Reviews and syntheses: The mechanisms underlying carbon storage in soil

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Abstract. Scientific research in the 21st century has considerably improved our knowledge of soil organic matter and its dynamics, particularly under the pressure of the global disruption of the carbon cycle. This paper reviews the processes that control C dynamics in soil, the representation of these processes over time, and their dependence on variations in major biotic and abiotic factors. The most recent advances in soil organic matter knowledge are:

- Most organic matter is composed of small molecules, derived from living organisms, without transformation via additional abiotic organic polymerization.

- Microbial compounds are predominant in the long term.

- Primary belowground production contributes more to organic matter than aboveground inputs.

- Contribution of less biodegradable compounds to soil organic matter is low in the long term.

- Two major factors determine the soil organic carbon production 'yield' from the initial substrates: the yield of carbon used by microorganisms and the association with minerals, particularly poorly crystallized minerals, which stabilize microbial compounds.

- Interactions between plants and microorganisms and between microbial communities affect or even regulate carbon residence times, and therefore carbon stocks.

Farming practices therefore affect soil C stocks not only through carbon inputs but also via their effect on microbial and organomineral interactions.

1   Introduction

Increasing organic carbon stocks in agricultural soils has emerged as an effective means to improve soils and increase plant productivity, delay the rise of atmospheric carbon dioxide and the rate of climate change, while maintaining the quality of downstream ecosystems. The recent spotlight of the climate change issue has considerably renewed scientific interest on soil organic carbon, which is now seen as a main compartment of the global C cycle, thus providing opportunities for mitigation. In this context, the "4 per 1000 initiative: soils for food security and climate" was launched in 2015. Considering that the total amount of organic carbon in soils at the global scale is about 2400 Gt of C, and that anthropogenic CO_2 emissions

30   are about 9.4 Gt C per year, a simple calculation suggests that an annual 4 per 1000 increase in the soil C stock could theoretically offset annual emissions (2400*0.04=9.6) (Minasny et al., 2017). Meanwhile, this initiative has given rise to a scientific controversy (Amundson and Biardeau, 2018, 2019; van Groenigen et al., 2017; de Vries, 2018; Baveye et al., 2018; VandenBygaart, 2018; White et al., 2018) Most of the criticism is focused on the political opportunity of the initiative, as well as on the calculation itself, which is based on several assumptions, some of which are actually highly debatable (e.g. the soil

35   depth to be considered). Other comments or questions have been more related to the processes underlying soil C storage: is there an upper limit to C storage in soils? What is the expected residence time of this carbon after its incorporation in soils? Is it possible to store more carbon without additional N and P inputs? Although substantial scientific knowledge exists on soil carbon dynamics, some controversy remains on these questions because recent findings are not always considered, or because of misuse of some of the concepts (e.g. confusion between soil C equilibrium and soil C saturation). Moreover, current soil C

40   stocks are spatially highly variable, and factors that could explain this variability are not fully understood, although it would be essential to clarify this aspect prior to any attempt to increase soil C stocks. Last but not least, questions remain about farming practices which could potentially increase carbon stocks. Apart from practices based on additional C inputs, there is no consensus on those based on other strategies, such as reduced tillage (Angers and Eriksen-Hamel, 2008; Dimassi et al., 2013; Dimassi et al., 2014; Haddaway et al., 2017; Luo et al., 2010; Virto et al., 2012). The gap between agronomic trials and

45   scientific knowledge on soil C dynamics is partly responsible for this limited understanding of interactions underlying the effects of farming practices on soil C stocks. In order to foster progress in this area and facilitate a proper interpretation of experimental results, this paper aims to provide a comprehensive and up-to-date review of processes that control the soil C dynamics, a representation of these processes over time, and their response to variations in major biotic and abiotic factors.

2   Main processes controlling the C stock and its dynamics in soils

50   Soil organic carbon (Figure 1) is distributed vertically with a strong concentration gradient decreasing from surface to depth: from 400 mg/g in organic "O" horizons at the soil surface, nearly 100 mg/g in the first cm of the organomineral horizon, and down to concentrations averaging less than 5 mg/g at 1 m depth. It has a wide range of ages, from a few days to several thousand years old (Figure 1). The soil carbon stock is the sum of what remains of each past annual input. It therefore depends on incoming carbon fluxes, biotransformations and stabilization duration, prior to the release of this element from the soil,

55   mainly in the form of CO_2 produced by decomposers' respiration. The main processes that regulate organic matter (OM) dynamics in soils are summarized in Figure 2.

2.1   Carbon inputs into soil: nature and fluxes

Organic matter entering the soil system is synthesized by higher plants. It reaches the soil through the roots (dead roots or root exudates) or in the form of shoot litter and via the restitution of unharvested aboveground plant parts. The soil carbon input

60   flux is the net primary production of the ecosystem minus the exported production, herbivore production and respiration. The

harvested primary production is transformed and some of it can subsequently be transferred to other soils as animal effluents (manure and slurry), or effluents and waste products from human activities (sewage sludge, compost from various sources, etc.).

2.1.1 Above- and below-ground input fluxes

65 The estimators of soil restitution fluxes are based on plant carbon allocation equations (allometric relationships) combined with carbon models. The harvest index (HI) is the harvested proportion of net primary production from the shoots, while the rest is returned to the soil. Note, for example, that HI values of 45–55% are commonly obtained for highly productive cereals. Genetic and agronomic optimization of yields generally increases the HI. It can therefore be said that, for a given crop production, carbon returns to soils increase with primary production, but the restitution/yield ratio decreases as the yield

70 increases.

Belowground input flux are much less documented but are considered to contribute more to organic matter than inputs from leaves and stems (Clemmensen et al., 2013; Rasse et al., 2005). The belowground to aboveground biomass (root/shoot) ratio is an indicator that is highly dependent on environmental conditions and is highly variable (10–30%. Rhizodeposition, which represents the contribution of carbon to the soil by living plants via roots, is an additional key factor. This may include root

75 renewal, release of cells or tissues (epidermis, root hairs, cap cells), macromolecules such as mucilage and extracellular enzymes, or small molecules, i.e. exsudates (Nguyen, 2003). Rhizodeposition is a series of processes generally related to the acquisition of water and nutrients by plants (including P, N, K, Fe and Mg). Carbon transfer from plants to symbiotic fungi is one of these processes. It is estimated that the rhizodeposition flux can be around 0.2–0.5 times the net root production (Nguyen, 2003; Jones et al., 2009; Balesdent et al., 2011). Belowground inputs are still largely unknown, highly variable, and

80 constitute a definite but still relatively unexplored lever driving carbon storage in soil. In general, the belowground proportion of primary production is greater when the soil conditions are limiting (water, nitrogen, phosphorus, iron). For example, for a cereal producing 8.5 t dry matter (DM)/ha of grain, the soil returns (stems, leaves) can be 7.5 t DM/ha (HI 53%) containing 450 mg/g of carbon, or 3.4 t C/ha. In addition, 1.3 t C/ha of roots (18% of aboveground production) and 0.4 t C/ha/year of rhizodeposition are added. The annual input to the soil is about 5.1 t C/ha/year. In grassland or fodder systems, a greater

85 proportion of the aboveground parts are exported or grazed, and belowground inputs account for the majority of the soil inputs.

2.1.2 Chemical nature of soil inputs

The main plant compounds that reach the ground are the plant structural constituents. These primarily include celluloses and hemicelluloses (neutral sugar polymers), then lignins (phenolic compound polymers), pectins (polymers containing charged sugars), proteins (structural or enzymes released by the roots), lipids from waxes, cuticles, bark and root cortexes. Plants also

90 release secondary metabolites. They can be polyphenolic compounds, tannins and a multitude of small molecules constituting root exudates (complex sugars, organic acids). The latter probably have a greater impact on carbon dynamics through their effects on microorganisms and on organic matter (OM) mobilization than as a structural OM source. Dead tissues that reach

the ground do not have the same composition as living tissues because the plant recovers many metabolites and mineral elements during senescence (particularly sugars and nitrogen compounds), while mainly leaving structural compounds. Green

95 manure differs from other plant inputs in this respect. Microbial products are generally composed of the same molecules except for celluloses and lignins. Compared to plant OM, microbial products are comparatively enriched with other polysaccharides, lipids, proteins, amino-saccharides, nucleic acids and a very diverse range of metabolites.

Soil organic matter is generated from all of these plant or microbial molecules or their monomers (Kelleher and Simpson, 2006). Non-industrial organic waste products are composed of mixtures of plant or microbial molecules or their monomers,

00 while compost and sewage sludge are enriched with microbial compounds in comparison to plant matter.

In addition to living compounds, byproducts of incomplete combustion may also be present, such as plant coal from fires, soot from regional or global fallout, biomass pyrolysis products (*terra preta*, biochar, coal mines and charcoal production site), and plastics. Soils can also contain local organic carbon from rocks, particularly from carboniferous shale (black shale, which gives soils a black colour).

05 ## 2.2   Organic matter transformation in soil

2.2.1   Physical and chemical biotransformation protagonists: fauna and micro-organisms

Biochemical reactions that occur during OM decomposition are mainly induced by microorganisms (fungi and bacteria), whether they are soil-borne or associated with fauna. The essentially mechanical action of soil fauna is often distinguished from the predominant biochemical action of microorganisms. Recent studies have highlighted the close complementarity of

10 all living organisms in the soil with regard to OM transformation.

Macrofauna (earthworms, termites, ants, etc.) act by fragmenting the litter, incorporating it into the soil profile and mixing the soil within the profile by bioturbation (Bohlen et al., 2004). Soil transit through the digestive tract of macrofauna (mainly earthworms) promotes contact between microbes and OM. Digestion alters the chemical structure of OM: (i) by selective digestion of peptide compounds, which alters their stability (Shan et al., 2010), (ii) by biochemical modifications due to

15 alternating extreme pH or redox conditions, or (iii) by physical modification of particles (Brauman, 2000). Many soil fauna groups are thus recognized as stimulating microorganism activity and soil organic matter biodegradation (Vidal et al., 2016; Brown, 1995).

Micro- and meso-fauna (mites, springtails, collembola, tardigrades, protozoa, etc.) mainly form a food web that regulates decomposing microorganisms, e.g. protozoa and bacterial nematodes tend to decrease the microorganism density (Bonkowski,

20 2004; Trap et al., 2016).

Microorganisms (fungi and bacteria) are the main drivers of OM chemical biotransformation. They represent the most taxonomically and functionally diverse living component of soil (Torsvik and Ovreas, 2002; Curtis and Sloan, 2005; Hättenschwiler et al., 2018). It is estimated that 1 g of soil can support up to 1 billion bacteria representing 1 million species (Gans et al., 2005), and 1000 fungal species roughly represent dozens of meters of mycelial filaments (Bardgett et al., 2005;

25   Buee et al., 2009). Microbial biomass is the mass of living microorganisms in soil and generally amounts to a few hundred grams of dry matter per square meter of soil, but most of the microbes are dormant or barely active (Lennon and Jones, 2011). The rhizosphere (soil zone near the roots) concentrates a large proportion of the soil's microbial activity (Nguyen, 2003). A systematic inventory of bacterial biodiversity (species richness) throughout the French national territory yielded an average of 1300 different genera at each sampling site—the richness variance could be explained by pH, grassland, forest and agricultural
30   land use, and the soil texture (Terrat et al., 2017). Microbial biomass is lowest in cultivated soil (Horrigue et al., 2016; Dequiedt et al., 2011).

2.2.2   Biotransformation reactions

Biotransformation reactions in soil are chemical reactions catalyzed by enzymes due to the activity of living soil organisms, in particular millions of microorganism species. These are both degradation and synthesis reactions. Uncatalyzed chemical
35   biotransformations are very rare.

The degradation reactions of organic compounds (so-called catabolic reactions) are mainly carried out by hydrolytic or oxidative depolymerization (Lehmann and Kleber, 2015)**.** The incoming plant compounds are mainly large molecules (Figure 3). These are cellulose, hemicelluloses, lignin, proteins, etc., all of which form "substrates". Due to their large size, their depolymerization first takes place outside microbial cells (Burns et al., 2013). Co-location between substrates and
40   microorganisms at the microbial habitat scale is essential for reactions to occur. Substrate/enzyme contact can occur by diffusion and advection of substrates and enzymes, or by microorganism growth and mobility. In addition, local environmental conditions (oxygenation, pH, water content, etc.) at the micrometer spatial scale must be favorable for microorganism activity (Chenu and Stotsky, 2002; Don et al., 2013; Pinheiro et al., 2015). In the particular case of fully or partially oxygen-depleted systems (so-called anaerobic conditions), oxygen cannot play its role as the final electron acceptor that accompanies C
45   oxidation during degradation. Oxidative degradation can occur with other oxidation-reduction reactions, but with reaction rates that could be 10 times slower (Keiluweit et al., 2017; Klupfel et al., 2014).

The action of extracellular enzymes continues until smaller reaction products (sugars, phenolic compounds, amino acids, lipids) can be transported through the microorganism cell membranes. The extracellular nature of reactions has several consequences, i.e. biodegradation has a high energy cost for organisms, while some compounds escape the cells and adsorb to
50   other organic or mineral compounds. Small molecules resulting from biodegradation can thus aggregate via weak bonds (hydrogen bonds or hydrophobic interactions) to form supramolecular assemblies (Sutton and Sposito, 2005) or with minerals to form organomineral associations (Kleber et al., 2015; Kögel-Knabner et al., 2008).

Small molecular weight organic compounds (organic acids, sugars, amino acids) can be absorbed into the intracellular environment of microorganisms for further biotransformation. Oxidative degradation can continue until its ultimate stage when
55   the elements are mineralized (CO_2, NH_4^+, H_2O, HPO_4^-, SO_4^{2-}). Mineralization is the result of the respiration and excretion of these inorganic compounds by organisms. Carbon mineralization is almost exclusively intracellular, despite the fact that extracellular catabolism of glucose has been observed (Kéraval et al., 2016).

The entire biodegradation chain is shown in Figure 3. From a quantitative standpoint, soils emit 10 times more CO_2 on a global scale from autotrophic (roots) and heterotrophic (microorganisms and fauna) respiration than human activities (IPCC 2013).

60 Unlike oxidative degradation, synthesis of new organic molecules from small organic molecular weight compounds occurs in microorganism cells in so-called anabolic reactions. Inorganic ions in the soil solution (orthophosphate, ammonium) are also involved in the synthesis of new molecules. These new molecules become cellular components or excreted metabolites (e.g. organic acids, polysaccharides, extracellular enzymes) and contribute to the soil OM pool. C incorporated by microorganisms and then re-incorporated into soil OM is repeatedly recycled. Thus, the fact that a molecule is quickly consumed by

65 microorganisms does not necessarily mean that its C will be rapidly mineralized into CO_2. The chemical stability or resistance to chemical attack of molecules reaching the soil is therefore not correlated with the soil's OM formation performance. The most biodegradable compounds have high long-term soil organic matter formation yields.

From a quantitative standpoint, the efficiency of C use by microorganisms (or CUE) can serve to estimate, for a given substrate, the quantity of microbial C formed in relation to the consumed C. The microbial material production flux is estimated at 0.3

70 to 0.4 times the plant material input flux to the soil (Sinsabaugh et al., 2014). This CUE varies according to: (i) the microbial species and their physiology, (ii) the availability of nutrient resource (N, P, S, etc.) required for microbial metabolism, (iii) interactions with the soil matrix and associated energy costs, and (iv) environmental conditions (temperature, pH, humidity, etc.) (Manzoni et al., 2012; Geyer et al., 2016; Lashermes et al., 2016; Mooshammer et al., 2014). It is also likely to change according to climatic and atmospheric conditions (Schimel, 2013; Allison et al., 2010; Sistla et al., 2013).

75 **2.2.3   Nature, properties and size classes of soil organic matter**

Soil OM therefore consists of a continuum of organic compounds at different stages of the biotransformation reactions described above, from particulate organic matter (POM) to the elementary building blocks of living organisms (simple sugars, phenolic compounds, amino acids, peptides, fatty acids, organic acids, lipids). The simplest molecules can form random assemblies via weak bonds, i.e. so-called supramolecular structures (Sutton and Sposito, 2005; Kelleher and Simpson, 2006)

80 (Figure 3).

Many studies have shown that compounds of microbial origin (polysaccharides, proteins, etc.) have a longer lifespan in soil than structural compounds in plants (celluloses, lignins, etc.). Ultimately, microorganisms are the main source of long-term stabilized organic compounds (relative to plants), (Derrien et al., 2006; Miltner et al., 2012; Kallenbach et al., 2016). (see stabilization processes in Section 1.4)

85 Oxidative depolymerization reactions systematically lead to a reduction in the size of molecules, but also to an increase in their aqueous solubility and an increase in their chemical reactivity. These properties are key to the behavior of soil solution compounds, particularly with respect to their ability to form organomineral associations (Kleber et al., 2015). Some organic compound functions are also pH dependent. One example is the carboxyl group, which is mainly in the form of COOH at pH below 4 but of COO- at pH above 5. The reactivity of soil OM is thus highly pH-dependent.

90   Finally, the average proportions of the different soil OM types and their size ranges are summarized in Figure 4. From an operational standpoint, C analysis of a soil sample is performed on "fine" soil, i.e. sieved to 2 mm, i.e. mainly C from simple and complex biopolymers (~75%), particulate organic debris (including carbonized debris) (~20%), microorganisms (~2%), microfauna (<1%) and the finest roots (<2%). These proportions are approximate and vary greatly between soils and horizons (Figure 1).

95   **2.2.4   The progressive decomposition model at odds with historical concepts**

In the progressive decomposition conceptual model described above, soil OM consists of a range of organic fragments and microbial products of all sizes at different decomposition stages (Figure 3). This mechanism is at odds with the historical "humification" model proposing the formation of "humic substances" by progressive condensation into macromolecules. Moreover, the different classes of humic compounds identified in the past (humic acids, fulvic acids, humins) do not

00   correspond to molecules existing *in situ*, but rather to physicochemical rearrangements of elementary molecules during their extraction (Sutton and Sposito, 2005). These different concepts (humification, humic substances, humic and fuvic acids, humins), which have been revealed as deficient by modern soil OM characterization methods, should no longer be used by the soil science community (Lehmann and Kleber, 2015), nor showcased in teaching courses.

The selective preservation model regarding some organic compounds has also been invalidated by dating techniques,

05   demonstrating that supposedly recalcitrant molecules are not specifically preserved in soil OM (Gleixner et al., 2001; Dignac et al., 2005; Amelung et al., 2008; Bol et al., 2009). Indeed, soil microbial communities, and implicitly the associated enzymatic repertoire, are able to degrade all types of substrate in almost any soil (Dungait et al., 2012). Soil OM preservation mechanisms are therefore not linked to their chemical recalcitrance but rather to other biological, physicochemical and structural factors (Schmidt et al., 2011), particularly their ability to associate with minerals. Organic matter transfers

10   **2.2.5   OM transfers within the soil profile**

Organic matter is transferred to the soil profile in particulate, colloidal or dissolved form.

Pedoturbation refers to the mixing of soil layers by physical processes in certain types of soil (frost, clay swelling-removal and crack filling), but mainly by biological processes. Otherwise bioturbation is when particulate transport is linked to biological action, i.e. when soil fauna (e.g. earthworms, ants, termites, voles and moles) bury plant residue, gradually mix the soil, or

15   move mineral material to the surface from deep horizons (Lavelle et al., 2016). The mixing process decreases exponentially with depth and becomes negligible below 50 cm over decades. Bioturbation is known to be more prevalent in permanent grasslands and fields under conservation agriculture than in conventional cropfields (Jagercikova et al., 2017).

Earthworms are essential actors in bioturbation as they ingest both organic matter (plant residue or other organisms, equivalent to 10–30 mg/g/day of dry OM) and minerals (Curry and Schmidt, 2007) and mix several dozen tonnes/ha/year of soil.

20   Earthworms bury these organomineral mixtures in the soil, excrete them along the galleries and, for some species, bring them to the surface as casts (Don et al., 2008). These biostructures represent hotspots of OM enriched in organic compounds (mucus)

that contribute to the stability of organomineral aggregates (Coq et al., 2007; Shan et al., 2010) and to C stabilization (Martin et al., 1990). It has been shown that the presence of earthworms can increase the C stock in soil by 30% (Zangerle et al., 2011). Water that circulates in the soil poral space is also a vector for vertical OM transport in the soil. By definition, this involves the transfer of particles less than 2 μm via leaching and of organic matter less than 0.45 μm by lixiviation. OM of less than 0.45 μm is called dissolved organic matter (DOM) and may involve OM that is free, adsorbed on minerals, co-precipitated with oxy-hydroxides, or complexed with metals. Translocation is a pedogenic mechanism that causes particles to migrate from the elluviating horizons to the illuviating horizons in which they are immobilized (Jagercikova et al., 2017). DOM molecules are generally small (less than 100 kDa, Figure 4 molecules shown on the bottom left), thus facilitating their diffusion. Water draining the upper soil horizons (organic horizons and surface mineral horizons) can have a high DOM content, while water draining the soil at depth generally has a low DOM content. DOM concentrations are also often correlated with the soil texture, with sandy soil solutions often having a higher DOM content than clay soils (under equivalent climatic conditions). There may also be marked seasonal variations in DOM. C exports via DOC flux have been found to range from 0.002 to 0.05 t of C ha^{-1}year^{-1} depending on the site (Doetterl et al., 2016), i.e. 0.7 Gt year^{-1} on a global scale.

2.2.6   OM transfers on the soil surface: erosion

Erosion is the major factor in soil degradation. It is mainly related to soil surface runoff and is therefore highly dependent on the climate, topography and land use. Wind erosion can also be significant, especially in arid regions. In undisturbed natural systems, material loss through erosion is generally offset by pedogenesis (Doetterl et al., 2016), whereas agricultural use increases erosion rates by 100-fold by removing natural vegetation and reducing surface organic matter in litter (Montgomery, 2007). With agricultural expansion, conservation agriculture has been introduced in many parts of the world to reduce soil erosion. The high spatiotemporal variability in soil erosion is thus associated with the history of land use and management. Surface horizons have been substantially depleted as a result of soil erosion (Lal, 2001). On a global scale, the quantity of soil C exported by lateral erosion is estimated at 0.3–1 Gt C/year. The omission of the fact that the erosion contribution to C flux budgets between soils and the atmosphere is often overlooked is a major source of error in the interpretation of the soil C dynamics model outputs (Chappell et al., 2016).

C transferred laterally by erosion is lost at the pedon scale, but the integration of processes at the watershed scale (detachment, transport, sedimentation, burial in lowland areas) results in C budgets that often generate debate regarding C sinks and sources (Doetterl et al., 2016; Mulder et al., 2015).

2.3   Stabilization and destabilization of soil organic matter

2.3.1   Organomineral interactions

Organomineral interactions are now recognized as being a key factor in stabilizing organic matter in soil. (Schmidt et al., 2011; Lehmann and Kleber, 2015; Mathieu et al., 2015). Soil minerals account for over 90% of the solid constituents in soil (Figure

4). The smallest minerals, mainly contained in the grain size class of less than 2 µm (classified as clays by agronomists), are highly effective in protecting OM. This particle size class includes a wide variety of minerals. Those with the greatest surface reactivity are the most involved in organomineral associations, and those with the highest specific surface area lead to greater quantities of stabilized OM. These include phyllosilicates (classified as clays by mineralogists), different forms of metal oxyhydroxides and poorly crystallized aluminosilicates (Basile-Doelsch et al., 2015; Kleber et al., 2015). Regardless of the nature of the minerals, the OM they stabilize are mostly made up of small molecules derived from microbial products (Miltner et al., 2012; Clemmensen et al., 2013; Cotrufo et al., 2015; Lavallee et al., 2018).

These minerals and poorly crystallized phases protect organic compounds through two main mechanisms (Kleber et al., 2015): (1) Adsorption on the surface of minerals is the first identified process (Kleber et al., 2007). When the adsorption affinity of an organic function on the mineral surface is greater than its affinity for the active enzyme site, oxidative degradation through enzymatic reactions cannot take place. Adsorption on mineral surfaces is localized. Organic compounds are adsorbed by patches but do not cover the entire surface of the particle (Vogel et al., 2014; Remusat et al., 2012).

(2) Co-precipitation leads to the formation of secondary mineral phases in the presence of OM. The size of these mineral phases ranges from one to a few dozen nanometers (Tamrat et al., 2018; Eusterhues et al., 2008; Levard et al., 2012; Rasmussen et al., 2018; Mikutta et al., 2006; Kleber et al., 2015; Torn et al., 1997; Tamrat et al., 2019). Allophanes, Fe and Al oxyhydroxides and chelates (organic ligands associated with a Fe or Al metal cation) are the most commonly described mineral phases. A molecular structure of nano-sized coprecipitates of inorganic oligomers with organic compounds has also been recently proposed (Tamrat et al., 2019). Poorly crystallized mineral phases can also be destructured by the action of organic ligands secreted by roots. Organic compounds then lose their mineral protection and can be used by microorganisms (Keiluweit et al., 2015).

A third process, i.e. cationic bridging by di- or trivalent ions, also plays an important role in OM stabilization in some soils. When this involves bridging between a mineral surface and an organic function—both negatively charged—it is referred to as "ternary complexation". In high pH and arid soils, cationic bridging with Ca2+ ions tends to override other organomineral bounds (Rasmussen et al., 2018; Rowley et al., 2018).

A conceptual representation of carbon stabilization by adsorption alone (above-cited point (1)) on clay minerals has given rise to the saturation concept (Hassink, 1997) whereby mineral surfaces are assumed to accommodate a limited amount of carbon, thus limiting soil carbon storage. However, the concept has yet to be sufficiently validated to be operational (West and Six, 2007) and the mechanism itself has been invalidated by certain observations (Vogel et al., 2014). In view of recent advances in knowledge of organomineral interactions, the saturation concept could now be revisited from a more mechanistic angle.

2.3.2 Soil structure and aggregation

Soil particle aggregation processes affect the OM mineralization rate (Rovira and Greacen, 1957). For example, the residence time of C in microaggregates (< 50 µm) is greater than that in macroaggregates (> 50 µm) (Golchin et al., 1994; Besnard et al., 1996; Six et al., 1998; Balesdent et al., 2000; Six et al., 2002; Chevallier et al., 2004). However, the structural difference

between micro- and macro-aggregates may not be the only factor underlying the difference in OM mineralization rate, because: (i) the nature of OM in these two entities may differ, and (ii) the lifespan of the macro- and micro-aggregates, which regulate the OM trapping time, is not the same (Plante et al., 2006). Nevertheless, aggregates, and especially microaggregates, are often used as fractions indicating the "degree" of physical protection of carbon. Conceptual models describe the C dynamics in the different aggregates by considering the formation-destruction cycles of the aggregates, but their parameterization remains complex (Stamati et al., 2013).

The action of the decomposers on their organic substrates (see para 1.2.2.1) takes place in the soil pore network. Since the smallest bacteria are in the micron range, the soil structure controls biodegradation at the micrometer spatial scale (Juarez et al., 2013) and may be related to different microbial communities in these habitats. The rate of mineralization of simple substrates thus partly depends on the size of the pores in which they are located (Killham et al., 1993; Ruamps et al., 2013). The geometry of the mineral particle associations creates microsites (micrometric to nanometric) in which OM is protected from enzymatic action. Within a microsite, regardless of whether or not organic compounds are directly bound to mineral surfaces, oxidative depolymerization (see para. 1.2.2.2) is significantly slowed down by limiting enzyme access and O_2 diffusion (Zimmerman et al., 2004; Chevallier et al., 2010; Keiluweit et al., 2017).

New models include an explicit 2D or 3D description of the pore network based on tomographic images (Monga et al., 2008; Monga et al., 2014; Blair et al., 2007; Falconer et al., 2015; Pajor et al., 2010; Resat et al., 2012; Vogel et al., 2015). They operate in short time steps and have been validated for simplified systems, but they cannot be used at the plot level. On the other hand, they should make it possible to prioritize the C dynamics control variables so as to be able to define soil structure descriptors other than those currently used in plot-scale models.

3 Time-dependent processes: dynamic representations

3.1 Kinetics, characteristic times, turnover, balance and mathematical modeling

Soil carbon is subject to permanent renewal. It is mathematically represented as a "dynamic system". Changes in the organic carbon stock can be described by a general differential equation:

$$dC/dt = I - kC \quad \text{[Equation 1]},$$

where C is the carbon stock (tC/ha), t the time (year), I the input (tC/ha/year) and k the proportion of mineralized carbon (or lost by erosion, etc.) per unit of time (year^{-1}). k is not fixed and is dependent on the conditions, quantity and nature of the carbon stock. k is the mineralization rate and kC is the mineralization flux (respiration).

The system is at equilibrium, as an annual average, if $dC/dt = 0$ (i.e. $I = kC$) and the carbon turnover time is $1/k = C/I$. Storage ($dC/dt > 0$) is the result of increased I inputs or a reduced k mineralization rate. The increase in carbon stock over a year cannot be greater than I. Conversely, the system C stock decreases if $dC/dt < 0$.

However, the average *k* value masks the high heterogeneity in carbon residence times. Isotopic tracing and soil respiration monitoring have helped monitor the fate of plant compound inputs in the soil at day to millennium time steps. Most of these inputs are mineralized and transformed into microbial products in less than a year, or a few years for ligno-cellulosic

20 compounds. The transformation products (10–20% of the carbon supply) are protected and mineralized very slowly over several decades. Figure 5 provides a numerical example of the fate of organic carbon reaching the soil.

The soil carbon stock is the sum of the remains of all these past annual inputs. Several kinetic parameters can be calculated. In the example in Figure 5, the OM mineralization rate is 5/45 tC/ha/year (11% year^{-1}). The vast majority of the carbon (37.5/45 tC/ha/year) consists of long-standing C. The average age of the carbon is 42 years. These slow kinetic parameters cannot be

25 explained by deterministic laws (e.g. enzymatic kinetics laws) but rather could be modelled by statistical approaches integrating hypercomplex functioning. Finally, dating methods have shown that, in addition to OM several decades old (Mathieu et al., 2015), organic materials that are inherited from a distant past.

Characteristic OM formation times are therefore long (several decades), OM currently present is inherited from past generations. Strictly speaking, kinetics representations should be based on continuous mathematical formalisms to predict

30 time-course variations in carbon stocks. In practice, however, compartmentalization approaches are used in conventional models (Bosatta and Agren, 1995). While remaining fairly faithful to reality, they enable the simplification of mathematical formalisms via discretization kinetics.

3.2 Ambiguous mineralization and biological activity paradoxes

In agronomy and ecology, the terms "mineralization" and "biological activity" implicitly imply that the rate of processes must

35 be taken into account but, as the definitions of these terms are generally unclear, they are often applied in a relatively unreliable manner.

In fact, "mineralization" implies" mineralization flux" (*kC*). It is measured *in situ* or *in vitro* and is very close to the average inputs from previous years, while being modulated by seasonal variations. The mineralization flux is therefore largely decoupled from changes in the organic reserves. It is sometimes reported that one treatment "increases" or "promotes" OM

40 mineralization, or that one system "mineralizes more" than another. The difference is generally related to differences in soil inputs more than to differences in the effectiveness of microorganisms.

The term "biological activity" is confusing. Three definitions could be considered:

(1) It could be defined as the respiratory flux (kC), i.e. equivalent to the mineralization flux described above.

(2) Alternatively, it could be defined as the efficiency or biodegradation rate (k), at equivalent biodegradable substrate

45 quantities. High "biological activity" is often considered beneficial for crop production. Active and efficient decomposing organisms enhance OM degradation. Nonmineralized C is transformed into microbial products that can be stabilized and/or represent a pool of readily available nutrients (Figure 3). However, at equal inputs, the higher the biological activity, the less C there is in the soil. Note therefore that maximum "biological activity" does not necessarily have to be sought—in order to

increase soil OM quantities, it might be preferable to slightly slow down the plant debris biotransformation process. A large

50   reservoir of elements could thus be created to achieve an equivalent annual average flux of released N and P nutrients. These elements would be less readily available but the same nutrient flux would prevail, thus ensuring a high degree of resilience to the agrosystem.

(3) On the other hand, when the term 'biological activity' refers to soil fauna activity, it could be highly variable depending on how the soil is managed.

55   ### 3.3   So-called "non-linear" processes

3.3.1   Linear processes, non-linear processes

Conventional models (Hénin and M., 1945; Jenkinson and Rayner, 1977; Parton et al., 1987; Andriulo et al., 1999), consider that parameters of the OM fate are independent of the input flux and OM quantities. This results in first-order differential equations ($\mathrm{d}C/\mathrm{dt} = \mathrm{I}\text{-}kC$ with k independent of C) and exponential kinetics. These models are considered linear: dual inputs

60   result in twofold increases in OM amounts. In change regimes, compartments fill or empty at their characteristic rate. However, there are now many indications of non-linear soil C dynamics processes (Table 1).

A major implication of non-linear behaviors is that OM is not homogeneously distributed, and that inputs, microorganisms and OM are not co-located (Vogel et al., 2015). Since they depend on local concentrations, non-linear process parameters are

65   dependent on the observation scale, i.e. the aggregate scale, profile, root distances, etc. The dynamics are not the same in situ and in homogenized in vitro systems. In vitro they depend on the experimental design and duration. This could likely explain the high discrepancy in the literature on carbon dynamics processes and mechanisms, and their broad quantification range. Although in vitro experiments help gain insight into the mechanisms involved, in situ experiments and observations at the square meter or plot scale, and at the decadal time scale, are obviously more relevant for addressing the carbon storage issue.

70   Non-linear representations thus predict less determined and reversible changes in organic stocks than linear models. However, non-linear processes have yet to be incorporated into operational C dynamics models. The saturation concept (see 1.4.1), which typically takes the impact of the mineral/OM ratio on carbon stabilization into account, also leads to a non-linear behavior.

3.3.2   Priming effect: now an important concept regarding the carbon storage issue

A major non-linear effect is called the "priming effect" (Fontaine et al., 2007; Kuzyakov et al., 2000; Sallih and Bottner, 1988).

75   In short, the supply of complex decomposable substrates (but not simple molecules such as glucose) provides competent microorganisms with the energy resource required to biodegrade stabilized OM. Typically, the soil OM residence time is thus shorter in soil zones that receive substantial inputs, such as on the surface, relative to deep horizons. Priming effect mechanisms are crucial in the dynamics of C, N and P elements. Theoretically, the priming effect is therefore based on the assumption that:

80 (i) carbon storage is not proportional to the inputs; and (ii) there is a risk of destabilization of pre-existing OM by carbon inputs, especially in deep horizons.

3.4   Renewal rates at the soil profile scale

Historical work on dynamic representations of C has mainly focused on the soil layer considered by agronomists, i.e. 0-30 cm depth. However, interest in understanding the subsoil mechanisms is growing because half of the soil carbon is located below
85 30 cm depth (Mulder et al., 2016); (Jobbagy and Jackson, 2000; Hiederer and Köchy, 2011). Carbon-14 (^{14}C) dating and natural tracing by ^{13}C have shown that the median age of carbon at 1 m depth is greater than 1000 years (Figure 1). Renewal is 7-10 times slower in the 30-100 cm layer than in the 0-30 cm layer (Mathieu et al., 2015; Balesdent et al., 2017; Balesdent et al., 2018). However, deep carbon is not inert. The above studies show that the 30-100 cm layer contains on average 25% of the "young" carbon stock (i.e. younger than 20 years) of the 0-100 cm layer in cultivated soils, and less than 20% in permanent
90 grasslands (Figure 6). Several studies have reported significant effects of land-use changes or agricultural practices on deep soil carbon, including a decrease in C through the cultivation of grasslands or forest areas (Guo and Gifford, 2002), an increase when forests are converted to pasture (Stahl et al., 2017), or the introduction of legumes (Guan et al., 2016).

4   Control of C residence times in soil: biotic and abiotic factors

The mechanisms described above are expressed to different extents in soil as a function of a series of 10 main factors that
95 control their intensity. These factors are comprehensively presented in Wiesmeier et al. (2019). Here we propose a synthesis of the co-dependencies of these factors (Table 2) by focusing on carbon residence time variation factors (but variations in stocks also depend on incoming carbon fluxes that are not considered here). In steady-state systems (stock at equilibrium and constant incoming fluxes), the mean residence time (MRT, expressed in years), is defined as the stock/incoming flux ratio (Eriksson, 1971) or as the mean age of C leaving the system (where age is the duration between the time when C enters the
00 soil and the observation time).

The nature of incoming C, particularly its biodegradability, has a counter-intuitive effect on carbon residence times (see "The progressive decomposition model" section). The nature of C affects MRTs through the microbial carbon use efficiency (CUE) and organomineral interactions.

Temperature is a major factor, among the best quantified, with mineralization rates rising by 2- to 3-fold at every 10°C
05 increase, but this effect depends on the soil, in particular their granulometry.

As the soil **water content** increases, mineralization rates increase linearly with moisture to a maximum (reached at around 20-50% of the volumetric soil water content according to the models (Sierra et al., 2015)), followed by a plateau and a decrease in relation to the oxygen deficit. The alternating desiccation-humectation cycles accelerate mineralization.

The partial pressure of oxygen. In saturated environments, if the environment becomes anaerobic, fermentation takes precedence over aerobic respiration, while the degradation of ligno-cellulosic debris is slowed or even stopped. However, there is no evidence of temporary anaerobic effects on carbon storage. Anaerobic environments are also unfavorable for the roots or wildlife and micro-organism activity. But ploughing is sometimes considered to accelerate biodegradation by aerating the soil. There is no scientific support for this effect.

Grain size is quite well correlated with carbon stocks at national levels. The <2 μm fraction content can lead to a carbon stocks variation by 2-fold. The <2 μm fraction contains between 0% and 50% of the C stocks in national soil C inventories. Fine granulometric fractions are often described as enriched with stable C, with MRTs longer than the average values in soil.

Mineralogy is a major determinant of OM stabilization but is still poorly quantified. It is combined with the nature of ions available in solution (Rasmussen et al., 2018). The mineralogy of phases interacting with SOM (particularly poorly crystallized minerals) is not static (Basile-Doelsch et al., 2015) and can be largely modified by land use, plants, pH and amendments.

Soil pH and ions in the soil solution. The soil pH determined by conventional measurements is an average value that does not reflect the spatial heterogeneity of pH at the micro- to nano-scale. The pH has a greater effect on the soil physicochemistry than on the microbial physiology. The presence of calcium or magnesium ions in solution (dominant at pH > 5) and of active limestone tends to insolubilize OM and adsorb it by electrostatic interactions, via Ca^{2+} bridges, thus reducing its biodegradation (Rowley et al., 2018). Aluminium has an equivalent role, but in acidic (< 4.5) and aluminous soil. Conversely, biodegradation rates are high in salty soil where Na^+ predominates in the exchange complex. The action of K^+ has not been assessed.

The availability and abundance of N, P and S elements has various and complex effects (see 2.5.2). While the degradation of ligno-cellulosic debris (low nitrogen) is temporarily delayed in the absence of mineral nitrogen, many other C, N and P stoichiometry effects are involved in priming, biotic interactions or carbon use efficiency (CUE).

Biodiversity. Since bacteria are major actors in OM mineralization as well as in the production of stabilized compounds, the effects of nematode and protist predation of bacteria, as well as bacterial regulation by fungi, is uncertain. The impact of pesticides on protists, nematodes and soil fungi could affect these regulations.

Biotic/abiotic interactions. The priming effect mechanism is involved in plant strategies for nutrient (N, P, K) acquisition. Plants release exudates and feed fungi from the rhizosphere that biodegrades OM (Fontaine et al., 2011) or even destabilizes organomineral associations (Keiluweit et al., 2015), while releasing nitrogen compounds or phosphorus. Many other plant-microorganism interactions mechanisms can, conversely, preserve OM (Northup et al., 1995; Averill et al., 2014), which allows the ecosystem to maintain a substantial reserve of elements and therefore a high degree of resilience.

Quantification of the effects of individually considered factors and mechanisms is still very incomplete, and perhaps inappropriate, because: (i) a single law controlling the MRT of the different C pools is not expected when several mechanisms are involved (Table 2); and (ii) several factors interact (Cotrufo et al., 2015). Quantification procedures described in the scientific literature are very confusing: many research groups estimate the weight of a factor by varying it and measuring mineralization flows, often in the short-term, despite the fact that these flows are not at all correlated with long-term carbon

MRTs. For example, the effect of temperature has given rise to a number of divergent results (Davidson and Janssens, 2006; Sierra et al., 2015). Responses are also highly dependent on the soil type (von Luetzow et al., 2008).

45   In current operational models, only temperature, soil moisture, grain size and substrate C/N are taken into account. However, there are other overriding factors. Priming effect modeling is emerging.

5   Conclusion

Soils in fields under conventional intensive agriculture have C stocks that are much lower than soils under grasslands or forests.

50   Carbon harvesting is not a major factor that could explain this difference—carbon inputs in croplands are often higher, at least in the absence of straw removal, as a result of maximized plant productivity. This suggests that agricultural practices can severely affect the residence time of organic carbon in soil in the long-term (decades), therefore acting on processes other than just the C input flux. OM observed in a soil at a given date is thus the result of a complex inheritance linked to the functioning (and possible use) of a soil over several hundreds (or even thousands) of years. In the light of recent research findings, several

55   candidate processes could contribute to C stabilization. Soil OM mainly consists of plant- and microbe-derived small organic molecules. In the soil, transfer and interaction processes with minerals redistribute these organic molecules and/or more or less permanently eliminate them from the action of micro-organisms. The long-term stabilization (this term is now preferred to the old term 'humification') is therefore not driven by the same forces as short-term degradation rates. A first group of processes rely on the role of vegetation, through the amount, bio-availability and activity of belowground plant inputs in the soil.

60   Degradability and direct inputs into the soil may alter the synergy between the stabilization by mineral phases and the efficiency of microbial products to associate with minerals at sub-micron scales. Plant-driven alteration of primary minerals may also facilitate the build-up of these organomineral associations. A second group of processes may rely on the decomposers' foodweb, since several studies have pointed out that the soil biodiversity affects the mineralization-stabilization balance, while highlighting the specific roles of fungi, predation or antagonisms with bacteria. Despite the fact that no clear assessments have

65   been reported, these studies suggest that plant biodiversity and the use of pesticides (typically fungicides and nematicides) may affect C storage. These effects of interactions between plants, microorganisms and mineral phases show that the combined effects of plant biodiversity/microbial biodiversity/mineralogy may contribute to ecosystem stability, through the maintenance of high levels of organic carbon. The question of the impact of pesticide use in conventional agriculture, which alters the soil biodiversity (especially fungicides and nematicides), on carbon storage must be addressed.

70   Finally, beyond tillage, crop residue restitution and of organic fertilizer inputs, agricultural practices, including so-called agroecological practices, may affect C storage through many factors including the nature and flow of belowground C, water content, pO^2, soil solution chemistry and pH, N and P availability, plant and microbial biodiversity as well as soil temperature. The interdependencies of the effects, their time dependence (short-term versus long-term responses), their relative importance with respect to C storage (or loss), are often not explained in detail, as they are very complex. Regarding C modelling, OM

75 decay dynamics are conventionally modelled by linear approaches, although many processes, considered individually, do not behave linearly. Greater insight into the mechanisms, their interdependencies, hierarchy and sensitivity to agricultural practices represents potential future action levers for C sequestration in soil. Due to the time-scale considered, retrospective studies or intercomparison of long-term experiments sites would be methods of choice.

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7   Author contributions

90 Isabelle Basile-Doelsch and Jerome Balesdent contributed equally to the French chapter "Les mécanismes à l'origine du stockage/déstockage de C dans les sols" of the above-cited INRA report. Isabelle Basile-Doelsch drafted the English version. Sylvain Pellerin commented the manuscript and led the INRA report.

8   Competing interests

95 The authors declare no competing interests.

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Table 1: Possible non-linear mechanisms of carbon decomposition or accumulation. Due to these mechanisms, decomposition rates are dependent on the amounts of carbon supplied or present. These processes can interact with each other.

MAIN NON-LINEAR MECHANISMS
Effect of organic matter on physical properties that affect biodegradation rates: - Water properties (porosity, wettability, evaporation, mulch) - Ground temperature (porosity, thermal conductivity, albedo, mulch)
Minerals/organic matter ratio modulating carbon stabilization
Physical protection ("glue" role of organic matter and microbial polysaccharides) favoring organomineral associations
Exsudation release of complexing organic acids that destabilize organomineral associations
Priming effect: stimulation of the biodegradation of stabilized organic matter by the energy supply from fresh matter
Carbon use efficiency depending on nutrients available to microorganisms
Toxicity of biodegradation byproducts to microbes (e.g. antibacterial litter, phenols)
Organic matter resources for fauna that promote organomineral stabilization (earthworms)

Table 2: Mechanistic analysis of factors influencing the carbon residence time in soil. (Fontaine et al., 2011; Schmidt et al., 2011; Kallenbach et al., 2016; Sinsabaugh et al., 2013; Rasmussen et al., 2018; Northup et al., 1995; Averill et al., 2014; Keiluweit et al., 2015; Bonneville et al., 2011)

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Factor changes (increase ↗, decrease ↘)		Effect on the intensity of the mechanism involved (increase ↗, decrease ↘, increase or decrease ↗↘)		Effect on carbon storage	Consideration in models Century, RothC
↗	Carbon input flux	↗	Source of organic matter	↗↗	Yes
↗	Decomposable carbon input flux	↗	Mineralization of old C by the priming effect	↘	No
↗	Biodegradabily of C input (plants, organic wastes)	↗	*Carbon use efficiency*	↗	No
		↗↘	Sorption, associations with minerals	↗↘	No
↗	Soil temperature	↗	Microbial activity	↘↘	Yes, all mechanisms combined
		↘	Sorption		
		↗	Diffusion		
↗	Water content (except pO$_2$)	↗	Microbial growth and mobility	↘	Yes, all mechanisms combined
		↘	Sorption		
		↗	Diffusion and transfer		
↘	O$_2$ (anaeroby)	↘	Microbial activity	↗	Yes
		↘	Oxydative degradation		No
↘	Granulometry: Mineral size	↘	Diffusion and transfer	↗	Yes, all mechanisms combined
		↗	Sorption		
↗	Mineralogy : - Short range order phases - Al, Fe, Ca complexes - 2:1 phyllosilicates	↗	Coprecipitation	↗↗	No
		↗	Complexation	↗	No
		↗	Sorption	↗	No
		↘	Transfer	↗	No
↗	pH	=	Microbial activity (4.5 <pH< 8.3)	0	No
		↗	Charge of organic and mineral surfaces	↗	No
		↗↘	Destabilization of organomineral associations	↗↘	No
		↘	Free Al	↘	No
		↗	Exchangeable Ca	↗	No
		↗	Fauna		
↗	Ionic species in soil solution	↗	Al^{3+}, Ca^{2+} concentration	↗	No
		↗	Na$^+$ concentration (salty soil)	↘	No
↗	N, P, S availability	↗	Decomposition of high C/N organic residue	↘	Yes
		↘	*Priming effect*	↗	No
		↗↘	*Carbon use efficiency*		No
↗		↗	Antibacterial compounds	↗	No

			Bacteriovorous predators	↗	No
	Activities of specific organisms, biodiversity	↗	Mycorrhizal symbiosis	↗↘	No
		↗	Earthworms (association with minerals)	↗	No
↗	Biotic/abiotic interactions (exsudates, excreta)	↗	Dissolution of short range order minerals	↗↘	No
		↘	Local pH	↗↘	No

50

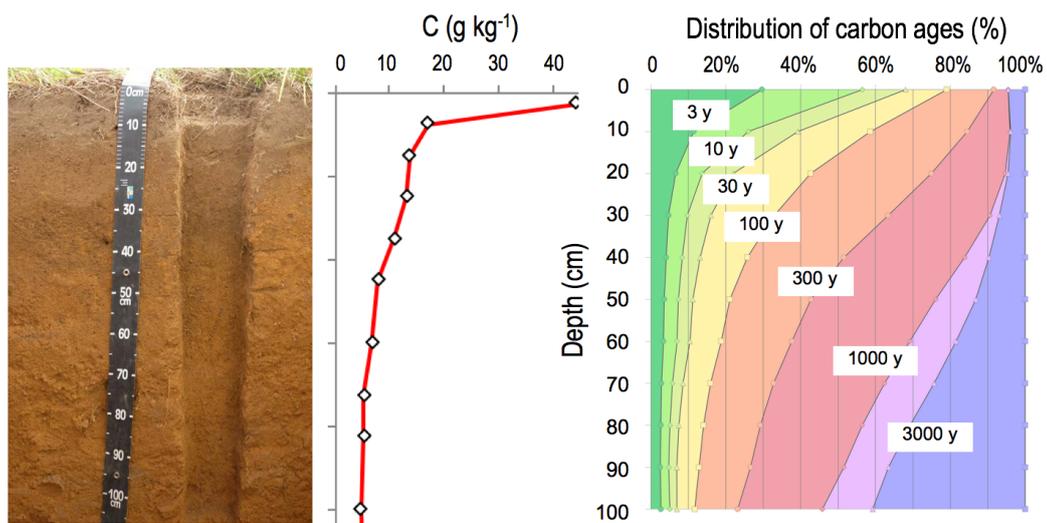



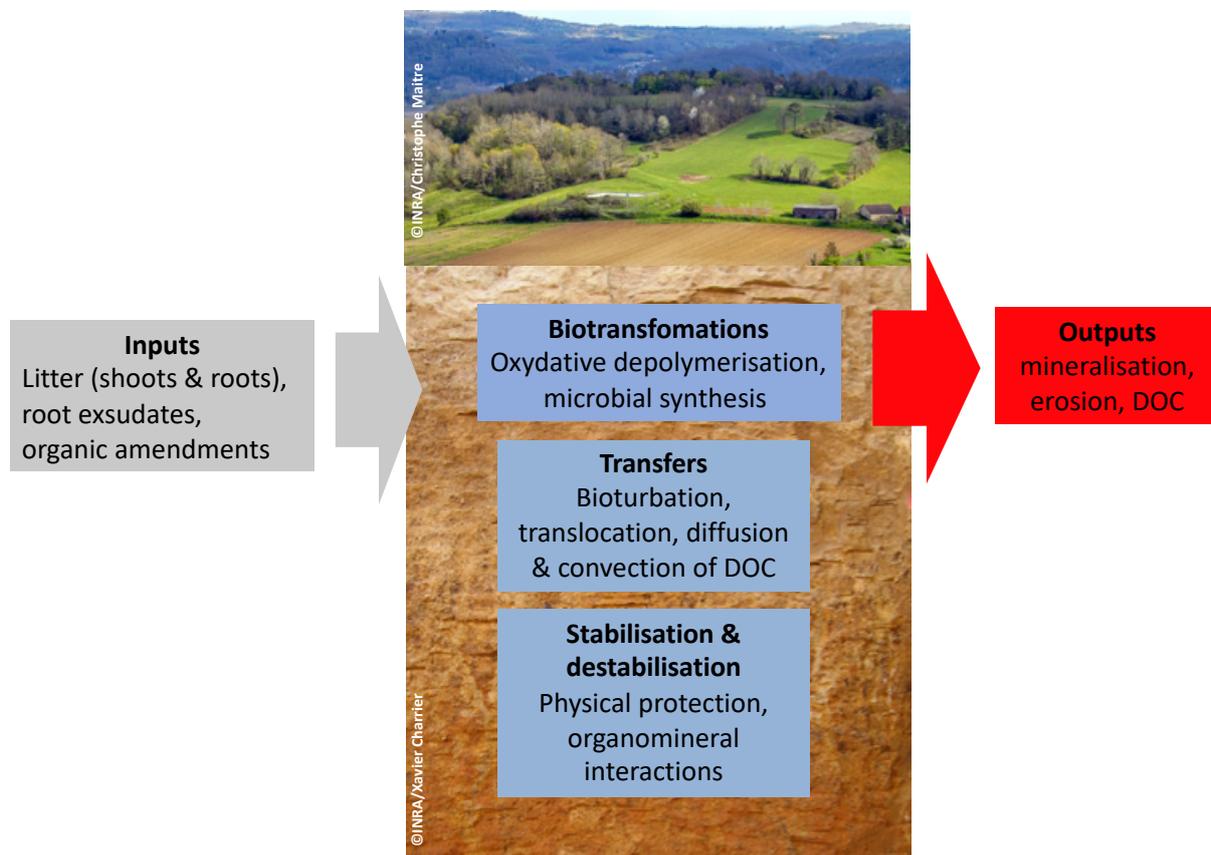
Figure 1: Grassland soil profile (left panel). The vertical distribution of organic carbon in this soil (central panel). A current distribution of carbon ages (right panel, based on data from Balesdent et al. (2018))

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Figure 2: The different processes that control carbon storage in soils (DOC: dissolved organic carbon)
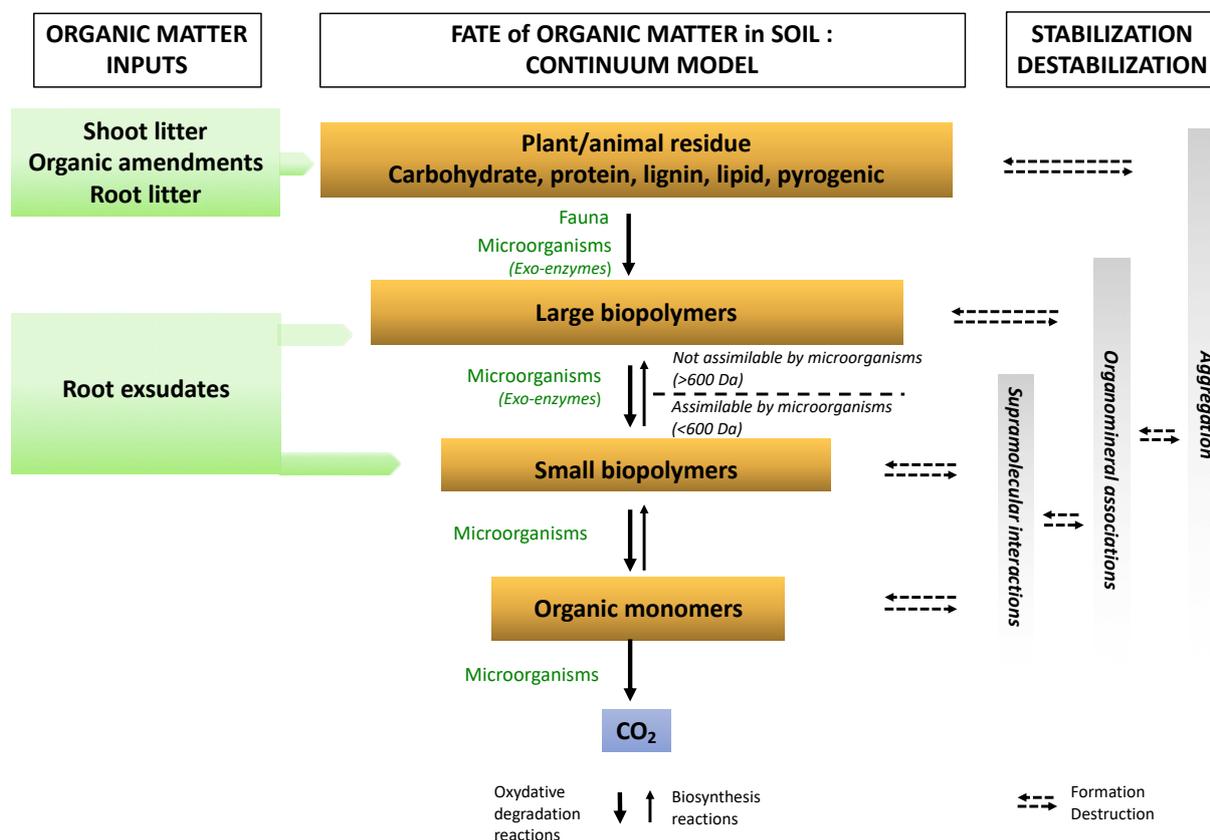
Figure 3: Representation of the soil OM biotransformation continuum model (adapted from Lehmann and Kleber (2015)). Organic matter enters the soil surface and deeper horizons in different forms. It is continuously degraded from plant and animal debris to the smallest molecules by the decomposer community. 600 Da (approximately 1 nm) represents the size at which molecules can be absorbed by microorganisms. Simultaneously, the rising oxidation state of the OM carbons increases the water solubility of the compounds, while also enhancing potential protection against further decomposition through greater reactivity to the OM (supramolecular associations), to mineral surfaces (organomineral interactions) and their incorporation into aggregates (aggregation). Solid arrows represent biotic processes and dotted arrows indicate abiotic processes.
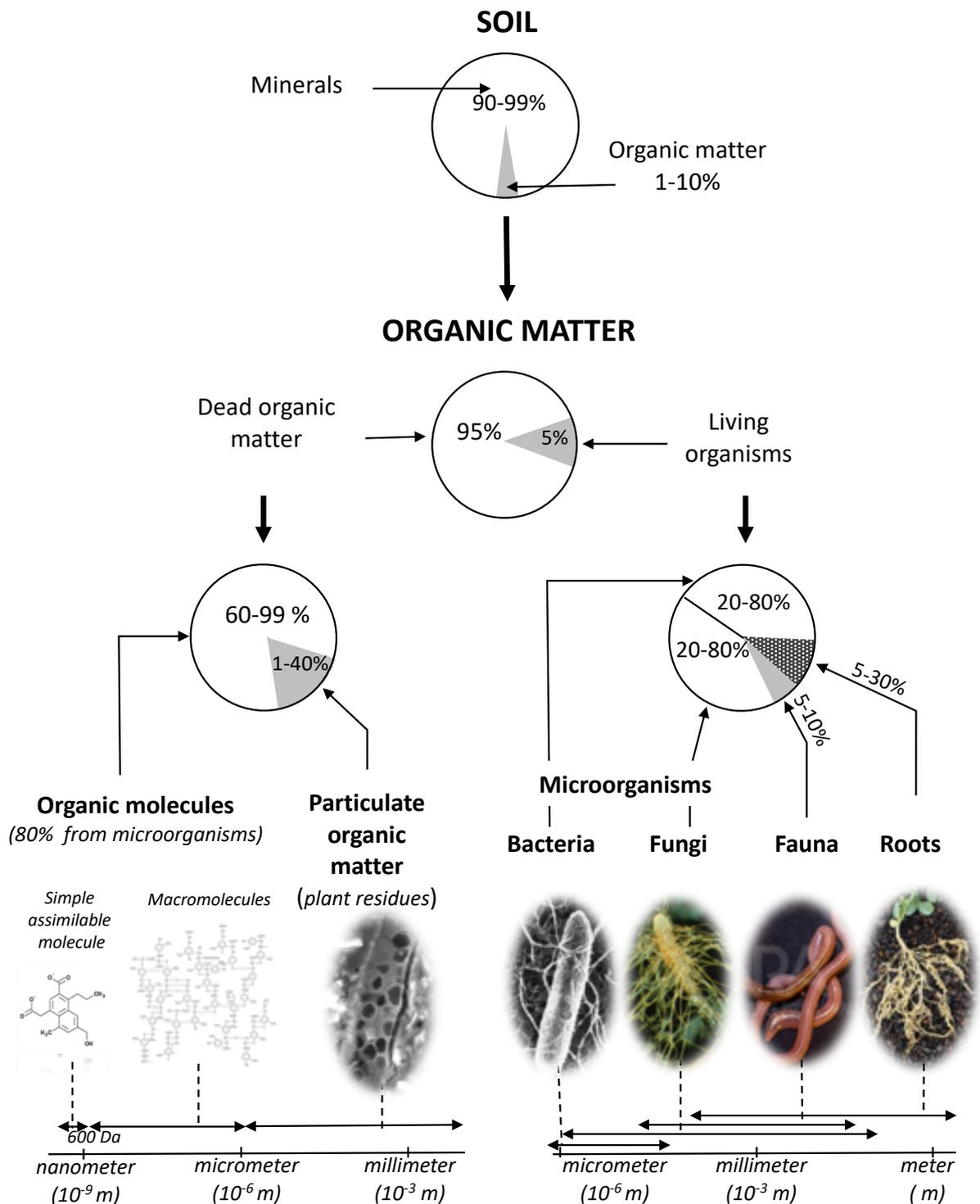
Figure 4: Nature, size range and indicative proportions of soil organic matter. Adapted from Calvet et al. (2011).
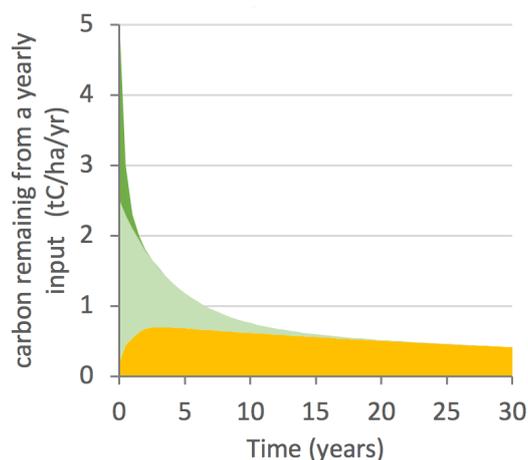
Figure 5: Simplified kinetic representation of the fate of plant organic inputs in soil, here 5 tC/ha/year. The kinetics is divided into three mineralization phases: fast, intermediate and slow. A soil that receives the same input each year therefore contains organic matter that can be divided into three corresponding pools, the size of which is represented in the figure by the colored areas. The numerical values are typical of the 0-30 cm layer of temperate crops. Old carbon represents organic material inherited from a distant past.
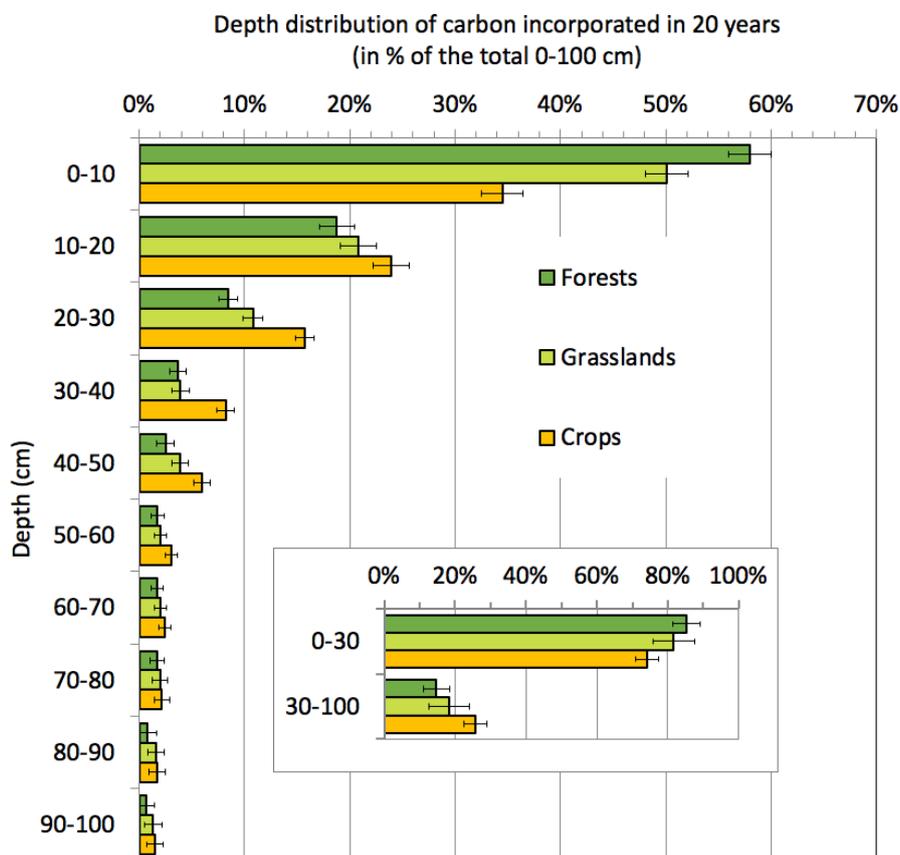
Figure 6: Vertical distribution of carbon incorporated by plant matter in the soil in 20 years under average temperate conditions. The quantity (in 10 cm increments) is expressed as a proportion of the total C incorporated in the first meter of soil. The value is a regression mean estimated from climate and land-use conditions. The error bars represent the 95% confidence interval of the estimate. (Based on data from Balesdent et al. (2018)).

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