:N ratios (Aitkenhead and McDowell, 2000). Podzolization can affect the SOC and soil organic nitrogen (SON) contents under such conditions. Croplands span the full range of mean annual, global temperatures. Disturbance, such as that caused by cultivation, usually results in decreased stocks of SOC with higher turnover times (Follett et al., 1997; Lal et al., 2015), whereas afforestation of agricultural land can lead to increased stocks (Morris et al., 2011; Mellor et al., 2013).

The deserts are affected by abiotic as well as biotic decomposition resulting in low SOC per unit area and low C:N ratios (Adair et al., 2008). Grasslands with high, beneath- to above-ground

Table 1
The global area, abiotic controls, net primary productivity, C inputs, terrestrial C, and turnover rates of soil C (adapted from Batjes, 2014; De Deyn et al., 2008; Horwath, 2015).

Biome	Area	MAP	MAT	Mean soil C	NPP	C inputs	Terrestrial C stock (PgC)	Gross SOC turnover time yr	
	% of total	(mm) yr^{-1}	°C	(kg m^{-2})	(PgCyr^{-1})	(kg m^{-2} yr^{-1})	Soil (0–3 m)	0–20 cm	0–300 cm
Tropical forests	12.2	1400–4500	23–28.5	12.0	20.1	2.03	692	5.3	22
Temperate forests	9.5	750–2500	9–14.5	8.7	7.4	0.85	262	9.5	26
Boreal forests	8.8	600–1800	-5–5	16.4	2.4	0.50	150	10	27
Tropical savannas	19.0	500–1350	18–28	5.4	13.7	0.48	345	6.2	30
Temperate grasslands	7.1	450–1400	−2–15	13.3	5.1	0.30	172	15.1	63
Mediterranean shrubland	3.1	400–600	15–20	7.6	1.3	0.46	124	16.7	70
Deserts	14.4	125–500	−4–25	3.4	3.2	0.08	208	25.4.	144
Tundra	7.0	250–1500	−15–5	19.6	0.5	0.10	818	52.3	165
Croplands	16.8	150–4500	−3–28.5	7.9	3.8	0.48	248	6.3	24
Wetlands g	2.2	250–4500	−2–28.5	72.3	4.3	0.17	450	150	945
Total	100			16.7	61.8	0.05	3051	NA	NA

MAP = mean annual precipitation; MAT = mean annual temperature; NPP = net annual primary productivity for the biome; NA = not applicable.

plant inputs usually have high SOC levels. In addition to the climatic-grass root-faunal interactions, there are effects of Ca concentrations (O'Brien et al., 2015) and the fact that smectitic clays, protective of SOC, are formed in grasslands (Yuan and Theng, 2012).

The tundra soils at 19.6 kg C m^{-1} (Table 1) contain a total of 818 Pg SOC with a turnover time of 165 yr. They have slow turnover rates in both the surface and subsurface even though mineral associations are less than those in other biomes (Tarnocai et al., 2009; Schuur et al., 2015). The tundra SOC stocks are continually being revised as more information becomes available. Hugelius et al. (2014) estimate the northern, circumpolar permafrost SOC stock to 3 m at 1035 ± 130 Pg rather than the 818 shown in Table 1. The large stock of SOC in the tundra soil, associated with ice and in estuarine sediments, could be very sensitive to warming (Ping et al., 2015). Many of the upland soils are expected to become drier. The wet environment in many lowland tundra sites prevents decomposition. Management scenarios that prevent drainage and maintain wetlands under global warming of the Arctic should be considered. Wetlands in all temperature regimes across the globe still retain high SOC levels with high C:N ratios attributable to the effect of anaerobiosis on decomposition (Aitkenhead and McDowell, 2000).

The gross, turnover time does not represent the true mean residence time (MRT) of the SOC due to the vast range in MRTs of the different pools-components (Bruun et al., 2005). Carbon dates (Campbell et al., 1967; Paul et al., 2001a ; Trumbore, 2009) show that measured SOC MRTs are much higher than the gross turnover times in Table 1. The majority of plant residues are decomposed in the first year, especially in the tropics (Trumbore, 1993). ^{13}C studies have shown that plant residues are transformed during decomposition into microbial products that interact with the soil matrix to protect 5–10% of the added grassland, plant residues as SOM over a 100 yr period (Follett et al., 1997). Approximately 10% of added ^{14}C is found in microbial tissue one year after addition, dropping to 4% after four years (Jenkinson and Ladd, 1981).

2. Plant inputs

Plant inputs drive decomposition and SOM formation and could be viewed as the controlling pump in the C cycle. There are indications that the native biota, adapted to a particular site, decomposes the litter from that site more rapidly than if the litter was placed on another site, i.e., has a home field advantage (Wallenstein et al., 2013). An adequate understanding of root inputs continues to be a problem (Follett et al., 1997; Adair et al., 2008; Hinsinger et al., 2012). Root-derived materials occur as exudates, fine and coarse root detritus, plant polysaccharides at the growing root tip, and mycorrhizal hypha (Calderón et al., 2012; Balestrini et al., 2015). On average, cereals, due to genetic selection for more above-ground growth, transfer 20–30% of their assimilated C to roots compared to the 30–50% for pasture grasses. However, because of the increased growth potential of cultivated cereals, the amount of the root-derived C is considered similar (Kuzyakov, 2010). This review showed root respiration accounted for 6–17% of the photosynthate for different plants, with 3–6% of the assimilated C transferred to soil. Another review (Jones et al., 2009) concluded that 20–40% of photosynthetic C is translocated underground. Of this, 5–55% remains in the roots (average of 19 ± 8%), 2–18% forms SOM, and 12 ± 5% is respired. Symbiotic root microbes, such as N fixers and mycorrhiza require extensive substrate (Paul and Kucey, 1981), but are so closely intertwined with root physiology that they are probably more closely associated with plant (autotrophic) than the soil-associated (heterotrophic) respiration.

The basic controls on plant photosynthesis, C translocation (Horwath et al., 1994; Rasse et al., 2005), and below-ground processes are similar throughout the large number of plant-microbial interactions in different ecosystems. The great range in the transfer of C to the roots, rhizosphere organisms, and soils is associated with differences in the plant-food web-abiotic controls in specific ecosystems (Moore and de Ruiter, 2012). Therefore, it is crucial to understand the factors involved in different ecosystems (Drigo et al., 2012).

An increased knowledge of the genetic information concerning symbiotic and rhizosphere organisms and their genes is giving us a better understanding of the C cycle (Balestrini et al., 2015). There is now a rich data source on gene expression and sequencing information, which provides insight into the controls on plant and microbial tissue decomposition, nutrient transfers, signal molecules, and enzyme production at the soil-root interface (Hinsinger et al., 2012; Pietramella et al., 2012).

Dahlman and Kucera (1968) used ^{14}C to show that the roots of a C_4, dominated tall-grass prairie had three times the biomass of the above-ground standing crop, but had a turnover time of three to four years. The above-ground biomass of a northern C_3 grassland was much smaller, but accounted for ~50% of the incorporated label; roots and rhizomes accounted for 25% and below-ground respiration and transfer to the soil for 25% (Warembourg and Paul, 1977). Sampling through the growing season made it possible to measure a root turnover of 155 days. Wheat shoots under similar conditions incorporated 69% of the label above-ground, 14% below-ground, and respired 17%.

Trees store much of their assimilated C in perennial wood. Data for a 5-yr-old poplar plantation (Table 2) showed that leaves and litter, which accounted for 37% of the biomass, contained 24% of the ^{14}C immediately after labeling. The label distribution in other plant parts was: 48% in stems and branches, 1.7% in fine roots, and 8.1% in coarse roots (Horwath et al., 1994). Root-soil-associated respiration accounted for 7.7% of the ^{14}C label; only 0.45% of the label went directly into the microbial biomass. Measurement after 328 days showed the expected loss of ^{14}C from the leaves after leaf fall, with 26% retention in the stem and branches and 9.7% in the roots. The root-soil respiration accounted for 15.3% of the label after one year, and the microbial biomass represented 0.3%. The microbial biomass lost 25% of its label after one year, verifying the slow microbial biomass turnover rates found in other studies (Paul and Voroney, 1980).

The microorganisms involved in symbiotic systems, such as N_2 fixation and mycorrhizal-P uptake, require extensive amounts of energy. A ^{14}C study showed that nodules in faba beans (*Vicea faba*) utilized 12% of the photosynthate, whereas the mycorrhiza utilized only 4% (Paul and Kucey, 1981). In both systems, the amount of ^{14}C attributed to symbiotic respiration-nutrient uptake was much greater than that fixed in the nodule or mycorrhizal tissues. Plants have some ability to compensate for the needs of their microbial

Table 2
Recovery of ^{14}C labeled C in different components of a poplar plantation (data from Horwath and Paul, 1994).

	Total C		^{14}C distribution	
			At labeling	After 328 days
	gC m^{-2}	% of total	%	%
Leaves/litter	448	37.0	24.0	0.2
Stems/branches	520	44.0	48.0	26.0
Roots <0.5 mm	52	4.4	1.7	1.3
Roots >0.5 mm	166	14.0	8.1	8.4
Root – soil respiration	–	–	7.7	15.4
Microbial biomass	103	1.5	0.4	0.3
Soluble C	75	–	–	–
Soil C	6788	–	1.2	1.4

partners by increased photosynthesis (Kucey and Paul, 1982). Calderón et al. (2012) applied a $^{14}CO_2$ pulse exposure to a *Sorghum bicolor-Glomus* association and found that mycorrhizal plants fixed 21% more CO_2 than non-mycorrhizal plants, but still had somewhat lower biomass production indicating there was an incomplete compensation of the needs of the mycorrhizal partners. This was also noted by Snellgrove et al. (1982). The mycorrhizal fatty acid, 16:1 *w*5, comprising 30% of the fatty acids of mycorrhizal roots, had a turnover time of 210 hr^{-1}. This was similar to the turnover time of fungal arbuscules (Cox et al., 1975) showing the importance of this fatty acid in endomycorrhizal-plant C transfers. The sorghum-mycorrhizal association transferred 6.3% of the tracer to the soil relative to only 2.3% in the non-mycorrhizal plants indicating the potential of mycorrhizal fungi to transfer assimilated C to soil.

There also are numerous indications that plant inputs can decrease SOM levels, such as in N mining and priming of the decomposition of native SOM (Kuzyakof and Domanski, 2000; Fontaine et al., 2003). Measurements with tracers and mass balance calculations that determine a net loss of SOM in the presence of added substrate show that priming is dependent on external factors (Bingeman et al., 1953). An example of N mining was shown when a corn crop, grown on soils with an extensive, active SOM pool, built up by previous legume crops or compost addition, contained more N than an adjoining wheat crop or even the N mineralized in a fallow plot (Sanchez et al., 2002). Roots can affect rhizosphere effects by drying the soil resulting in decreased decomposition, and dissolved organic matter in the soil can move to the root surfaces by mass flow.

The significance of plant-functional traits (De Deyn et al., 2008) and plant-derived C on soil biota and SOM formation (Bardgett, 2005) is not yet fully understood. Plant-microbial-SOM interactions are complex (Balestrini et al., 2015) and transfer rates vary widely with different symbiotic partners (Hinsinger et al., 2012) and in different ecosystems (Jones et al., 2009). Fortunately some of the techniques in use today will be of use in our research. Spence et al. (2011), using HR-MAS NMR, concluded that 50% of SOM is derived from microbial products. Workers such as Pisana et al. (2013) have used biological marker analysis to identify plant residue products, such as suberin and cutin and long chain aliphatics, in SOM. Simpson et al. (2011) reviewed such studies relative to molecular interactions that affect global processes. Gillespie et al. (2014) combined XANES spectroscopy (Lehmann et al., 2005) at the C and N edges with microbial biomarkers to measure the biochemical composition of the SOM of the soil fine fraction and the relative contribution of fungi and bacteria to this SOM. Chenu et al. (2015) provides information on other techniques, such as Nano-SIMS, IR spectroscopy and electron and atomic microscopy that can help determine the fate of plant residues in soil.

3. The nature and formation of soil organic matter

3.1. Historical perspectives

Ancient Chinese dynasties (2357–2261 BCE) recognized differences in soil color in soil classification for taxation purposes (Coleman et al., 2004). The ancient Vidic civilization of India classified soils by color, land forms, erosion, vegetation, land use, and human health implications (Paul, 2007). Waksman (1938), in his treatise entitled “Humus,” stated that the literature from Theophrastus (373–328 BCE) to Wallerius (1709–1778 CE) equated the words “humus” with the color of the surface, soil layer. Dark colored soils were known to be more fertile, more easily cultivated, and to hold more water. Linneaus (1707–1778), the great Swedish botanist, classified garden soils as *Humus daedalea* and field soils as *Humus rualis* (Feller, 1997). He possibly foretold the difficulties in microbial classification, before the advent of the molecular age, when he placed all organisms, seen under the microscope by Leeuwenhoek, under the genus *Chaos* (Paul, 2007).

Archard in 1786 and Berzelius in 1806 extracted humic substances from soil with alkali and showed their interaction with metals (Paul, 2007; Warkentin, 2006). Müller's studies in 1881 showed the role of earthworms in the production of nutrient-rich soil (Mull) relative to the nutrient poor litter layer (Mor), with little biological activity (Hillel, 1991; Feller, 1997; Feller et al., 2003). The work of Dokochaev and Kustyechev in 1883 (Kononova, 1961) led to modern concepts of soil formation and ecosystem studies, including the interactions of climate, vegetation (biota), parent materials, topography (the landscape), and time. Hilgaard recognized the role of cations, especially calcium, in SOM stabilization. Heber, Deherain, and Omylyanski established the role of biological-abiotic controls on humus formation, plant residue structure, and decomposition (Paul, 2007). Schreiner and Shorey (see Waksman, 1932) used available biochemical fractionation techniques, to isolate 40 identifiable materials including hydrocarbons, sterols, organic acids, aldehydes, carbohydrates, and organic P compounds (Stevenson, 1994). However, the amounts extracted were too small to assign a structure to SOM. Löhnis and Fred (1923) suggested that old humus is richer in N and much of the CO_2 is derived from fresh litter with higher C:N ratios. Waksman and Tenney (1927) contributed greatly to the knowledge of residue composition and decomposition. Waksman (1932) gives detailed data on the chemical composition of various plant parts at different stages of decomposition and said, “This mass of undecomposed, partially decomposed, and transformed materials makes up soil organic matter which is being modified constantly.” He also noted the production of stable soil nitrogenous compounds from amino acids of the proteins in plants and stressed the importance of fungi in SOM formation.

3.2. Humus structure

Today, we again are looking at what constitutes humus-SOM (Schmidt et al., 2011; Chenu et al., 2015; Horwath, 2015). Piccolo (2001) suggested that humic substances are composed of supramolecular structures of self-assembling, relatively small, heterogeneous molecules. This involves weak dispersive rather than covalent bonding. He suggested that the large molecular weights, previously demonstrated by ultra-centrifugation and gel chromatograph, were artifacts. Schnitzer and Monreal (2011) agreed, suggesting molecular weights of 6400–7800 arising from 755 to 950 atoms. These molecular weights place a restriction on the involvement of larger-molecular weight, aromatic structures, or proteins. Pisana et al. (2013) listed the average proportions of the major groups in SOM identified by nuclear magnetic resonance (NMR) as alkyl = 31%, O-alkyl = 39%, aromatic = 19%, and carbonyl = 10%. The long chain alkyl compounds increased linearly with an increase in MAT from 2 to 26 °C (Pisana et al., 2014).

Kononova (1961) and Schnitzer and Monreal (2011) argue for the occurrence of humic materials in soils. They recognized that there is some uptake of O_2 during NaOH fractionation, but stated that this can be eliminated by extraction under N_2. NMR data that identifies primarily functional groups (Simpson et al., 2011) has been used to argue for a non-humic nature of SOM (Feng and Simpson, 2011). These studies are usually conducted on soils previously treated with HF that results in a loss of 10–30% of its SOC (Chenu et al., 2015). The material lost is associated with the labile pool composed largely of carbohydrates and N compounds, which are primarily responsible for soil fertility (McLauchlan and Hobbie, 2004; Zegouagh et al., 2004).

The big difference between the views expressed by Kononova (1961) and Schnitzer and Monreal (2011), relative to those of

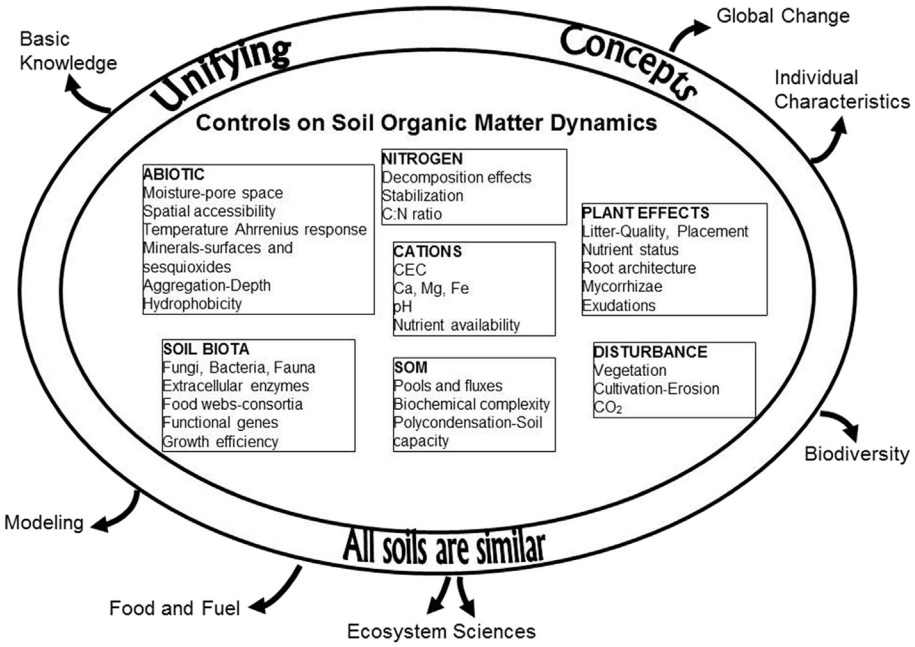

Fig. 1. The biotic and abiotic controls on soil organic matter formation and dynamics are interactive and highly integrated.

Schmidt et al. (2011), Simpson et al. (2011), and Lehmann and Kleber (2015), involves the extent to which covalent bonds hold the superstructure, humus molecule, or micelle together. Clapp et al. (2005) quote Burdon who in 2001 wrote that there is no biochemical or chemical knowledge to suggest that humic structures would be formed in the soil environment. On the other hand, Haider et al. (1975) reference many articles where enzymatic and autoxidation of phenols to quinones leads to covalent bond formation with amino acids. Many fungi and bacteria were found to increase the reactions as were clays. Clemente and Simpson (2013) suggest that organic protection by lignin or lignin-oxidation products against chemical oxidation does occur. The hydrophobicity of the lipids is also a factor (Kögel-Knabner et al., 2008), as are the stabilizing effects of cations (Stevenson, 1994). Some of the stable, hydrophobic materials are often similar to plant waxes, cutins, and suberins (Simpson et al., 2011; Baldock and Broos, 2012).

The extraction of humic compounds by alkali or resins has provided information on molecular weights, optical and colloidal properties, and chemical composition (Stevenson, 1994; Clapp et al., 2005). The words “humic compounds” tend to be associated with specific types of extraction. “Humus” is a more useful general term. The words “macromolecules,” “organic aggregates,” and “micelles” have been suggested as other alternatives. In 1930, Schmook (see Waksman, 1938) described the nature and structure of humus as mixtures of related compounds having similar structures, with N coming from proteins as an integral part of the structure. Lignin was thought to be a precursor of SOM after it was modified and interacted with microbial products (Paul and Clark, 1986; Stevenson, 1994). Now lignin is considered to be decomposed in soil and microbial products arising from the transformation of non-lignin plant residues are considered more important (Cotrufo et al., 2013). However, lignin and the lignin-to-N ratios are still considered to be major control agents in litter decomposition and stabilization (Parton et al., 2015).

The nature of SOM is best understood through a knowledge of the controls on its formation and dynamics (Fig. 1). Chemical composition (recalcitrance), physical protection, and matrix interactions (clay, silts, sesquioxides, and cations) are often cited as the major controls on SOM formation and dynamics (Stevenson, 1994; von Lützow et al., 2007). In many soils, silts comprised primarily of quartz and feldspar, contain one-quarter to one half the amount of SOC per unit weight as the clay. Brady (1984) states that the silts also contain approximately one-third the sesquioxides and equivalent Ca and Mg as the clays, possibly in fine clay coatings of chemically-oxidized quartz and feldspars. Spatial effects and resource availability are important especially in the subsurface (Chabbi et al., 2009) and in aggregates of surface soils (O'Brien and Jastrow, 2013; Segoli et al., 2013). Clays produce higher microbial biomass, stabilized microbial products (Sorensen, 1972; Amato and Ladd, 1992), enzymatic interactions (Ladd and Butler, 1975; Sinsabaugh and Follstad Shah, 2012), and increased quinone formation (Haider et al., 1975).

A generalized structural diagram, adapted from Horwath (2015), represents present knowledge about the general composition of SOM including its interactions, bonding mechanisms, cations, and clay effects (Fig. 2). The diagram illustrates the aromatic and aliphatic nature, the relationships among functional groups, and organo-mineral interactions. Near edge structure X-ray absorption, fine structure (NEXAFS), synchrotron near edge structure (XANES), and Fourier transform infrared (FTIR) showed interior pore regions of micro-aggregates where SOM is complexed with minerals (Gillespie et al., 2014; Horwath, 2015). Outer layers contain more oxidized C dominated by carboxyl and O-Alkyl functional groups. The preferential adsorption of amino compounds to clay surfaces (Nannipieri and Paul, 2009) results in enrichment of ^{15}N relative to ^{13}C or ^{14}C compounds (Sorensen, 1975). These compounds are thought to form a stable inner core to which other organics are sorbed (Sollins et al., 2006).

The role of the complex interactions of SOM in ecosystem functioning (Kögel-Knabner et al., 2008; Cheeke et al., 2013) can best be established by a combination of fractionation, incubation, and chemical characterization methodologies. Combining tracer studies with observations at the μm scale with NanoSIMS made it possible to examine the locations of these interactions (Chenu et al., 2015). This verified earlier electron micrographs that cell debris, such as cell walls and mucilage, are often directly associated with mineral particles (Foster and Martin, 1981; Campbell and Porter, 1982; Foster et al., 1983). Pyrolysis-molecular beam, mass spectroscopy (py-

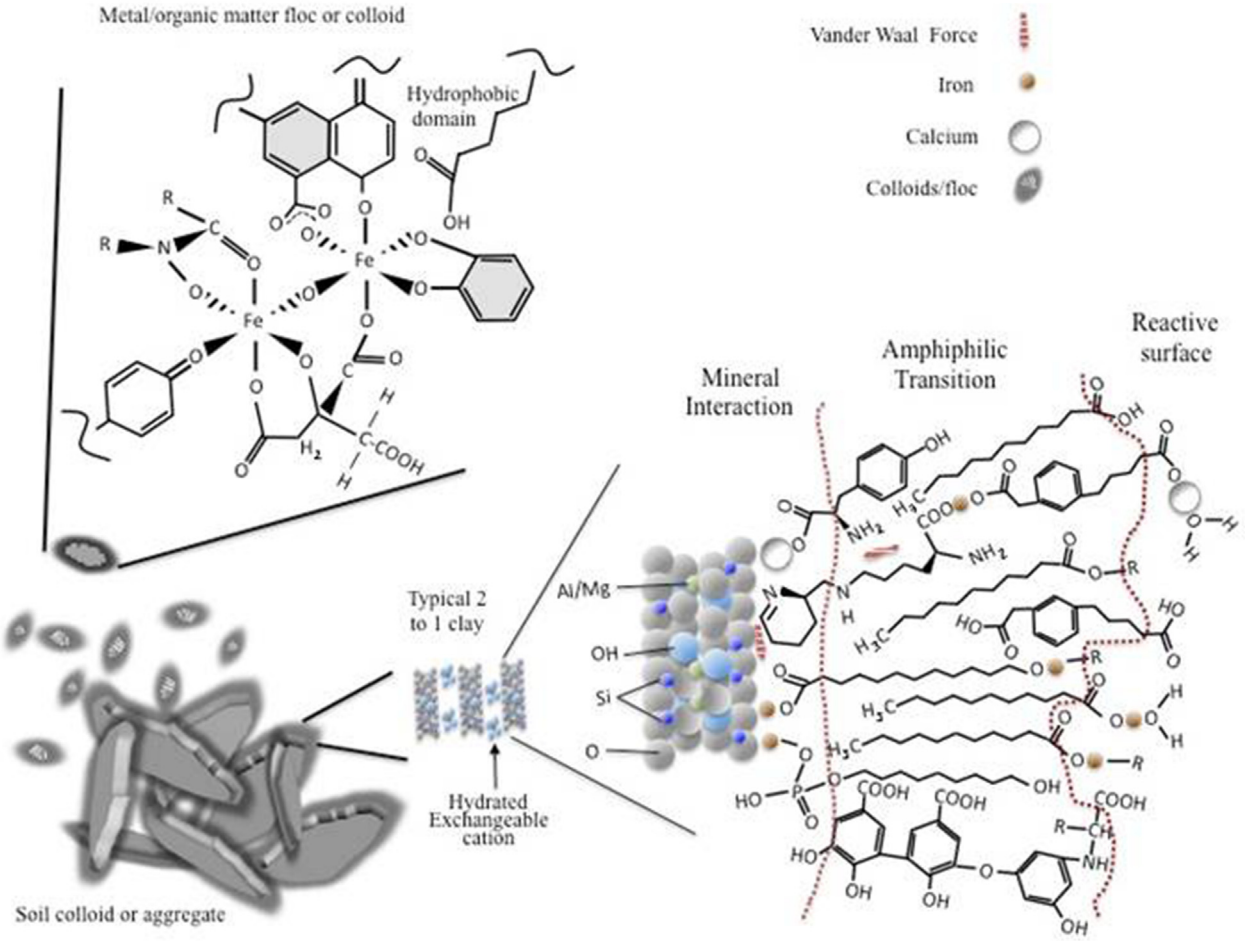

Fig. 2. Suggested structures for soil organic matter. The flocculation process of dissolved SOM with metals, such as Fe, is one mechanism leading to stable soil C. The flocs interact with SOM on minerals and aggregates. The SOM interacts with minerals by forming layers of different chemical properties (adapted from Horwath, 2015).

MBMS) (Hoover et al., 2002) of soil showed that the ~50% of the SOM that is pyrolyzed (Paul et al., 2011) contains: 5–10% aromatics and lignin monomers, 10–15% carbohydrates, 25–35% N compounds, 7–10% lipids, and 5–10% phenols (Haddix et al., 2011).

Acid hydrolysis, together with ^{14}C carbon dating, can be used to determine the resistant fraction that on average is 1400–1800 yr older than the total SOC (Leavitt et al., 1997; Paul et al., 2006). The N of even the non-hydrolyzable fraction is largely amide in nature (Plante et al., 2009). Mid-infrared spectroscopy (MiDIR) (Calderón et al., 2013) shows the effects of soil minerals and adsorption and is useful for measuring the characteristics of the LF and POM fractions, which are so important in C cycling. There are at least 10^6 natural products, including secondary metabolites of microbial origin (Alexander, 1961; Waide, 1975; Bérdy, 2005). Schnitzer and Monreal (2011) emphasized the role of these secondary microbial metabolites in SOM formation stating that abundant arylaromatic products (polyketides) could form a significant core of the thousand-year old humic acids that have been isolated from many soils (Campbell et al., 1967; Scharpenseel and Schiffman, 1977; Scharpenseel et al., 1989).

4. Turnover of specific SOM components

4.1. Historical perspectives

Measures of SOM dynamics could not be conducted until the advent of tracers when Norman and Werkman (1943) incorporated ^{15}N-labeled soybean residues into soil. Their mass spectrometer measurements of the stable isotope showed that 26% of the labeled N was recovered by a subsequent crop, with most of the tracer remaining in the soil. The growth of plant materials in a ^{14}C atmosphere and incorporation of the residues into soil in both laboratory and field studies made it possible to follow both the labeled and non-labeled SOC (Coleman and Fry, 1991). Thus, both the C and N components of SOM could be followed (Norman, 1946; Broadbent and Norman, 1946; Broadbent, 1947).

The basic equations for tracer use (Broadbent and Bartholomew, 1948; Bingeman et al., 1953; Kirkham and Bartholomew, 1954, 1955) still apply today. These workers also redeveloped the original Löhnis concept of priming as the additional decomposition of native SOM in the presence of the added substrate. The word priming can be used in two contexts: 1) the use of ^{13}C, ^{14}C, or ^{15}N data to measure the increased decomposition (turnover) of the native SOM in the presence of the added substrate, and 2) the use of the tracer to measure not only the increased turnover of SOM, but also to calculate whether there was a true net change of soil C in the presence of an added substrate. This requires consideration of the amount of added C or N remaining and involves the use of a mass balance equation to calculate the total SOM gains or losses.

The proportion of added residue remaining in various soils and climates is similar if the incubations have been carried out long enough to establish a steady state for that environment (Jenkinson, 1965, 1971, 1990). The addition of plant residues or microbial materials, and the measurement of their decomposition rates in soils

(Mayaudon and Simonart, 1958, 1963), showed that the ^{14}C from both substrates rapidly entered all fractions, but to different extents, depending on that soil fraction's turnover rate.

There are a number of reviews that provide access to the original ^{14}C papers. Some of these include: Chahal (1968) "Biosynthesis and characterization of soil polysaccharides;" Wagner (1968) "Significance of microbial tissue to soil organic matter;" Finch et al. (1971) "The biochemistry of soil polysaccharides;" Marshall (1971) "Sorptive reactions between microorganisms and clay particles;" Haider et al. (1975) "Humus biochemistry;" Wagner (1975) "Microbial growth and carbon turnover;" Sorensen (1977) "Factors affecting the biostability of metabolic materials in soil;" Paul and van Veen (1978) "The use of tracers to determine the dynamic nature of organic matter;" Foster and Martin (1981) "*In situ* analysis of soil components of biological origin;" Jenkinson and Ladd (1981) "Microbial biomass in soil: measurement and turnover;" Stout et al. (1981) "Chemistry and turnover of naturally occurring resistant organic compounds in soil;" Ladd and Martin (1984) "Soil organic matter studies;" Dinel et al. (1990) "Soil lipids: origin, nature content, decomposition and effect on soil properties;" Smith and Paul (1990) "The significance of soil microbial biomass estimates;" and Kögel-Knabner and Kleber (2012) "Mineralogical, physiochemical and microbiological controls on soil organic matter stabilization and turnover."

4.2. Soil polysaccharides

Plant carbohydrates, comprised primarily of glucose from cellulose, and xylose and arabinose from hemi-cellulose, are the primary source of energy in soil (Chahal, 1968). The traditional method of measuring SOC polysaccharides, involving hydrolysis to constituent monomers, showed some xylose and arabinose, which indicated plant remains (Finch et al., 1971). Mannose, fucose, and rhamnose are widespread in fungi. The primary sugars in bacteria are glucose, fructose, mannose, galactose, rhamnose, and fucose. The production of these compounds can be used to estimate microbial growth, but may also accumulate in the microbial products, especially in extracellular slimes-biofilms (Redmile-Gordon et al., 2014). They also and react with humic substances (Cheshire et al., 1974). The role of polysaccharides in aggregation is well-established (Acton et al., 1963; Six et al., 2002a; Fry, 2015). The N-acetylglucosamine of chitin, in fungi cell walls, and N-acetylmuramic acid, of bacterial cell walls, can be used in specific compound, stable isotope probing to determine fungal to bacterial ratios (Gillespie et al., 2014; Kandeler, 2015).

4.3. Soil lipids

Lipids, such as free fatty acids and phospholipids, are of interest because specific lipids (Wagner and Muzorewa, 1977) are associated with various microbial groups, and their tracer contents can be readily measured (Vestal and White, 1989). The separation of ^{13}C-labeled, fatty acid-phospholipids (PFLAs) thought to occur only in living cells (Kandeler, 2015) is fast, reproducible, and easily measured by GC-C-IRMS. Interpretation is limited by the somewhat restricted number of peaks that identify major groups of organisms, their variable occurrence in cells (Dinel et al., 1990), the somewhat erratic ^{13}C natural abundance in different components (Pelz et al., 2005), and the difficulty in distinguishing between plant and microbial fatty acids. The incorporation of the tracer indicative of actively growing cells can be a useful adjunct to soil metagenomic-pyrotagged sequencing (Myrold et al., 2013) to determine community composition (Bottomley et al., 2012).

McMahon et al. (2005) following microbial community dynamics via PLFA analysis after the addition of ^{13}C-wheat straw and incubation confirmed earlier observations that Gr^- bacteria were most active when growing on soluble extracts. The fungi, represented by 18:*w*6.9, were dominant in decomposition of insoluble residues. Labeled ergosterol can be measured as a fungal marker (Kandeler, 2015). The determination of waxes and resins that comprise 1–5% of SOC in mineral soils and up to 20% of organic deposits (Wagner and Muzorewa, 1977) require pretreatments, such as NaOH hydrolysis before GC analysis. pyMBMS (Hoover et al., 2002) can identify them directly. Waxes and resins play special roles in the formation of SOM micelles and hydrophobicity (Kögel-Knabner et al., 2008). Higher molecular weight lipids from cutins and suberins can differentiate root from leaf residue (Feng and Simpson, 2011).

4.4. Soil phenol-aromatics

The transformations of aromatics in SOM have received attention due to their similarity with what were thought to be humic constituents (Clapp et al., 2005). Labeled (^{14}C) cellulose decomposed four times as fast as labeled lignin even though they are physically related in plants (Crawford et al., 1977). Lignins are usually degraded by cometabolism and phenol-oxidase enzymes with little or no production of microbial biomass or incorporation into resistant SOM (Haider et al., 1975). During degradation, the aromatic component of lignin molecules is often broken up while still attached to a larger unit (von Lützow et al., 2007). Thus, lignin itself is not a major constituent of SOM, but is still considered of importance in modeling litter dynamics (Parton et al., 2015).

The brown-black color of humus has been related to light absorption at specific wavelengths (Kononova, 1961; Shields et al., 1968). White rot fungi, which completely degrade lignin and its byproducts, do not form colored compounds in soils (Haider et al., 1975). Brown rot fungi, which only partially degrade aromatics and attack side chains, produce many brown-colored intermediates (Haider, 1992; Stevenson, 1994) that may undergo further oxidation-reduction in soils (Horwath, 2015). Phenolic compounds and lipids are abundant in silts, whereas N components and carbohydrates tend to concentrate in the clays. This conclusion is supported by the observation that silts contain more non-hydrolyzable C than clays (Paul et al., 2006; Plante et al., 2009).

4.5. N compounds

Nitrogenous compounds comprise approximately 20–35% of the SOC (Bremner and Hauck, 1982; Haddix et al., 2011). Amino sugars are important C and N constituents of SOM, and if associated with resistant, melanic, fungal constituents from dark-colored fungi, can be quite resistant to decomposition (Wagner, 1968, 1975). The C:N ratio of plant residues varies from 250:1 to 20:1 depending on the plant and plant part. Fungi are nearer to 10 to 15:1 and bacteria closer to 5:1. Soil organic matter, normally said to have a C:N ratio of 10–13:1, approaches 8 to 10:1 when the plant residues in the light fraction (LF) and particulate SOM (POM) are removed. Clays in cultivated soils approach 6:1. Such a low ratio does not allow for the presence of much N-free carbohydrates, lipids, or phenols-aromatics in the clay fraction (Paul et al., 2011). However, the presence of fixed ammonia in the clay fraction can affect the C:N ratio of this fraction (Jannson, 1958, 1963).

Earlier humic-formation theories (Kononova, 1961) postulated interactions of amino acids with sugars through the Maillard reaction and with phenols through condensation reactions (Haider et al., 1975; Horwath, 2015). Today's theories of SOM stabilization postulate direct adsorption of amino acids to clays (Sollins et al., 2006; Yuan and Theng, 2012) and the general belief that most soil N is composed of proteinacous-derived and cell wall

constituents (Stevenson, 1994; Di Costy et al., 2003; Nannipieri and Paul, 2009). Pyrolysis analysis (Schulten and Leinweber, 1993; Schulten, 1996) shows significant concentrations of cyclic N monomers in soil. The possibility that these are formed during analysis has been considered (Schulten and Leinweber, 1999); however, it is now believed that considerable quantities of these non-plant N compounds do occur in soil (Gillespie et al., 2014).

Derivatization of amino sugars allows for the separation and measurement of the compounds and associated tracers by gas chromatography-mass spectrometry (Kandeler, 2015; Bai et al., 2013). Liquid chromatography eliminates contamination of SOC with non-labeled C compounds associated with derivatization. Microbial products (Sorensen, 1975, 1977) rapidly enter what is known as the slow fraction of SOM with only a small amount being identified as microbial biomass. All of this helps explain why the modern literature still agrees with Löhnis and Fred (1923), that on average, 1% of the soil N becomes mineralized over a year's time (Robertson and Groffman, 2015).

5. Turnover of soil organic matter-humus constituents

5.1. Tracer applications

A further understanding of humus turnover in ecosystem dynamics and sustainability, global change, and soil fertility requires us to go beyond the simple gross turnover estimates of Table 1. Meaningful pool sizes and reaction rates are required (Manzoni and Porporato, 2009; Manzoni et al., 2012). The measurement of SOM fractions has proven successful when used together with: 1) modeling (Jenkinson and Rayner, 1977; Parton et al., 2015), 2) comparison of management techniques (Paul et al., 1997), 3) determination of pedogenic-soil forming factors (Scharpenseel and Schiffman, 1977; Trumbore, 1993), 4) depth (Stout et al., 1981; Goh, 1991), and 5) mineral interactions (Anderson and Paul, 1984; Torn et al., 1997).

The dynamics of field soils are best determined by two techniques: 1) carbon dating that utilizes the ^{14}C produced in the atmosphere by solar radiation, or 2) C_3–C_4 plant switches that provide a ^{13}C signal. Radiocarbon (^{14}C) has a long half-life, and such measurements are significant over periods of 100 to 50,000 yr (Stout et al., 1981). The production of ^{14}C during hydrogen bomb testing produced a spike of ^{14}C beginning in 1954, peaking in 1963–1964, and gradually declining to where it is now immeasurable (O'Brien and Stout, 1978; Chenu et al., 2015). This has proven useful for the determination of turnover times of SOC components with a rapid turnover, such as roots and litter (Trumbore, 2009).

Balesdent et al. (1988) demonstrated that the different discrimination against the naturally occurring ^{13}C isotope during photosynthesis by C_3 and C_4 plants produced a usable signal in the SOM if there was a C_3–C_4 plant switch, such as the growth of C_4 maize on a previous C_3 forested soil or the growth of C_3 wheat on a previous C_4 grassland (Boutton, 1996). Automatic instrumentation for measuring $^{13}CO_2$ evolution, and the measurement of ^{13}C of specific compounds, such as fatty acids and chitin, are making rapid analysis of SOM dynamics and the identification of specific SOM constituents in stable isotope probing possible (Chen et al., 2012; Kandeler, 2015).

The use of mass spectrometers coupled to pyrolysis units has shown that the ^{13}C content of the pyrolysis products mirror their nonvolatile precursors allowing this technique to be used to determine the dynamics of soil constituents (Gleixner, 2013). Another use of ^{13}C occurs when the DNA of soil organisms is exposed to a ^{13}C substrate. The heavy DNA produced by the incorporation of the isotope is separated by ultracentrifugation and analyzed for microbial diversity using nucleic acid, molecular techniques (Thies, 2015). Another ^{13}C opportunity occurred when CO_2 derived from fossil fuels, thus having a different ^{13}C signature, was used in free atmosphere CO_2 enhancement (FACE) experiments under field conditions (Leavitt et al., 1997; Norby and Zak, 2011). Controls on decomposition and SOM stabilization (Fig. 1), such as soil texture, plant type, moisture, and N availability, have been shown to have interactive effects on the SOC dynamics of different sites (Hungate et al., 1996; Leavitt et al., 2001).

Table 3
Dynamics of soil fractions of a northern cultivated grassland (Mollisol) with 5.6% SOC (adapted from Campbell et al., 1967; Anderson and Paul, 1984; Paul et al., 2004).

Fraction	% SOC	MRT yr	Fraction	% SOC	MRT yr
LF	5	3	Whole soil	100	870
POM	10	12	Fine clay	8	170
Acid extract	14	325	Course clay	31	1255
Fulvic acids	15	495	Fine silt	29	968
Humic acids	40	1235	Coarse silt	25	800
Humin	31	1140	Non-hyd. Humin	23	1230
Non-hyd. HA	29	1400	Non-hyd. SOC	57	1350
Hyd. HA	11	25	Ca humates	21	1410

LF = light fraction; POM = particulate organic matter; HA = humic acids; Non-hyd. = Non hydrolyzable.

The turnover dynamics measured with tracers are dependent on the length of the tracer exposure. MRTs measured in laboratory incubations that are limited to a few years are shorter than those measured in the field where the C_3–C_4 plant switch is usually measured in decades (Collins et al., 2000). Carbon dates measure SOM dynamic of constituents, which can be millennia in length. However, they also reflect shorter term disturbance, such as management (Campbell et al., 1967; Mathieu et al., 2015). Paul et al. (2006) related field ^{13}C measurements that averaged 20 yr of tracer exposure to ^{14}C carbon dates from surface and depth measurements made on five soil types in the US Corn Belt to obtain the following equation:

$$^{14}C\ MRT = 176(^{13}C\ MRT)^{0.54} \quad (1)$$

This equation has the potential to relate the extensive number of ^{13}C field measurements to their longer, much more difficult to obtain carbon-dating equivalents. The length of the ^{13}C field or laboratory exposure should be considered if different from the 20 yr used to establish this equation.

5.2. Soil fraction dynamics

An understanding of SOC-fraction dynamics is best achieved by examining fraction-tracer data from different soils. A Canadian, Chernozemic (Mollisolic) soil with a mean annual temperature (MAT) of −2 °C and 5.6% SOC had an overall MRT of 870 yr (Table 3). In the absence of a C_3–C_4 vegetation switch in this cool climate, the data for the LF and POM fractions were derived from SOC-fraction changes during long-term incubation (Paul et al., 2004) and comparison to sites with ^{13}C data (Gregorich et al., 1995; Haile-Mariam et al., 2008). The light fraction (LF), comprising intra-aggregate plant residues (Hurisso et al., 2013), was the youngest fraction with an MRT of 3 yr. The inter-aggregate particulate organic matter (POM) comprising the other portion of fairly decomposable SOC (Jastrow, 1996; Jastrow and Miller, 1998) had an MRT of 12 yr. The MRT of the humic acid fraction at 1235 yr was much older than fulvic acids at 470 yr showing that this fractionation does differentiate on an MRT basis (Martel and Paul, 1974a, b). Hydrolysis of the old humic acids increased the MRT by 165 yr, while producing a soluble fraction of 25 yr (Campbell et al., 1967), showing that

Table 4
Use of long-term incubation, acid hydrolysis,^{13}C plant switches, and ^{14}C carbon dating to measure the kinetics of SOC pools in a cultivated, Colorado grassland soil with 1.1% C, a microbial biomass of 377 μg Cg^{-1} soil and 110 yr of cultivation-plant switch (data from Follett et al., 2007; Paul et al., 1997, 2011).

	% of total soil C	% native vegetation remaining after cultivation	MRT (yr)
Cult. Soil (^{14}C)	100	–	1015
Microbial, Labile	2	–	0.6
Microbial, Non-labile	2	–	14
Active Soil C (Inc)	8	–	11
Slow Soil C (Inc)	32	–	72
Resistant Soil C (^{14}C)	60	–	2658
Cult. Whole Soil (^{13}C)	100	70	186
Light Fraction (^{13}C)	11	16	108
POM (^{13}C)	8	17	110
Silt (^{13}C)	30	61	199
Coarse Clay (^{13}C)	22	81	304
Fine Clay (^{13}C)	15	85	540

(^{13}C) (^{14}C) = method of measurement.

although the humic acid was an old, measurable fraction, it contained a small proportion of young SOC (Paul et al., 2006). The coarse clay comprised 31% of the SOC and dated 1255 ± 80 yr. The Ca humates isolated with by humic fractionation after removal of Ca were similar in MRT to the nonhydrolyzable humic acids (Table 3). The fine clay, comprising 8% of the soil mass, adsorbed microbial metabolites and dated only 170 ± 50 yr (Anderson and Paul, 1984).

Analysis of SOC dynamics for a warmer grassland (MAT of 9 °C) with 1.1% SOC included vegetation comparisons, long-term incubation, and ^{14}C and ^{13}C together with fractionation (Table 4). The SOC had a field MRT of 1015 yr; the 60% of the SOC that was non-hydrolyzable (Poirier et al., 2005) had an MRT of 2658 yr (Follett et al., 2007). In spite of the great MRT of both the whole soil and the non-hydrolyzable fraction, this soil evolved 33% of its SOC during an 842-day incubation. The LF and some of the POM, in addition to the labile microbial biomass, are responsible for much of the mineralizable C of this soil. This soil also has a low level of aggregation, which has been shown in other soils to protect the labile pools (Mikha et al., 2013). Measurement of microbial biomass kinetics (Follett et al., 2007; Paul et al., 2011) showed that 1.2% of its SOC occurred in a labile microbial fraction with an MRT of 0.6 yr; another 2.3% of the SOC was stable microbial biomass with a field equivalent MRT of 14 yr. The drop in the microbial biomass C accounted for 24% of the mineralized C during the first 172 days of incubation. From day 332–842, the drop in biomass contributed just 6% of the mineralized C. The LF and POM of this soil, together representing 19% of the SOC, contained some prairie-derived SOC attributable in part to their 7% pyrogenic C (charcoal) (Lavallee et al., 2015).

Table 5
The use of ^{13}C changes of Hoytville soil fractions during long-term incubation of a corn-field soil (1.96% SOC after 30 yr continuous corn) derived from a forest to determine the C_3 and C_4 dynamics of the light fraction (LF), POM + sand, silt, and clay (data from Haile-Mariam et al., 2008; Lavallee et al., 2015).

	Whole soil	LF	POM plus sand	Silt	Clay
SOC day 0 (%)	100.0	3.5	11.0	23.0	53.0
SOC day 800 (%)	100.0	1.0	14.0	26.0	51.0
C:N day 0	9.6	20.0	15.0	10.0	6.5
C_4 C from corn (%)	23.0	84.0	56.0	20.0	11.0
C_4 MRT yr	18.2	3.7	7.8	12.8	26.8
^{13}C Day 0‰	−22.1	−14.1	−17.8	−22.4	−23.5
C_3 MRT yr	173.0	17.0	38.0	139.0	261.0
Black C%	5.0	3.9	2.0	6.3	10.6

The SOC dropped from 1.9% C at day 0–1.6% C at day 800. The sum of fractions does not add to 100 because of SOC losses during the fractionation, especially during the density fractionation.

The data from Table 4 can be used to test Equation (1). Conversion of the ^{13}C data for the total soil to a ^{14}C field-equivalent via this equation yielded a MRT of 2435 yr (data not shown) relative to the measured carbon date of 1020 yr. The average of silt and coarse clays with a calculated, ^{13}C equivalent age of 2565 and 3478 yr, respectively, was similar to the carbon date of the non-hydrolyzable C at 2658 yr. This badly degraded soil had a very old, fine clay fraction as measured by ^{13}C. Equation (1) was developed on soils with an average of a 20 yr C_3–C_4 switch rather than the 10 yr switch on this site. This confirms earlier comments that equation (1) and all other tracer measurements should be interpreted relative to the time of the experiment.

A third study involved acid hydrolysis, ^{14}C dating, and ^{13}C measurement of the C_3 and C_4 dynamics using data from long-term incubation. The native, Ohio Mollisol was developed under a poorly drained, maple forest. The cultivated, continuous corn on this site had 1.96% SOC with an MRT of 920 yr (Table 5). The 45% of the SOC that was non-hydrolyzable at 1770 yr MRT was assumed to be the resistant SOC pool for curve fitting purposes. The active pool accounted for 3% of the SOC with an MRT of 91 days. Fractionation and ^{13}C analysis (Table 5) showed that the light fraction, with a C:N ratio of 20 (Haile-Mariam et al., 2008), accounted for 3.5% of the SOC at the initiation of the incubation, with 84% of its C derived from corn. The slow pool (Gregorich et al., 1995, 1996), with 52% of the SOC and an MRT of 45 yr, is the seat of soil fertility. The POM plus sand, had 56% of its C originating from corn, and had a corn-derived C_4-MRT of 7.8 yr. The non-corn C_3 of this fraction was five times as old. Black carbon (Krull et al., 2006; Cheng et al., 2008) constituted 3.9% of the C of this fraction, with a ^{13}C signature of −24‰, showing that it was derived primarily from the original forest vegetation (Lavallee et al., 2015). The silt had more of its C derived from corn than did the clay fraction. The C:N ratios decreased from LF at 20:1 to clay at 6.5:1 showing the effects of decomposition and the importance of proteinaceous material stabilized by clay. Bradford reactive soil protein or glomalin (Rillig et al., 2003), said to be formed by arbuscular mycorrhyzal fungi or extracted as humic substances (Schindler et al., 2007), constituted 5% of the SOC (Haile-Mariam et al., 2008) and contained only 10% C_4 -corn C.

The MRT of the SOC of this soil increased by a factor of 5 or more at depth (Scharpenseel et al., 1989; Paul et al., 2001a) (Table 6). The MRT of the residue of acid hydrolysis doubled at depths for all soils showing that the procedure removed significant amounts of young C. However, the amount of non-hydrolyzable SOC decreased with depth, confirming previous observations (Martel and Paul, 1974a, b), that factors other than recalcitrance are involved in the great age. The observations (Chabbi et al., 2009; Rumpel and Kögel-Knabner, 2011; Dungait et al., 2012) that much of this great age is

Table 6
The role of depth and non-hydrolyzable C on the dynamics of SOC (data from Paul et al., 2001a).

Soil type	Depth cm	SOC %	SOC MRT yr	NHC %	NHC MRT yr	CO_2 MIN%
Northern US Prairie	0–20	1.75	792	50	2180	6.8
(Mollisols)	25–50	0.86	2860	42	5881	5.6
	50–100	0.36	5260	29	10,480	4.4
E. Dec. Forest	0–20	1.31	794	45	1928	6.3
(Alfisols)	25–50	0.47	2113	35	4856	7.2
	50–100	0.26	4128	34	8520	6.9

MIN = Mineralized. All MRT are based on carbon dating.

not due to recalcitrance, but rather inaccessibility, are supported by the similar percentage of SOC (Table 6) that is released by mixing-incubation of the subsurface and surface soils (Collins et al., 2000). Mathieu et al. (2015) through a meta-analysis of carbon dates concluded that while the age of topsoil SOC is controlled primarily by climate and cultivation, the age of deeper horizons is dependent on pedological traits, such as clay content and minerology that influence accessibility.

Lajtha et al. (2014), in a similar study, used ^{13}C and ^{14}C together with incubation and density fractionation of forest and restored grassland plots. Root and litter inputs on their prairie site appeared to have similar effects on SOC levels. The estimates of labile C were similar between control and litter plots.

The above data shows that although a number of fractionation tracer techniques are required to characterize all fractions there is a consistency between soils and fractions. The subsurface soils are much older and have different controls than the surface. There also is agreement between these data and other literature. This all gives support to the hope that actual pools and fluxes can be used for modeling purposes to better understand ecosystem dynamics and responses to global change.

6. The role of microbial products in SOC formation and dynamics

Microbial products have long been considered to be the major components of SOM (Löhnis and Fred, 1923; Waksman, 1932; Wagner, 1975; Miltner et al., 2011), yet we don't fully know how they are produced or where and how they are stabilized (Cotrufo et al., 2013). Measurement of biomass size changes, during long-term laboratory incubation (Table 4), showed that 35% of the original biomass had a field-adjusted MRT of 0.6 yr. The other 65% was old with a field equivalent MRT of 14 yr. The microbial biomass C at 3.8% of this SOC is in the upper range of 2–5% found for most soils (Schnurer et al., 1985; Smith and Paul, 1990). The microbial biomass, as a percent of the SOC, increases with soil quality as affected by manure, compost additions, or rotations, including legumes (Anderson and Domsch, 1980, 1989). Also, the proportion of the biomass that is labile with incubation is more sensitive to soil quality than the total biomass (Alvarez et al., 1995; Follett et al., 2007). Other factors affecting the biomass include the clay content and pH values. There is both a greater biomass and a greater carbon utilization efficiency (CUE) in clay than sandy soils (Amato and Ladd, 1992). Also, acidic soils have different decomposition kinetics (Jenkinson and Ladd, 1981) and a different community composition (Fierer et al., 2009) than those with higher pH values. Fungi (especially mycorrhyzal fungi) are more common in litter layers, at the soil surface and on the surface of aggregates (Fry, 2015). Bacteria and archaea are more often found at depth and soil biota are restricted to pores >0.8 μm, so only 20–50% of the soil pore volumes are available for decomposition.

The experiments of Oades and Wagner (1970), Jenkinson (1971), Martin et al. (1974), and Sorensen (1972, 1981), and reviews

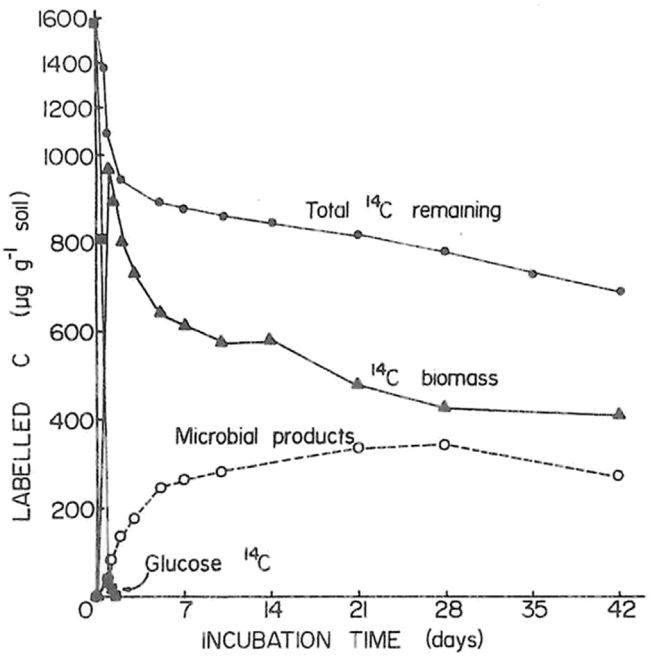

Fig. 3. The relative decomposition of ^{14}C glucose and ^{14}C wheat straw in a northern Prairie soil (from Voroney et al., 1989).

(Webley and Jones, 1971; Paul and van Veen, 1978), delineate the principles affecting microbial growth and its effect on SOM formation. These established that: 1) the level of substrate addition does not appreciably affect the amount remaining, 2) priming of *in situ* SOM at times does occur, 3) acid hydrolysis is superior to humic fractionation for separating differentially labeled constituents, but not satisfactory for determination of pool sizes, 4) the label rapidly enters all soil fractions, and 5) different temperatures of incubation, while following Arrhenius (Q_{10}) kinetics, do not appreciably alter the amount of added substrate remaining after steady state is achieved. These observations have been confirmed in the more recent experiments on the effects of global warming (Alvarez et al., 1995; Steinweg et al., 2008; Conant et al., 2011).

An extensive series of experiments, with ^{14}C-labeled plant residues, glucose, and cellulose that were incubated for up to 6 yr (Sorensen, 1972, 1975, 1977, and 1981) showed that ^{14}C cellulose produced less amino acid ^{14}C than that added as ^{14}C glucose. Due to the recycling of ^{15}N in soil during microbial growth, and the preferential retention of amino compounds in clays, ^{15}N compounds have greater MRTs than ^{14}C labeled compounds. Sorensen and Paul (1971) found that after a 200-day incubation with ^{14}C and ^{15}N, the remaining ^{14}C had an MRT of 3.2 yr compared to a 6.4 yr MRT for ^{15}N. Some of the ^{14}C and ^{15}N was associated with fine clay, nano-sized (<0.04 μm) particles (McGill et al., 1975). Enzyme production (Ladd and Paul, 1973), estimated at 2–5% of the microbial biomass (Sinsabaugh et al., 2013), could be one of the components

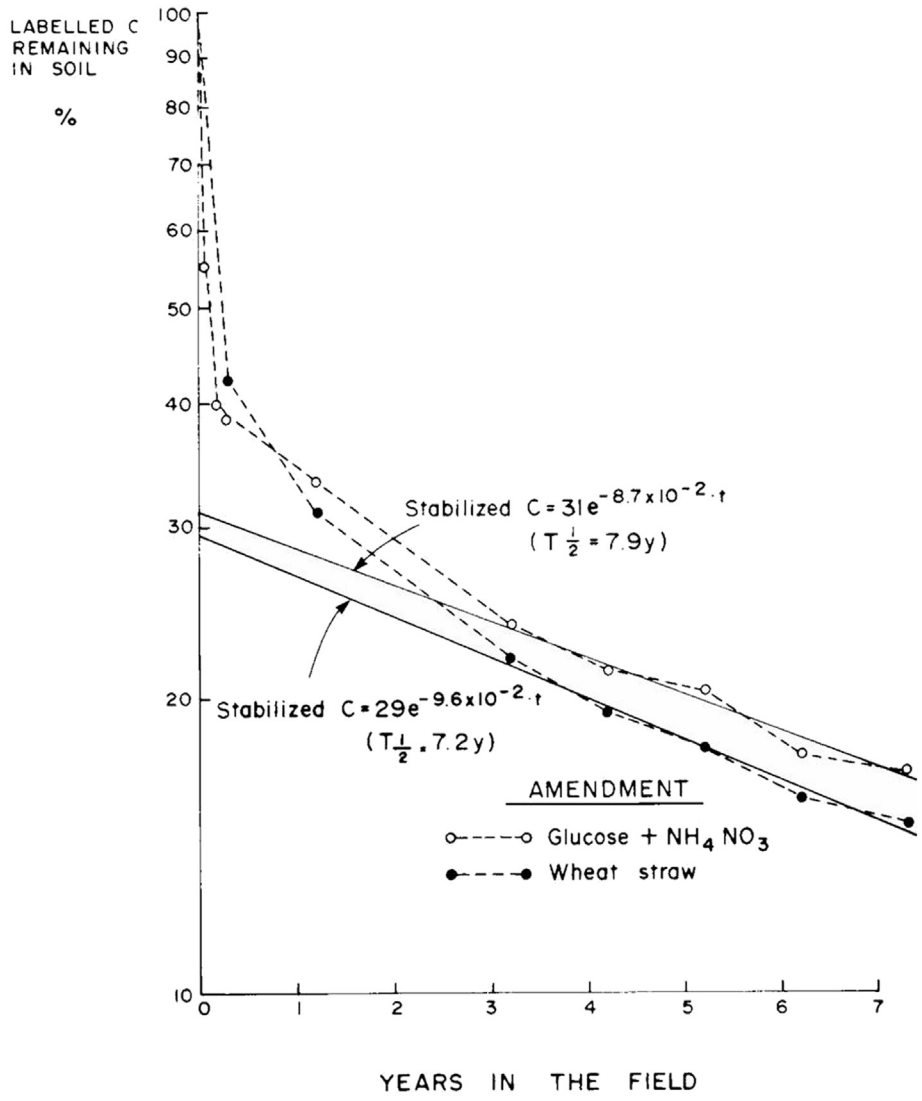

Fig. 4. Decay rates and pool sizes of microbial biomass and microbial products present in soil after growth on ^{14}C glucose in a laboratory incubation (from Paul and Voroney, 1980).

of the microbial products. Plants and soil fauna are also sources of soil enzymes (Nannipieri and Small, 2006; Gianfreda et al., 2012).

Further indication of the role of microbial products comes from a 7 yr field study involving glucose and wheat straw additions (Voroney et al., 1989). Although the decomposition rate of the glucose was faster initially, a greater amount of stable SOC was formed from the ^{14}C glucose than from the ^{14}C wheat straw (Fig. 3) with a field decomposition rate constant $T_{1/2}$ of 7.9 yr for the glucose-derived ^{14}C, corresponding to an MRT of 11.5 yr.

Visual proof of associations between bacterial cell components with clays and humified materials was demonstrated by Foster and Martin's (1981) electron, microscope photos. Miltner et al. (2011) provided further visual examples in arguing for a significant contribution of microbial biomass to SOM formation. Clay-SOM interactions are usually associated with adsorbed humus, sesquioxides, and cations (Yuan and Theng, 2012) that affect the soil biota, its substrate, and extracellular enzymes (Marshall, 1971; Gianfreda et al., 2012; Kögel-Knabner and Kleber, 2012).

Much of the biomass is at a resting state at any one time. Paul and Voroney (1980) added 1600 μg ^{14}C as glucose to soil in a laboratory incubation. At the end of day one, there was no measurable glucose, but 950 μg ^{14}C remained in microbial cells, showing 60% CUE (Fig. 4). The original ^{12}C biomass lost 12% of its C in the presence of the labeled glucose with a decay rate of 1.27×10^{-1} day. The decay rate constant of the non-active pool of the unlabeled biomass in the presence of glucose at 5.5×10^{-3t} was equivalent to an MRT (1/k) of 182 days. The labeled biomass could be separated into three pools. The active component accounted for 40% of the glucose-C immobilized and decayed at a rate constant of 1.2 day^{-1}. The smaller, second component had a decay rate of 9.08×10^{-2} day^{-1}. The third component at 534 μg^{14} C had a decay rate of 5.5×10^{-3t}. This was equivalent to the biomass decay rate of the unlabeled soil. Others confirm that only 2–14% of the total microbial biomass is active at any one time (Stursova et al., 2012).

Further information on organism growth and organic matter interactions was shown in a study where long-term incubation reduced the mineralizable SOC by 18–20% with a 50% drop in the chloroform-extractable biomass (Birge et al., 2015). The respiration of CO_2 from added corn or wheat residue, however, was the same (~40%) in the fresh and the biomass-depleted soil. The insensitivity of decomposition to microbial biomass size also has been demonstrated where chloroform treatment for microbial biomass measurements, killed 99.9% of the culturable biomass (Shields et al., 1973; Kemmitt et al., 2008). Reinoculation was not required to

achieve decomposition with mineralization of ~45% of the killed biomass-C during 10 days at 25 °C (Jenkinson and Ladd, 1981; Smith and Paul, 1990; Hurisso et al., 2013).

The above data is relevant to questions about how microbial biomass estimates should be incorporated into modeling SOM dynamics relative to microbial growth (Sinsabaugh and Follstad Shah, 2012), CUE (Sinsabaugh et al., 2016), and enzyme kinetics (Schimel, 2001) or first order dynamics (Parton et al., 2015). It also gives support to the Kemmitt et al. (2008) hypothesis that physical characteristics, not the microbial biomass, controls decomposition in soils. Also to be considered is the possibility that external enzymes independent of the biomass are contributing to decomposition (Nannipieri and Small, 2006; Gianfreda et al., 2012.)

The interactions of organism growth, organic matter, and tracers have recently become more tightly fused through the use of stable-isotope probing (SIP) (Chen et al., 2012). The incorporation of substrate-^{13}C through added labeled compounds into the rhizosphere, mycorrhizal fungi, or plant litter can now be used to: 1) measure the relationship between CUE and SOM formation (Sinsabaugh et al., 2016), 2) identify community composition through DNA and RNA-SIP, gene expression (Pietramella et al., 2012), as well as PLFA formation (Myrold et al., 2013), and 3) movement of plant residues and microbial products into and through soil humus (Kandeler, 2015; Thies, 2015). Organisms in the β- and γ-subgroups of Protobacteria (Killham and Prosser, 2015) utilize soluble constituents and are representative of Wynogradsky's zymogenous bacteria (Waksman, 1932; Alexander, 1961). Phylla, such as Actinobacteria, Planctomycetes, and Firmicutes, are involved in complex molecule decomposition and are therefore representative of Winogradsky's autochthonous organisms. The Ascomycota fungi represent the dominant fungal forms and are also active decomposers. Fusarium which is often associated with plant diseases (Taylor and Sinsabaugh, 2015) has been shown to be a major straw decomposition organism (Chattopadhyay et al., 2016).

7. Modeling in soil organic matter and tracer research

Models organize and analyze data, test and develop concepts, predict future processes, and expand understanding across scales (Campbell and Paustian, 2015). They are central to the understanding of soil organism-organic matter interactions, which is why there are >250 published models (Manzoni and Porporato, 2009). The publications by Smith et al. (1997), Schimel (2001), Manzoni et al. (2012), Moore and de Ruiter (2012), Sinsabaugh and Follstad Shah (2012), and Parton et al. (2015) give background information and comparisons between models. These models explore a variety of topics including: substrate-enzyme-microbe interactions (Sinsabaugh et al., 2016), food web-faunal effects (Osler and Sommerkorn, 2007), and global climate change (EPA, 2015).

Manzoni and Porporato (2009) note that in 1936, Nikiforoff suggested that humus formation involved pools with different turnover times, although the term “active organic matter” was used much earlier (Waksman, 1932). Jenny (1941) restated Dokuchaev's five soil forming factors of climate, parent material, topography, organisms, and time in an equation format. Jenkinson and Rayner (1977) used long-term Rothamsted field, ^{14}C addition, and carbon dating data to publish a simulation model that described organic matter turnover. Their model, now adapted as Roth C (Jenkinson, 1990), used an inert fraction that was included to help the model describe the high ^{14}C MRTs found in SOM, especially at depth. Previous discussions in this and other publications point out that there is no inert pool, not even black carbon is inert (Kögel-Knabner et al., 2008; Lavallee et al., 2015).

The McGill et al. (1975) model included a sub-model that described the transformation of microbial biomass. The van Veen and Paul (1981) model that used first order kinetics, with a microbial biomass pool, recognized the effects of physical protection by aggregates and clay-associated materials. The values for the effects of protection were determined by comparing the decomposition of amino acids in the presence and absence of clays. The effects of cultivation were modeled by using long-term climate data and alteration of the physical protection factors due to disturbance and erosion (Voroney et al., 1981). Aggregates are an important part of physical protection (Six et al., 2002a, b). Segoli et al. (2013) utilized data from incubation experiments to calculate and validate biological and environmental influences on the rates of formation and breakdown of micro and macroaggregates. Their model estimated the turnover rate for macroaggregates at 31 days and 181 days for microaggregates. These were laboratory incubations, the turnover rates measured in the field with tracers would be much longer (Collins et al., 2000).

Biological decomposition is enzyme mediated; therefore, one must ask how can a SOM decomposition model not include them? However, 50% of the models listed by Manzoni and Porporato (2009) are based on first order kinetics. Some models, such as Century (Parton et al., 1987, 2015), use first order kinetics with an implicit recognition of microbial enzymes in the decay functions for the various pools. Moisture and temperature are among the major control variables of all the models tested. Their overriding importance in decomposition (Adair et al., 2008), together with the extensive mathematical fine tuning of decomposition rates, have helped many of the models to be reasonably predictive of natural processes.

Extensive field and laboratory information is required to obtain actual pools and fluxes. Paul et al. (1999) inserted analytically-derived, kinetic pools and fluxes into the daily version of the Century model (Parton et al., 1998, 2015) to simulate daily field CO_2 evolution rates over a season in a number of cropping systems. Long-term incubations (Collins et al., 1999), ^{13}C estimates of field turnover rates (Collins et al., 2000), together with acid hydrolysis (Leavitt et al., 1997) and carbon dating (Paul et al., 2001a) provided an estimate of the active slow and resistant (passive) pools. The model accurately predicted field-measured CO_2 evolution rates on a daily basis over the growing season. It overestimated CO_2 fluxes after harvest in the fall. This was attributed to the fact that the model did not consider a lag period during which the above-ground residues lose their hydrophobicity, and are comminuted and colonized by the soil biota before the residue is in intimate contact with the soil biota and its enzymes.

The extensive studies and models on organism-enzyme interactions (Weintraub and Schimel, 2003; Sinsabaugh and Follstad Shah, 2012) usually involve Michaelis-Menten kinetics (Schimel, 2001). The amount of substrate turned into microbial products is central to SOM dynamics (Cotrufo et al., 2013; Sinsabaugh et al., 2016) and can be handled directly (Sinsabaugh et al., 2013) or indirectly as in the decomposition rate constants in first order models (Jenkinson and Rayner, 1977; Parton et al., 1987). Biotic information is most often included in food webs (Zwart et al., 1994; Coleman et al., 2004) and can become complicated if not process-function based (Moore and de Ruiter, 2012).

In addition to modeling, we need to ensure our data helps us interpret information on ecosystem dynamics. We can test our knowledge about organism biomass activity and SOM dynamics by relating it to measured field respiration rates and ecosystem productivity. The CO_2 flux of 5.6 Mg C ha^{-1} yr^{-1} released from poplar soils (Fig. 5), relative to 4.2 Mg C ha^{-1} yr^{-1} for a corn-soybean rotation (Hamilton et al., 2015) reflects the higher NPP in the poplar plantation. The higher levels of SOM on the poplar site altered the kinetically-determined sizes and dynamics of the active and slow pools (Collins et al., 1999; Paul et al., 1999, 2001b). The

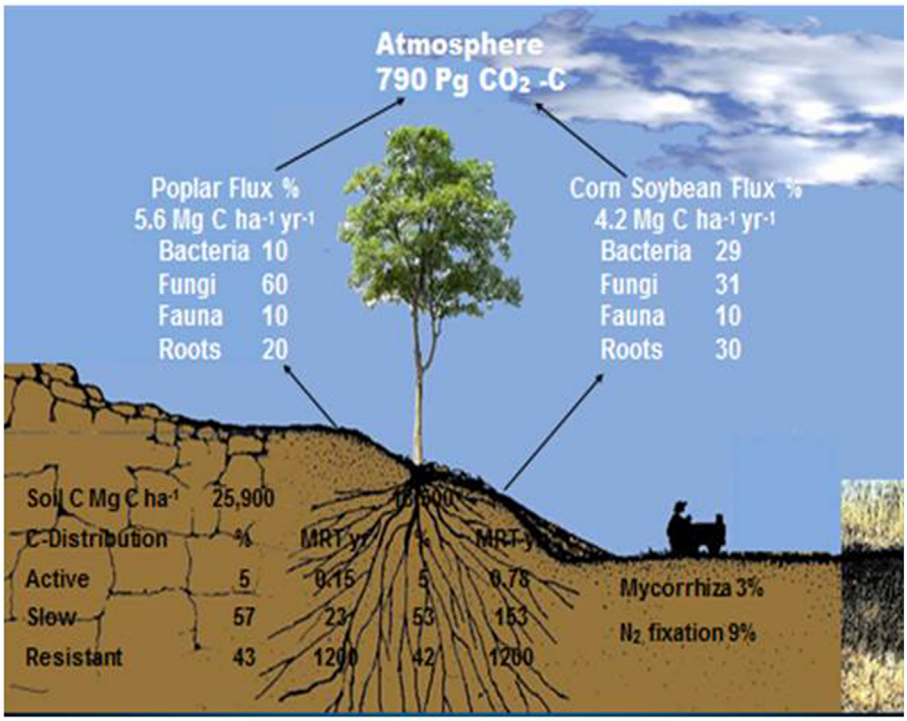

Fig. 5. Soil organic matter pools (0–25 cm) and atmospheric C fluxes (% of total) through bacteria, fungi fauna, symbionts, and roots for a poplar plantation and corn-soybean rotation at KBS-LTER MI.

figure in tying the various sections of this review together points out the relationship between plant growth, microbial respiration, SOM pool sizes, and even the effects of symbiotic organisms. The data for the contributions of the fauna, bacteria, fungi, and roots (Fig. 5) are based on the knowledge of biomass size obtained via microscopy and chloroform-fumigation (Horwath and Paul, 1994) and knowledge of microbial growth determined by ^{14}C thymidine incorporation (Harris and Paul, 1994). The numbers reflect the increase in fungal biomass in the poplar plantation as the trees switched from a vesicular arbuscular to an ectotrophic mycorrhizal symbiosis at ~5 yr in age, which affected the underground C transfers (Horwath et al., 1994).

8. Looking forward

Plants, as ecosystem C pumps, produce the substrate for soil biotic activity and SOM formation (Paul, 2015). Over the long term, net primary production must slightly exceed decomposition for SOM to accumulate. Even though much is known about plant-soil -biota controls (Balestrini et al., 2015), their interactive effects make it difficult to predict individual ecosystem effects (Hinsinger et al., 2012). These effects include: 1) the range in amounts and chemistry of above and below-ground plant C allocation with plant type, soil depth and season, 2) the ability of plants to compensate, in part, for the needs of symbiotic partners, 3) the soil drying effects on the soil biota and the mass movement of DOC as the plants withdraw water, and 4) the interactions with root-associated organisms including food webs.

The role of non-culturable organisms and genes can now be better understood with the finding of huge reservoirs of previously unknown genetic material (Pietramella et al., 2012; Taylor and Sinsabaugh, 2015). Physiological, gene expression, enzymatic, and food web data are also needed to gain a better understanding of microbial products in humus formation. The role of resting organisms (Jenkinson and Ladd, 1981), maintenance energy (Babiuk and Paul, 1970), enzyme stabilization (Sinsabaugh et al., 2013), priming (Kirkham and Bartholomew, 1954), CUE (Sinsabaugh et al., 2016), and how microbial products are stabilized (Miltner et al., 2011), must be better understood. Compound specific isotope studies (Chen et al., 2012; Gleixner, 2013) and tracer dynamics (Chenu et al., 2015), conducted together with enzyme (Sinsabaugh and Follstad Shah, 2012; Kandeler, 2015) and microbial community studies (Thies, 2015), will prove most useful in addressing these questions.

The concepts discussed in this review have implications for soil ecosystem functioning, nutrient cycling, pollution control, biogeochemistry, feeding an expanding global population and global change. Additional areas where more information is needed include: the timing and distribution of above- and beneath-ground plant inputs, residue and SOM composition (Chenu et al., 2015), temporal and spatial scaling (Hinckley et al., 2014), and microbial community composition (Kong et al., 2011). We are still not able to reliably control the effects of root-associated diseases, the ability of plants to compensate for C requirements of symbionts, or the effects of competition in attempts to inoculate desirable organisms into soil.

Microbial parameters still not well understood include CUE relative to SOM formation, maintenance energy of soil organisms, carbon overflow, and polysaccharide excretion under nutrient deficiency and cometabolism. We are finally able to characterize the vast numbers of organisms in soil. But, how important is community diversity? How can we express soil biota activities and interactions relative to food webs, predators, and parasites, including relative unknowns such as viruses? There is a great deal of microbial-enzyme data that is still difficult to interpret, such as: the role of resting soil populations, gene control by induction and inhibition, external enzyme diffusion and stoichiometry, degradation of and inhibition by specific organics, as well as the Arrhenius-based activation energy effects which are now being investigated in regard to increased temperatures across the globe.

Hopefully, this review helped identify the extensive historical literature, especially that on tracers, which can further develop future basic concepts about decomposition, microbial growth, and microbial product formation relative to SOM dynamics. The case studies were included to show the usefulness of multiple data sets. Some of the available information discussed in this review includes:

1) The combination of methods, including tracer additions, long-term incubation, ^{14}C carbon dating, and ^{13}C natural abundance measurements, which have helped to develop kinetically-defined SOC pool sizes and turnover rates.
2) Physical fractionation, especially when combined with tracers, to provide pool size and turnover information on actual SOM fractions, such as the LF, POM, silt, and clay.
3) All SOC pools contain young and old constituents due to their dynamic nature.
4) Physically isolated fractions reflect decomposition stages with decreasing C:N ratios and increasing MRT as the fractions move from the LF to the clays.
5) In some soils, fine clays are associated with recent microbial products and have low MRTs; in other soils this is not the case.
6) Much of the pyrogenic or black carbon is associated with the silt and clay-sized pools and has high MRTs, but it is not inert.
7) Tracer measurements are dependent on the time length of exposure. Data should be expressed relative to the length of exposure. The empirically-derived equation that relates ^{14}C dates to field-determined ^{13}C rates requires more validation at different time scales to relate data from short-term experiments to the pedological controlled values that occur in the field.
8) Silt-sized materials have less SOC per unit weight than clays. Their MRTs are often slightly lower than those of clays. We still don't have definitive knowledge concerning the mechanisms of SOC protection by silt-sized particles.
9) Since N is a strong controller of SOC dynamics, further integration of the data from both C and N tracers would be very useful.
10) The soils at depth are thousands of years older than those found at the surface, yet when brought to the surface, they often are fairly rapidly decomposed indicating that decomposition at depth is heavily controlled by spatial effects-resource availability.
11) All soils have similar controls allowing for the development of overall concepts, modeling, and extrapolations to larger landscapes. The expression of the controls at different sites results in the individual site characteristics.

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