



Soil carbon sequestration – An interplay between soil microbial community and soil organic matter dynamics

Siddhartha Shankar Bhattacharyya^a, Gerard H. Ros^b, Karolina Furtak^c,
Hafiz M.N. Iqbal^{d,*}, Roberto Parra-Saldívar^{d,*}

^a Department of Agronomy, Faculty of Agriculture, Bangladesh Agricultural University, Mymensingh 2202, Bangladesh

^b Environmental Systems Analysis Group, Wageningen University and Research, Wageningen, the Netherlands

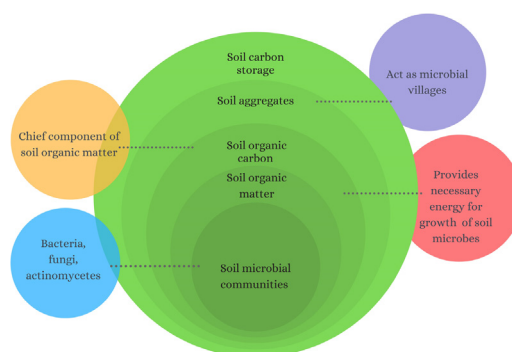
^c Department of Agricultural Microbiology, Institute of Soil Science and Plant Cultivation - State Research Institute, Czartoryskich 8, 24-100 Puławy, Poland

^d Tecnológico de Monterrey, School of Engineering and Science, Monterrey 64849, Mexico

HIGHLIGHTS

- Soil microbial community (SMC) is the heart of soil carbon sequestration (SCS).
- SMC regulates soil organic matter (SOM) decomposition and transformation.
- Soil aggregates and SOM determines the rate of SCS.
- Reintroduction of decayed SMC under different agricultural systems would ensure sustainability in long-term C storage.

GRAPHICAL ABSTRACT



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ABSTRACT

Soil carbon sequestration (SCS) refers to the uptake of carbon (C) containing substances from the atmosphere and its storage in soil C pools. Soil microbial community (SMC) play a major role in C cycling and their activity has been considered as the main driver of differences in the potential to store C in soils. The composition of the SMC is crucial for the maintenance of soil ecosystem services, as the structure and activity of SMC also regulates the turnover and delivery of nutrients, as well as the rate of decomposition of soil organic matter (SOM). Quantifying the impact of agricultural practices on both SMC and SCS is key to improve sustainability of soil management. Hence, we discuss the impact of farming practices improving SCS by altering SMC, SOM, and soil aggregates, unraveling their inter- and intra-relationships. Using quantitative and process driven insights from 197 peer-reviewed publications leads to the conclusion that the net benefits from agricultural management to improve SCS would not be sustainable if we overlook the role of soil microbial community. Reintroduction of the decayed microbial community to agricultural soils is crucial for enhancing long-term C storage potential of soils and stabilize them over time. The interactions among SMC, SOM, soil aggregates, and agricultural activities still require more knowledge and research to understand their full contribution to the SCS.

Abbreviations: AMF, Arbuscular mycorrhizal fungi; C, Carbon; CC, Cover cropping; CR, Crop rotation; CT, Conventional tillage; CUE, Carbon use efficiency; EEG, Easily extractable glomalin; EPS, Extracellular polymeric substances; FDA, Fluorescein diacetate; MBC, Microbial biomass carbon; MBN, Microbial biomass nitrogen; NT, No-tillage system; OM, Organic matter; PLFA, Phospholipid fatty acid; POC, Particulate organic carbon; RPE, Rhizosphere priming effect; RT, Reduced tillage; SCS, Soil carbon sequestration; SMC, Soil microbial community; SOC, Soil organic carbon; SOM, Soil organic matter; ST, Strip tillage; TG, Total glomalin; WSA, Water stable aggregates.

* Corresponding authors.

E-mail addresses: hafiz.iqbal@tec.mx (H.M.N. Iqbal), r.parra@tec.mx (R. Parra-Saldívar).

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1. Introduction

Soil carbon sequestration (SCS) has become one of the popular methods for capturing and storing atmospheric Carbon (C) into soils for a longer time (Lal, 2004; Schlesinger and Amundson, 2019; De Stefano and Jacobson, 2018; Liang et al., 2019a). Different methods or improvised agricultural operations for increasing SCS have been proposed. For instance, grassland settlement in abandoned and deteriorated agricultural fields, no-tillage (NT) systems, crop rotation, fertilization and organic amendments, and cover cropping (CC) may lead to systems increasing soil C stocks (Yang et al., 2019a; Francaviglia et al., 2017; Cha-un et al., 2017; Coonan et al., 2019; Tautges et al., 2019; Luan et al., 2021). However, the effectiveness of these practices highly rely on microbial activities (Peigné et al., 2007), and hence the role of the soil microbial community (SMC) should be understood to develop and adopt effective agronomic measures for SCS. Their key role in regulating C stocks and fluxes, and their interaction with soil particles, is however often overlooked. Needless to say, the microbial community is the most important regulator of soil C cycling, C biogeochemical cycles (Beauregard et al., 2010; Hartmann et al., 2015; Khatoun et al., 2017; Jansson and Hofmockel, 2020). Microbial diversity and biomass alter rhizosphere processes and determine the long-term viability of agricultural lands, in particular for carbon dynamics (Hartmann et al., 2015). Intensification of agriculture has substantially impacted the size and composition of SMC thereby altering the processes driving C sequestration (Kallenbach et al., 2019; Wallenstein, 2017). Selecting appropriate agronomic measures to increase C stocks require insights in the interplay between management, rhizosphere dynamics and the intermediating role of SMC.

Numerous studies have shown that cover cropping, organic amendments, tillage practices and crop diversification affects both soil functioning and microbial communities (Beauregard et al., 2010; Kim et al., 2020). Combining diverse crop rotation schemes (corn-cotton) along with manures (broiler litter) may yield in stable aggregates and higher microbial biomass in silty clay loam soils (Adeli et al., 2009). Reduced tillage (RT) and no tillage practices (NT) may increase arbuscular mycorrhizal spores (AMF) and dehydrogenase enzymatic activity (Celik et al., 2011) whereas Li et al. (2020) showed in a global meta-analysis that changing conventional to no till systems could increase total phospholipid fatty acid (PLFA) by 11%, fungal PLFA by 17%, and total microbial biomass by 4%. How these changes in soil microbial community affect the net C sequestration however is still unclear.

Earlier studies showed that microbial biomass, soil aggregate stability and SCS are interrelated (Garcia-Franco et al., 2015). Stable soil aggregates are needed to increase C stocks and their stability is enhanced by the plant leaf litter or root deposits with a phenolic and lignin composition (Blanco-Canqui and Lal, 2004; Liu et al., 2019). Soils with higher levels of macro-

aggregates have more potential to sequester carbon (Luan et al., 2021) since they protect C from decomposition by physical and chemical processes (Cantón et al., 2009; Murugan et al., 2019; Wilpiszeski et al., 2019), determine 80% of SCS in karst soils (Liu et al., 2019) and are identified as the main factor controlling SCS in black soils of China (Zheng et al., 2018). Macroaggregate formation is coupled with SMC activities and both regulate 82% of the variation in SOC storage (Zhang et al., 2018). Agricultural operations often tend to decrease the persistence of soil aggregates, also modifying the SMC structure (Kraut-Cohen et al., 2020). Since the microbial community structure also regulates nutrient turnover and supply, as well as SOM decomposition rates, the microbial community has been identified as critical driver for the conservation of soil ecosystem services (Nsabimana et al., 2004). Likewise, microbial necromass is gaining attention because of its high capability of producing stabilized SOM and stable C (Ma et al., 2018; Buckeridge et al., 2020). Kallenbach et al. (2016) concluded higher amounts of SOM might be linked with fungal abundance and microbial biomass instead of mineral composition of soil. This stabilization might be linked with “bacterial and fungal cell wall envelopes” (Miltner et al., 2012). All these aforementioned studies demonstrate the irreplaceable role of SMC in maintaining the optimum level of C in agricultural soils (Fig. 1), and hence a deeper understanding of the effects of agricultural practices on SMC and their impact on SCS is needed to identify those practices that have a persistent effect on soil organic carbon dynamics (Frasier et al., 2016).

This paper reviews existing knowledge on the role of soil microbial community on the fate of soil carbon in response to agronomic measures. We hypothesize that optimizing soil and nutrient management for carbon sequestration (while stimulating co-benefits for agronomic and environment) requires foremost insights in the role of the soil microbial community structure and their response to management practices applied. Management practices stimulating microbial communities to form soil aggregates, to alter their feeding strategies, and to reduce their access to carbon and nutrients might enhance the carbon sequestration potential.

The literatures used in this study were collected, synthesized and collated from previous studies appeared in peer-reviewed journals. Search engines used for literature searching were “Web of Science”, “Scopus”, “Google scholar” and search keywords include “soil organic matter” AND “soil microbial community” or “agricultural soils and soil biota” or “Conventional tillage”; “soil carbon”, SOM and MBC” etc. Peer reviewed studies include i) long- and short- term field researches, and ii) meta-analyses. Throughout the study, we used following definitions: climate (Köppen-Geiger classification), soil type (sand, clay, loam), crop type (arable and grasslands), and duration of effects (short-term and long-term).

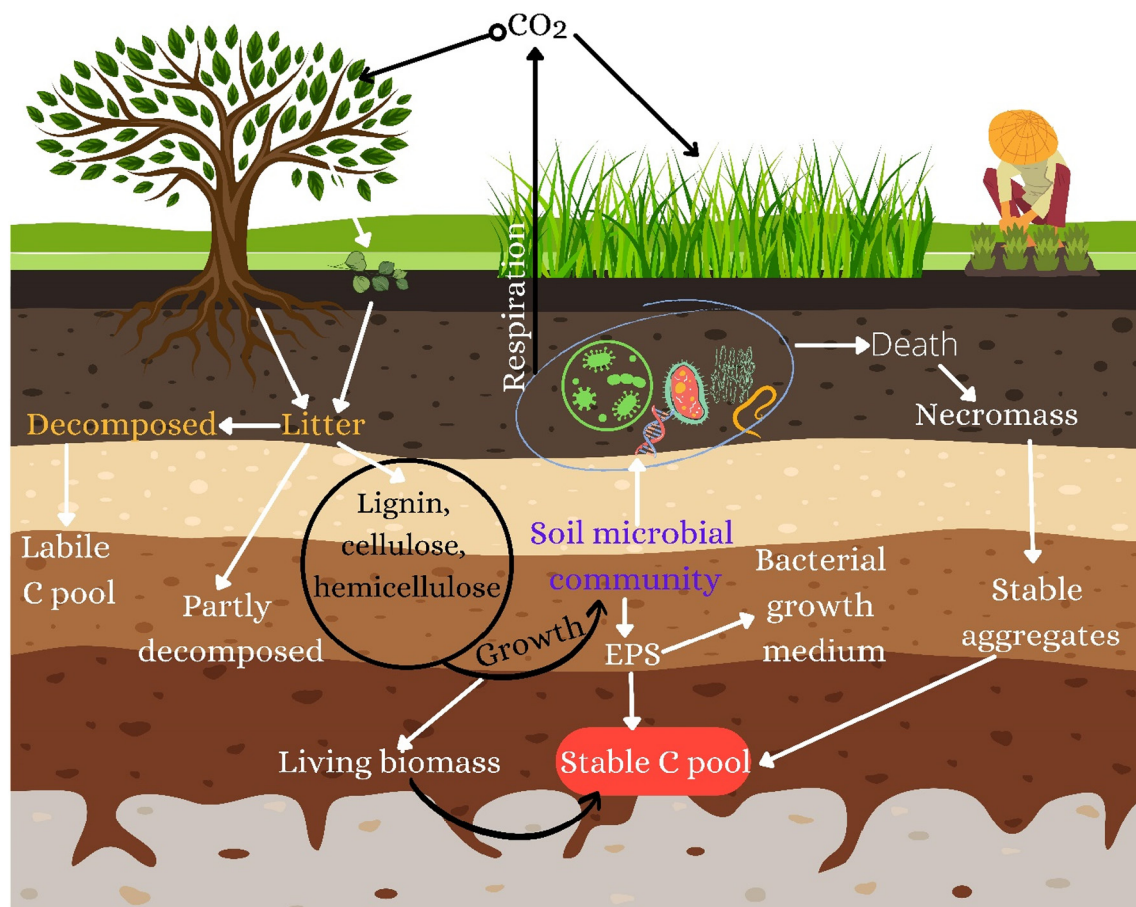


Fig. 1. Conceptual schematic representation of soil microbial communities' relationship with different soil C pools.

2. Role of the soil microbial community in soil organic matter dynamics

2.1. Microbial origin of SOM

For many years, soil organic matter (SOM) formation was thought to be related to plant inputs and their composition. Stable SOM is derived from recalcitrant complex plant polymers, such as lignin derivatives and long-chain lipids (Berg and McClaugherty, 2020). This paradigm ignored the fact that soil microorganisms are capable of degrading a wide range of plant compounds as long as they accessible and abiotic factors are favorable for carbon synthesis in their biomass (Paul, 2016). With advances in molecular techniques and a conceptual shift from plant-based concepts, the role of soil microbial communities (SMCs) in association with C accessibility has gained widespread acceptance (Lehmann and Kleber, 2015; Paul, 2016). SOM accumulation might even be more controlled by distinct microbial communities than by clay mineralogy (Kallenbach et al., 2015) and microbial biomass residues (necromass) might even serve as a primer stabilizing SOM, leading to the conclusion that SOC storage is heavily influenced by anabolic activities of microorganisms, emphasizing that the most persistent organic matter may not be composed of plant litter or their residues but carbon that has first passed through microbial biomass (Liang et al., 2019b).

The viability of soil microorganisms depends largely on organic matter quality and availability (Nguyen and Marschner, 2016). If substrates start to run out or their supply is interrupted, SMC may enter a dormant state by taking up spore forms, or they die, thus reducing their biomass, as confirmed by laboratory experiments (Shahbaz et al., 2017). After cell death, organic compounds contribute to microbial necromass, and this necromass can make up more than half of soil organic carbon (Miltner et al., 2012; Liang et al., 2019a; Fig. 2).

Necromass formation strongly depends on the composition of the SMC. Microbial populations use one of three main life strategies indirectly controlling their potential to sequester carbon in soil: r-, K- and L-strategies, with the composition and size of the active fraction depending on environmental conditions (Swift et al., 1979). The L-strategy is considered stress tolerant, the K-strategy is considered slow and efficient growth in almost all environments, and the r-strategy is considered to grow rapidly in favorable environments but to decline rapidly under any constraints. The ability to rapidly increase growth rates enables microorganism with r-strategies to compete with others and to rapidly rebuild populations when fresh substrate is introduced. But under unfavourable conditions, r-strategies do not maintain their population but activate biomass reduction mechanisms (autolysis) to producing necromass (Miltner et al., 2012), which serves as substrate for surviving microorganisms (Bradley et al., 2018; Shahbaz et al., 2017). Thus, r-strategies represent a microbial functional group with great potential to accelerate SOM decomposition. The formation of necromass allows microorganisms to survive when the energy supply to the environment is reduced, i.e. in a closed system where no fresh matter appears (Shoemaker et al., 2021).

Studies using molecular biomarkers (sugars, amino sugars, proteins and lipids) show that SMC is the source of organic compounds stabilized in SOM in the long term (Schimel and Schaeffer, 2012; Derrien et al., 2006; Liang et al., 2019b). Importantly, microbial metabolism of relatively simple C substrates (e.g. root exudates) can manifest SOM chemical heterogeneity, similar to that in soils under complex plant communities (Castle et al., 2016). Using microbial biomarkers, such as amino sugars or phospholipid fatty acids (Joergensen, 2018; Condron et al., 2010), some suggested that it may be possible to manipulate some SMC groups to control SOM formation (Jastrow et al., 2007; Liang et al., 2019a). Field research has shown that higher plant diversity results in higher soil C levels, being explained

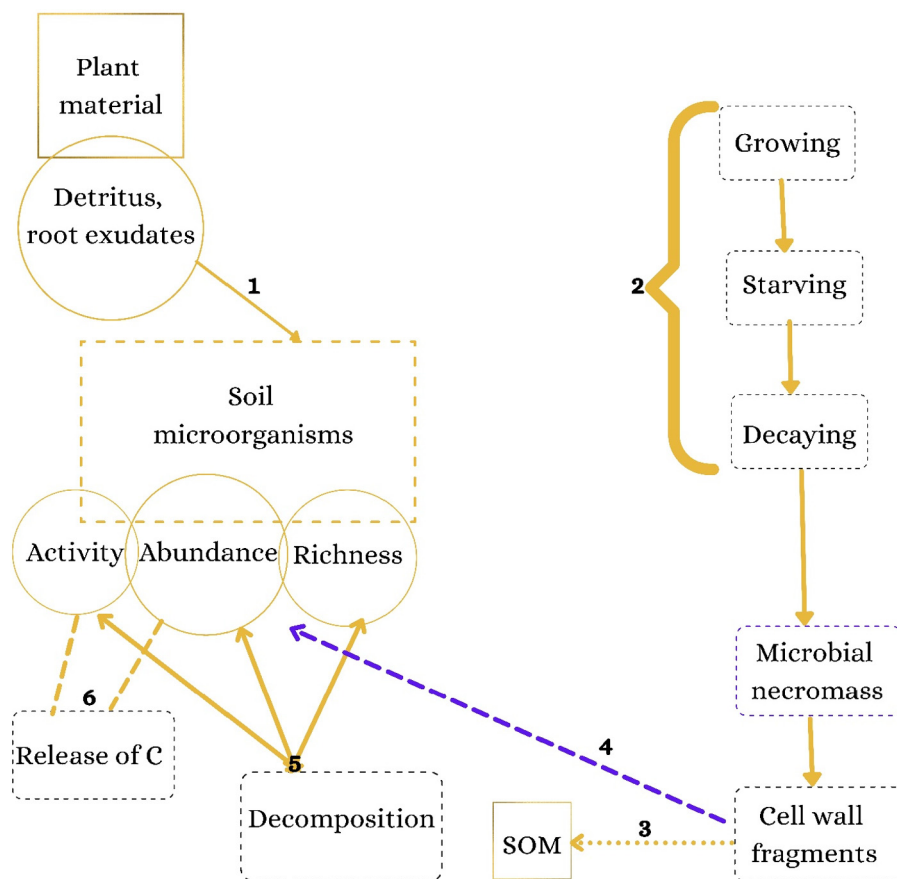


Fig. 2. Simplified model for the formation of SOM from bacterial necromass and relationship between SMC and decomposition: (1) plant residues introduced into the soil are used by microorganisms for growth; (2) when substrates become limited as a result of microbial growth, microorganisms begin to starve and then die, and their biomass is broken down into fragments; (3) the result of the breakdown is, among other things, flat fragments of cell walls that remain in the soil as necromass, which is partially converted into SOM, by surviving microorganisms; (4) some of the fragments are reused by bacteria as substrate for growth; (5) diversity, abundance and activity of SMC influences the type of decomposition processes and their rate; (6) the amount and type of C in the soil affects microbial abundance and activity (according to Miltner et al., 2012 and Condon et al., 2010).

by rhizosphere induced changes in SMC. Above ground plant diversity was indeed correlated with higher microbial necromass biomarkers and arbuscular mycorrhizal fungal biomarkers (Liang et al., 2016; Malik et al., 2016).

The microbial growth strategies of SMC groups are influenced by abiotic factors and soil quality (Maharjan et al., 2017) suggesting that climate, land use, and soil and nutrient management affect microbial growth and the decomposition and stabilization rates of necromass. In a fertile soil, r-strategies predominate, in a medium soil K-strategies and in a poor soil L-strategies (Panikov, 2010). Recently, Liang et al. (2019a) showed that the proportion of necromass in SOC varies with soil and land use with proportions over 50% for cropland, around 36% for grassland and about 22 to 38% in temperate forest soils (Liang et al., 2019b; Ni et al., 2020). The bacterial necromass contribution to SOM have been shown to increase with depth in grassland and forest soils. However, this pattern might be altered by soil management as opposite findings have been presented for cropland soils (Wang et al., 2021). In addition, formation and consumption of necromass are also influenced by soil pH, bulk density, mean annual temperature and even historical precipitation (Buckeridge et al., 2020; Zhang et al., 2021). This leads to the conclusion that the necromass contribution to SOM can be altered by management practices affecting the microbial community structure and activity (Buckeridge et al., 2020).

Microbial remains are not resistant to degradation, so their persistence must result from stabilization processes occurring in the soil (Kästner and Miltner, 2018). This stabilization has been explained by pile formation from dead cell envelope fragments (Miltner et al., 2012) where cellular debris is arranged in a stable agglomerates that limit their accessibility for

other microorganisms. It is noteworthy that some microbial groups produce specific defensive compounds preventing them for microbial uptake such as polyhydroxy-alkanoic acids, but how these contribute to SOM formation remains unknown (Condon et al., 2010). Despite the high importance of microorganisms in SOM formation, experimental evidence for SMC involvement in SOM formation is still limited by methods using specific microbial biomarkers (Kallenbach et al., 2016), hampering a comprehensive and quantitative analysis of the microbial contribution to SOM stabilization. Recently, Liang et al. (2019a) came up with a framework to develop quantitative assessments of microbial necromass from amino sugar data, and new quantitative insights are still on the way.

2.2. Biological processes controlling soil carbon storage

Decomposition includes the physical breakdown and biochemical transformation of complex organic molecules of dead materials into simpler organic and inorganic molecules. During the formation of SOM, decomposition products of plant and microbial origin enter the soil, being subjected to further decomposition and humification, which also involves the participation of SMC that further oxidize and assimilate SOM (Robertson and Paul, 2000). Also, the amount of SOM accumulated depends not only on the quantity and quality of organic matter inputs, but also on the physico-chemical environment and soil food web available (Torri et al., 2014). For example, acidic pH and dried conditions delay SOM degradation (Saviozzi et al., 2014; Torri et al., 2014). Considering the contribution of microbial necromass to SOM, changes in the environment affecting the size, growth rate and productivity of SMCs may affect the stable

accumulation of SOM (Kallenbach et al., 2015, 2016). Furthermore, biotic organic C undergoes transformations upon exposure to SMC, resulting in chemical stabilization (Schimel and Schaeffer, 2012; Christensen, 2001). Incorporation of SOM-derived C into microbial biomass corresponded to increased enzyme activity, which is indicative of SOM co-metabolism (Shahbaz et al., 2017).

In more detail, decomposition is primarily driven by activities of bacteria, actinomycetes, fungi and protozoa (Condon et al., 2010), where bacteria dominate in the long term (Malik et al., 2016). Approximately 10–15% of the C decomposition can be directly attributed to soil organism's activity (Hopkins and Gregorich, 2009). Heterotrophs derive energy and C for growth from organic compounds. They can be divided into microorganisms that use labile organic matter (known as zymogenic biomass) and those that decompose more resistant, older forms of C (known as autochthonous biomass). Heterotrophs have been identified as the organisms that control and regulate SOM decomposition, nutrient cycling and energy flow (Schmidt et al., 2011; Han et al., 2016; Table 1).

The microbial community can play multiple roles in SOM breakdown and C sequestration. Microorganisms play a key role in two critical, contrasting mechanisms: not only reducing SOC stocks through decomposition but also increasing SOC stocks through the formation of microbial biomass and stabilization of its residues associated with minerals, within soil structures, or by incrustation with Fe or Si precipitates (Kästner and Miltner, 2018; Liang et al., 2016; Kallenbach et al., 2015). In addition, abiotic and biotic factors affect the abundance, activity and composition of the SMC (Furtak and Gałazka, 2019) and they on their turn affect the decomposition of SOM (Ekschmitt et al., 2008; Fig. 1). For example, strong relationships between SOM, clay content, bacterial biomass and hydrolytic enzyme activities have been found (Wilkerson and Olapade, 2020) though a change in SOM only has not necessarily huge impacts on microbial diversity (Paterson et al., 2007; Webster et al., 2000). Others showed that carbon inputs varying in composition altered the soil microbial diversity and that this diversity was more important in controlling C decomposition rates than their abundance (Jiang et al., 2008; Shahbaz et al., 2017; Table 1). Plant diversity also affects the composition of SMCs as well as their spatial distribution due their impact on soil porosity. This subsequently changes the spatial distribution of SMCs and their impact on carbon contents and bulk densities affecting C stocks (Kravchenko et al., 2019). Plant-soil-microbiome interactions are therefore identified as responsible for SCS (Kravchenko et al., 2019).

The amount of C used for microbial growth relative to total C uptake, also called Carbon Use Efficiency (CUE), has an effect on microbial residue production (Kallenbach et al., 2015). When CUE increases, more C is consumed for biomass synthesis, which increases carbon stabilization (Kallenbach et al., 2016). It is assumed that C storage is possible when the metabolic energy required to decompose organic matter introduced into the soil is greater than the energy gained from catabolism occurring in microbial cells (Torri et al., 2014). The CUE of the microbial community is affected by the quality of the organic residues applied (Roller and Schmidt, 2015). For example, highly reduced C substrates are usually associated with high CUE but it can also be used by copiotrophs that have a naturally low CUE (Geyer et al., 2016). Sugars, starch and simple proteins are degraded most rapidly, followed by proteins, hemicelluloses and cellulose

whereas lignins and fats are broken down the slowest. For the most easily degradable substrates the highest CUE values are observed (~70–75%), while for less degradable substrates of lower quality, e.g., oxalic acid, the CUE is lower (~3–4.5%) (Frey et al., 2013).

Much of the C in soils comes from labile compounds processed by SMC and stabilized as residues in so called organomineral complexes (Miltner et al., 2012). Increases in C stocks are largely dependent on the fate of newly added C rather than the degradation of native SOM (Lange et al., 2015). High SMC activity triggered by organic matter inputs might trigger mineralization of this native SOM (Soriano-Disla et al., 2010), a process often referred as the “priming effect” (Dalenberg and Jager, 1989), in particular in soil with low clay content. Microbial necromass and other microbial by-products can be selectively preserved through interactions with soil minerals like clay and incorporation into soil aggregates (Kallenbach et al., 2016; Heckman et al., 2013). Through the formation of organo-mineral complexes or the compression of substances in small soil pores, the organic matter becomes inaccessible to microorganisms and their enzymes (Six et al., 2002).

2.3. Physical processes affected by SMC controlling soil carbon storage

Soil structure and soil organic matter are interlinked and sensitive to crop and soil management. Soil structure is formed by soil aggregates and these are the secondary particles (structural units) formed through the combination of mineral particles with organic and/or inorganic binding agents. Microbial extracellular polymeric substances (EPS)- containing polysaccharides, proteins, nucleic acids and lipids - can enrich and boost up the aggregate stability (Costa et al., 2018). The heterogeneous composition of EPS enables the SMC for being dehydrated and provides the necessary resistance against different agricultural operations. Due to its chemical nature EPS might serve as an adhesive compound, adhering to clay and ions and thereby binding fine particles tightly together (Shanmugam and Abirami, 2019), while acting as a growth medium for other soil microorganisms too (Wang et al., 2015). Biological aggregating agents such as extracellular polysaccharides, fungal mycelia, hyphae and glycoproteins produced by microorganisms stimulate the formation of stable aggregates (Tang et al., 2011; Barbosa et al., 2019). On the other hand, the aggregate size distribution also controls the colony development of bacterial and fungal communities (Ai et al., 2018; Bai et al., 2020; Fig. 3), thereby affecting the C decomposition and stabilization (Pathan et al., 2021). Hence, the SMC influences soil aggregation by i) building a bridge and changing surfaces to facilitate aggregate formation, ii) separating organo-mineral complexes to inhibit further entrance into aggregates, and iii) binding of soil particles via released extra- and intracellular single-stranded DNA (Pathan et al., 2021).

Bacterial and fungal communities are spatially distributed in soils following aggregate size (Tong et al., 2019) thereby affecting their potential to alter C stabilization. Recently, Zheng et al. (2021) revealed that microaggregates contain more bacteria than macroaggregates, with no major interaction between the bacterial and fungal communities. Soil aggregates fractions have often separate microenvironments subjugated by distinct microbiota, and the configurations of these microbial groups may vary (Ruamps et al., 2011) due to resource availability and species

Table 1
Selected SOM elements and SMC-derived enzymes involved in their transformation.

SOM component	Enzyme involved in transformation	Source of enzyme	References
Cellulose	Cellulases cellobiohydrolases	Fungi (eg. <i>Aspergillus</i> sp., <i>Trichoderma</i> sp., <i>Phanerochaete</i>)	(López-Mondéjar et al., 2016)
Hemicelluloses	glucosidases hemicellulases	Bacteria (eg. <i>Pseudomonas</i> sp., <i>Cellulomonas</i> sp.,)	
Chitin	Chitinases chitinase	Bacteria (<i>Actinobacteria</i> sp., <i>Proteobacteria</i> sp., <i>Firmicutes</i> sp.) Fungi (<i>Trichoderma</i> sp., <i>Verticillium</i> sp.)	(Wieczorek et al., 2019)
Lignin	Lignin peroxidase Mn(II)-peroxidases quinone reductases	Fungi (eg. <i>Basidiomycetous</i> sp., <i>Phanerochaete</i> sp.)	(Liers et al., 2011)
Proteins	Proteases	Bacteria (eg. <i>Bacillus</i> sp.) Fungi (eg. <i>Cladosporium</i> sp.)	(Gurumallesh et al., 2019)

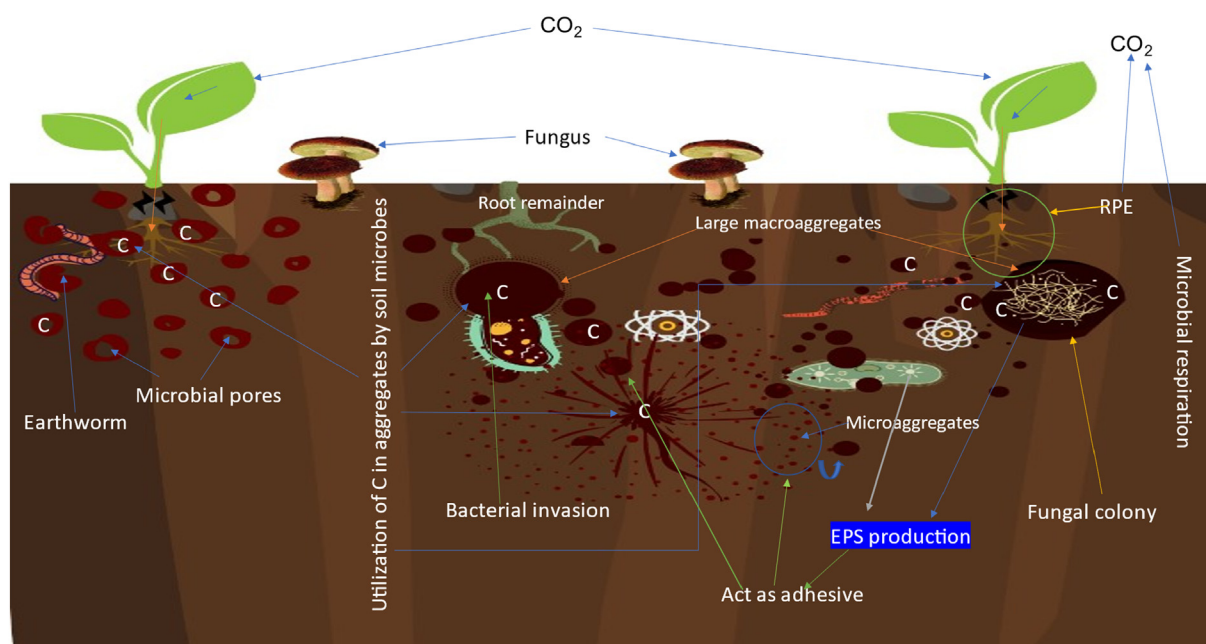


Fig. 3. Conceptual schematic diagram showing interlinkages among C cycling, soil microbes and soil aggregation. Abbreviations: RPE = Rhizosphere priming effect, EPS = Extracellular polymeric substances.

requirements. Large macro-aggregates contain greater number of gram-positive bacteria and Eukaryotes compared to other aggregates (Briar et al., 2011), and small macroaggregates may favor fungal populations (Tong et al., 2019) affecting SOC accumulation in soils (Zhang et al., 2018). Not all microbial populations have the same capacity to form steady aggregates (Liang et al., 2019a; Lehmann et al., 2020; Table 3) due to variation in biopolymer production and necromass growth. Likewise, Fokom et al. (2012) found SCS is highly correlated with glomalin (glycoprotein) and stable aggregates content in soil ($r^2 = 0.76$, $P < 0.01$). Glomalin associated with AMF has a huge potential to promote macroaggregates formation through concurrently binding of microaggregates (Wilson et al., 2009). Soils that contain higher glomalin content may have more water stable aggregates (Table 2). High levels of microaggregates however may limit the necromass induced SCS (Luan et al., 2021). Large macro-aggregates are also less stable and can be easily broken down into small macro-aggregates and then into micro-aggregates.

Aggregate turnover, being defined as the destruction and production of aggregates, is very important for SCS since it determines the C stabilization on the long term. Aggregate turnover is inextricably linked with rhizosphere priming effect (RPE) and soils can be managed in such a way that both are stimulated to increase C sequestration (Wang et al., 2020a; Murugan et al., 2019). Huo et al. (2017) stated RPE might augment SOC mineralization rate by 59%. The reasons behind such a higher rate might be higher microbial activity, biomass turnover and accelerated evapotranspiration (Cheng, 2009; He et al., 2020). As mentioned, the SMC controls aggregate turnover and hence affects the C sequestration rate (Fig. 3). Wilson et al. (2009) discovered an 85% increase in water stable macroaggregates along with improved SCS as a result of improved AMF hyphal abundance during a 24-

year experiment in prairie soils. Changes in SCS can be attributed to AMF's increased weathering capabilities (Verbruggen et al., 2021). Raising the prevalence of the Basidiomycota fungal division and the Mortierellomycota phylum in aggregates has been proposed as a possible C sink (Tong et al., 2019). Taskin et al. (2021) demonstrated that microbial species diversity (*Bradyrhizobium* spp.) correlates with stabilized C within macroaggregates, whereas Chen et al. (2017) showed that improved macroaggregation is the central nexus for increasing total organic C (Chen et al., 2017).

3. Influence of agricultural practices on SMC and associated C sequestration

Agricultural practices change the soil microbiome and also modifies the associated microenvironment conducive to the composition, abundance and activity of SMC and associated SCS. Agricultural land use affects soil C content and cycling either positively or inhibitory. Additionally, a study by Tscharnkte et al. (2012) showed that there are about 1000 species of microorganisms in natural soil not cultivated for agriculture, and about 140–150 species in 1 g of agricultural soil. Studies show that in agricultural soils the number of functioning taxonomic units (OTUs) can be up to 30% lower than in uncultivated soils (Wolińska et al., 2017). In this section the five most relevant agronomic practices affecting soil quality, SMC and SCS are evaluated.

3.1. Conventional versus organic farming

Ponge et al. (2013) demonstrated conventional agricultural activities have extensive impact on SMC i.e., increasing intensity (i.e., increased use

Table 2
Relationship between glomalin, soil C, N contents and aggregates (Fokom et al., 2012).

Land use types	EEG (mg/g)	TG (mg/g)	C (%)	N (%)	C/N	OM (%)	WSA (1–2 mm) (%)
Forest	10.56(0.98) ^a	15.67(1.36) ^a	1.56(0.02) ^a	0.150(0.01) ^a	10.40(0.07) ^a	2.68 ^a	64.57(1.36) ^a
Fallow	07.41(1.73) ^b	13.06(2.32) ^b	1.52(0.03) ^a	0.138(0.00) ^b	11.01(0.15) ^b	2.62 ^a	52.0(4.95) ^b
Field crops cultivation	06.51(0.84) ^b	08.45(1.14) ^c	1.46(0.05) ^b	0.129(0.01) ^c	11.31(0.03) ^b	2.51 ^b	43.5(0.73) ^c

Abbreviations: EEG = Easily extractable glomalin, TG = Total glomalin, WSA = Water stable aggregates.

Table 3

Some selected soil microbial genus, species and associated strains involved in aggregation process.

Genus	Strain(s)	Nature	Species	Role	Reference(s)
<i>Rhizobium</i>	KYGT207	Bacterial	<i>R. sultae</i>	Water stable aggregates formation	Kaci et al. (2005)
<i>Glomus</i>	–	Fungal	<i>G. mosseae</i> <i>G. intraradices</i>	Can produce higher macroaggregates and increase stability within particles.	Bedini et al. (2009)
<i>Fusarium</i>	RLCS05	Fungal	<i>Fusarium</i> spp.	Huge potential of forming water stable aggregates.	Liang et al. (2019a)
<i>Mucor</i>	RCLS19	Fungal	n.s.	Facilitate stable aggregates formation	Lehmann et al. (2020)
<i>Gibberella</i>	RLCS08	Fungal	<i>G. tricineta</i>	Best soil aggregator	Liang et al. (2019b)

Note: n.s. = not specified.

of fertilizers and plant protection products, deep ploughing, use of high-performance machinery) caused decreasing species richness and diversity of soil biota (Table 4). In addition, taxonomic and phylogenetic richness, diversity and heterogeneity may decrease in conventional farming systems (Lupatini et al., 2017). It is evident that row-crop systems with cover crops can accumulate C even under very intensive cultivation (Kallenbach et al., 2015; Syswerda et al., 2011), while some vigorous cropping systems may increase C very slowly despite large additions of organic substances and no disturbance (Sprunger and Philip Robertson, 2018; Chimento et al., 2016). Organic manure addition is helpful for the proliferation of SMC, it substantially changes the SMC composition (Ponge et al., 2013), ultimately, improves SCS. In research by Pulleman et al. (2006) the total SOM content was 15, 24 and 46 g kg⁻¹ in conventional, organic and grassland fields, respectively.

According to the European Commission, 2022, the term “organic farming” is used to define agriculture which aims to minimize human impact on the environment while maintaining the natural functionality of the agricultural system (https://ec.europa.eu/info/food-farming-fisheries/farming/organic-farming/organics-glance_en). Practices used in organic farming include crop rotation, use of crop diversity, animal and plant combinations, organic fertilizers and biopreparations (Abdelrahman et al., 2020). It is hypothesized that these practices in the long term can result in an increase of organic C and N in soil. The area of organic crops in the world is increasing year by year. In organic farming, production aims to close nutrient cycles where plant and animal residues are returned to the soils. This improves soil quality through the accumulation of organic matter in the soil. Several researches have reported positive effects of organic farming on soil quality, including SMC abundance and activity (Lori et al., 2017). Santos et al. (2012) showed that organic farming increased by 100–300% the content of the soil microbial biomass. The use of organic fertilizers, including manure, increases the number of bacteria that break down organic matter (Hartmann et al., 2015). Organic system can increase the abundance of microorganisms in soil, especially fungi including *Cladosporium* sp. and *Mucor* sp., which can inhibit pathogen growth in the soil (Tautges et al., 2016). Organic farming system has the potential to increase the taxonomic, phylogenetic and heterogeneous richness of soil microbes compared to the conventional system (Lupatini et al., 2017; Hartmann et al., 2015). Bonanomi et al. (2016) even concluded that organic farming can improve the soil microbial balance previously damaged by conventional farming. Summarizing, this type of farming is beneficial to improve SMC structure, composition and diversity in soils owing to the decreased or even no use of chemical compounds. However, increases in SOM or fractional C as a result of organic practices are usually evident after long-term application

(Yang et al., 2019b). After 21 years of organic farming in Switzerland, it was found to reduce SOM losses over time, and biomass and SMC activity increased (Fließbach et al., 2007). A long-term study in eastern Nebraska on rainfed soils found the greatest changes in N and organic C (SOC) levels in the soil profile in soils with low initial SOM content (Varvel and Wilhelm, 2011). This is related to the sudden introduction of additional fresh organic matter. Organic farming which is known for utilizing less or even no chemical inputs during crop production show favorable condition to SMC by augmenting the abundance and diversity of SMC because of higher SOM, SOC and TN contents (Düring et al., 2002; Leite et al., 2010; Santos et al., 2012).

3.2. Tillage

Tillage is the age-old practice of cultivating soils. Different tillage practices are advocated globally since tillage practices may exert strong influence on SMC (Zhang et al., 2012; Wang et al., 2020b; Mbuthia et al., 2015) and associated C sequestration (Li et al., 2019); even, non-significant impact has been reported (Schlatter et al., 2017). Tillage mainly disrupts soil aggregates (Jiang et al., 2011) and aggregates are the habitats of soil microbial communities. As for example, conventionally tilled (CT) soils may have 32% less MBC content and 40–60% less AMF compared to NT soils (Helgason et al., 2010). Again, copiotrophs are an important element of soil C cycles and also contribute to the higher microbial C use efficiency (Yaghoubi Khanghahi et al., 2020). Pulleman et al. (2006) showed that after 70 years, SOM content and mineralization decreased as a result of tillage and arable cropping compared to pasture, but were significantly higher in organic than in conventional farming. Liu et al. (2016) reported in Australian calcisol, chisel tillage, which using a heavy duty cultivator with special spring or fixed tines (reduced tillage), has a greater effect on topsoil than NT (without disturbing the soil) because it raises MBC by 34%, abundance of copiotrophic bacterial group e.g., *Firmicutes* sp., disaccharides, and sugar alcohol by 75%, 114%, 37%, 178%, and 167%, respectively. Schmidt et al. (2018) concluded that NT may increase bacterial and archaeal populations and diversity across the whole soil profile over CT. Also, the microbial communities remain tillage stress-resistant. Zhang et al. (2018) reported NT soils may contain 30% higher gram-positive bacteria, 12% higher gram-negative bacteria, 72% higher fungi, and 45% lower actinobacteria over CT. Contrarily, CT may favor copiotrophic bacteria whereas NT favors oligotrophic bacteria (Degruene et al., 2017). Kabiri et al. (2016) indicate that reduced tillage has a positive effect on soil microbial biomass carbon (MBC) and nitrogen (MBN) compared to CT. These studies indicate that NT shows more obvious input to the abundance,

Table 4

Different land use impact on soil biota (adapted and slightly modified from Ponge et al., 2013).

Abundance (ind·m ⁻²)	Permanent meadow	Meadow in rotation	Crop in rotation	Permanent crop	Slurry	No slurry
Anecic earthworms (ind·m ⁻²)	64.5 ± 13.5	58.4 ± 12.2	22.0 ± 6.6	28.3 ± 4.4	41.2 ± 8.7	25.3 ± 4.6
Endogeic earthworms (ind·m ⁻²)	229 ± 58	211 ± 28	134 ± 25	167 ± 23	230 ± 42	124 ± 16
Total macroarthropods and mollusks (ind·m ⁻²)	349 ± 51	312 ± 66	130 ± 20	173 ± 22	232 ± 45	137 ± 19
Saprophagous macroarthropods and mollusks (ind·m ⁻²)	69.6 ± 22.7	67.4 ± 17.4	23.8 ± 7.6	24.6 ± 6.7	40.5 ± 13.6	15.7 ± 3.5
Epigeic springtails (ind·m ⁻²)	810 ± 240	3520 ± 1130	5540 ± 2370	4100 ± 890	2480 ± 800	5150 ± 1340
Phytoparasitic nematodes (ind·g ⁻¹ dry soil)	1560 ± 240	1050 ± 200	620 ± 90	490 ± 60	470 ± 90	500 ± 80
Bacterivorous nematodes (ind·g ⁻¹ dry soil)	574 ± 88	621 ± 82	687 ± 155	588 ± 52	669 ± 70	578 ± 69
Microbial biomass (mg C·kg ⁻¹)	553 ± 45	385 ± 27	269 ± 29	243 ± 11	369 ± 75	460 ± 72

diversity of soil microorganisms, specifically augment copiotrophs and higher MBC over CT. NT remains more preferable for SMC, though it may depend on specific pedo-climatic conditions. NT equipped with organic amendments may improve microbial community diversity and stability (Wang et al., 2017). Additionally, as compared to CT, strip tillage (ST) is associated with higher bacteria by 49%, effective bacteria by 27%, active and total fungi by 37%, and nematodes by 275% (Leskovar et al., 2016). A study by Bailey et al. (2002) showed that tilled soils had lower fungal activity and lower C content than soils managed to native or no-till systems. In addition, the C content correlated with fungal activity in all tested samples.

3.3. Crop rotation

Crop rotation (CR) alters the soil microbial parameters and thereby the microbes associated C sequestration. Venter et al. (2016) reported CR can enhance microbial richness and diversity by 15 and 3.4%, respectively. Wheat-soybean rotation may improve AMF, zoospore fungi and sac fungi (Guo et al., 2020; Ai et al., 2018). Soybean-wheat rotation may reduce microbial richness and diversity as opposed to wheat-wheat rotation (Yin et al., 2010). Rice-maize-mungbean rotation may enhance soil bacteria (e.g., Proteobacteria, Acidobacteria, Chloroflexi, Verrucomicrobia) composition, abundance and diversity compared to rice-rice-rice rotation (Xuan et al., 2012). This type of variation under different crop rotation practices might cause fluctuations in soil C storage and its varied utilization by SMC. Venter et al. (2016) stated that inclusion of legumes in CR, particularly, may not influence SMC diversity or richness (Venter et al., 2016). But Borase et al. (2020) found after a long-term CR practice including legumes that it increased SOC stock, MBC and soil enzymatic activities (acid/alkaline phosphatase, beta-glucosidase and arylsulfatase). Similarly, the legume-AMF and rhizobia symbiosis acts as a barrier, decreasing the effect of agricultural operations on SMC (Schmidt et al., 2017). Therefore, inclusion of legumes in CR might be helpful to conserve the SMC. Different crops and weeds exhibit allelopathic impacts on SMC. As a result, SMC in the rhizosphere varies (Costa et al., 2006). But this is not widely investigated. In a study with alligator weed widely grown in Brazil, Ge et al. (2018) indicated allelochemicals secretion from this species could decrease the soil enzymatic activity also, the relative abundance of SMC. These secretions may also inhibit the germination of crop species. Contrarily, Meiners et al. (2017) found sufficient abundance of SMC could avert the allelopathic potential of plants, specifically, by increasing germination around 25–54%.

3.4. Cover crops

Cover cropping (CC) is a proven means for optimized SCS. Poeplau and Don (2015) estimated CC can contribute to $0.12 \text{ Pg C year}^{-1}$. Since SMC regulates crop residue breakdown and CC can add more residue C in soil (Sainju et al., 2007). For this season CC can exert significant contribution in the soil microbial parameters i.e., colony structure, MBC, MBN, PLFA, abundance, diversity and activity of soil organisms (Kim et al., 2020). Effect of some selected CC on the abundance of different soil microbes are presented in Fig. 4. CC may increase total PLFA. MBC, MBN contents by 24, 40 and 54%, respectively while soil total bacteria and fungi may rise 7–31% (Muhammad et al., 2021). CC's actual impact on MBC, MBN and PLFA contents may vary according to the climatic conditions, e.g., meta-analysis performed by Kim et al. (2020) revealed MBC, MBN was highest under tropical conditions while greater PLFA contents observed in temperate zones, but, continental climate produced lower MBC, MBN and PLFA under CC. Inclusion of CC under temperate and tropical climatic conditions may induce 18.7% and 7.2% SOC stock changes, respectively (Jian et al., 2020). Hallama et al. (2019) suggested combining CC establishment with other management activities such as tillage to optimize the CC's effect on soil microbiological attributes. However, benefits from CC on soil microbiome may be hindered in case of continental climate, NT systems or after chemical elimination from the field. (Kim et al., 2020).

3.5. Fertilization & manure addition

Fertilization is an important aspect of agriculture. Different fertilization modes (synthetic fertilizers or organic addition) may cause variations in soil nutrients, pH, and soil microorganisms over the long term, ultimately, influence the production and decomposition of SOC by microbial communities (Neumann et al., 2013; Lupatini et al., 2013; Williams et al., 2013; Beauregard et al., 2010). Fertilization and manure incorporation are more likely to affect the microbial community composition. In rice fields, for example, it was found that both mineral and organic fertilization led to increases in MBC content of 29 and 61% sequentially over the unfertilized control. (Geisseler et al., 2017). Across all studies, mineral fertilizer does not seem to have lasting negative effects on soil microorganisms. In a long-term experiment in an alpine pasture by Yuan et al. (2020) and colleagues revealed P addition could avert the decomposition rate of SOM, also, can increase particulate organic carbon (POC 9.1%) because of

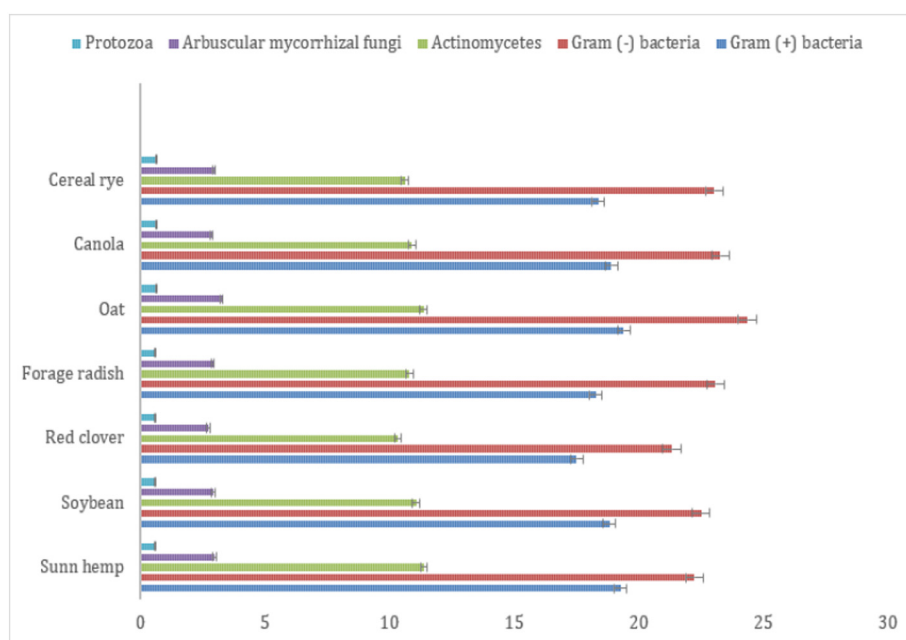


Fig. 4. Effect of cover crops on abundance of different soil microbes (Data from Finney et al., 2017).

lower fungal biomass. They also found N & P addition can substantially alter the soil microbial parameters e.g., decreased MBC, MBN and PLFAs. Similar results were previously reported by Li et al. (2018). P fertilization inhibits the soil microbial (bacteria, fungi, AMF) activity, but, no effect on diversity and richness (Beauregard et al., 2010). N fertilization in sub-alpine meadow may inhibit species richness, increase MBC, augment SOC decomposition, and decrease SCS (Li et al., 2016). SOC breakdown derived from N fertilization might be linked with the action of extracellular enzymes. Jian et al. (2016) observed that N fertilization would change combined hydrolase enzyme activities, potentially reducing MBC. Microorganisms' susceptibility to long-term fertilization might be reduced with clay fractions because of high buffering ability, shielding microbial cells from alterations even after a century (Neumann et al., 2013).

The influence of organic matter supply on the contribution of SMC to soil C regulation can be explained in several ways:

- (1) Higher organic matter additions may increase decomposition and reduce C storage through reduced microbial C use efficiency (Manzoni et al., 2012);
- (2) Higher organic matter additions, inputs of labile C or nutrients resulting in either enhanced mineralization of SOM in soil, which is called a *positive priming effect* (Fontaine et al., 2007; Hicks et al., 2019);
- (3) Higher additions of organic matter can increase C skimming through increased accumulation of microbial necromass over time (Liang et al., 2011).

Organic fertilization may reduce the relative abundance of bacterial communities in all aggregates, while increasing the fungal population in macroaggregates. Again, organic fertilization can decrease bacterial community abundances while increasing fungal populations, resulting in SCS in soil aggregates (Tong et al., 2020). Manure and slurry can improve MBC both quantitatively and qualitatively e.g., Grunwald et al. (2016) found presence of average 356 mg MBC kg⁻¹ of soil. Since MBC ensures higher stability of aggregates, such presence of MBC confirms their importance in SCS. However, after a 33-year trial, Guo et al. (2020) found that adding compost or manure, or combining compost with chemical fertilizers, would increase the presence of Deltaproteobacteria and Bacteroidetes while also reducing agricultural management-related pressures on them. Bai et al. (2020) suggested after a 6 years experiment straw derived biochar may favor diversity and richness of bacterial communities in topsoil and evenness in the whole soil profile. Combination of biochar with chemical fertilizer may induce fungal dominated microbial communities in tropical soils although it may result in increased MBC and MBN contents (Oladele et al., 2019). These studies suggest that SCS is highly dependent on fertilization, manure addition and also on SMC. In addition, the C content correlated with fungal activity in all tested samples (Fig. 5).

4. Conclusions and perspectives

We conclude that optimizing soil and nutrient management for carbon sequestration while stimulating co-benefits for agronomy and environment requires a key role for the soil microbial community structure for several reasons i.e., i) SMC is controlling the rate of C decomposition, ii) SMC is controlling formation of soil aggregates, thereby creating protected environments for C breakdown and altering the physical accessibility of organic compounds for uptake within the root zone and iii) impact of agronomic measures is largely mediated by short and long-term dynamics of SMC.

SOM is produced in soil from humus which is formed by the relentless decomposing activities of SMC on plant derived litters or other alike substances. Agricultural operations tend to disrupt this incessant cycling of SOM, consequently, pose a threat to other soil microbiological parameters crucial for long-term C storage and SCS. We showed that SOM and SOC deposition, decomposition, transformation and stabilization are fully reliant on SMC structure, abundance, composition, living and dead biomass production and associated EPS. Although the decomposition of SOM is mainly dependent on SMC, its rate is influenced by numerous environmental factors. These include natural factors such as temperature, humidity, oxygen,

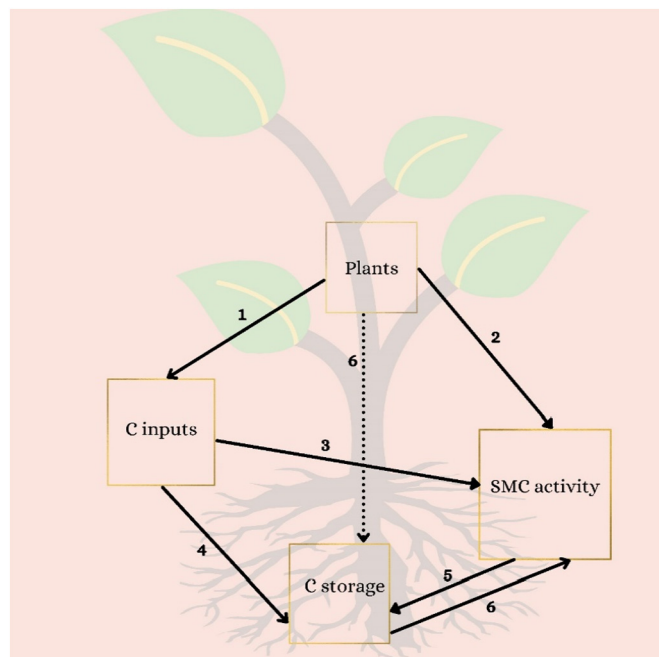


Fig. 5. Relationships between plant, microorganisms and C storage in soil (according to Lange et al., 2015): (1) Plant→C inputs: plant diversity increases the amount of C entering the soil (Ravenek et al., 2014; Jiang et al., 2008); (2) Plant→SMC activity: plant cover affects SMC (its activity, diversity) (Kravchenko et al., 2019; Torri et al., 2014); (3) C inputs→SMC activity: more C affects SMC activity (Manzoni et al., 2012; Fontaine et al., 2007); (4) C inputs→C storage: higher C input from biomass results in increased C storage (Sollins et al., 1996); (5) SMC activity→C storage: SMC affects C storage through a variety of process (Kallenbach et al., 2015, 2016; Miltner et al., 2012; Schimel and Schaeffer, 2012; Liang and Balser, 2011); (6) C storage→SMC activity: higher soil C content increases SMC activity (Nguyen and Marschner, 2016; Fontaine et al., 2007; Paterson et al., 2007).

nutrient availability, as well as anthropogenic factors caused by soil management - interference with the structure, fertilization, planting density. There are a number of interactions between all these factors and the microbial community, many of which have not been investigated to date. For these reasons, determining the unambiguous influence of SMC on SOM distribution is very difficult, as it would require controlling/eliminating other parameters (Reed and Martiny, 2007). SOM SOC, soil aggregates act as the major pathways of SCS and long-term C storage under diverse agricultural practices and this C storage potential of soils is determined by the SMC. Moreover, soil enzymes, EPS, and MBC (both live and dead) are the key contributors in i) stabilizing C reservoirs and ii) creating stable aggregation, and all of these factors are closely connected with SMC. Wilson et al. (2009) found decrease in abundance of AMF because of agricultural activities caused poor soil aggregation, no alternative process could avert it. Again, approximately 5 Gt of anthropogenic C emission could be abated per year through AMF (Parihar et al., 2020). Role of such fungi or bacteria can't be underestimated to mitigate the hazardous impact of climate change. We suggest reintroducing the decayed SMC, which can sustainably promote the emergence of new species and their flourishing establishment in agroecosystems. Since SOC is the most dominant component of SOM, we can only expect long-term soil C storage if we have a strong SOM content, and this radical change could be real if we take care of the soil microbial communities. However, the following research questions should be taken into consideration in future researches:

1. how does spatial distribution of microbial biomass in soil affects soil structure, porosity, effective turnover and C sequestration in soil?
2. how can SMC attain resistance against various agricultural operations if sufficient amount of EPS degrading enzymes are present in soil?

3. interplay between microbial necromass and soil minerals under various agricultural systems.
4. how does the quality, quantity and forms of organic matter in soil determine the distinct role of soil microbial community in different soil processes required for long-term C storage or cycling?

CRediT authorship contribution statement

Siddhartha Shankar Bhattacharyya: Conceptualization, Data Analysis, Tables, Figures Writing - Original and Final Draft, Reviewing and Editing. **Gerard H. Ros:** Conceptualization, Writing - Final Draft, Reviewing and Editing. **Karolina Furtak:** Data Analysis, Tables, Figures, Writing-Original and Final Draft, Reviewing and Editing. **Hafiz M.N. Iqbal:** Conceptualization, Supervision, Reviewing and Editing. **Roberto Parra-Saldívar:** Conceptualization, Supervision, Reviewing and Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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