



Stabilisation of soil organic matter: interactions between clay and microbes

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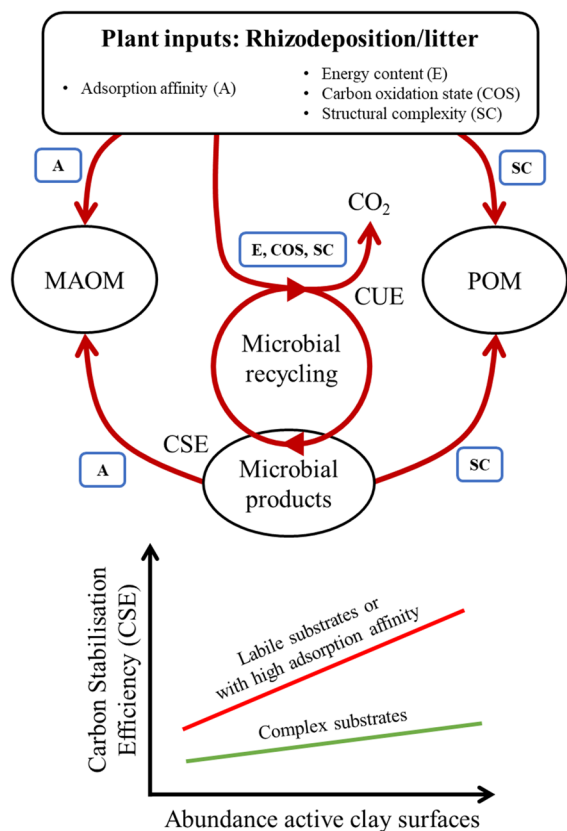
Abstract Soil organic matter (SOM) plays a central role in the global carbon balance and in mitigating climate change. It will therefore be important to understand mechanisms of SOM decomposition and stabilisation. SOM stabilisation is controlled by biotic factors, such as the efficiency by which microbes use and produce organic compounds varying in chemistry, but also by abiotic factors, such as adsorption of plant- and microbially-derived organic matter onto soil minerals. Indeed, the physicochemical adsorption of organic matter onto soil minerals, forming mineral associated organic matter (MAOM), is one of the significant processes for SOM stabilisation. We integrate existing frameworks of SOM stabilisation and illustrate how microbial control over SOM stabilisation interacts with soil minerals. In our new integrated

framework, we emphasise the interplay between substrate characteristics and the abundance of active clay surfaces on microbial processes such as carbon use efficiency and recycling. We postulate that microbial use and recycling of plant- and microbially-derived substrates decline with increased abundance of active clay surfaces, and that the shape of these relationships depend on the affinity of each substrate to adsorb, thereby affecting the efficiency by which organic matter remains in the soil and is stabilised into MAOM. Our framework provides avenues for novel research and ideas to incorporate interactions between clay surfaces and microbes on SOM stabilisation in biogeochemical models.

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Graphical abstract



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Introduction

Soil organic matter plays an important role in soil fertility and structure. It is one of the major components of the global carbon (C) cycle as it contains more C than in terrestrial plant biomass and atmosphere combined (Field et al. 2004; Schlesinger 1990). It also plays a crucial role in soil surface-atmosphere exchange of greenhouse gases (Grandy and Neff 2008; Grandy and Robertson 2006; Kuzyakov 2011). Owing to its large size, relatively small changes in the SOM stock can have a significant impact on the atmospheric carbon dioxide (CO₂) concentration (Eglin et al. 2010; Magdoff and Weil 2004; Scharlemann et al. 2014). Protecting SOM from microbial decomposition (SOM stabilisation) is therefore important to mitigate

climate change, but the mechanisms of SOM stabilisation still remain poorly understood.

Most C components of plant organic matter input into the soil are decomposed biotically by microbes and respired into the atmosphere over short (<50 years) time scales (Dwivedi et al. 2019). However, a significant portion of the C in SOM is not respired but can become abiotically (i.e., chemically, or physically) protected before or after microbial processing. As such, organic C in soil can persist over much longer (100 s to >1000 years) time scales (Dwivedi et al. 2019). The age of C in SOM tends to increase with soil depth (Balesdent et al. 2018; Schrumpf et al. 2013). This is because microbial SOM processing is often more abundant at shallow soil depths, whereas stabilisation of SOM onto mineral surfaces becomes more dominant in the deeper soil (>30 cm) (Jackson et al. 2017). Increased residence time of SOM with soil depth has also been associated with variation in the chemical properties of organic inputs and lower nutrient availability in sub-surface soil, which may inhibit microbial activity (Rumpel and Kögel-Knabner 2011). Thus, both biotic factors (e.g., plant inputs, microbial composition) and abiotic factors (e.g., clay content, mineralogy) are critical regulators of SOM formation and stabilisation.

Soil organic matter is considered as one of the most complex and least-understood components of soil (Magdoff and Weil 2004). It is a heterogeneous mixture of organic compounds with variable composition and decomposition rates (Chenu et al. 2015; Kleber and Johnson 2010). There are multiple functional pools in SOM, each stabilised by a specific mechanism, and each having a certain turnover rate. A simple approach to isolate functional SOM pools into mineral-associated organic matter (MAOM) and particulate organic matter (POM) has been proposed to understand and predict broad-scale SOM dynamics (Lavallee et al. 2020). They defined MAOM as the fraction of SOM consisting of single molecules or microscopic fragments of organic material that are directly from plant material or have been chemically transformed by the soil biota, and that is associated with minerals and protected from decomposition. On the other hand, POM is the lightweight and relatively undecomposed fraction of organic matter that includes easily decomposable (labile) compounds and mostly plant-derived compounds that are structurally

complex and have high activation energies compared to MAOM (Cambardella and Elliott 1992; Lavallee et al. 2020; von Lützow et al. 2008). Because of the strong physicochemical sorption of OM with clay minerals and metal oxides (Kleber et al. 2021; Rasmussen et al. 2018), the MAOM fraction has been acknowledged as an important pool for the long term C stabilisation in the soil (Grandy and Neff 2008; Jagadamma et al. 2012; Kiem and Kögel-Knabner 2003; Kögel-Knabner 2002; Marschner et al. 2008; Rumpel et al. 2010; von Lützow et al. 2007).

It has become increasingly clear that microbial products (e.g., necromass) are important for MAOM formation (Kallenbach et al. 2016; Liang et al. 2019), particularly in environments that provide favourable conditions for microbial growth (Angst et al. 2021a). Therefore, the efficiency of SOM stabilisation through the formation of organo-mineral complexes (or MAOM) will also depend on how efficiently plant compounds are turned into microbial products that interact with minerals (Bradford et al. 2013; Cotrufo et al. 2013). An important parameter in this regard is the microbial growth efficiency, or carbon use efficiency (CUE), i.e., the proportion of C substrates (here, we focus on non-microbial products) that is used by microbes for their growth instead of being respired. When a greater proportion of C substrate is used for microbial growth, this can ultimately result in more stable C into organo-mineral complexes (Cotrufo et al. 2013). However, microbial CUE can vary strongly with substrate type, nutrient availability, and other soil conditions (Manzoni et al. 2012), and much uncertainty remains about how this affects SOM stabilisation through MAOM formation. Furthermore, the formation and persistence of MAOM will depend on how strongly organic compounds adsorb onto mineral surfaces, which can vary among organic compounds and type of mineral (Kleber et al. 2021; Sokol et al. 2019). The interactions between organic compounds and clay minerals would also affect the proportion of C that remains unprotected in the soil. Unprotected C has a greater possibility of being recycled by microbes (i.e., more frequent decomposition cycles of dead microbial cells by living microbes), eventually resulting in more C lost as CO₂ and less C remaining in the soil (Angst et al. 2021b; Hagerty et al. 2014) that could potentially form stable complexes with minerals. To account for microbial recycling effects, Geyer et al.

(2020) defined microbial “C stabilisation efficiency” (CSE), a metric that includes microbial products for C growth and use in the CUE equation.

From the above, it becomes clear that biotic processes such as microbial decomposition, CUE and recycling of substrates do not operate independently from abiotic processes such as adsorption onto soil minerals to stabilise SOM through the formation of MAOM. However, these interactions have rarely been considered in experimental studies or current frameworks of SOM stabilisation. Indeed, we know very little about how microbially controlled SOM stabilisation (including rate and strength of stabilisation) depends on abiotic processes such as adsorption and type of soil minerals. Here, we first discuss current models of SOM stabilisation and then propose a new framework integrating abiotic (variation in the abundance of clay particles that have the capacity to adsorb organic compounds on their surfaces, referred to as active clay surfaces hereafter) and biotic mechanisms (microbial CUE and recycling of substrates) of SOM stabilisation. Our framework highlights the need to incorporate interactions between clay surfaces and biotic controls on SOM stabilisation in biogeochemical models.

Models of SOM stabilisation

Traditional models of SOM dynamics assume the decomposition of plant litter based on simple first-order kinetics that do not account for the formation of organo-mineral complexes through abiotic control (e.g., CENTURY and RothC models, Coleman and Jenkinson 1996; Parton et al. 1983). However, studies using solid-state ¹³C nuclear magnetic resonance (NMR) spectroscopy have revealed that much of SOM is microbial-derived and has few similarities with plant litter (Knicker 2011). Also, microbial necromass can make up more than half of all topsoil organic C in agricultural, grassland, and forest ecosystems (Liang et al. 2019), although plant biomolecules, such as lipids, lignin, and sugars, might also contribute to the formation of organo-mineral complexes (Angst et al. 2021a). Regardless, it has become clear that stabilisation of SOM is not solely based on intrinsic properties of the organic matter that control (first-order) decomposition rates but is influenced by

physicochemical interactions with the soil environment (Schmidt et al. 2011).

Cotrufo et al. (2013) proposed the microbial efficiency-matrix stabilisation (MEMS) framework, where SOM is stabilised through the formation of organo-mineral complexes, with labile plant compounds being the dominant source of these complexes. The idea behind this framework is that labile plant compounds are used more efficiently by soil microbes than relatively recalcitrant plant compounds and therefore a greater fraction of labile plant compounds end up in the microbial necromass or as a microbial by-product (e.g., extracellular enzymes) that can react with soil minerals to form organo-mineral complexes (MAOM). However, this may also depend on the extent of soil C saturation or the inherent capacity of soils to stabilise C (Castellano et al. 2015). In contrast, some plant compounds that are relatively slow to decompose, such as slow-decaying plant litter may eventually be lost to the soil as CO₂ when their conversion to microbial necromass is low. If this indeed occurs in different soil types and land uses, this will profoundly change the current view of how the quality of plant inputs influences SOM stabilisation.

Later, Liang et al. (2017) introduced another conceptual framework for soil C stabilisation, referred to as the microbial C pump mechanism, where microorganism-mediated processes lead to SOM stabilisation. Two major pathways were described in this model by which microorganisms influence SOM formation: (1) *ex-vivo* (extracellular) modification, in which extracellular enzymes attack and transform plant residues, resulting in the deposition of plant-derived C that is not readily assimilated by microorganisms; and (2) *in-vivo* turnover of organic substrates (e.g., cell uptake–biosynthesis–growth–death), resulting in the deposition of microbial-derived C. In both pathways, microorganisms contribute to the formation of POM and MAOM fractions. The relative importance of *in-vivo* turnover and *ex-vivo* modification varies with different environmental conditions, and similar to the MEMS framework, this model also advocates that microbial necromass and metabolites are the precursors for SOM stabilisation. They further illustrated that the pathway of C is differently driven by bacteria and fungi with different trophic lifestyles, such as autotrophic or heterotrophic lifestyles, substrate-use, and host species.

Sokol et al. (2019) proposed a spatially explicit set of processes that link the plant C source with MAOM formation. They suggested that the formation of MAOM in areas of high microbial density (e.g., rhizosphere zone and other microbial hotspots) should primarily occur through an *in-vivo* microbial turnover pathway and favour C substrates that are processed first by microbes. In contrast, in areas of low microbial density (e.g., certain regions of the bulk soil), MAOM formation should primarily occur through direct sorption of the intact or partially oxidised plant compounds to un-colonised mineral surfaces, particularly substrates with a strong ‘sorptive affinity’ to mineral surfaces. Through this framework, they describe how the primacy of biotic *vs.* abiotic (e.g., abundance of clay particles) controls on MAOM dynamics is not mutually exclusive but instead spatially dictated.

This spatial control over SOM stabilisation or persistence was also highlighted in the ‘functional complexity’ concept proposed by Lehmann et al. (2020). They postulated that an increase in spatial heterogeneity in the soil, combined with an increase in the molecular diversity of substrates, can reduce SOM decomposition. They argued that spatial heterogeneity decreases the likelihood that microbes are in direct contact with their substrates, while a greater molecular diversity in substrates reduces decomposition because of a reduced energy return on investment in different types of extracellular enzymes.

However, none of these above-described conceptual frameworks considers the interactions between clay particles and biotic processes in relation to the SOM stabilisation. For instance, the rate and strength of substrate adsorption to minerals will be influenced by clay content and clay mineralogy, which in turn will influence the microbial C use and recycling. In other words, if more of the substrate is directly and rapidly adsorbed onto minerals (including microbial products), then there will be less opportunity for microbes to recycle C, while there is also evidence that a decline in C availability can also directly influence microbial CUE (Min et al. 2016). Microbial use of substrates will further depend on the adsorption strength or affinity that can significantly vary among substrates, all of which would influence microbial C use and recycling of different substrates. Soils differ widely in clay content and mineralogy, interactions between abiotic and biotic processes will have

important consequences for SOM stabilisation. Therefore, we propose a framework integrating the existing concepts on interactions between abiotic and biotic controls on OM stabilisation in soils varying in the abundance of active clay surfaces.

Framework to integrate interactions between abiotic and biotic processes on SOM stabilisation

Our framework integrates existing concepts and is primarily based on four principles described below. While the first three principles have been included in other frameworks of SOM stabilisation, the fourth principle is what makes this integrated framework distinct from others. We first illustrate these principles using three different types and contrasting plant organic matter inputs, which include glucose and oxalic acid, two simple and labile compounds that are frequently found in root exudates, and a plant litter (either from roots or shoots) that is structurally more complex (i.e., has a greater molecular diversity) and overall is slower to decay than the labile compounds. Plant litter consists of different compounds (lignin, cellulose, etc.) that vary greatly in composition depending on its source, the purpose of using plant litter here is to contrast rhizodeposition compounds

with plant litter, since plants do not produce solely lignin or cellulose. We then describe six different scenarios about the fate of these three substrates in soils with either low or high abundance of active clay surfaces.

Principle 1 Microbial CUEs differ intrinsically among different substrates, which can be related to their energy content, C oxidation state, and structural complexity (Fig. 1a).

As a general rule, compounds that have a large energy content result in a high microbial CUE of such compounds (Fig. 1a). This is because microbes are frequently C-limited rather than being energy-limited, whereby energy-rich compounds liberate enough energy for maximum C-assimilation and growth resulting in a high microbial CUE (Gommers et al. 1988). However, the microbial CUE is not only determined by the energy content of a substrate but also depends on metabolic pathways (Dijkstra et al. 2015, 2011) and C oxidation state of the substrate (Gunina et al. 2014, 2017; Manzoni et al. 2012). For instance, sugars are thought to be used more for anabolism (particularly when microbes are C-limited), and therefore result in a high microbial CUE, while carboxylic acids, such as oxalic acid, are used more for energy production, resulting in a much lower microbial CUE

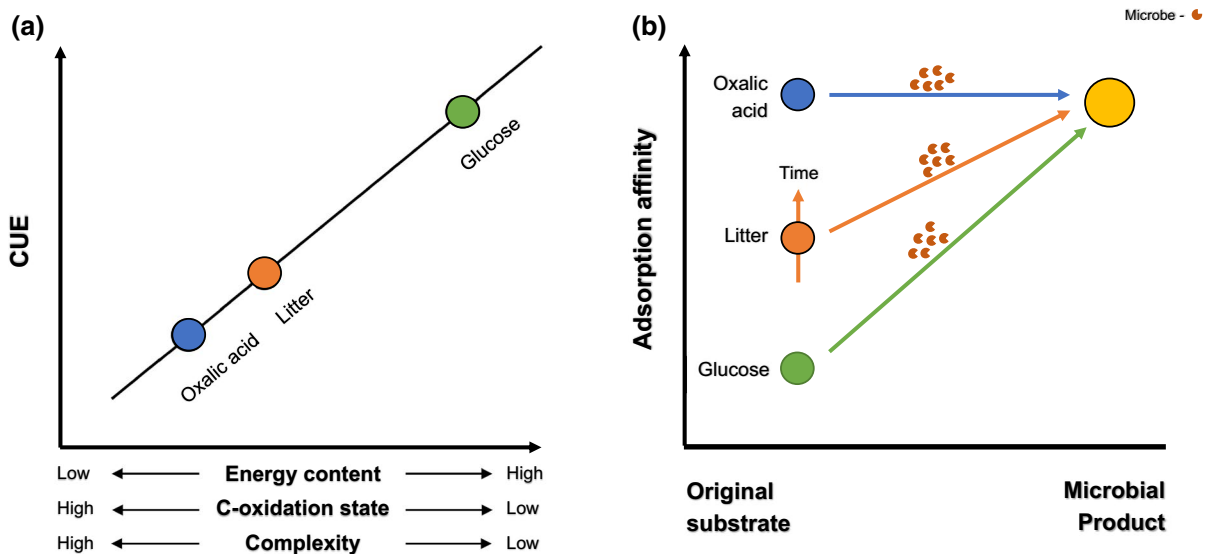


Fig. 1 Schematic representation of the influence of energy content, C-oxidation state, and complexity of three contrasting substrates on microbial carbon use efficiency (CUE, **a**); and the adsorption affinity of original substrates and microbial products (**b**)

(Gunina et al. 2014). The structural complexity of a substrate may also affect CUE. Microbes need to produce extracellular enzymes to break down substrates before they can be taken up. Because the production of extracellular enzymes requires energy, and a greater number of enzymatic steps are required to breakdown more complex substrates, complex substrates have a relatively low microbial CUE (Ågren and Bosatta 1987). Therefore, a more complex nature of plant litter (and its breakdown products) is thought to result in a lower microbial CUE compared to labile and more simple substrates used for anabolism (Cotrufo et al. 2013).

Principle 2 Substrates (including microbial products) differ in their adsorption affinity to clay minerals, while the adsorption affinity of microbial products is usually higher than or as high as for the substrates they were derived from (Fig. 1b).

Adsorption of organic compounds onto clay minerals occur through different mechanisms, including ligand exchange reactions, hydrophobic interactions and van der Waals forces, hydrogen bonding, and cation bridging (Gu et al. 1994; Sposito 1984; Yeasmin et al. 2014). Ligand exchange between the carboxyl and hydroxyl functional groups of organic compounds and mineral surfaces has been considered as one of the most dominant adsorption mechanisms (Gu et al. 1994), and therefore, carboxylic acids (such as oxalic acid) tend to have a high adsorption affinity to clay minerals, particularly iron oxides (Jagadamma et al. 2012, 2014; Yeasmin et al. 2014). In contrast, without carboxyl or hydroxyl functional groups, glucose has a much smaller tendency to directly adsorb onto clay minerals (Fischer et al. 2010). Fresh plant litter also tends to have a low density of these functional groups, but decomposition could result in increased formation of COOH and OH functional groups on material that remains undecomposed (Kögel-Knabner et al. 1988). It can therefore be expected that the adsorption affinity of plant litter would increase with time. Other chemical characteristics, such as hydrophobicity and aromaticity could also influence the adsorption affinity of plant litter (Kaiser and Zech 1997; Keiluweit and Kleber 2009).

However, regardless of the type, once substrates are processed and incorporated into microbial biomass, the microbial products, including microbial

necromass and extracellular enzymes, have chemical structures that are expected to have a greater adsorption affinity compared to the substrates they have derived from, possibly because of higher density of carboxyl or hydroxyl functional groups. For instance, specific extracellular enzymes produced by microbes usually contain a large number of functional groups and therefore have a tendency to adsorb onto soil clays minerals (LePrince and Quiquampoix 1996; Olagoke et al. 2020). Recently, this principle was also indirectly shown where rapid formation of microbial products from glucose resulted in increased sorption to clay, thereby preventing further decomposition of these microbial products (Geyer et al. 2020). Indeed, it has been suggested that MAOM formation is largely driven by adsorption with microbial products (Kallenbach et al. 2016; Miltner et al. 2012). However, most of these studies measured adsorption of microbial products that are left behind, and there is therefore the possibility that microbial products with low adsorption affinity are produced, and that are consequently decomposed.

Principle 3 Substrate complexity and adsorption affinity will affect C flow into MAOM and POM (Fig. 2).

This principle builds on prior conceptual frameworks (Cotrufo et al. 2013; Kaiser and Kalbitz 2012; Sokol et al. 2019) and predicts that both substrate complexity and adsorption affinity affect the C flow into MAOM and POM (Fig. 2). Labile and relatively simple compounds with low adsorption affinity, such as glucose, are readily taken up by microbes and therefore are not likely to be directly adsorbed onto minerals (Fischer et al. 2010). However, these compounds can still strongly contribute to MAOM formation through the in-vivo microbial pathway (Cotrufo et al. 2013; Liang et al. 2017; Fig. 2a), unless the capacity of soil to adsorb compounds has been saturated (Castellano et al. 2015; Stewart et al. 2007). Labile and relatively simple compounds that have a high adsorption affinity, such as oxalic acid, are more likely to be directly adsorbed onto minerals and can escape microbial uptake, particularly when they are produced at locations with low microbial density (Sokol et al. 2019, Fig. 2b). In contrast, compounds that have greater structural complexity (e.g., structural

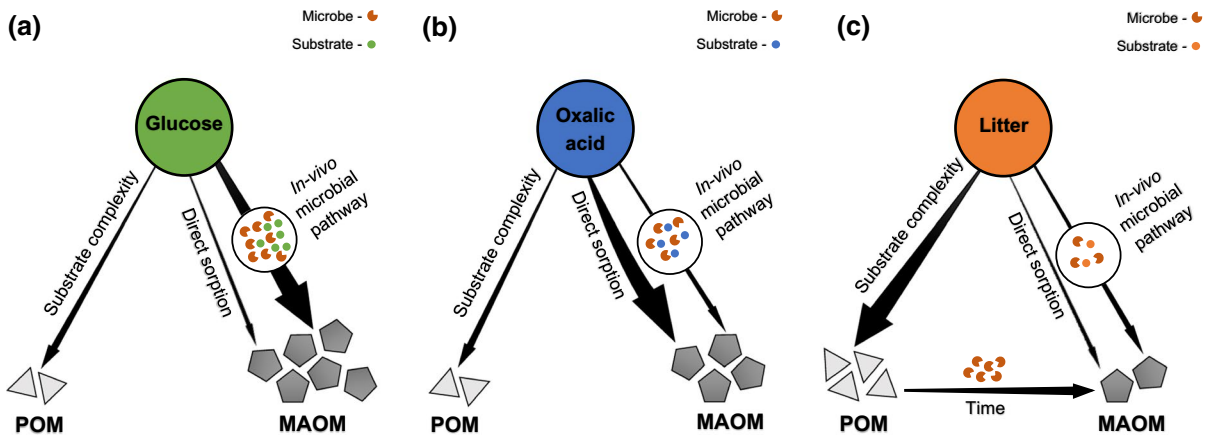


Fig. 2 Simplified scheme of particulate organic matter (POM) and mineral associated organic matter (MAOM) formation with glucose (a), oxalic acid (b) and litter (c). We identify

three distinct pathways, (1) partial decomposition of structurally complex substrates, (2) direct sorption, and (3) the in-vivo microbial pathway

residues derived from plant litter that have undergone comminution) will not be readily decomposed and adsorbed to minerals, and therefore contribute mostly to POM (Fig. 2c). However, with time more of this material will be modified through microbial decomposition, which increases their likelihood to contribute to MAOM.

Principle 4 An increase in the abundance of active clay surfaces will increase adsorption, decrease microbial recycling, increase microbial CSE due to C flowing into MAOM, and the magnitude of this effect will depend upon the intrinsic microbial CUE and adsorption affinity of each organic compound (Fig. 3).

A first feature of this principle is represented by the potential for adsorption of organic C onto clay minerals, which will increase with increased abundance of active clay surfaces (e.g., Jeewani et al. 2021, Fig. 3a). The abundance of active clay surfaces will also determine the maximum capacity (i.e., saturation) for soils to form complexes with organic C (Dexter et al. 2008; Hassink 1997; Klopfenstein et al. 2015), while the actual rate of adsorption may be greater in soils that are further from C saturation (Castellano et al. 2015; Stewart et al. 2008). Furthermore, we only focus here on the role of active clay surfaces, but we would like to point out that the adsorption capacity of soils will also be influenced by the type of clay minerals and by the thickness of

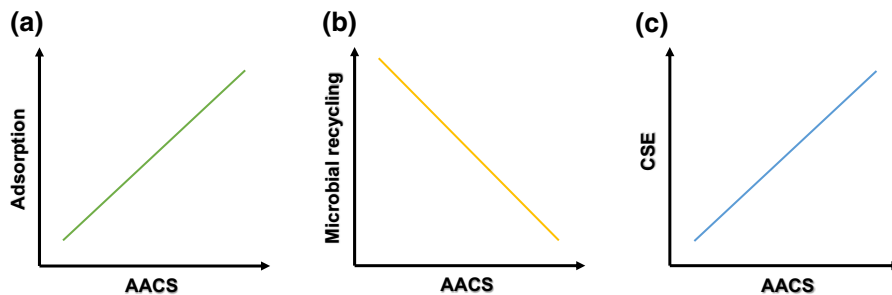
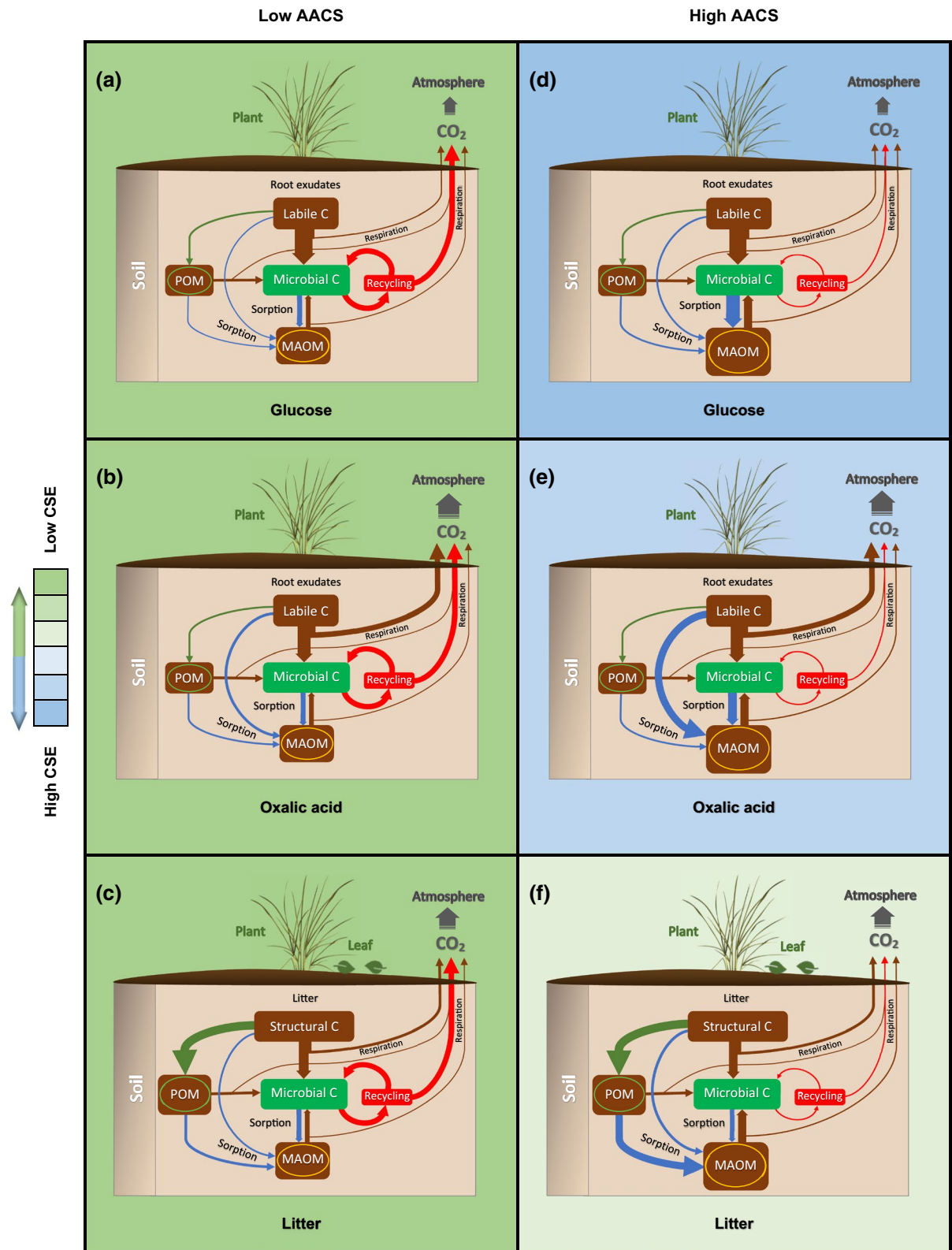


Fig. 3 Simplified representation of the influence of the abundance of active clay surfaces (AACS) on adsorption (a), microbial recycling (b) and carbon stabilisation efficiency (CSE, c) of substrates. While relationships are presented as linear, it is

possible that they may be non-linear (e.g., smaller increase in adsorption and CSE or smaller decrease in microbial recycling with increased AACS)



◀**Fig. 4** Framework depicting the fate of glucose (**a, d**), oxalic acid (**b, e**), and plant litter (**c, f**) in soils with low (**a, b, c**) and high abundance of active clay surfaces (AACS) (**d, e, f**). Glucose and oxalic acid are represented as labile C, while plant litter is structural C. Green arrows indicate C flowing into the particulate organic matter pool (POM), brown and red arrows indicate microbial uptake and respiration, and blue arrows indicate adsorption onto minerals forming mineral associated organic matter (MAOM). Microbial recycling pathways are further made distinct with red arrows. The thickness of the arrows indicates the relative size of the C flows. The background colour of each panel indicates the variation in microbial carbon stabilisation efficiency (CSE), as indicated by the colour bar on the left

C accrual on a clay surface (Churchman et al. 2020; Jindaluang et al. 2013; Kalbitz et al. 2000; Schweizer et al. 2021; Singh et al. 2016). When there is a greater adsorption capacity, there will be less substrate available for microbes, including microbial products (e.g., Swenson et al. 2015), and therefore, an increase in abundance of active clay surfaces would reduce microbial recycling of C (Fig. 3b). When there is less opportunity for microbes to recycle C, this will result in reduced loss of C as CO₂, and therefore, a greater abundance of active clay surfaces would increase the microbial CSE (Fig. 3c). The CSE differs from CUE in that CSE includes microbial use of microbial products (Geyer et al. 2020).

Interactions between substrate type and abundance of active clay surfaces: six scenarios

We postulate six different scenarios based on the abovementioned four principles for each of the three substrates (glucose, oxalic acid, and plant litter) in soils with either a low or high abundance of active clay surfaces (Fig. 4). For each of these substrate types, we elaborate on how an increased abundance of active clay surfaces alters the C dynamics and why specific C flows are high or low based on the four principles stated above.

Soils with low abundance of active clay surfaces

In soils with low abundance of active clay surfaces, we postulate that most of the labile C (glucose, oxalic acid) will be taken up by microbes, and little C will flow into the POM pool (Fig. 4a, b). In contrast, much

of the structural C (plant litter) is not readily taken up by microbes and will flow into the POM pool (Fig. 4c). Because of the low abundance of active clay surfaces, the capacity to adsorb C will be low for all three substrate types, and also adsorption of POM-derived compounds, directly or indirectly through the microbial pathway, will be small (Haddix et al. 2020). As a consequence, there will be much opportunity for microbes to recycle microbial products, resulting in relatively high recycling rates for all three substrates. High rates of recycling, where microbial products are repeatedly used with time, in soils with low abundance of active clay surfaces will generally have low microbial CSEs (Angst et al. 2021b). Although there will be intrinsic differences in microbial CUE among substrates, because of repeated recycling with time, microbial CSE will be low for all substrates. Indeed, during repeated recycling, increasingly more microbial C will be respired and lost to the atmosphere. The MAOM pool in soils with low abundance of active clay surfaces will be small, and most of the soil C will exist in the POM pool, particularly when substrates are added as plant litter.

Soils with high abundance of active clay surfaces

In soils with high abundance of active clay surfaces the role of adsorption will be more prominent. Direct adsorption of labile substrates with a high adsorption affinity (e.g., oxalic acid) can be high, where it competes with microbial uptake (Fig. 4e). On the other hand, labile substrates with a low adsorption affinity (e.g., glucose) will not be directly adsorbed onto minerals but immediately taken up by microbes, and only after the formation of microbial products, will adsorption onto minerals occur (Fig. 4d). Assuming that fresh plant litter will have a low adsorption affinity, initial adsorption of plant litter will be small, also because it is not readily taken up by microbes. However, with time it is expected that after modification by microbes, the modified litter in the POM pool will have a greater ability to form MAOM (Fig. 4f, also see Haddix et al. 2020). Because of the high adsorption affinity of microbial products, there is less likelihood of recycling of microbially derived compounds (Samson et al. 2020b), and therefore we expect that microbial recycling will tend to be lower in soils with high abundance of active clay surfaces. Indeed, (Angst et al. 2021b) also suggested a greater retention

of C derived from plant litter in a clay-rich soil due to reduced microbial recycling. As a consequence, we also expect that the microbial CSE of different plant substrates should be higher in soils with high abundance of active clay surfaces (as observed by Angst et al. 2021b for grass litter), and particularly for labile compounds that intrinsically result in a high microbial CUE, such as glucose. Due to the high adsorption of microbial products and other compounds with high adsorption affinity, we predict relatively large MAOM pools in soils with high abundance of active clay surfaces, although where plant litter is an important component of plant input, POM may also remain high.

Further considerations

In our new framework, we have attempted to integrate interactions between abiotic and biotic processes in relation to SOM stabilisation and showed possible scenarios for the SOM stabilisation in soils with low and high abundances of active clay surfaces. We understand that this framework does not specifically consider the role of soil aggregation, which can also be important for SOM stabilisation and depend on clay content (Chivenge et al. 2011; Six et al. 2004, 2002; von Lützow et al. 2006). For instance, recently it was suggested that clay may be more important for protecting SOM through aggregation rather than mineral adsorption (Schweizer et al. 2021). Also, our framework does not explicitly consider the effects of variability in the soil microbial community (e.g., variation in bacteria and fungi) on SOM stabilisation (Kallenbach et al. 2016). Published studies have suggested that fungi-dominated soils may accumulate more C than bacteria-dominated soils because fungi produce more structural compounds than bacteria and have a relatively high CUE (Six et al. 2006; Thiet et al. 2006). However, evidence for this remains inconclusive, as it has also been suggested that fungi have a lower CUE than bacteria, possibly because fungi produce C-costly enzymes to break down complex structures (Poll et al. 2006; Ullah et al. 2021). Soil pH can have a strong influence on the soil microbial community composition and microbial CUE (Jones et al. 2019; Zheng et al. 2019), therefore may influence SOM stabilisation (O'Brien et al. 2015), which has not been considered here. Furthermore, our

framework only focuses on the abundance of active clay surfaces but not on the clay mineralogy, which remains key area for future research as different minerals have different organic matter adsorption affinities (Churchman et al. 2020; Jones and Singh 2014; Kalbitz et al. 2000; Singh et al. 2016; Yeasmin et al. 2014, 2017, 2020). Finally, our framework does not include the role of plant roots other than being a source of SOM substrate (either as exudates or root litter). However, roots can cause rhizosphere priming, destabilising SOM, possibly both POM and MAOM pools (Dijkstra et al. 2021). We therefore believe it is critically important to understand the different roles of soil aggregation, microbial community, and plant roots on SOM stabilisation in soils that vary in clay content and mineralogy.

Conclusions

Mechanisms leading to the decomposition of SOM are well documented, although uncertainties persist regarding the stability of SOM. To address this critical gap, a robust predictive understanding and modelling of the SOM dynamics are essential for examining short- and long-term changes in soil C storage (especially the microbial dynamics and different pools such as POM and the more stable MAOM) and feedbacks with climate. While several frameworks about SOM dynamics and stabilisation have been put forward focusing on plant inputs and microbial interactions, there is still a lack of empirical and conceptual understanding of how these biotic controls on SOM stabilisation interact with abiotic soil factors such as the abundance of active clay surfaces (but see Samson et al. 2020a). Our framework advances this understanding by linking plant C source and chemistry with adsorption and microbial pathways of POM and MAOM formation in soils varying in the abundance of active clay surfaces. We believe that accounting for interactions between biotic and abiotic controls on SOM stabilisation is necessary to understand how efficiently C substrates of different chemistries are incorporated into POM and MAOM in different soils.

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Author contributions MRI and FAD designed the framework and BS contributed to the concept. MRI prepared the initial manuscript. FAD and BS finally reviewed and edited the manuscript.

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Declarations

Competing interests The authors declare no competing interests.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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