

Increasing soil carbon storage: mechanisms, effects of agricultural practices and proxies. A review

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Abstract The international 4 per 1000 initiative aims at supporting states and non-governmental stakeholders in their efforts towards a better management of soil carbon (C) stocks. These stocks depend on soil C inputs and outputs. They are the result of fine spatial scale interconnected mechanisms, which stabilise/destabilise organic matter-borne C. Since 2016, the CarboSMS consortium federates French researchers working on these mechanisms and their effects on C stocks in a local and global change setting (land use, agricultural practices, climatic and soil conditions, etc.). This article is a synthesis of this consortium's first seminar. In the first part, we

present recent advances in the understanding of soil C stabilisation mechanisms comprising biotic and abiotic processes, which occur concomitantly and interact. Soil organic C stocks are altered by biotic activities of plants (the main source of C through litter and root systems), microorganisms (fungi and bacteria) and 'ecosystem engineers' (earthworms, termites, ants). In the meantime, abiotic processes related to the soil-physical structure, porosity and mineral fraction also modify these stocks. In the second part, we show how agricultural practices affect soil C stocks. By acting on both biotic and abiotic mechanisms, land use and management practices

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(choice of plant species and density, plant residue exports, amendments, fertilisation, tillage, etc.) drive soil spatiotemporal organic inputs and organic matter sensitivity to mineralisation. Interaction between the different mechanisms and their effects on C stocks are revealed by meta-analyses and long-term field studies. The third part addresses upscaling issues. This is a cause for major concern since soil organic C stabilisation mechanisms are most often studied at fine spatial scales (mm– μ m) under controlled conditions, while agricultural practices are implemented at the plot scale. We discuss some proxies and models describing specific mechanisms and their action in different soil and climatic contexts and show how they should be taken into account in large scale models, to improve change predictions in soil C stocks. Finally, this literature review highlights some future research prospects geared towards preserving or even increasing C stocks, our focus being put on the mechanisms, the effects of agricultural practices on them and C stock prediction models.

Keywords Soil organic C · C dynamics · Stabilisation mechanisms · Mineralisation · Agricultural practices · Indicators · Models · Macrofauna · Microorganisms · Litter · Root inputs · Organomineral associations · Porosity

Contents

1. Introduction
2. Soil C storage mechanisms: state of the art
 - 2.1. Action of living biomass on soil organic C dynamics
 - 2.1.1. Plants, rhizosphere and soil organic C storage—importance of root systems
 - 2.1.2. Impact of living organisms on soil C sequestration—the macrofauna case
 - 2.1.3. Diversity and physiology of microorganisms—drivers of soil C dynamics
 - 2.2. Abiotic soil organic C stabilisation mechanisms
 - 2.2.1. Localisation in the physical structure of soil
 - 2.2.2. C stabilisation mechanisms involving organomineral interactions
3. Mechanisms of OM dynamics affected by agricultural practices
 - 3.1. Review of the main agricultural practices
 - 3.2. Impact of agricultural practises on soil organic C storage
4. How could a better accounting of OM stabilisation mechanisms improve the prediction of soil organic C stock evolution?
 - 4.1. Finding indicators to improve prediction of changes in soil organic C stocks
 - 4.2. Better integration of OM stabilisation mechanisms in large-scale C dynamics models

- 4.3. Modelling OM mineralisation at the micro-scale could help in describing macroscopic C fluxes
- 4.4. Data needed to constrain various approaches to enhance prediction of soil C stock evolution patterns
5. Conclusion
- Acknowledgments
- References

1 Introduction

The increasing atmospheric concentration of greenhouse gases (GHG), particularly those containing carbon (CO_2 , CH_4), is a consequence of human activities and is associated with climate change. Anthropogenic carbon emissions are partially balanced by carbon (C) sinks in oceans, vegetation and soil (Le Quéré et al. 2015). Soils contain approximately three times more C than the atmosphere (2400 vs. 800 GtC) (Jobbágy and Jackson 2000), in the form of organic C borne in organic matter (OM). On decadal time scales, soils can serve as a C sink or source depending on their properties, on the climate, land use, etc. (Eglin et al. 2010).

Global models linking the atmospheric CO_2 concentration to temperature show that a 3.5–4 Gt/year decrease in atmospheric C would limit the temperature increase to $+1.5/2^\circ\text{C}$ by 2050 (Meinshausen et al. 2009; Minasny et al. 2017), i.e. the threshold beyond which climate change would have a significant impact (IPCC 2013). This annual decrease in the atmospheric CO_2 concentration could be fulfilled by annually increasing C stocks in the top 30 cm soil horizon by 0.4% (4 per 1000) (Balesdent and Arrouays 1999; Paustian et al. 2016).

In this context, the 4 per 1000—Carbon Sequestration in Soils for Food Security and the Climate initiative, launched by France in 2015 ahead of COP21 in Paris (<http://4p1000.org/>), aims to bring together governmental and non-governmental stakeholders devoted to improving soil C stock management. Positive effects on food security and climate change are expected through the collective objective of increasing C stocks on a global scale in agricultural areas (croplands, grasslands, forests), on which human action can be oriented towards C storage (Paustian et al. 2016). Indeed, increasing soil OM stocks is also beneficial for soil fertility, since OM mineralisation might be a source of nutrients for plants. But this requires implementing agricultural practices adapted to local conditions that will increase soil C inputs, with outputs remaining stable or decreasing, thus maximising soil C storage.

Soil OM is not homogeneous, and some OM is quickly mineralised after entering the soil, while some persists for very long periods (Schmidt et al. 2011). Conceptual pools were sometimes associated to functional pools tentatively separated from soils according to chemical or physical fractionation

(e.g. Balesdent 1996; Zimmermann et al. 2007; Crow et al. 2007; Moni et al. 2012). In recent years, the significance of the chemical fractions obtained after the so-called humic substances separation have been questioned since they are probably artefacts formed during the drastic chemical extraction treatment (Schmidt et al. 2011). Reconciling conceptual and experimental pools of soil C with different dynamics is still a matter of research, especially when soil organic matter is now accepted as a continuum of organic molecules possibly associated with minerals (Lehmann and Kleber 2015).

Three soil conceptual C pools are generally defined according to their degradation rate (Fig. 1) (von Lützow et al. 2008). Labile OM turnover occurs within a day to a year. OM turnover in the intermediate pool occurs within a few years to decades. Both pools originate predominantly from plant, animal, bacterial and fungal residues. The intermediate pool is also supplied by OM degradation products from the labile pool. This OM pool is rather active with rather fast turnover, so it is highly influenced by soil management practices. Finally, the turnover of the stable OM pool occurs on time scales ranging from decades to centuries. It originates from labile and intermediate pools and involves most of the soil organic C (Torn et al. 2009). It consists of plant, animal, bacterial or fungal residues and microbial metabolic products. OM in the stable pool can be found in aggregates and/or adsorbed on mineral surfaces.

The challenge for the 4 per 1000 initiative is to increase the size of the intermediate and stable C pools in order to maximise the sustainability of additional C storage, i.e. maximising the residence time of this additional C in soil. C storage/release in these reservoirs is driven by biotic and abiotic mechanisms that operate at fine spatial scales within the soil organomineral matrix. It is essential to understand these mechanisms and interactions so as to be able to anticipate and control changes in soil C contents in an ever-evolving environment (changes in land use, agricultural practices, climatic

or edaphic conditions, etc.). Many research groups are addressing these scientific challenges while striving to overcome scientific knowledge gaps on these mechanisms. However, it is hard to compare this information on various spatiotemporal scales, which has led to the creation of a national research network in France (to be expanded internationally) to federate the strengths of our scientific community on this issue.

The CarboSMS (Carbon Stabilization Mechanisms in Soil) research network was launched in late 2015 and currently consists of about 110 members. Some 70 researchers attended the CarboSMS kickoff meeting at the *Ecole Normale Supérieure* (ENS) in Paris on 10 March 2016. The present article summarises the outcome of this meeting. In the first part, we present recent advances on the mechanisms involved in soil organic C sequestration and then discuss the effects of agricultural practices on these mechanisms in the second part. Finally, in the third part, we show how it is essential to account for these mechanisms in global models and define indicators to describe C dynamics in order to enhance the prediction of the patterns of change of soil organic C stocks.

2 Soil C storage mechanisms: state of the art

Two main types of mechanisms influence the stabilisation/destabilisation of soil organic C: biotic mechanisms related to living soil biomass and soil biodiversity (plants, fauna, microorganisms) and abiotic mechanisms (localisation in the soil physical structure and degradation/stabilisation hotspots, organomineral interactions). For the sake of clarity, these mechanisms will be discussed successively in the following section, although they occur simultaneously in soils, combining or neutralising their effects.

2.1 Action of living biomass on soil organic C dynamics

2.1.1 Plants, rhizosphere and soil organic C storage—importance of root systems

The effects of plants on soil OM are twofold. First, as autotrophic organisms, plants are the main source of soil organic C through their litter production (shoots and roots), root exudates (released through passive and active mechanisms) and via symbiotic (nitrogen-fixing and mycorrhizal) associations. Second, plants contribute to soil OM stabilisation mechanisms by producing poorly degradable compounds and by promoting stable aggregate formation. By limiting erosion, plants also contribute to soil OM conservation.

Plants have a broad range of root systems and their influence on soil OM varies with the plant species and root functional traits (i.e. architecture, morphology, physiology, chemical composition and symbiotic associations, Fig. 2).

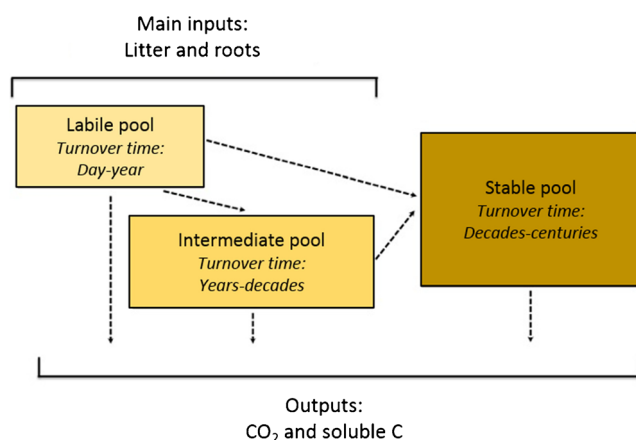


Fig. 1 Conceptual pools of soil C depending on its turnover time: labile, intermediate and stable pools

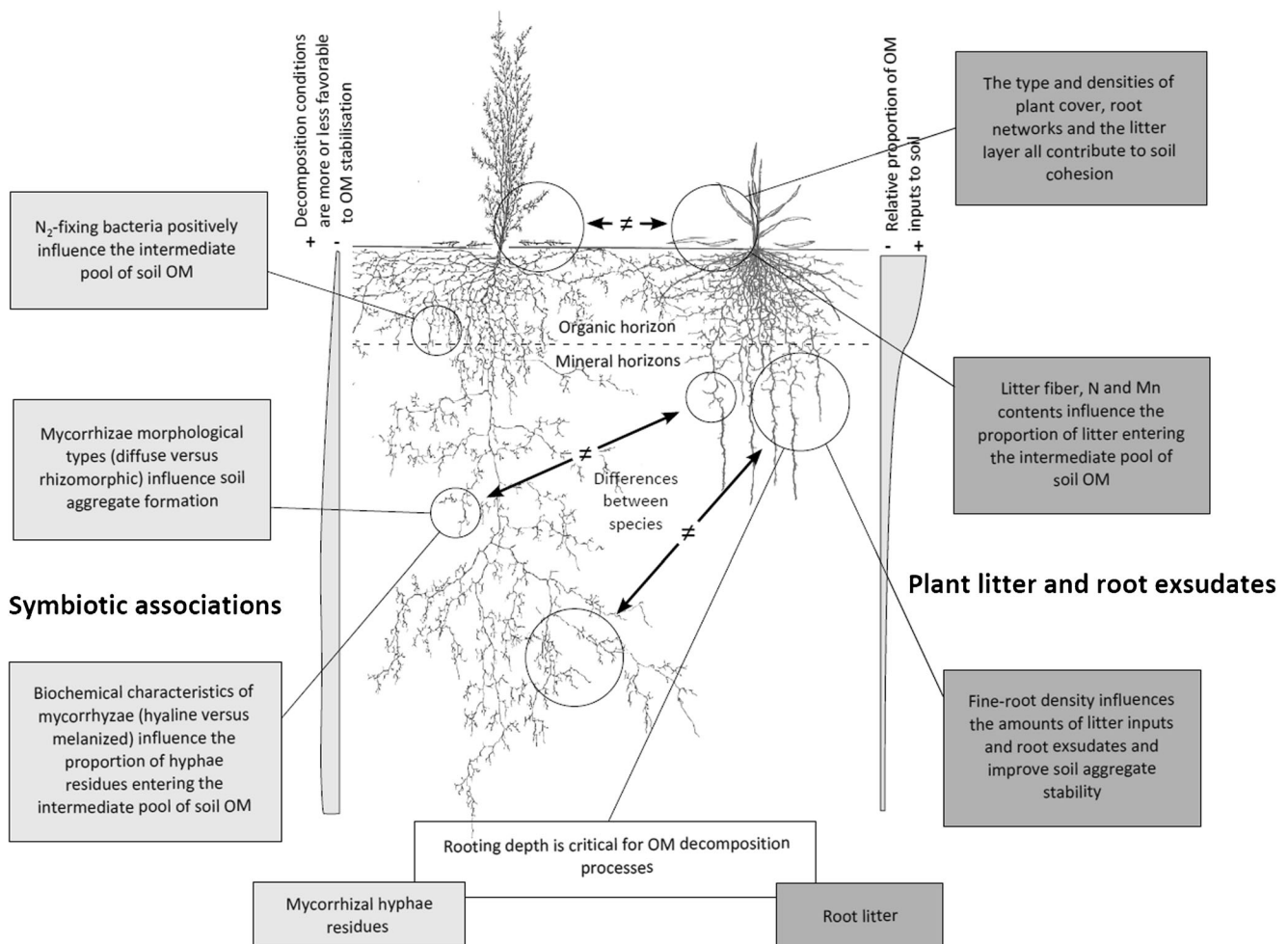


Fig. 2 Differences in functional traits and symbiotic associations between different plant species influence soil organic matter stabilisation. Adapted from Freschet et al. (in press)

OM fluxes from plants to soils C inputs to the soil consist of above- and belowground litter (leaves, branches, stem, roots...), but also of rhizodeposits and of compounds that are directly transferred to mycorrhizal fungi. Root litter contributes about one third of total litter inputs in grassland soils and half in forest soils (Freschet et al. 2013). Rhizodeposition represents about 11% of the C assimilated by plants or 27% of that allocated to roots (Jones et al. 2009; Balesdent et al. 2011). The type and intensity of mycorrhizal associations, and therefore of C transfers to mycelial hyphae, depend respectively on the plant phylogenetic identity and on soil factors, especially on the availability of soil nutrients (Soudzilovskaia et al. 2015).

Some recent and debated studies suggest that belowground inputs largely contribute to OM, which is stabilised in soils on the medium to long term (Balesdent and Balabane 1996; Kuzyakov and Domanski 2000; Mendez-Millan et al. 2010; Clemmensen et al. 2015), especially in deeper soil horizons (Rasse et al. 2005; Rumpel and Kögel-Knabner 2011; Mendez-Millan et al. 2012). In particular, the study by

Jobbágy and Jackson (2000) showed that the vertical root distribution corresponds to that of soil organic C for different plant species and soil types. Indeed, root litter decomposition is generally 30% slower than leaf decomposition (Birouste et al. 2012; Freschet et al. 2013). In addition, aboveground litter inputs are only partly transferred into the mineral soil (Garten 2009), where the decomposition rate decreases with increasing depth (Garcia-Pausas et al. 2012; Poirier et al. 2014; Prieto et al. 2016).

The contribution of belowground input to C storage occurs through the persistence of plant residues or via the stimulation of soil microbial activity and the increase of the contribution of microbial necromass to the slow cycling soil OM pools (Beniston et al. 2014; DuPont et al. 2014; Lange et al. 2015; Morriën et al. 2017).

The architecture and rooting profile of species are thus critical traits that control the amount and location of C inputs in the soil profile. Amongst herbaceous plants, monocots generally produce greater root biomass than forbs (Poorter et al. 2015) and have higher fine root densities (Craine et al. 2003),

suggesting larger C inputs to soil. Lange et al. (2015) also demonstrated that higher plant diversity increases rhizosphere carbon inputs.

Quality of OM inputs and impact on their decomposition rate

The chemical composition [e.g. concentration in C, lignins, nitrogen (N) and manganese (Mn)] of aboveground and belowground litter inputs and root exudates varies markedly between plant species and influences OM decomposition kinetics on time scales ranging from year to decade (Jones et al. 2009; Machinet et al. 2011; Birouste et al. 2012). It is commonly recognised that a high lignin content leads to the accumulation of particulate OM in the soil (Cotrufo et al. 2015) and increases the plant residue contribution to the intermediate OM pool (Fig. 1). The litter Mn content stimulates lignin degradation through the formation of Mn peroxidases involved in lignin oxidation (Berg 2014; Keiluweit et al. 2015a). High N levels in plant litter and residues generally increase their initial decomposition rate, and result in the accumulation of microbial residues that persist in the soil. At the same time, high N levels in plant residues inhibit the specific decomposition of lignins (Berg et al. 2010; Dignac et al. 2002; Martins and Angers 2015), probably due to the recombination of N with partially decomposed lignin molecules (Berg et al. 2010).

The type and intensity of mycorrhizal associations strongly influence the OM fate in soils (Fig. 2) (Clemmensen et al. 2013, 2015). Roots colonised by ectomycorrhiza, as well as mycelial hyphae from both ecto- and endomycorrhiza, decompose more slowly than non-mycorrhizal roots (Langley et al. 2006). Moreover, mycorrhizal hyphae differ in their morphological (diffuse vs. rhizomorphic) and biochemical (hyaline vs. melanised) characteristics (Fernandez and Kennedy 2015). Melanised compounds could be involved in fungal OM persistence in soils (Fernandez et al. 2016). Several recent studies suggest that the chemical composition of OM inputs may not explain their persistence in soils beyond a decade, but has an impact on the C pool cycling over year to decade. Over longer time scales, this persistence would depend more on environmental conditions (Amelung et al. 2008; Derrien et al. 2006; Thevenot et al. 2010; Schmidt et al. 2011; Andreetta et al. 2013; Lehmann and Kleber 2015; Mathieu et al. 2015).

Impact of plant residue inputs on soil OM degradation (priming effect)

Fresh OM inputs that are easily used by soil microbial decomposers, such as root exudates, leachates and the labile portion of litter, can also stimulate native soil OM degradation. This so-called priming effect can be explained by three potentially co-occurring mechanisms (Löhnis 1926; Fontaine et al. 2004, 2007; Blagodatskaya and Kuzyakov 2008): (1) increased activity and development of microbial communities specialised in acquiring labile resources (r-strategists) resulting in increased soil enzymatic activities with potentially negative effects on soil OM storage; (2) stimulation of microbial communities adapted to the degradation of

less degradable substrates (K-strategists), which depends on the nutrient availability in soils (Fontaine et al. 2011; Derrien et al. 2014); and (3) the action of root exudates (e.g. oxalic acid) disrupting soil organomineral associations and providing microorganisms with access to previously stabilised organic compounds (Keiluweit et al. 2015b).

Aggregate stability and soil layer cohesion Plants contribute to the formation of stable aggregates (OM protected from degradation, see Section 2.2.1 below) in soil through fine roots and mycorrhizal associations (Tisdall and Oades 1982). High fine root and mycelial hyphae densities improve aggregate stability (Fig. 2) (Wu et al. 2014; Erktan et al. 2016) through different mechanisms: (1) increased production of root exudates, such as polysaccharides, which act as a glue between soil particles, (2) better soil particle trapping facilitated by the entanglement of roots and hyphae, (3) increased wetting-drying cycle frequency in soil in relation to water acquisition by roots, (4) input of plant residues containing specific constituents (e.g. hemicellulose, suberin or phenolic compounds) that contribute to macroaggregate stability and (5) stimulation of the production of microbial metabolites involved in microaggregate stability (Martens 2000; von Lützow et al. 2008; Martins and Angers 2015). These processes vary between plant species, but also depend on mycorrhizal fungi (Rillig et al. 2015). Hyphae with a diffuse morphology, thus promoting soil-hyphal interactions, could therefore have a greater impact on soil aggregate formation than hyphae of rhizomorphic types (Fernandez and Kennedy 2015). Finally, polysaccharides secreted by N₂-fixing bacteria also have a positive effect on soil aggregate formation (Martins and Angers 2015).

Vegetation also contributes indirectly to soil C storage/release by affecting soil physical structure. The density and permanence of aboveground plant cover, as well as the plant's ability to accumulate litter, protect topsoil from structural breakdown under the action of rainfall (Fig. 2) (Le Bissonnais et al. 2005). Species with high root length density (e.g. monocot species) and high root branching intensity (e.g. annual species) within topsoil also limits surface erosion and water runoff by promoting soil particle trapping (Gyssels et al. 2005). High root length density and fast root turnover also promote the formation of galleries that increase the soil porosity and limit water runoff (Gyssels et al. 2005). However, this also increases soil moisture and may improve conditions for soil OM decomposition in deeper soil horizons. Finally, species with deep root systems, high root length density and high root branching intensity can improve the cohesion between soil layers and limit landslides (Stokes et al. 2009).

In conclusion, plants influence labile, intermediate and stable soil C pools. The effects of plants on soil OM stabilisation and protection seem to be mostly positive, although the balance between positive and negative effects (i.e. over-mineralisation) will differ according to interactions between plants and the soil abiotic and biotic conditions. For instance,

plant–microbe, plant–plant, plant–animal (herbivory-related) and plant–soil interactions and their effects on C stabilisation mechanisms have yet to be extensively explored. Furthermore, although chemical recalcitrance has been shown to have little influence on long-term soil C stabilisation (Marschner et al. 2008; Schmidt et al. 2011; Dungait et al. 2012), it may influence the intermediate C pool (Fig. 1) and the secondary consumption/transformation of these OM by macro- and microorganisms (Moorhead et al. 2014). The search for new indicators of C dynamics linked to the chemical composition of plant tissues could improve our knowledge on these mechanisms. In this context, another major challenge is to gain greater insight into the role of the functional diversity of plants and of their symbionts in soil OM stabilisation/destabilisation mechanisms. This challenge requires stronger interactions between soil science, plant and microbial ecology and the development of long-term comparative laboratory and field studies before testing the relevance of these mechanisms in models. To this aim, experimental platforms (e.g. Ecotrons) and stable isotope techniques to differentiate C fluxes would help to gain insight into how the spatial distribution of roots and their symbionts can influence OM stabilisation through mechanisms related to soil physical properties, as presented in the Section 2.2 of this review.

2.1.2 Impact of living organisms on soil C sequestration—the macrofauna case

The diversity of organisms hosted in soils is huge in terms of size and function, encompassing megafauna, macrofauna, microfauna and microorganisms. Soil macrofauna includes organisms larger than 2 mm with high taxonomic diversity, including millipedes (diplopoda and centipedes), woodlice, earthworms, some springtails, numerous spiders and insects (ants, beetles, termites), in addition to vertebrates such as rodents (mice) and insectivores (moles, shrews). Functionally, these animals can be grouped according to their diet (zoophagous, herbivorous, root-feeding, saprophagous, soil-feeding, etc.) or to their impact on their physical and chemical environment. The best known group includes ‘ecosystem engineers’ (earthworms, ants and termites). These organisms often represent a large biomass in soils (individually for earthworms or socially for termites and ants), having a substantial influence on soil OM dynamics (Chevallier et al. 2001) (Fig. 3).

Processes promoting C stabilization In tropical and temperate regions, it is widely recognised that long-term OM stabilisation is controlled by interactions between microorganisms (fungi and bacteria), ecosystem engineers (roots, earthworms, termites, ants) and the soil mineral matrix (Lavelle 1997). Ecosystem engineers act by fragmenting litter, incorporating it into the soil profile,

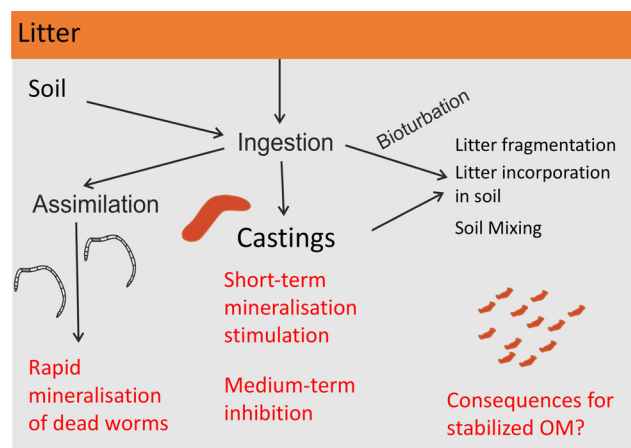


Fig. 3 Earthworm activity affects organic matter dynamics via litter consumption and soil particle ingestion

mixing soil by bioturbation in the profile and influencing dissolved OM transport (Bohlen et al. 2004).

Ecosystem engineers also promote C stabilisation by forming biogenic structures (biostructures such as castings, galleries, veneers, fungi wheels, termite or ant hills). The C in these structures can be stabilised through organomineral associations, depending on ingested OM composition (Vidal et al. 2016). The type, shape and characteristics of these biogenic structures vary depending on species, land-use patterns and seasons (Decaëns et al. 2001; Hedde et al. 2005; Mora et al. 2005). The C distribution in these structures, e.g. concentration decreasing from the centre outwards, varies between species. For a given species, the C distribution in biogenic structures varies according to their habitats and depends on the soil depth (Don et al. 2008; Jiménez et al. 2008). The physical degradation rate of these structures influences C stabilisation time scale, as well as nutrient release and availability in soils (Le Bayon and Binet 2006; Mariani et al. 2007a; Mariani et al. 2007b; Jouquet et al. 2011). Furthermore, the type of OM (macro-debris, particulate matter or microbial metabolites) and its location (intra- or inter-aggregate), which differ between ecosystem engineers, are also drivers of C dynamics in these biogenic structures (Six et al. 2000; Bossuyt et al. 2004; Six et al. 2004; Bossuyt et al. 2005).

Processes promoting C mineralisation The transit of soil particles through the gut of macrofaunal organisms promotes contact between microbes and OM, leading to alteration of the chemical structure of the OM. This alteration occurs (1) by selective digestion of peptide compounds which alters their stability (Shan et al. 2010), (2) through biochemical changes due to a succession of extreme pH or redox conditions (Brauman 2000) or (3) by physical remodelling of the particles (West et al. 1991). Many groups of soil fauna are known

to stimulate microbial activity and OM mineralisation in the short term (Brown 1995; Winding et al. 1997).

Micro- and meso-fauna also contribute to the decomposition of litter and plant debris, in that their activity regulates the activity of the soil microbial communities. For example, the grazing of bacterial-feeding protozoa or nematodes tends to reduce the microbial density. However, it also stimulates the activity of the microbial communities, which tends to increase OM mineralisation rate. This is known as the microbial loop principle (Bonkowski 2004).

In conclusion, trophic activity and the production of biostructures by soil fauna, especially by the ecosystem engineers, impact soil C dynamics: OM mineralisation is often stimulated in the short term, but stabilised in the longer term. As a result, the quantitative effects are highly variable (Fig. 3). Further research is necessary to gain insight into and predict these effects, while taking the functional traits of the organisms and their environment into greater account. At larger spatiotemporal scales, the functional domain defined by the properties of biogenic structures (e.g. termitosphere, myrmecosphere or drilosphere) strongly influences C storage in the soil profile, which affects the overall ecosystem functioning.

There is also a lack of knowledge about (1) the impact of the biochemical quality of OM on its use by soil organisms since the OM they ingest is chosen not only according to its degradability but also to its stoichiometric composition, in relation to decomposer needs; and (2) the digestive system of organisms, its effect on microorganism selection and the effect of this selection on biogenic structures. Little is also known about the effect of changes in environmental conditions (water and nutrient availability) on biogenic structures. Research on the effects of cultivation practices (tillage, pesticide use, etc.) on the soil fauna density and on their trophic interactions that affect soil C stabilisation would also be necessary (see Section 3).

Finally, future research on C stabilisation mechanisms in soil hosting macrofauna should assess the balance between the beneficial effects of these organisms on C storage and their negative effects due to the GHG they emit (CH_4 , N_2O) (Lubbers et al. 2013; Chapuis-Lardy et al. 2010). In the long term, research projects should also consider the ability of soil fauna to generally positively influence plant biomass production (Scheu 2003), thus likely increasing soil OM inputs (see Section 2.1.1).

2.1.3 Diversity and physiology of microorganisms—drivers of soil C dynamics

Within soil decomposers, microorganisms are the most taxonomically and functionally diversified component (Torsvik and Øvreås 2002; Curtis and Sloan 2005). It is estimated that 1 g of soil can host up to 1 billion bacteria, representing

1 million species (Gans et al. 2005), and up to 1 million fungi comprising up to 10,000 species (Hawksworth 1991; Bardgett 2005). However, the number of neighbouring microorganisms with which a single bacterium interacts, within a distance of about 20 μm , is relatively limited (120 cells on average) (Raynaud and Nunan 2014).

By their activity, microorganisms play a very important role in the ecosystem services provided by soils. At the ecosystem scale, soil microorganisms are vital with regard to (1) nutrient recycling (N, phosphorus, sulphur, potassium, etc.), essential for plant growth and ecosystem dynamics; (2) soil OM storage, crucial for preserving the soil structure and fertility; and (3) soil OM degradation, which could dramatically change the global climate equilibrium (van der Heijden et al. 2008). Furthermore, microorganisms are the main source of organic compounds stabilised in the long term (compared to plants) (e.g. Simpson et al. 2007; Schimel and Schaeffer 2012), as indicated by studies using molecular biomarkers such as sugars and amino sugars, proteins and lipids (Derrien et al. 2006; Miltner et al. 2012).

The soil microbial compartment, despite its central role in soil OM transformation, is still often considered as a group of ubiquitous organisms with high functional redundancy (Nannipieri et al. 2003), on the basis of the postulate put forward by Beijerinck (1913) that ‘everything is everywhere, but, the environment selects’. As such, microbial communities are still often included in compartment models of soil C dynamics as a functional black box generating fluxes whose intensity depends only on abiotic factors such as temperature, humidity, pH, etc., thus excluding the hypothesis that the diversity and composition of microbial communities as well as trophic interactions (competition, commensalism, etc.) between populations can play a functional role (McGill 1996; Gignoux et al. 2001).

This vision could be partly explained by the technical limitations that have long hindered the characterisation of the vast diversity of microbial communities in soils, thus preventing (1) the identification of microbial populations involved in soil OM degradation and (2) the assessment of the role of microbial diversity in soil OM transformation. However, significant progress has been made (Fig. 4), especially since the beginning of the ‘omics’ era and the advent of molecular tools, which are currently able to characterise the taxonomic and functional diversity of communities in situ and without a priori (Maron et al. 2011; Nagy et al. 2016). Recent studies using these tools have suggested that microbial diversity is an important parameter that can modulate soil OM turnover, and thus the balance between soil C storage and atmospheric CO_2 emissions (Tardy et al. 2015; Ho et al. 2014; Baumann et al. 2013; Bell et al. 2005). Future studies should improve the overall understanding of microbial mechanisms involved in this balance (complementary niches, facilitation, etc.). However, other studies have indicated that diversity does not have a role in the balance between C storage and CO_2

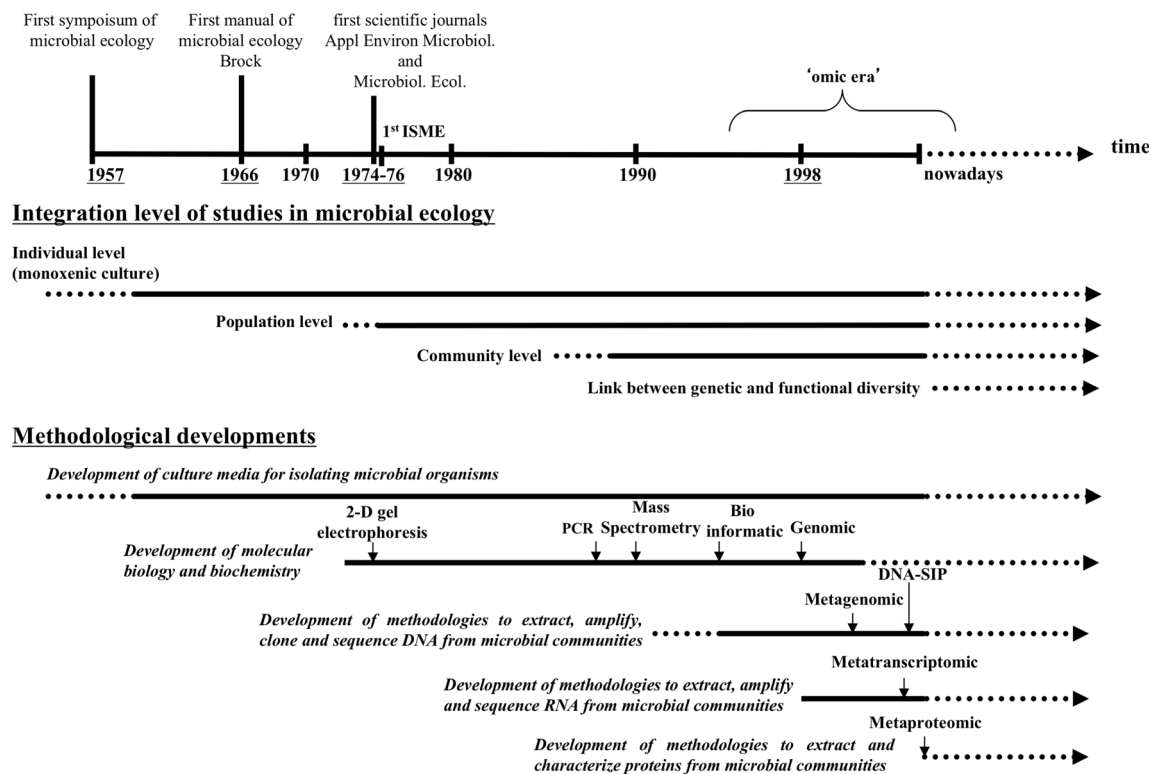


Fig. 4 History and methodological developments in microbial ecology. Excerpt from Maron et al. (2007), with permission of Springer

emissions (Wertz et al. 2006; Wertz et al. 2007; Griffiths et al. 2001 and Griffiths et al. 2008). Long-term studies at experimental sites but also in monitoring networks at national or international scales (Gardi et al. 2009) will help to gain insight into the spatiotemporal variability of processes related to microbial diversity and their impact on soil organic C storage.

Advances in microbial ecological knowledge are crucial for understanding how microorganisms use C and therefore impact its long-term fate in soil (Schimel and Schaeffer 2012). A substantial proportion of soil C originates from labile compounds metabolised by microorganisms and stabilised as microbial residues in organomineral complexes (Miltner et al. 2012; Clemmensen et al. 2013; Cotrufo et al. 2015; Haddix et al. 2016). The C use efficiency of microorganisms is used to estimate, for a given substrate, the ratio between mineralised C and C incorporated in soil OM. This C use efficiency varies depending on the microbial species and their physiology, nutrient availability (N, phosphorus, sulphur, etc.) necessary for microbial metabolism, interactions with the soil matrix and the environmental conditions (temperature, pH, moisture, etc.) (Manzoni et al. 2012; Mooshammer et al. 2014; Geyer et al. 2016; Lashermes et al. 2016). Moreover, it is likely to change depending on the climatic and atmospheric conditions (Allison et al. 2010; Schimel 2013; Sistla et al. 2014).

Considering the major contribution of microbial communities in processes driving soil C dynamics, managing the microbial component could be a lever for optimising

soil C storage (Jastrow et al. 2007). Future research should aim at classifying the impacts of climate parameters, land-use patterns and microbial diversity on C storage, while also focussing on improving the models by explicitly incorporating microbial diversity to improve the prediction of soil C dynamics.

2.2 Abiotic soil organic C stabilisation mechanisms

2.2.1 Localisation in the physical structure of soil

Soil is a heterogeneous environment, which has an impact on soil organic C dynamics. At the landscape scale, soil heterogeneity is driven by the soil texture and mineralogy, and by topology and management practices. At the plot scale, agricultural practices and plant species are the determinants of heterogeneity (Etema and Wardle 2002; Chevallier et al. 2000). At the fine process scale, the degree of heterogeneity depends on the soil physical structure, which corresponds to the spatial arrangement of solid particles (mineral particles, OM) and pores in which fluids, decomposers and soluble compounds circulate (Chenu and Stotzky 2002; Monard et al. 2012). Understanding how the soil physical structure affects OM dynamics is crucial with a view to preserving or even increasing organic C stocks in soils. On the one hand, climate change, and especially the water regime, affects the environmental

conditions at the microbial habitat scale, while on the other, land use and agricultural practices markedly affect the soil structure.

As mentioned above, biotic processes can have a great effect on aggregation: plants with their roots, macrofauna when they digest organic and mineral soil components together, and microbes by acting on their close organomineral environment at the nanoscale. Abiotic C stabilisation mechanisms are thus highly linked to biotic mechanisms.

Soil organic C dynamics are slowed down by inclusion in aggregates From the mid-twentieth century, experimental studies have demonstrated that aggregation decreases the soil OM mineralisation rate (Rovira and Greacen 1957). Experiments were designed to measure CO₂ production after grinding of soil aggregates and to compare it to the CO₂ emitted by the same soil with preserved aggregates. The results showed that grinding increased soil organic C mineralisation, and that the rate increased with the fineness of the grinding. Since then, many studies based on physical fractionation methods have helped to isolate different types of soil aggregates and understand their roles in protecting OM. By analysing samples of soils that had undergone conversion from a C₃ to a C₄ photosynthesis type of vegetation (or the reverse), and using the difference in C isotopic composition between OM from C₃ and C₄ plant types, it was shown that (1) the C residence time was greater when plant debris was included in aggregates than when it was not associated with aggregates, and (2) the C residence time in micro-aggregates (<50 µm) was longer than in macro-aggregates (>50 µm) (e.g. Golchin et al. 1994; Besnard et al. 1996; Six et al. 1998; Six and Jastrow 2002; Chevallier et al. 2004). However, the structural difference between micro- and macro-aggregates might not be the only factor that could explain these contrasted OM mineralisation rates because (1) the OM nature and quality may differ in micro- and macro-aggregates, (2) micro- and macro-aggregates might host different microbial communities (Hemkemeyer et al. 2015) and (3) the stability of macro- and micro-aggregates, which regulates the OM storage duration, is not the same (Plante and McGill 2002). However, aggregates, and especially micro-aggregates, are used as fractions to indicate the degree of physical protection of C as estimates of the pools involved in the compartment models on C dynamics at multi-annual time scales (e.g. Zimmermann et al. 2007, for RothC). Conceptual models describing C dynamics in different aggregates, considering aggregate formation-destruction cycles, have recently emerged, but their parameterisation is not yet possible since these models are too complex and not sufficiently constrained (Stamati et al. 2013).

Decomposers act on organic substrates in the soil pore network OM mineralisation requires contact between the substrates and decomposing microorganisms, or their enzymes, at

the micrometre scale of the microbial habitat (Chenu and Stotzky 2002). Several recently developed techniques have helped gain insight into the mechanisms by which the physical structure of soil regulates OM mineralisation. Microtomography helps estimate the size and shape of the pores and their degree of connectivity. Nanoscale secondary ion mass spectrometry (nanoSIMS) and synchrotron radiation [scanning transmission x-ray microscope (STXM) and near edge x-ray absorption fine structure (NEXAFS)] imaging can locate OM and microorganisms at the micrometre scale, while also providing chemical information complementary to that obtained through fluorescence microscopy studies of thin soil sections (Raynaud and Nunan 2014). It has been shown that OM-decomposer co-localisation accelerates biodegradation (Vieublé Gonod et al. 2003; Pinheiro et al. 2015; Don et al. 2013), while accessibility of OM to microbes might be a major driver of soil C dynamics (Dungait et al. 2012). This contact can occur by substrate and enzyme diffusion and advection, or via microorganism growth and mobility (Fig. 5). Furthermore, the local environmental conditions (oxygen, pH, water content, etc.) at the micrometre scale have to be favourable for microorganism activity. The soil structure controls biodegradation at the micrometre scale (Juarez et al. 2013). The mineralisation rates of simple substrates thus depend on the size of the pores in which they are located (Killham et al. 1993; Ruamps et al. 2011) and could be related to the different microbial communities present in these habitats (Hemkemeyer et al. 2015; Hatton et al. 2015).

In conclusion, by combining experimental approaches involving microcosms, isotopic labelling, 3D imaging and modelling, significant progress should be achieved in the coming years in understanding how the soil structure controls OM dynamics and incorporating these controls into models. Studies at fine spatial scales will be particularly useful to link

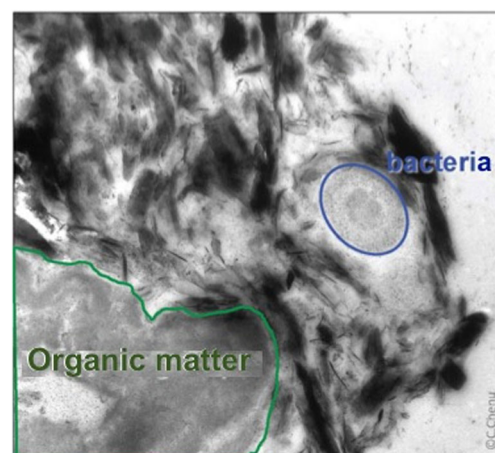


Fig. 5 Organic matter biodegradation requires direct contact between microorganisms or their extracellular enzymes and organic substrates, and local conditions favourable for microorganisms. This transmission electron microscopy image of a thin soil section shows that, even at the micrometric scale, microorganisms and organic materials can be physically separated (Chenu et al. 2014a)

C storage mechanisms to the soil C saturation concept, as discussed in the third part of this review (Section 4).

2.2.2 C stabilisation mechanisms involving organomineral interactions

Mineral protection of soil OM—an old story The idea that soil OM can be protected from the mineralising activity of microorganisms by soil minerals emerged more than 200 years ago (Thaer 1811 in Feller and Chenu 2012). This protection has been included in soil C dynamics models for over 70 years (Henin and Dupuis 1945). Smaller minerals, mainly contained in the clay particle-size fraction (less than 2 μm), most efficiently protect OM. This particle-size class consists of a variety of minerals: clay minerals (phyllosilicates), as well as different forms of metallic oxyhydroxides and poorly crystallised aluminosilicates (allophane or imogolite types). These finely divided minerals protect OM by adsorption (e.g. Jones and Edwards 1998) or by trapping OM within sub-micron aggregates, thus physically protecting it from the degrading action of soil microorganisms (Chenu and Plante 2006). The OM degradation rate is also decreased, and stabilisation increased, when organic molecules are located in parts of the pore network (neck diameter between 10 and 1000 nm) that are saturated with water, thus limiting oxygen and enzyme diffusion (Zimmerman et al. 2004; Chevallier et al. 2010).

Chemical interactions and heterogeneous soil OM distribution OM adsorption by soil minerals may derive from different types of interaction: anionic ligand exchange, cationic ligand exchange, cationic bridges or so-called weak interactions (including van der Waals forces, hydrogen bonding, hydrophobic interactions). The type of interactions involved depends on the mineral phases and OM chemical functions (von Lützow et al. 2006). Although theoretically these different types of interactions are expected, it is however very difficult to directly observe them in soil samples and to highlight any chemical specificity of organomineral interactions using current state-of-the-art techniques (Lutfalla 2015).

Moreover, direct observations on natural samples using microscopic techniques combined with increasingly powerful characterisation tools (atomic force microscopy, nanoSIMS, STXM–NEXAFS, etc.) showed that OM is adsorbed on mineral surfaces in the form of patches and does not cover the entire particle surface (e.g. Ransom et al. 1998; Chenu and Plante 2006; Remusat et al. 2012; Theng 2012; Rumpel et al. 2015). An isotopic labelling study further revealed that newly adsorbed OM preferentially binds to existing patches and not to free mineral surfaces (Vogel et al. 2014). These results suggest that the capacity of different minerals to protect OM would depend on their ability to adsorb a large number of patches. This could explain why the correlation between

specific mineral surfaces and their ability to protect OM is poor or nonexistent (Kögel-Knabner et al. 2008).

High importance of low-crystallised mineral forms and mineral weathering Andosol observations, chemical extraction results and fine-scale observations suggest that poorly crystallised mineral forms (pedogenic oxides and amorphous or slightly crystallised aluminosilicates) are particularly efficient in stabilising soil OM (Torn et al. 1997; Kleber et al. 2015). They complex soil organic compounds to form organomineral nano-complexes (noted here nanoCOMx), a few nanometres to a few hundreds of nanometres in size, which contain high C concentrations. They can be observed by direct transmission electron microscopy analysis (Wen et al. 2014). Close correlations between the metallic oxyhydroxide and C contents have been highlighted using indirect chemical extraction methods (Bruun et al. 2010; Mikutta et al. 2006), thus demonstrating the importance of nanoCOMx for soil OM stabilisation. NanoCOMx have mainly been studied in controlled conditions whereby they are synthesised by adsorption and co-precipitation (especially for Fe and Al) in batch experiments, but further research is needed on the identification and quantification of these mechanisms in soils (Kleber et al. 2015).

Andosols, which have a particularly high OM content, are the systems of choice for studying nanoCOMx formation in soils (Torn et al. 1997). The weathering of primary mineral phases produces partially crystallised phases (proto-imogolites), which complex the OM before reaching their final crystalline growth stages (imogolite and/or allophane). These proto-imogolite/OM interactions thus have a dual feedback effect: (1) they stabilise organic compounds over periods of up to several thousands of years (Basile-Doelsch et al. 2005), and (2) they stop crystal growth of the secondary mineral phases (Levard et al. 2012). Based on these mechanisms, a new conceptual model of soil OM stabilisation was proposed to highlight the synergy between the continuous alteration of minerals and nanoCOMx formation dynamics (Basile-Doelsch et al. 2015) (Fig. 6). The findings of some studies carried out on mineral surfaces tend to confirm this model (Bonneville et al. 2011; Kawano and Tomita 2001). Future research is needed to validate this model on various mineralogical phases in different soil types.

Finally, unlike crystallised minerals, the kinetics of alteration of poorly crystallised minerals in soils may span just a few years to decades, which is of the same order of magnitude as the time scales at which C dynamics are considered in the climate change context. Contrary to general opinion, OM mineralisation in organomineral complexes could well be due to destabilisation of mineral phases, which are no longer regarded as immutable at yearly to decadal timescales. Keiluweit et al. (2015b) showed, for example, that some oxalate type constituents of root exudates destabilised

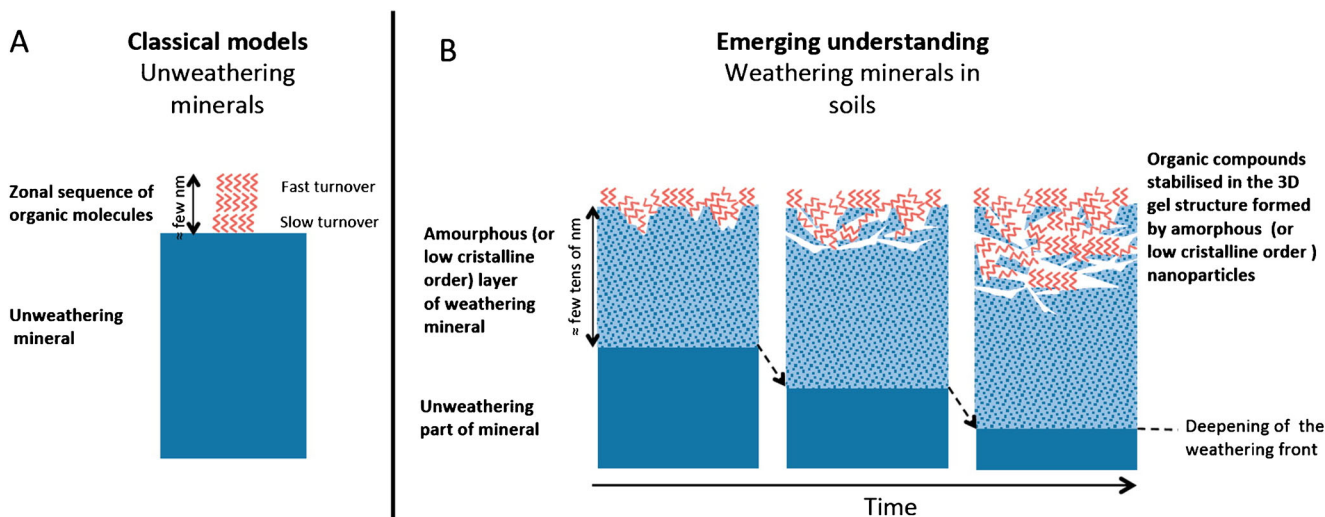


Fig. 6 Conceptual models of organomineral interactions differing with regard to the mineral surface properties. **a** In conventional models, organic compounds form a series of layers, and the turnover rate decreases when the molecule gets closer to the mineral surface. **b** The model proposed by Basile-Doelsch et al. (2015) considers that the

alteration of minerals generates nanometre amorphous minerals. Their high reactivity and specific surface area promote their interactions with organic compounds (excerpt from Basile-Doelsch et al. 2015, with permission of ACS Publications)

oxyhydroxide minerals and released initially complexed native OM. These compounds, which become accessible to microorganisms, may be mineralised. The destabilisation of nanoCOMx mineral components has also been shown in agricultural systems (Wen et al. 2014), and in some cases associated with substantial OM loss.

Until recently, analytical methods have not been effective to achieve sufficiently detailed characterisation of the organic component of organomineral complexes to highlight differences depending on the mineral phases to which they are associated. Future research on organomineral complexes will benefit from recent progress in analytical methods. To enhance integration of theoretical knowledge of these complexes, future studies on their formation and dynamics will have to move from the laboratory to the field in order to understand how these mechanisms are affected by agricultural practices.

3 Mechanisms of OM dynamics affected by agricultural practices

The soil C stock depends primarily on land-use patterns. For French soils, Martin et al. (2011) showed that the 0 to 30 cm mineral horizons contained on average 80 tC ha⁻¹ under forest and grassland, 50 tC ha⁻¹ under crops and 35 tC ha⁻¹ in vineyard soils (Table 1). Any land-use change therefore has a marked effect on the C stock. Meta-analyses on this subject have shown massive C loss following the cultivation of forests and grasslands. The meta-analysis of Guo and Gifford (2002), based on 74 publications, showed that soil C decreases when cropland replaces native forest (−42%) and pasture (−59%). It

also revealed a drop in C stocks from plantations to grassland (−10%) and from native forest to plantations (−13%). The rapid decrease in C stocks in cultivated soils can be explained by the generally lower C inputs (Lal et al. 2004) and faster OM mineralisation rates due to more intense tillage, which mixes deeper soil horizons and partly destroys the aggregation (Wei et al. 2014). However, soil C stocks increase after conversion from native forest to pasture (+8%), crop to pasture (19%), crop to plantation (+18%) or crop to secondary forest (+53%) (Guo and Gifford 2002). Observations by Attard et al. (2016) showed the asymmetry of the mechanisms: the loss of organic C stocks after cultivation of grassland soil was fast while the replenishment of these stocks was slow because it depends on the slow installation and growth of plant roots in the previously cultivated soil. Furthermore, recent observations showed that C stock evolution related to land-use changes are mediated by soil parent material (Barré et al. 2017): the differences in soil C stocks between old forests and croplands were higher on calcareous bedrocks than on loess deposits.

Operationally, these results concerning the impacts of land-use changes on soil C stocks underline the fact that the spatial patterns of land-use or rotations must be considered with caution. However, soil C stocks also depend on the agricultural practices implemented, which determine the input and output C fluxes in soils, depending on soil and climatic conditions. The following section identifies the main agricultural practices and examines their impact on the soil C stock.

3.1 Review of the main agricultural practices

Various management operations (Table 1) can be implemented depending on the land use. The following categories can be

Table 1 Specificities of different types of land use (non-exhaustive list) in metropolitan France (croplands, urban gardens, grasslands, vineyards, forests and agroforestry systems) in terms of C content, soil and climatic conditions, vegetation, soil structure, residue management, exogenous organic matter inputs and other practices, and their spatiotemporal variability [compiled on the basis of interviews with a dozen professionals working at the crossroad between academia and agriculture (agricultural technical institutes, French National Forestry Office, etc.)]

	Forests	Grasslands	Agroforestry	Croplands	Vineyards	Urban gardens
Average stocks (tC ha^{-1} of 0–30 cm, Martin et al. 2011)	80	80	Not mentioned	50	35	Variable
C contents (g kg^{-1} soil, Joinel et al. 2016)	33.83 [1.48–159]	29.82 [4.49–243]		16.92 [2.57–58.20]	11.21 [3.41–39.3]	28.15 [9.79–59.30]
Average [min–max]						
Soil and climatic conditions	Poor acidic soils, sometimes flooded	Eventually soils on slopes, diversity of climates	Diverse	Marked human action	Often basic soil and warm climates	Strong artificialisation
Plant species		High biodiversity, including legumes	Avoid competition between tree species and crops	Low biodiversity	Potentially grass bands in the ranks	Aesthetic criterion
Residue management	Depends on export of harvest residues (branches <7 cm in diameter)	Depends on grazing and mowing intensity	Export of wood biomass (except leaves) and crops, residues are sometimes returned to the soil	Export of harvest, residues are sometimes returned to the soil	Leaves and crushed shoots eventually returned to the soil	Export of fallen leaves and mowing lawns
Exogenous OM inputs		Manure	Eventually	Contribution of exogenous OM from urban area, or manure	No exogenous input	Large inputs of exogenous OM from urban origin
Practices modifying soil physical structure	Stump and eventual tillage when planting, compaction after heavy engine traffic at thinning (every 10 years approximately)	Often aggregated structure, sometimes tillage	Tillage or no-tillage in tree rows	Tillage or no-tillage	Soil scratching, eventually decompaction	Packed, waterproof, volumes constrained by the pipe network
Other practices	Fertilisation rarely practiced, amendment if trees decline	Fertilisation, irrigation, associations with legumes	Fertilisation, irrigation, inorganic amendment, pesticides			
Temporal specificity	Forest revolution, about 60–200 years	Sometimes leys	C dynamics must be rationalised according to forest revolution duration	Annual crops, sometimes intermediate crops		Rapidly changing physical and chemical properties
Spatial heterogeneity	Related to root distribution, organic surface horizon	Especially related to grazing intensity	Lines of trees on grass bands	Eventually hedges and grass bands	Vine rows and eventually grass inter-rows	Very heterogeneous, alignment of trees, fragmented, discontinuous

distinguished: choice of plant species, vegetation density, plant export intensity (crop residues returned to the soil or exported, grazing/mowing of grasslands, export of harvest residues in forest ecosystems, etc.), addition of exogenous OM, irrigation, fertilisation, tillage, etc. These practices mainly control the spatiotemporal distribution of OM inputs to soil, along with the sensitivity of OM to mineralisation, both of which affect soil OM stocks (Jastrow et al. 2007).

Choice of plant species The choice of plant species has an effect on the chemical quality of soil OM (Rumpel et al. 2009; Armas-Herrera et al. 2016) and modifies the processes governing the dynamics of soil organic C. In forests, for example, although aboveground litter production is similar for softwood and hardwood trees, the litter degradation mechanisms differ (Berg and Ekbohm 1991; Osono and Takeda 2006). In deciduous forest, litter generally decomposes faster and the residues are more deeply incorporated in the soil profile because of the biochemical properties of their tissues and their impact on the soil chemistry, thus impacting, for example, the presence and activity of earthworms (Augusto et al. 2015). As noted above (Section 2.1.2), these organisms have a strong influence on soil OM dynamics. In grasslands, legume–grass associations promote soil C storage (Li et al. 2016). In agricultural systems, varieties allocating more resources to the harvested part (grain) are often selected to increase yields. This selection decreases the biomass allocated to vegetative parts, including roots which contribute more than other plant organs to the intermediate OM pool (Section 2.1.1).

Soil OM inputs The intensity of plant harvesting for plantation management directly impacts plant-derived soil OM inputs (leaf litter, crop residues, roots, etc.). In grasslands, these inputs depend on the number of grazing animals and the mowing frequency (Conant et al. 2001); in agricultural systems, on crop residue export (Saffih-Hdadi and Mary 2008); in forests, on the thinning regime and the exportation of branches of less than 7 cm diameter (called harvest residues) (Jandl et al. 2006); inputs in urban soils depend on the mowing frequency in parks and on the removal of fallen leaves (Qian and Follett

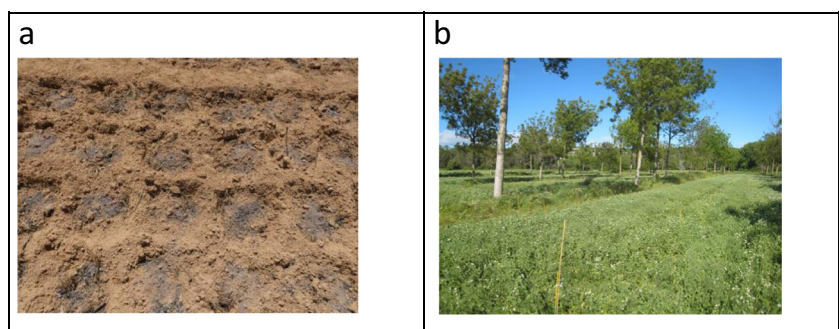
2002; Lal and Augustin 2011). Exogenous OM is sometimes added to reduce chemical input and to recycle waste. Exogenous OM may be animal manure (Chotte et al. 2013), compost or sewage sludge (Hargreaves et al. 2008; Lashermes et al. 2009), or pyrogenic residues (biochar) (Steiner et al. 2007; Andrew et al. 2013).

The frequency and spatial distribution/localisation of soil OM inputs differ amongst land uses. It is assumed that vegetation cover present throughout the year increases soil OM inputs, as it is the case for permanent grassland, under grass bands or when intermediate crops are cultivated during the winter season. C dynamics in soils under ley grasslands show a legacy grassland effect during cropping years, leading to longer residence times of C in their fine fractions compared to continuously cropped soils (Panettieri et al. 2017). Soil OM inputs in forests are also a function of the age of trees at cutting (input of younger trees being lower than input of older ones). Spatially, the distribution of plant inputs may be modulated (Fig. 7) by seeding (or planting) density, by the localised addition of composts, by planting of grass bands in vineyards, by growing hedges in croplands or rows of trees in agroforestry systems or by aesthetic management of parks and gardens in urban areas (Freschet et al. 2008; Strohbach et al. 2012; Kulak et al. 2013; Cardinael et al. 2015).

These practices can increase the quantities of C added to the soil, but the extent to which they also affect C stabilisation mechanisms is unclear. Additional soil OM mineralisation can, for example, be observed following a fresh OM input (see the priming effect paragraph, Section 2.1.1).

Practices that stimulate both primary production and decomposer activity Tillage, soil decompaction after heavy machinery passages or removal of stumps after clear-cutting a forest stand are also practices that impact not only primary production and soil OM inputs but also OM mineralisation and therefore soil to atmosphere C fluxes. These operations affect soil properties, likely including its structure, decomposer activity (Lienhard et al. 2013) and consequently soil organic C stocks (see Section 2). Primary production and decomposer activity are also impacted by facilities for soil and water conservation in dry areas, by the use of inorganic amendments or

Fig. 7 The spatial distribution of organic matter can be modulated by localised compost inputs (**a** Madagascar) or by setting up rows of trees in the plots (**b** Agroforestry, Melle, France). Source: T Chevallier and R Cardinael



by systematic fertilisation in some cropping regions or in urban gardens (Miller et al. 2005; Edmondson et al. 2012). However, for economic reasons, fertilisation practices are very limited in forests or in poor agricultural areas.

3.2 Impact of agricultural practices on soil organic C storage

French experimental field studies on long-term variations in soil C stocks Numerous studies have already been conducted on the effects of agricultural practices on soil C storage. We present the results of three recently published experiments located in France spanning decadal to multi-decadal periods. One study concerns forests under conventional management, while two were focused on large-scale cropping systems with exogenous OM amendments or reduced tillage.

Changes in C stocks in forest soils were monitored in the French Permanent Plot Network for the Monitoring of Forest Ecosystems (RENECOFOR) by repeated measurements in 102 plots managed by the French National Forestry Office at 15-year intervals (Jonard et al. 2017). The observations revealed an average annual increase in C stock of $0.34 \text{ t ha}^{-1} \text{ year}^{-1}$. This precisely corresponds to a 4‰ annual increase (average stocks in litter and in the top 40 cm soil horizon were 81.6 tC ha^{-1} = $0.34/81.6 = 0.004$). The stock increase was larger in coniferous than in deciduous forests (Jonard et al. 2017) and was not linked to increased aboveground inputs. Weak links were noted with the litter quality (C/N), the history and management of the stand (regular vs. irregular forests).

The effects of the addition of exogenous OM were studied in the Qualiagro long-term field experiment, located at Feucherolles, near Paris (France). Various composts and manures were applied at a rate of 4 t ha^{-1} every other year. The soil C contents, measured every other year for 15 years, showed significant C accumulation, i.e. $0.20\text{--}0.50 \text{ tC ha}^{-1} \text{ year}^{-1}$ for soil amended with manure and urban compost (Peltre et al. 2012). These organic amendments thus had a positive effect on C storage, in addition to economic and agronomic benefits (improvement of soil fertility and physical structure). However, negative effects were observed, particularly related to fluxes of elements other than C. Organic amendments often contain large quantities of N and P, thus inducing a risk of over-fertilisation, N_2O emission and NH_3 volatilisation. Organic amendments also present a risk associated with the organic contaminants, metal contaminants or pathogens that they may contain (Smith 2009). It is necessary to better characterise the OM input, the reversibility of its accumulation and effects on the dynamics of other elements (N, P, etc.) in order to better understand and predict the positive and negative effects of waste-derived organic amendments (Noirot-Cosson et al. 2016).

The long-term effects of tillage were studied for 41 years in a large-scale cropping area in the Paris Basin (Boigneville) (Dimassi et al. 2014). In this field experiment, no significant

effects of tillage or crop management were observed on C stocks over 41 years. Reducing tillage, however, resulted in rapid soil C accumulation in the first 4 years, and then the C stocks only slightly changed over the next 24 years ($+2.17 \text{ tC ha}^{-1}$ with reduced tillage, $+1.31 \text{ tC ha}^{-1}$ with no tillage), but additional stored C was later lost (Dimassi et al. 2014). The lack of ploughing caused soil OM stratification and changes in soil functioning, nutrient availability, soil water holding capacity, microbial diversity, the amount of fresh C incorporated in the soil and, accordingly, the priming effect. The water regime could be the determining factor of C storage/destocking in these situations. OM mineralisation was favoured during wet years or when the soils were irrigated, particularly at the surface where the majority of C accumulated when ploughing was stopped. Conversely, C accumulated during dry years. As already suggested by Balesdent et al. (2000), this study highlighted the importance of identifying, quantifying and classifying the different mechanisms according to the soil and climatic conditions in order to be able to model and predict soil organic C stocks under different agricultural and forestry practices.

Meta-analyses Meta-analyses are useful for comparing results obtained in various long-term studies in similar experimental fields to determine whether the processes triggered by a specific agricultural practice are widespread. Hereafter, we present some examples of recently published meta-analyses on the impacts of irrigation (Zhou et al. 2016), tillage (Virto et al. 2012), liming (Paradelo et al. 2015) and fertilisation (Han et al. 2016; Yue et al. 2016) on soil C stocks.

The findings of a meta-analysis by Zhou et al. (2016) suggested that the water availability changed the plant C allocation and the soil OM turnover. Drought led to an increase in the root/shoot ratio and a decrease in heterotrophic soil respiration, while irrigation led to an increase in soil respiration but also to higher biomass inputs.

Regarding soil tillage, the meta-analysis of Virto et al. (2012) shows the same trends as the long-term observation by Dimassi et al. (2014). No-tillage had little effect on the soil organic C stocks (see also Luo et al. 2010). However, secondary practices of no-till cropping systems (implemented to offset the lack of tillage, as the choice of cropped species and the number of rotations) showed positive effects on C storage (Virto et al. 2012).

Paradelo et al. (2015) reviewed the results of 29 studies considering the effects of liming on soil C stocks. Their meta-analysis did not reveal an unambiguous effect of liming on C storage. The compiled studies had been carried out under a wide range of experimental conditions. Moreover, they did not allow quantification of the three key processes driving the dynamics of organic C in soils affected by liming: crop

production, decomposer activity and soil structure (see Section 2).

Yue et al. (2016) compared 60 studies on the impact of N inputs on C stocks. Their meta-analysis highlighted an increase in soil C inputs and no change in output fluxes related to increased N inputs. Regarding organic C stocks, the results showed an increase in C in the organic horizons and the soil solution, but no change in the C stock in the mineral soil horizons, contrary to the findings of the meta-analysis on forest soils conducted by Janssens et al. (2010). However, meta-analyses average the results obtained in different contexts and with different timescales, which may overlook effects that could be observed at a given site. The meta-analysis of Han et al. (2016) confirmed the results of Yue et al. (2016). If fertilisation is complemented by organic amendments, then the increase in C stocks would be even higher since organic amendments directly contribute to soil OM stocks.

In conclusion, due to the lack of knowledge on the mechanisms impacted by agricultural practices, it is hard to predict their effects on soil C stocks. Agricultural practices, which increase soil OM inputs, are often considered to have a positive impact on C storage (Pellerin et al. 2013; Chenu et al. 2014b; Paustian et al. 2016). However, their impact on mechanisms that contribute to the storage/destocking of soil C (see Section 2) are not yet clearly understood. Meta-analyses and long-term field studies showed that the relative intensity of mechanisms contributing to storage and those contributing to destocking may change over time. These studies also showed that it is essential to understand how the soil and climatic conditions modulate soil organic C stabilisation mechanisms.

In addition, while considering practices in terms of the C cycle and increased soil C stocks, the importance of interactions with cycles of other nutrients present in OM (N, P, S, etc.) should not be overlooked. Finally, regardless of the land use, it should be kept in mind that the main challenge for all agricultural stakeholders is to ensure a production level that will provide enough food in the context of world population growth and sufficient income for farmers, while maintaining employment. Preserving or increasing OM stocks are also levers with regard to these issues (Manlay et al. 2016).

4 How could a better accounting of OM stabilisation mechanisms improve the prediction of soil organic C stock evolution?

Working at the scale of mechanisms often implies working at fine spatial scales (mm– μm), only assessing the potential role of specific mechanisms and studying them in specific conditions (laboratory experiments or experiments in specific soil and climatic conditions). Predicting changes in the soil organic C stock through the understanding of mechanisms raises at

least two crucial related issues that will be discussed in this section: (1) upscaling (from μm^3 to dm^3 and then to the plot, landscape and global scale) and (2) validation (from the potential action of a mechanism to its quantitative expression in different soil and climatic contexts). Regarding the upscaling issue, there are at least three possibilities: (1) finding an indicator that describes one or more mechanisms, (2) introducing more mechanisms in soil organic C dynamics models (RothC or Century types) or (3) identifying variables measured at the microscopic scale that allow, through appropriate modelling, prediction of macroscopic trends. Each of these approaches must then be validated on suitable datasets (Fig. 8).

4.1 Finding indicators to improve prediction of changes in soil organic C stocks

Several indicators have or could be developed to improve the prediction of soil organic C stocks, particularly in a context of land use and practice changes (see IPCC 2006, detailing the method currently used to estimate changes in soil C stocks).

The most currently discussed indicator is probably the C saturation deficit. Hassink (1997) proposed that the proportion of the fine fraction ($<20\ \mu\text{m}$) of a soil implies an upper limit to its capacity to store stable C. This theoretical limit can be calculated (C_{sat}) by particle-size measurements ($C_{\text{sat}} = 4.09 + 0.37 \times (\text{clay} + \text{fine silt})$) (Hassink 1997). Sequestration by the fine fraction is due to the physical and physicochemical protection provided by finely divided minerals (see Section 2.2.2). The C saturation deficit is obtained by subtracting this theoretical C_{sat} value from the actual OM concentration in the fine fraction of the soil. This indicator has recently been used to draw the first map of the potential of organic C storage in the fine fraction in the 0–30 cm horizon of French soils (Angers et al. 2011). However, this indicator of the potential gain of soil organic C has so far never been validated and its relevance for predicting C stock patterns consecutive to a change in land use or farming practices remains to be evaluated (O'Rourke et al. 2015).

Another approach, somewhat similar to that of Hassink (1997), was proposed to assess French soil C storage capacity. Rémy and Marin-Laflèche (1974) defined some benchmark OM levels according to clay and carbonate soil contents. Roussel et al. (2001) used this chart to estimate the OM deficit compared to the benchmark OM contents for French soils. The authors thus subtracted OM contents referenced in the French Soil Analysis Database (BDAT) from the benchmark OM contents listed on the chart proposed by Rémy and Marin-Laflèche (1974). However, the link between the potential of OM gain and the OM deficit calculated using the Rémy and Marin-Laflèche (1974) chart remains to be validated and the area of validity of this chart is still an open issue (Roussel et al. 2001).

Conversely, indicators of the risk of soil organic C loss could be developed. For example, C in a soil with a high

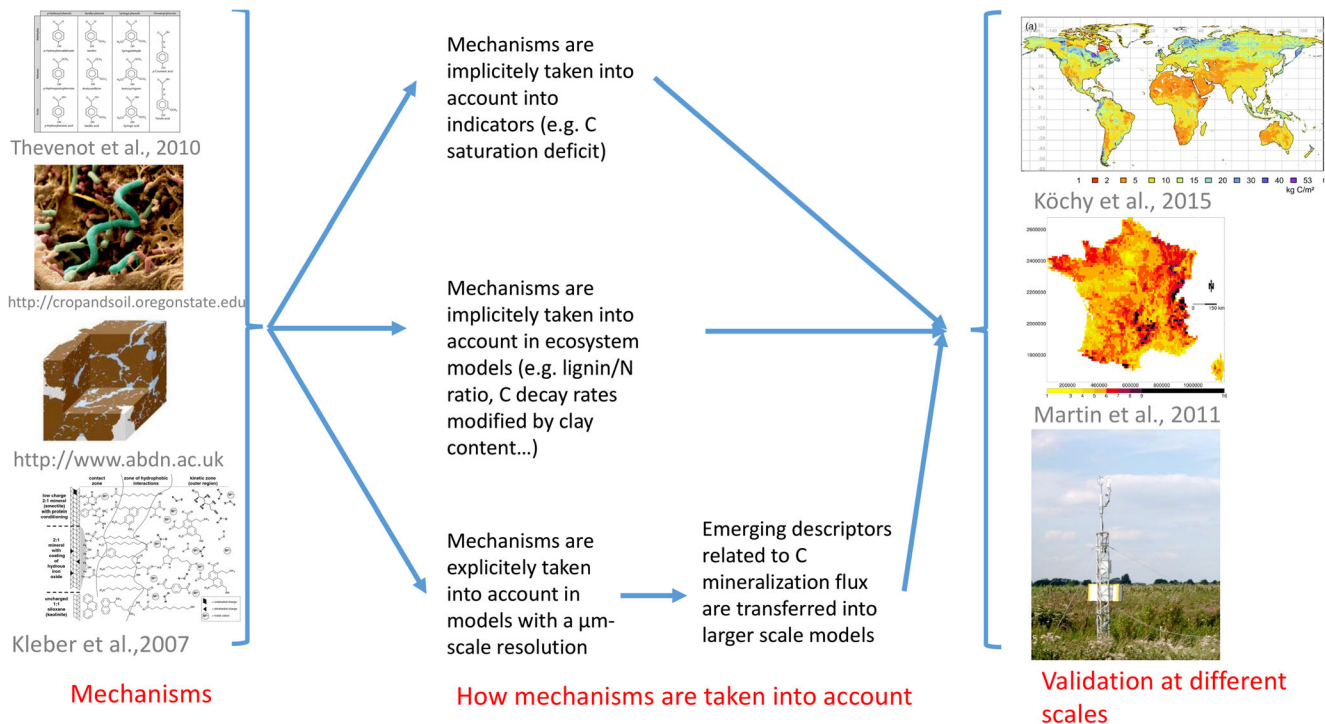


Fig. 8 From the identification of stabilisation mechanisms to their effective consideration to improve the prediction of soil organic C stock evolution

particulate OM content may be more rapidly lost compared to C in a soil that has a greater portion of C associated with the mineral matrix (Arrouays 1994; Jolivet et al. 2003). Particulate OM contents, which are easily measured by standardised methods, could thus be an indicator of the potential for soil C loss. Other studies suggest that the biogeochemical stability of C might be connected to its thermal stability (Plante et al. 2011; Saenger et al. 2013, 2015; Barré et al. 2016). In this case, thermal measurements could serve as a proxy for assessing the amount of organic C that may be lost following a land use or cropping practice change. Using thermal measurements to assess the C sequestration potential could also be considered.

Other indicators based on biotic mechanisms of soil organic C sequestration (see Section 2.1) could probably be used, such as the bacteria/fungi ratio or indicators based on soil fauna, vegetation or litter layer. Soil type and mineralogy are also potential relevant indicators (Mathieu et al. 2015; Khomo et al. 2016). It should be kept in mind that the measurement of these indicators should be rapid and inexpensive to enable them to be tested in a large variety of soil and climatic contexts. Finally, the indicator necessarily represents the sequestration mechanisms in partial and degraded form, but its predictive value will only be satisfactory if it has a sound scientific basis and has been subject to a specific validation process. These conditions have currently not been met for any indicator, thus broadening the prospects for research, validation and implementation of such indicators of soil C stock changes. In

addition, selecting relevant indicators for C storage initiatives is still a complicated task. Indeed, indicators could trace the C storage potential of soils (like those described above) or other variables such as the storage rate, input fluxes, average mineralisation rate, mean residence time in soil, etc.

4.2 Better integration of OM stabilisation mechanisms in large-scale C dynamics models

The prediction of the evolution of C stocks by Earth-system models is very uncertain (e.g. Friedlingstein et al. 2006). A comparison of Earth-system models showed, for a given anthropogenic GHG emission change scenario, that these models can predict a soil organic C stock evolutionary pattern for the twenty-first century ranging from -50 to $+300$ GtC (Eglin et al. 2010). The difference between the extremes of the predicted values corresponds to about 40% of the current atmospheric C stock. A better prediction of the evolution of the atmospheric CO_2 concentration is crucial to reduce uncertainties about soil C stock changes. Soil C stabilisation mechanisms are not yet taken into sufficient consideration in large-scale models (Luo et al. 2016). In particular, biological regulation (macrofauna, microorganisms) and soil structure (Wieder et al. 2015) are barely taken into account in these models despite the fact that they are major drivers of soil C dynamics, as noted above (see Section 2).

Furthermore, most of these models fail to reproduce the interactions between primary production and organic C

residence time in soils. These two variables control the amount of C stored in soils, but independently (Todd-Brown et al. 2013). However, explicitly integrating stabilisation mechanisms into these models is a difficult task. We must first find a suitable mathematical formalism to describe the mechanism to be added, incorporate it into the model and test whether the model performance has actually been improved.

By this approach, various studies have been aimed at introducing the priming effect in C dynamics models (Guenet et al. 2013; Perveen et al. 2014). An equation describing the soil OM mineralisation rate as a function of the fresh OM content, proposed by Wutzler and Reichstein (2008) and adapted by Guenet et al. (2013), was introduced in the ORCHIDEE model. This function actually improved the performance of the model for representing incubation data from laboratory experiments. Simulations based on various scenarios highlighted that soil storage capacities predicted by the two versions of the model could differ by up to 12 GtC (i.e. 0.8 tC ha⁻¹) for the twenty-first century (Guenet et al. *submitted*).

The explicit representation of all sequestration mechanisms in Earth-system models is not yet possible since it would necessitate excessively long calculation times and since the equations needed to describe many mechanisms have yet to be accurately formulated. They could however be quickly improved by increasing the number of comparisons between statistical and mechanistic models and by testing the mechanistic models on databases that exist or are under development.

However, the lack of precise data still hampers the use and improvement of models, especially at large spatial scales and in the vertical profile (Mathieu et al. 2015; He et al. 2016; Balesdent et al., *in press*). There are indeed very strong uncertainties with regard to C stock estimates and the input data of these models (soil parameters, land use, C inputs, etc.). The progress achieved in the GlobalSoilMap project in developing well-resolved global maps of soil characteristics (Arrouays et al. 2014) is also essential for improving the representation of sequestration mechanisms in Earth-system models.

4.3 Modelling OM mineralisation at the micro-scale could help describing macroscopic C fluxes

Another approach is to precisely describe soil OM mineralisation in micro-scale models and investigate how these models could usefully fuel C dynamics models operating at larger scales (plot, landscape, global). For example, a few models have emerged during the past decade, explicitly describing the functioning of soil micro-organisms in interaction with their substrates, their environment and soil OM (Schimel and Weintraub 2003; Fontaine and Barot 2005; Moorhead and Sinsabaugh 2006; Allison 2012). Some of these models include the representation of several functional groups of microorganisms (e.g. copiotrophic and oligotrophic categories) with

homogeneous ecological functioning features. These new models including microbial processes are more consistent with the actual processes and can be more generally applied for various environmental situations. However, they are more complex, often theoretical and not calibrated (Guisan and Zimmermann 2000). One current challenge is to improve their predictive accuracy by testing them on suitable experimental observations (Schmidt et al. 2011). This requires research conducted on various scales (populations, communities, ecosystems) to (1) prioritize key factors for predicting soil C dynamics and interactions with nutrient cycles, and (2) integrate robust and simplified functions in larger scale models.

A new generation of mechanistic models has also emerged that take the effects of the soil physical structure on the activity of decomposers and on C mineralisation into account. These models include an explicit 2D or 3D description of the pore network based on computer tomography images (Monga et al. 2008, 2014; Falconer et al. 2007, 2015; Pajor et al. 2010; Resat et al. 2012; Vogel et al. 2015). They operate over short time scales and have been validated for simplified systems. These models should facilitate the classification of variables controlling C dynamics in order to define soil structure descriptors other than those currently used in models at the plot scale so as to improve them.

An effective strategy could be to use emerging properties from micro-scale models that explicitly take fine-scale soil heterogeneity into account to fuel ecosystem models. Otherwise, simplified versions of fine-scale models that capture fine-scale soil heterogeneity could be designed and integrated in ecosystem models. However, such upscaling from micrometre to plot and then global scales is a difficult task spanning a vast field of research.

4.4 Data needed to constrain various approaches to enhance prediction of soil C stock evolution patterns

Irrespective of the approach used to connect the stabilisation mechanisms to the evolution of soil C stocks, the predictions must be compared to field data. Changes in C stocks are hard to detect in the short term (<10 years), which is a methodological challenge for the implementation of the 4 per 1000 programme. The detection of changes in soil C stocks currently involves repeated analyses over time in long-term field studies (Fornara et al. 2011) or chronosequences (Pöplau et al. 2011). In addition, to assess whether predictions of a particular approach could be generalised, it would be useful to compare the predictions to data collected for different plant covers in various soil and climatic contexts. As such, networks of long-term field experiments and soil monitoring programmes mentioned above (Section 3) are particularly useful. For instance, at sites equipped with flux towers, C stocks, soil

properties and site management history are monitored, in addition to ecosystem to atmosphere gas fluxes. Many such sites have been developed in recent years, and there are currently about 600 worldwide for a variety of ecosystems, thus enabling relevant data synthesis. For example, a recent study evaluated changes in primary production in grasslands according to the nitrogen fertilisation and climate (annual rainfall and temperature) conditions (Gilmanov et al. 2010; Soussana et al. 2010), while also assessing organic C sequestration in grassland soils according to the nitrogen fertilisation, harvested biomass (agricultural practices) and soil and weather conditions. Other syntheses of data from flux tower sites showed that the C balances were instead controlled by management practices in young forests and by climate variations in mature forests (Kowalski et al. 2004). Soil organic C storage was found to increase with the number of days of plant growth (Granier et al. 2000).

Another interesting example is the use of Free-Air CO₂ Enrichment experimental systems, which artificially increase the atmospheric CO₂ concentration. Such experiments have been developed for several years now and have generated essential information on the response of ecosystems to increased atmospheric CO₂ concentrations (Ainsworth and Long 2005). Regarding the soil, they have shown that C stock increases when nitrogen is available and does not vary when nitrogen is limiting, despite increased input via litter production (Hungate et al. 2009). These data were compared with large-scale model outputs for different output variables (Walker et al. 2015).

Networks of sites thus enable us to estimate the importance of stabilisation mechanisms for C storage, to classify them (by exploring databases) and to validate approaches designed to improve prediction of soil C stock evolutionary patterns. However, changes in soil C stocks are often not observable for several years after a change—this key factor highlights the fact that such sites must absolutely be maintained in the long term.

In conclusion, enhanced integration of soil OM stabilisation mechanisms in models to improve predictions of the evolution of soil C stocks is not easy. Several approaches could be proposed, each with their positive and negative features. Building soil C storage indicators based on mechanisms is the simplest approach, but they may have very limited predictive value if they have a weak scientific basis due to the excessive uncertainty level. Finding a suitable and robust formalism to incorporate the mechanisms in large-scale models is often a major research challenge in itself. Linking stabilisation mechanisms and modelling of soil C stock dynamics requires collaboration of scientific communities conducting research on mechanisms and modelling—this is the only way to accurately assess medium- and long-term variations in soil organic C stocks in a changing environment.

5 Conclusion

The currently favoured solution of the 4 per 1000 initiative to increase soil C stocks is to increase soil C input fluxes through management practices adapted to local conditions. These practices not only influence soil C inputs but also soil C stabilisation and destabilisation mechanisms and therefore soil C outputs.

Recent studies have improved the overall understanding of biotic and abiotic mechanisms involved in soil organic C stabilisation/destabilisation. Belowground plant contributions have a major role in soil C storage/destocking. Contrary to aboveground litter that might be quickly mineralised, root inputs could greatly contribute to C inputs that may be stabilised in soils, although they may also induce over-mineralisation of native OM, especially when nutrient resources are limited. Plant residues supply intermediate and labile soil C pools, and, through their chemical composition, control their dynamics. They also indirectly act on the stable C pool by promoting aggregate formation through roots and mycorrhizal associations. Microorganisms and soil fauna have a central role in soil C storage/destocking mechanisms because they consume and transform OM. Their metabolic activity produces CO₂ and CH₄ (destocking) when they consume applied (exogenous) and native (endogenous) OM. However, the action of soil organisms is generally considered to produce secondary compounds that ultimately contribute to soil C stabilisation, either via their chemical recalcitrance or via the interactions they establish with mineral soil ions and surfaces. Soil organisms are also essential for nutrient recycling, and preserving ecosystem balance and biodiversity. All of these co-benefits tend to indicate that soils with high biological activity have a higher C storage potential. However, their management requires increased knowledge on the interacting mechanisms and is more operationally difficult. The 4 per 1000 initiative will have to consider these antagonist biotic mechanisms in its recommendations in order to balance higher soil C stabilization with respect to C mineralisation.

The action of decomposers on OM depends on the arrangement between particles (inorganic and organic) and on the network of pores in which the fluids, decomposers and their enzymes circulate. Recent studies have also highlighted the central role of mineral phases in protecting OM. However, it appears that all mineral surfaces do not have the same ability to protect organic compounds and that organomineral complexes evolve over time due to weathering processes. Recently developed tools should lead to significant progress in the understanding and modelling of the influence of the soil matrix structure on soil C storage/destocking.

The effects of OM stabilisation mechanisms must be studied throughout the soil profile, including deep soil horizons (up to parent material), since plant root systems have a very high impact. C dynamics models should

therefore not be limited to the soil surface since deep soils are also impacted by agricultural practices and land-use patterns. These models should try to find indicators that explicitly take the different soil compartments into account and no longer consider the microbial component as a 'black box', while also considering the soil fauna. Research on the validation of indicators of these mechanisms is essential in order to take the complexity of the equation involving biological factors, physical interactions, soil and climate conditions, land-use patterns, practices and management into account.

This review highlighted three essential needs for future research on soil C storage: long-term monitoring of experimental sites; reliable and precisely resolved data (soil parameters, land-use patterns and practices), particularly at large spatial scales; and multidisciplinary interactions between researchers in the fields of soil science and ecology. Indeed, although the different mechanisms are often studied separately, they should be studied together as they are related. These complex interactions drive C dynamics. Finally, it is crucial to strengthen interactions between operational and academic communities in order to accurately identify the challenges that still need to be addressed to enhance the overall understanding of the impact of agricultural practices on soil C storage, to disseminate new knowledge and translate it into practical recommendations.

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