

Understanding and fostering soil carbon sequestration

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E-CHAPTER FROM THIS BOOK



Understanding soil organic carbon dynamics at larger scales

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1 Introduction

In this chapter, we focus on the effects of biotic and abiotic factors controlling soil organic carbon dynamics at continental to global scales. On the side of natural effects, we highlight processes that can control carbon inputs, turnover, and stabilization in soils. On the side of anthropogenic effects, we focus on the role of climate change as well as historic and modern land conversion. We hereby divide anthropogenic effects into direct and indirect disturbances done by humans. Both overarching sections close with a short synthesis.

2 Natural processes affecting soil carbon dynamics¹

The cycling of carbon (C) between plants, soil and the atmosphere is undoubtedly one of the most important fields of soil research in the twenty-first

¹ This section was written by Sebastian Doetterl.

century. At global scales, the amount of C involved in this cycle is primarily a function of organic matter entering soil through plant growth, its transformation within and incorporation into soil, and the specific nature of interactions with the soil (mineral) matrix under varying environmental conditions. Given the importance of healthy soils for supporting diverse ecosystems and the delivery of a multitude of ecosystem services including global climate regulation, it is still surprising to see that, despite thousands of studies on soil properties, plant-soil interactions and soil biogeochemistry, only relatively few soil types (namely those in wealthy countries in temperate climate zones) are well studied (see Kögel-Knabner and Amelung, 2021). While these studies have greatly improved our understanding of fundamental physicochemical soil organic carbon (SOC) stabilization and destabilization processes in soils, the understanding of biogeochemical cycles in many other soil systems cannot be simply derived from findings of specific, well-studied soil types. Too diverse are the controls of processes in soil types of contrasting pedoclimatic environments that ultimately control (SO)C sequestration. Consequently, biogeochemical models developed for specific soil types are not necessarily representative for other soil systems and may only be applied with great uncertainties and potentially result in false estimates of responses of soil C cycling to global change. Lack of understanding of spatial patterns of and links between biogeochemical cycles is thus one of the largest sources of uncertainty for predicting terrestrial C cycling in global models overall (Friedlingstein et al., 2020). With examples from different climate zones, we highlight in the following chapter some key processes and gaps in our understanding of C cycling at larger scales and how closing those gaps may help to better predict SOC sequestration of soils with global significance (Fig. 1).

2.1 Controls on carbon input, turnover and sequestration²

2.1.1 Global carbon reservoirs

Carbon is cycling within and across different earth spheres, being stored, transformed, and moved at different rates through sedimentary rocks, rivers, lakes, oceans, the soil system (mineral, organic, and permafrost soil), terrestrial vegetation, and the atmosphere. Besides the total concentration, C stored in different earth systems can be characterized according to the mean residence time (i.e. time needed to exchange each C atom of the considered system or subsystem at least once). Based on the C mean residence times, different systems can be subdivided into active and inactive drivers of C dynamics. Under undisturbed conditions, almost the entire C stored in sediments or sedimentary

² This section was written by Gina Garland and Sebastian Doetterl.

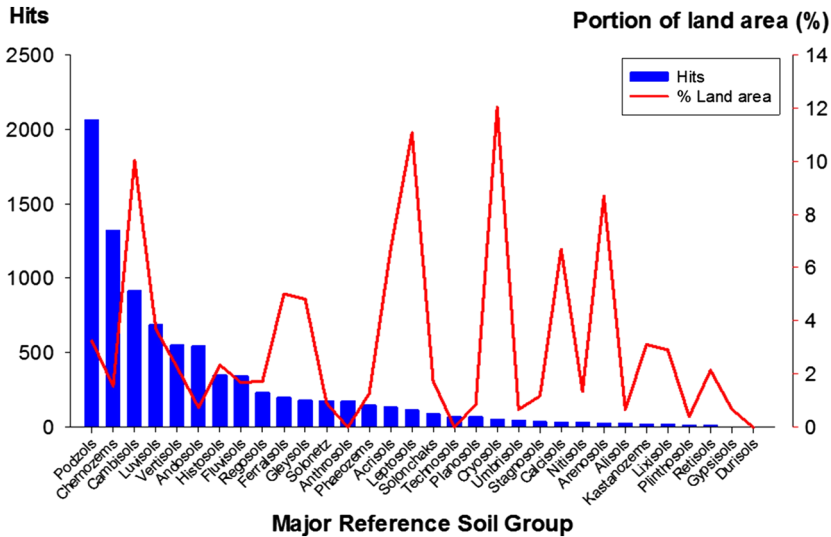


Figure 1 Database hits for joint search of the key words ‘soil organic matter and Podzols’ or with any other major Reference Soil Group according to IUSS Working Group WRB (2015), using the literature search program SciFinder Scholar (www.scifinder.cas.org; March 14, 2020; blue bars). The red lines represent the contribution of each soil group to total land area, as given in IUSS Working Group WRB (2015; Annex 1 - Description, distribution, use and management of Reference Soil Groups). The figure illustrates the frequency of organic matter research for a given soil group. It is not designed to give a full honest overview, because the search did neither include the key words soil organic carbon, nor any soil group as translated to other classification systems. Reprint of Kögel-Knabner and Amelung (2021).

rocks, for example, is considered to be inactive with mean residence times of up to millions of years (Mackenzie et al., 2004). The C stored in the deep ocean waters and sediments is also considered to be inactive, with mean residence times of more than 1000 years. In contrast, C stored in the atmosphere, in the surface oceans, in living vegetation, and in soil organic matter is considered to be relatively active, with mean residence times ranging from seconds to centuries (e.g. Killough and Emanuel, 1981; Trumbore, 2000). However, fossil fuel C from sedimentary deposits is an example of how an inactive C reservoir can be rapidly transformed into a highly active driver of global C dynamics due to its anthropogenic uses.

Besides geologic systems (upper mantle, continental crust, oceanic crust), sediments at the surface of the earth containing calcite and dolomite deposits and rocks as well as organic matter are by far the largest C reservoir (7.78×10^7 Gt) with fossil fuel-C accounting for less than 0.5% of the total 5000 Gt sedimentary organic C (Mackenzie et al., 2004). The world oceans store about 38000 Gt of C whereby the surface ocean waters (first 100 m) that are directly

interacting with the atmosphere contain about 700 Gt dissolved C and 3 Gt of C stored in the oceanic biota (e.g. Houghton, 2007; Mackenzie, et al., 2004). The living vegetation of terrestrial ecosystems stores 450–650 Gt organic C whereas soils contain 1500–3000 Gt organic C (first 2 m) (Sanderman et al., 2017; Friedlingstein et al., 2020).

Current global carbon models estimate that soils store approximately 81% of terrestrial C stocks amounting to approximately 1500 Gt C, which is more than the atmosphere (800 Gt C) and terrestrial vegetation (500 Gt C) combined (Erb et al., 2018; Friedlingstein et al., 2020; FAO and ITPS, 2015; IPCC, 2013). However, this number does not include soil in the permafrost region. Data from Tarnocai et al. (2009) and Hugelius et al. (2013, 2014) suggest that up to 1700 Gt of organic C can be found in shallow and deep permafrost soils. As such, the importance of soils as sources and sinks for atmospheric CO₂ is increasingly recognized at both the scientific and policy-making levels. Thus, on-the-ground measures to protect and increase this important C stock are currently being explored at a vigorous pace. Strong expectations are placed on soils as a critical element for combatting the current global climate crisis (Richter and Yaalon, 2012). This has in turn spurred the continuous improvement of Earth system models to determine accurate estimates of SOC stocks, the main drivers of the dynamic processes contributing to these stocks, and how they may change over time under varying climatic conditions and human activities (Chapin et al., 2009; Todd-Brown et al., 2014; Kawamiya et al., 2020).

2.1.2 Plant-soil relationships as a key component to understand soil organic carbon dynamics

One important factor to consider as a regulator for SOC stocks is vegetation (Chapter 3 of this book). Although this pool accounts for only 19% of terrestrial C stocks, it is one of the key drivers of C input into soil systems and thus the overall significance of plants in maintaining SOC stocks must not be overlooked. Indeed, it is this plant-soil feedback (Laliberte et al., 2013; Pugnaire et al., 2019), or the process by which plants modify the biotic and abiotic soil properties through feedback mechanisms, which drive not only the input of C into the system, but are also one of the key components of pedogenesis in general, along with parent material, climate, topography, and time (Dokuchaev, 1886, 1899; Jenny, 1941). In fact, through time, soil-plant interactions evolve from initial soil formation stages, where the composition and size of the soil organic matter stock is primarily determined by plant-derived inputs (Khedim et al., 2021) to later stages, where soil properties such as mineralogy and texture play an increasingly dominant role in stabilizing these different organic matter pools accumulating in the soil (Chorover et al., 2004; Mikutta et al., 2006, 2009;

Kleber et al., 2021). Ultimately, soil properties determine the capacity of soils to accumulate C (Paul, 2016). However, even at these later soil developmental stages, vegetation still plays an important role for soil carbon sequestration (Chapters 2 and 3 of this book), as the main transporters of atmospheric C into the soil system.

The net amount of SOC sequestered in a given system depends not only on the initial C introduced via plants but also on a variety of biotic and abiotic processes including rates of decomposition and the capacity of soils to adsorb organic matter onto soil minerals (Kleber et al., 2021). However, in general terms, the higher the net primary productivity (NPP), or the total vegetative biomass produced within a given ecosystem or land use type, the higher carbon inputs to soils (Smith, 2008) and subsequently the higher potential SOC sequestration. As such, the specific type of vegetation in a given area plays an important role in overall SOC dynamics, including distribution of SOC pools at different soil depths (Jobbagy and Jackson, 2000). For example, current estimates of carbon stored in different vegetation types show that forests contain the largest proportion of terrestrial C pools, with 359 Gt C stored in the vegetation and 787 Gt C in forest soils (IPCC, 2022). This is in large part because growth often occurs year round, and also because the forest litter C sources tend to be more recalcitrant than other vegetation types (Smith, 2008). Though less than forests, tropical savannas (66 Gt C in the vegetation and 264 Gt C in the soil) and natural grasslands (9 Gt C in the vegetation and 295 Gt C in the soil) are also known to sequester large quantities of C, much of which is through decomposition from their proportionally large root systems (IPCC, 2022; Soussana et al., 2006; Lorenz and Lal, 2018; Ma et al., 2021). Croplands, on the other hand, tend to provide relatively few C input (3 Gt C in the vegetation and 128 Gt C in the soil) due to the removal of biomass C during crop harvest (IPCC, 2022). However, the specific amount for a given area depends greatly on the management practices employed (see Sections 2.2–2.4 and Chapters 15–24 of this book).

2.1.3 Impact of climate on plant species distribution and soil organic carbon cycling

While the integral role of plant growth in driving both pedogenesis and SOC dynamics is unquestioned, various abiotic factors influencing these biological communities at the global scale must be considered in addition. It is well known, for example, that climatic patterns can drive and shape soil formation and SOC accrual through both physical and chemical weathering of parent material (Ehlers and Goss, 2016; Torn et al., 1997). This impacts SOC dynamics not only directly, but also indirectly through effects on geomorphology, vegetation patterns, and soil (geo)chemistry. Indeed, both historic and current temperature and precipitation patterns, coupled with parent material and

topography, have a direct influence on global aboveground and belowground biodiversity patterns, including plant species distribution and productivity (Adler et al., 2013; Zuckerberg et al., 2020). As access to global databases and advanced modeling and experimental approaches expands, it is increasingly clear that such climatically driven changes in the composition and functioning of biological communities have a significant impact on the global carbon cycle (Peng et al., 1998; Gerten et al., 2008; Crowther et al., 2019; Lu et al., 2019; Eglinton et al., 2021).

For example, in colder high latitude and high altitude climate regions, low temperatures can limit both plant growth and soil microbial activity, which in turn reduces decomposition of organic material and therefore the turnover and availability of key plant nutrients such as nitrogen and phosphorus (Hobbie, 1992; Paul, 2016). In natural ecosystems, such strong controls on nutrient availability in turn significantly influence the capacity of different plant species to grow (Hobbie, 1992) and thus significantly shape global plant distribution patterns (Aerts and Chapin, 1999). Similarly, it has often been noted that plant diversity tends to decrease from the equatorial region toward the poles due to the interactive effect of temperature and precipitation patterns (Hillebrand, 2004; Laliberte et al., 2020). Yet even within a given ecosystem type, regional climatic differences can impact SOC dynamics as well. For example, global temperature patterns in forests are known to directly influence the allocation of new carbon supplies to different tissue types. For example, trees in colder climates allocate more new C to roots in comparison to shoots (Reich et al., 2014; Ma et al., 2021). This difference in C allocation not only influences C uptake through photosynthesis, but also decomposition rates and nutrient availability, which in turn impacts C input into the soil, its turnover and potential sequestration as SOC (Kirschbaum, 1995, 2000; Davidson and Janssens, 2006). Furthermore, as vegetation patterns are strongly influenced by anthropogenic factors (i.e. management practices), the relative impact of climate on SOC sequestration must be assessed considering these other important drivers (Smith, 2008; Morris et al., 2020).

In addition to changes in temperature, moisture availability as driven by precipitation patterns are also known to greatly impact plant species distribution and biological activity (Schaffer and Rodriguez-Iturbe, 2018), and thus both directly and indirectly SOC dynamics. For example, in arid and semiarid regions, rates of microbial decomposition decrease drastically during the dry season, thus reducing nutrient turnover and availability to plants and ultimately reducing NPP (Manzoni et al., 2012a). As new soil C inputs are primarily plant derived, this impacts not only the total SOC content, but also the transport of more mobile SOC compounds (i.e. dissolved organic compounds) to greater soil depths and thus the soils' capacity to accumulate SOC (Kaiser and Kalbitz, 2012). At the same time, under these dry and nutrient

poor conditions, microbial C decomposition is reduced as well, leading to sometimes contrasting feedbacks between low C input but high SOC accrual. Conclusively, these processes highlight the interacting and complex abiotic controls on SOC storage under different climates, changing in importance as pedogenesis progresses (Rumpel et al., 2002; Quideau et al., 2001).

2.2 Soil microorganisms as agents of carbon turnover at the global scale³

2.2.1 The effect of soil microbiome composition on carbon dynamics at global scales

Belowground ecosystems are hosting very diverse microbial communities, with the number of species present in a gram of soil typically exceeding a thousand (Gans et al., 2005; Torsvik et al., 1990), and the number of individuals ranging from millions to billions (Raynaud and Nunan, 2014; Torsvik et al., 2002). Despite their microscopic size, soil microbes are important drivers of terrestrial biogeochemical cycles as they are responsible for the formation and turnover of soil organic matter (Chapter 2 of this book), and through SOC mineralization also control the amount of nutrients available to plants.

Globally, the amount of microbial biomass carbon has been estimated at 16.7 Gt C in the top 0.3 m of soils (ca. 2.3 % of SOC) and 23.2 Gt C in the top meter (ca. 1.5 % of SOC) (Xu et al., 2013). Soil fungi constitute the largest biomass (ca. 12 Pg C), followed by bacteria (ca. 7 Gt) and Archaea (ca. 0.5 Gt) (Bar-On et al., 2018). The largest stock of soil microbial biomass carbon is located in tundra, while desert ecosystems contain the lowest amount of microbes (Xu et al., 2013). In general, managed soils (i.e. grassland and agriculture) contain less microbial biomass carbon compared to soil under natural vegetation (Xu et al., 2013). At the global scale, the mass of soil microbes thus follows the opposite trend of aboveground biomass, with the greatest abundance in Arctic and sub-Arctic ecosystems (Crowther et al., 2019). This seems counterintuitive, as larger microbial abundances lead to faster rates of soil organic matter processing and thus lower SOC stocks. However, cold temperatures at high latitudes reduce the rate of soil organic matter mineralization, leading to large SOC stocks, which support large microbial abundances.

Not only the abundance of soil microbes affects soil biogeochemical cycles, also the microbial community composition is important. Bacteria are the phylogenetically most diverse group on earth (Hug et al., 2016) with the numbers of species in the millions. Similarly while the number of described fungal species is ca. 100 000 (Blackwell, 2011), their total number is estimated to

³ This section was written by Marijn Van de Broek and Aline Frossard.

be as high as 5.1 million species (O'Brien et al., 2005). The immense diversity of belowground microorganisms has been shown to have a significant impact on biogeochemical cycles in terrestrial ecosystems (Bardgett and van der Putten, 2014). Microbial diversity is driven by spatial heterogeneity (Bardgett and van der Putten, 2014), which varies from the micrometer to millimeter scale in soils (Vos et al., 2013) to the continental scale (Fierer et al., 2009). While in the past the great local diversity in soil microorganisms has obscured spatial patterns in their community composition, recent meta-analyses of high-throughput sequencing data have shown that at the global scale, microbial community composition is related to soil pH (Lauber et al., 2009; Tedersoo et al., 2014), aridity (Maestre et al., 2015), plant diversity (Prober et al., 2015), and plant productivity (Delgado-Baquerizo et al., 2018). In addition, there appears to be no clear relationship between latitude and belowground species richness as is the case for aboveground species (Bardgett and van der Putten, 2014). The ratio of plant-to-fungi richness, for example, decreases exponentially from the equator toward the poles (Tedersoo et al., 2014). The effect of the composition of the soil microbiome on soil organic matter transformation processes is more important for specific processes which can only be performed by specialized microbial groups, such as N transformation processes and lignin decomposition, compared to more general processes, such as mineralization of labile plant litter compounds such as sugars, which can be performed by a broad range of soil microorganisms (Crowther et al., 2019; Baumann et al., 2013). The latter, referred to as functional redundancy, seems to be a common characteristic of many microbial systems (Louca et al., 2018), although reduced microbial diversity was shown to affect specific decomposition functions (Baumann et al., 2013). However, a common paradigm is that not changes in microbial species diversity level, but rather community composition, are more important for soil organic matter cycling (Bardgett and van der Putten, 2014).

The two microbial functional groups whose effect on soil organic matter cycling has been studied most intensively at the global scale are arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal mycorrhizal fungi (EMF). While both form symbioses with plant roots to facilitate plant nutrient uptake, at least some EMF have the capacity to produce oxidative and hydrolytic extracellular enzymes to mineralize organic matter and obtain nutrients (Chalot and Brun, 1998; Courty et al., 2010). In contrast, AMF lack this capacity and rely on saprotrophic microbes for organic matter mineralization (Smith and Smith, 2011). While ca. 2% of plant species associate with EMF, EMF-associated trees represent ca. 60% of all trees on earth (Steidinger et al., 2019). There are two main mechanisms by which the type of mycorrhizal symbiont associated to trees has an impact on SOC dynamics. The first one is related to the ability of EMF to produce extracellular enzymes, thereby affecting nutrient availability for microorganisms and plants. This may lead to decreasing microbial activity

and soil organic matter mineralization, while on the other hand facilitating plant NPP, and thus organic carbon inputs to the soil (Orwin et al., 2011). The second mechanism is related to the quality of plant leaf litter produced by AMF and EMF-associated trees. It has been shown for mature forests in the United States that AMF-associated trees produce litter of high quality, which decomposes faster compared to litter of lower quality produced by EMF-associated trees (Phillips et al., 2013). This has a substantial effect on SOC stocks, as showed that soils in ecosystems dominated by AMF-associated trees store 70% less SOC per unit nitrogen compared to soils in ecosystems dominated by EMF dominated trees (Averill et al., 2014). In addition, Averill et al. (2014) showed that mycorrhizal association with trees has a larger effect on SOC stocks compared to climatic or edaphic factors. This knowledge has been used to successfully improve the representation of the soil microbial communities in SOC models, both at the local (Brzostek et al., 2014; Fatichi et al., 2019; Fisher et al., 2010) and global scale (Sulman et al., 2019).

2.2.2 The role of soil microorganisms in the formation and loss of soil organic carbon

While historically input quantity and quality of plant material was considered as the main driver of soil C storage and stabilization, recent paradigms have recognized soil microbial metabolism, through assimilation, growth, and necromass production, as a key control for both soil C losses and stabilization in soils (e.g. Cotrufo et al., 2013, Chapter 2 of this book). In fact, a recent review concluded that SOC stabilized through mineral interactions consists of some plant but mostly microbial-derived compounds (Angst et al., 2022). Many soil microbes utilize this soil organic matter as their main source of energy by assimilating organic molecules, after which a portion of carbon is lost in the form of CO₂ produced during microbial maintenance, growth, and enzyme production with the rest being incorporated into microbial biomass or released into mineral soil again. Since most biomolecules are polymers and too large for direct microbial uptake, many soil microbes have the ability to produce extracellular enzymes which mediate the depolymerization of large organic molecules. This microbial extracellular enzyme activity (EEA) is then directly linked to resource availability (e.g. Burns et al., 2013). The induction of enzyme synthesis and secretion by microbial cells is hereby mainly governed by local substrate concentration. Low availability of carbon or nutrient compounds will trigger the synthesis of the corresponding enzyme to facilitate nutrient release into the soil solution for uptake by plants and microorganisms. However, enzyme production is costly for cells and EEA is usually reflecting cellular resource and energy economics by maximizing the benefit while minimizing the costs. When cells endure pressure to lower the energetic demands of

extracellular enzyme production, a sufficient concentration of the reaction products need to be maintained to support cellular functions and maintain viability (Burns et al., 2013). Modeling results indicate that a minimum of 2% of microbially assimilated C must be allocated to enzyme production to sustain microbial biomass of decomposer communities at constant levels (Schimel and Weintraub, 2003). However, the percentage of C allocated to enzyme production sufficient to maintain cell viability is likely to vary according to soil environmental factors (pH and temperature) as well as quality and substrate availability, diffusion conditions, and extracellular enzyme survival and sorption to soil minerals (Burns et al., 2013). Globally, extracellular enzyme stoichiometry is strongly constrained, with an averaged C:N:P ratio of 1:1:1, based on log-transformed potential activities of C-, N-, and P-acquiring enzymes. Although mechanisms are currently mostly unknown, data gathered from many different soils confirmed that the regulation of extracellular enzymes contribute to match the microbial stoichiometric demand. As an example, an increased N availability through the excretion of N acquiring enzymes (e.g. aminopeptidases) in soil was shown to stimulate C mobilizing enzymes (Allison and Vitousek, 2005) and to enhance the activity of the phosphatase (Mooshammer et al., 2012). In this way, the investment of microorganisms to acquire N also includes mining for P to maintain an elemental stoichiometric ratio. Moreover, once excreted from cells, several extracellular enzymes can be stabilized by binding to clay minerals and organic matter compounds to retain their activity, though often reduced in comparison to free enzymes, for prolonged periods of time (Burns et al., 2013). It has been suggested that stabilized enzymes associated with organic and inorganic colloids could contribute through extracellular metabolism substantially to soil respiration (Kandeler, 1990; Maire et al., 2013) but quantitative assessments of this contribution are still lacking.

In addition to being the main agents of SOC mineralization, microorganisms play a key role in soil organic matter formation and ultimately stabilization (Chapter 2 of this book), depending on their location in the soil matrix. In the rhizosphere surrounding living roots, microbes receive carbon either from rhizodeposition or from decaying roots (Chapter 3 of this book). In mineral soil, however, microbes utilize SOC that is located in patches on soil minerals and which is often not directly plant derived but already processed through one or several microbial life cycles before being stabilized on mineral surfaces (see also Section 1.3 for more detail). While the composition of the soil microbiome will have a substantial effect on the rate of carbon mineralization in the rhizosphere, spatial (in)accessibility of SOC to microbes can become a substantial additional limitation for carbon mineralization in mineral soil (Schimel and Schaeffer, 2012). Ultimately, the fraction of carbon utilized by soil microorganisms will depend on their carbon use efficiency (CUE). The microbial CUE refers to the balance between SOC retained in microbial biomass versus

the amount of C respired and released to the atmosphere (Sinsabaugh et al., 2016, 2013; Spohn et al., 2016). CUE can also be represented as a function of stoichiometric environmental resource supply in relation to biomass composition (Sinsabaugh et al., 2016). Microbial CUE can be higher when SOC availability is limiting and microbial catabolic and anabolic metabolism is coupled. In contrast, nutrient limitation can reduce CUE by uncoupling catabolism and anabolism which increases the cost for extracellular enzyme production (Blagodatskaya and Kuzyakov, 2008). Thus, CUE is expected to vary greatly along gradients of resource availability (Sinsabaugh et al., 2017). Moreover, environmental variation in soil temperature and moisture alter the microbial metabolism thereby affecting CUE by shifting the balance between microbial growth and respiration (Allison et al., 2010; Manzoni et al., 2012b).

Thus, microbial mediation of soil organic matter formation can occur via two major mechanisms: (1) the *ex vivo* one by which extracellular enzymes attack and transform plant residue, resulting in plant-derived SOC and (2) the *in vivo* turnover of organic substrates via cell uptake, biosynthesis, growth, and death resulting in microbial-derived SOC (Liang et al., 2017). The necromass left by dead microorganisms is then either recycled as a new substrate for microbial growth or adsorbed to mineral surfaces and stabilized in the soil (Miltner et al., 2012). The balance between microbial catabolic activity, releasing CO₂ to the atmosphere and anabolic activity, which contributes to necromass formation, controls largely the magnitude of soil C sequestration (e.g. Liang et al., 2017). Necromass mostly includes organic matter from fragmented cell membranes and former intracellular compounds such as enzymes, ribosomes, and small biopolymers not recycled by the active microbial pool. In a comprehensive review, it was reported that about 30% of stable SOC is derived from microbial necromass in temperate forests, while microbial necromass contributes to more than half of the total SOC in grassland and agricultural soils (Liang et al., 2019). Moreover, the authors of that study observed that the proportion of the fungal necromass (more than 70% of total necromass) is much higher than the bacterial one (less than 30% of total necromass), independently of land use type.

In conclusion, the heterogeneous nature of soil and its chemically diverse compounds produce large variations of elemental stoichiometry, which microorganisms have to manage. Moreover, the C:N:P ratio of soil microbial biomass was observed to be significantly smaller and less variable than that of their substrates in the surrounding soil. This implies a certain degree of homeostasis (i.e. stoichiometric invariance) of microbial cells (Cleveland and Liptzin, 2007), which can constrain microbial activities. The resulting stoichiometric imbalance between microbial cells and their resource (i.e. the surrounding soil) is very important for carbon and nutrient cycling and microbial growth and functioning (Mooshammer et al., 2012, 2014). However, it is not

clear yet how soil microbes regulate C:N:P homeostasis (i.e. stoichiometric imbalance toward the surrounding soil). Four complementary mechanisms allowing microbial communities to adapt to environmental constraints have been proposed (Mooshammer et al., 2014): (1) microorganisms reduce their stoichiometric resource imbalance by adjusting C:N:P ratios internally (i.e. cellular stoichiometry), (2) microorganisms adjust the production of extracellular enzymes in order to maximize the mobilization of substrates, which are rich in limiting nutrients, (3) microorganisms ingest any available elements in their surrounding and excrete nutrient in excess to their demand, while keeping the limited ones in their cells, and (4) specialization of microorganisms, such as nitrogen-fixing prokaryotes or saprophytic fungi, which increase the availability of limiting nutrients (N and P), which are then available to other microorganisms. However, the relative importance of these mechanisms to overcome stoichiometric resource imbalances and how these imbalances affect the metabolization of organic matter and SOC sequestration via the composition and functioning of microbial communities is poorly understood.

2.3 Geochemical perspective on the properties of soils to store carbon⁴

2.3.1 Soil-forming processes at larger scales

Climate has important direct and indirect consequences on soil C cycling and ultimately sequestration. Globally, SOC stocks are generally positively correlated with moisture and negatively correlated with temperature (Post et al., 1982), whereas the longest SOC turnover rates are usually found in cold or dry regions where biological activity is constrained (Carvalhais et al., 2014; Shi et al., 2020). However, large variability in SOC stocks and turnover rates still exist within one climate zone, due to variation in soil internal properties that evolve in response to the soil-forming factors, namely soil physicochemical properties (Torn et al., 1997; Rasmussen et al., 2018; von Fromm et al., 2021).

At global scales, geology, climate, vegetation, and their interactions drive soil biogeochemical cycles and soil development (Fig. 2). Direct and indirect effects of human-related activities on soils have been recognized for long as a sixth soil-forming factor with local to global impacts on soil functions and development (Amundson and Jenny, 1997). Among the number of ecosystem services provided by soils, the biogeochemical cycling of key nutrients and water is one of the most important functions for regulating environmental systems. For example, water input and percolation rates in

⁴ This section was written by Jean-Thomas Cornelis, Sophie Opfergelt and Sebastian Doetterl.

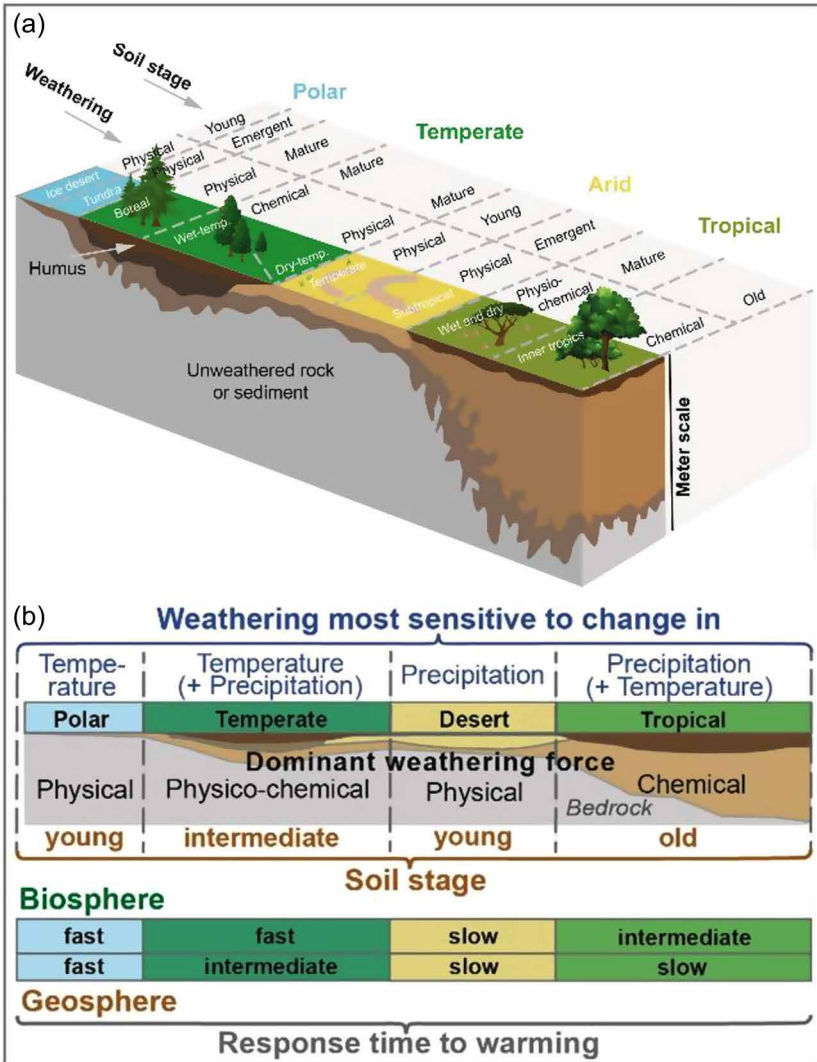


Figure 2 (a) Distribution of weathering forces and soil development stages at the global scale. (b) Conceptual design of sensitivity of bio- and geosphere to climate change in relation to weathering and rate of expected change (modified after Doetterl et al., 2018).

soils are key drivers of thermodynamics and kinetics of soil biogeochemical reactions (Chadwick and Chorover, 2001), which in turn govern the ability of soils to retain nutrients and to stabilize organic matter against decomposition (Witzgall et al., 2021). With the rising human influence on soils, we entered an era in which anthropogenic soil disturbance needs to be considered as the main driver of soil development in many ecosystems. Thus, there is an urgent

need in revisiting our understanding of the main controls on the upper and lower boundaries of soils and the development direction of key soil properties (Cline, 1961; Richter and Billings, 2015). For example, soil moisture is spatially variable across climate zones as a function of atmospheric and land surface conditions (Lawrence and Hornberger, 2007). From a geochemical perspective, the transition from alkaline to acidic soil domains is globally driven by water balances (Slessarev et al., 2016). Shifts in hydrology and soil saturation/aeration regulate redox conditions potentially altering carbon storage in soils through variations in microbial activity (Lehmann et al., 2020) and/or electron transfer between minerals and organic matter (Kleber et al., 2021). Similarly, hydrology controls carbon inputs through its effect on biomass production and microbial decomposer communities controlling SOC turnover (see Sections 1.1 and 1.2). However, human disturbances of the water cycle are not adequately represented at scales at which soils differ in their development and geochemical characteristics (Vörösmarty and Sahagian, 2000). Furthermore, most of our mechanistic understanding of soil processes and warming is derived from studies in temperate zones (Haaf et al., 2021; Kögel-Knabner and Amelung, 2021). A holistic, global assessment on factors controlling soil respiration except for basic variables that integrate various processes at once (clay content) has not been done yet (Davidson and Janssens, 2006). In addition, current terrestrial biosphere models (TBM) use highly simplified approaches to represent carbon (C), nitrogen (N), and phosphorus (P) dynamics in soils and do not consider hydrology or geochemistry-related differences in soil properties and soil formation that affect C, N, and P cycling. Soil is not mechanistically represented in these models but is treated as a black box with a given mostly budgetary function for key nutrients.

2.3.2 Soil formation as control on (bio)geochemistry and soil organic carbon storage

Environmental factors controlling soil development (Chadwick and Chorover, 2001) can lead to the formation of soils with very contrasting contents, availability and speciation of major (Ca, Mg, K, P, Si) and trace elements (Fe, Mn, Mo, Zn) (Jobbagy and Jackson, 2001). Changing soil-forming conditions can affect the geochemistry of such elements and thereby the capacity of soils to store organic carbon. The chemistry of these elements is also sensitive to changes in water-related soil-forming conditions (change in drainage and redox conditions). At global scale, SOC retention in terrestrial ecosystems is forced by climate-driven thresholds, which govern prevailing mineral-related carbon stabilization mechanisms in which a range of elements play a key role (Kramer and Chadwick, 2018). For example, in humid regions, it is well-established that Al, Fe, and Mn

geochemistry is central with regard to the ability of soils to store SOC (Kleber et al., 2021; Allard et al., 2017; Johnson et al., 2015; Stuckey et al., 2018). In the warming Arctic, permafrost thaw is not only associated with direct losses of labile organic matter but also with changing conditions for Fe-bearing mineral dissolution (Monhonval et al., 2021; Opfergelt, 2020; Patzner et al., 2020), which are intimately linked with redox-sensitive elements and a lowering of the potential for soils to store SOC through organo-mineral associations. Similarly, decreasing soil drainage in warming high-latitude peatlands is considered to decrease Fe export from soils as Fe-organic complexes, which in turn has potential implications for the part of organic matter stored in soils as chelated with Fe ions (Opfergelt et al., 2017). In dry regions with alkaline and less acidic soils conditions, other elements such as calcium may take over the role of the main binding partner for organic matter (Rowley et al., 2018). Thus, shifts in hydrology and soil saturation/aeration shape the biogeochemical cycling of key elements (Si, Al, and Fe) involved in secondary mineral formation (clay minerals and Fe-, Al-oxyhydroxides) or redox-sensitive elements (Fe, Mn, or Mo) with key ecological functions (Herndon et al., 2020). The distribution and mobility of both cations and anions in soils shows stark contrasts between tropical (Fritsch et al., 2009) and temperate regions (Fekiacova et al., 2017; Otero et al., 2009) due to the varying development and weathering stages of soils, with often sharply contrasting pH and redox conditions. In tropical soils, hematite (Fe_2O_3) is the main soil constituent involved in organic matter stabilization while soil-forming processes in temperate zones lead to the formation of goethite (crystalline FeOOH) and/or ferrihydrite (amorphous $\text{Fe}_2\text{O}_3 \cdot 0.5\text{H}_2\text{O}$), which are key constituents to SOC stabilization (Kleber et al., 2015). Beyond soil redox controls, it is worth pointing out that soil aeration can also have indirect effects by moderating the bioavailability of trace elements (Fe, Mo, Mn, Zn) that are key in biomass production and in microbial enzymatic ability to process soil organic matter.

In conclusion, these examples remind us that the control of environmental conditions on soil development and soil properties will be highly influential on biogeochemical cycles and thus SOC sequestration through direct (adsorption of organic molecules) or indirect (interaction with trace elements acting as enzymatic cofactors) effects on organic matter storage between contrasting climate regions. Furthermore, the relative importance of various environmental controls (Fig. 3) on the carbon cycle changes over time as soils develop. Thus, soil processes as controls on geochemistry and the intertwined interactions with trace elements should certainly deserve further investigations with regard to SOC stabilization at a global scale. The role of trace elements such as Mo certainly should receive more attention. This is exemplified by the role of Mo in biomass production as a cofactor in the N-fixing enzyme nitrogenase that is associated with roots (Barron et al., 2009; Bellenger et al., 2008). Another

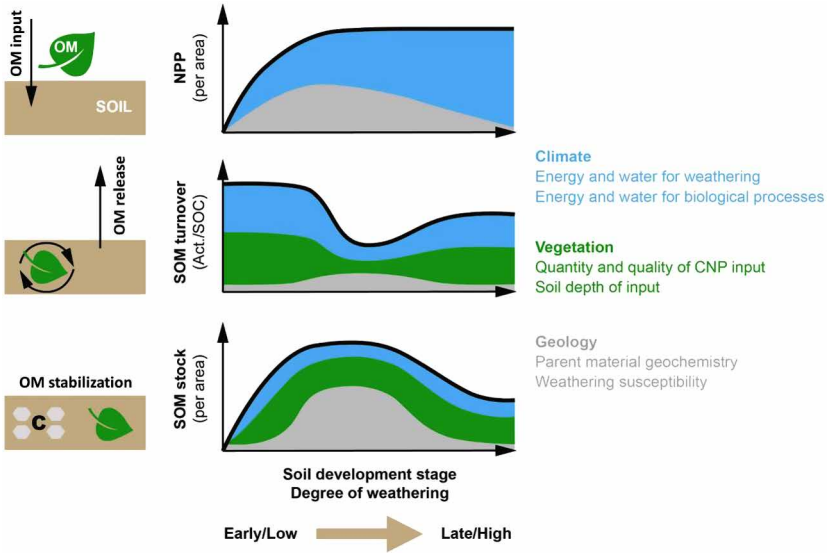


Figure 3 Representation of biological (vegetation and microbial) processes in focus and their hypothesized trajectories along timelines of soil development. Upper panels: NPP and OM input. Middle panels: OM matter release and microbial OM cycling in soils. Lower panels: OM stabilization with minerals and SOM stock. Y-axis represents size of stock or flux. X-axis represents the degree of soil development. Colored area in plots represent the effect size of key environmental controls (climate, vegetation, and geology) on the respective process in focus at various soil development stages.

element is Mn, a cofactor of Mn peroxidase, strongly controlling the later stage of soil organic matter decomposition (Berg et al., 2007).

3 Carbon cycling in the Anthropocene: direct and indirect human disturbance of soil and its impact on soil organic carbon

The global influence of human activity on soils and the biogeochemical cycles therein is an important factor determining our influence on the environment as a species with reach to almost all terrestrial ecosystems. For thousands of years, humans have altered soils directly through changing land use and the deliberate modification of soil properties to satisfy their needs. With climate change, humans now also alter soils indirectly and in regions where humans are not present in large numbers or where no direct interest in the use of soils exists. In the light of the rapidly increasing global impact of human activity on soils and ecosystems, the following section aims at illustrating the main processes and drivers for historic and future patterns of SOC gains and losses

through examples of anthropogenic activity, which have altered soils at large scales.

3.1 The role of human-induced climate change⁵

3.1.1 Temperature effects on soil organic carbon cycling

Temperature describes the amount of thermal energy present in a system, with higher temperatures typically leading to increased reaction rates of processes such as microbial decomposition of soil organic matter and greenhouse gas (GHG) fluxes to the atmosphere (Carey et al., 2016). The relationship between reaction rates and temperature is generally positive and nonlinear (e.g. exponentially increasing). However, not all warming results in increased C loss from soils. For example, warming temperatures during the winter in temperate ecosystems can melt the insulating snow layer and paradoxically result in soil freezing (Reinmann and Templer, 2016). Winter soil freezing can reduce SOC loss due to decreases in microbial biomass and exoenzyme activity (Sorensen et al., 2016). At high temperature extremes decomposition may also be slowed, either due to the denaturing of enzymes involved in decomposition (Schipper et al., 2014), microbial acclimation (Bradford et al., 2010; Bárcenas-Moreno et al., 2009), community shifts (DeAngelis et al., 2015), or interactions between temperature and soil moisture. At higher temperatures, surfaces tend to increase their evaporation, resulting in potential water stress, which can inhibit soil microbial activity (e.g. warming-induced drying decreases biological activity) (Hicks Pries et al., 2017). Contrastingly, in cold regions, warming can lead to higher water availability (e.g. water is less frozen throughout the year) and stimulate plant growth and microbial activity alike. This increased activity could potentially lead to higher C input to soils (see the following section for details).

Most of our hypotheses for how soils will respond to warming temperatures come from field warming experiments. These experiments typically measure total SOC stock over a period of 1–25 years, though most data from warming experiments are the result of manipulations of <5 years (Crowther et al., 2016; van Gestel et al., 2018). Crowther et al. (2016) found that the majority of soil warming experiments measured a loss in SOC stocks. However, a later study by van Gestel et al. (2018) found that when including more data points than in the original study, the SOC stock warming response was not significantly different from zero. Indeed, soil responses in field warming experiments are very heterogeneous. This may be partially accounted for by the difficulty of

⁵ This section was written by Rose Abramoff and Sophie von Fromm.

measuring a relatively small change to a large pool, and by changes to plant inputs induced by warming. Field-scale warming experiments consistently report increased rates of C lost as CO₂ from the soil surface (Carey et al., 2016; Haaf et al., 2021), SOC losses from subsoil (Soong et al., 2021) but also increased plant inputs, which may offset to some extent these losses.

Soil warming may not affect all SOC pools equally. Historically and for the purpose of modeling, soils have been divided into conceptual pools based on their turnover time such as *Active*, *Slow*, and *Passive* (Parton et al., 1987). More recent conceptual and simulation models consider SOC pools that are measurable by fractionation or extraction (Abramoff et al., 2018; Robertson et al., 2019). Two common SOC pools measured by density fractionation are particulate organic matter (POM) that represents incompletely decomposed plant material, and mineral-associated organic matter (MAOM) that consists of organic matter that is complexed in some way with mineral surfaces (Kleber et al., 2021). Warming temperatures typically cause loss of total SOC in the absence of changes to plant inputs, yet the amount of C in some functional fractions of soil such as POM and/or MAOM may increase (Rocci et al., 2021). Recent studies have highlighted the differences in the vulnerability of POM and MAOM to warming (Rocci et al., 2021; Lugato et al., 2021; Soong et al., 2021), with POM generally found to be more vulnerable to warming than MAOM. For example, Lugato et al. (2021) used a space-for-time approach to infer the vulnerability of POM and MAOM to global warming, showing that estimates of POM and MAOM were lower in warmer than in colder locations. This inferred sensitivity was greater for POM than it was for MAOM, although there were differences across land use types (e.g. more absolute POM loss in forests, more absolute MAOM loss in croplands). Similarly, Soong et al. (2021) noted that there was a significant decrease in POM concentrations at 1 m depth after 3.5 years of soil warming in a conifer forest, while MAOM concentrations increased in the subsoil. The increase in MAOM concentrations may have been due to an increase in microbial activity and dissolved organic C (DOC) concentrations, which were also observed at this depth, and the more rapid and selective decomposition of the easily available POM relative to the total SOC stock.

While there is still little evidence available on the effects of temperature on POM and/or MAOM fractions at the field level, there are theoretical (Conant et al., 2011) and modeling (Sulman et al., 2018; Abramoff et al., 2019) studies that make different assumptions about the temperature sensitivity of MAOM (from negative to neutral to positive) depending on the bond type and whether the majority of bonds involved in the organo-mineral associations are expected to be endo- or exothermic. These studies find large potential variations in the modeled SOC stock as a result of these assumptions.

The large variation in SOC temperature response observed in field experiments and for different soil functional fractions underlines that

temperature is not the only driver for the response of soils to warming, and it may not even be the main driver. Rather, soil responses to warming interact with the local vegetation, climate, geochemistry, and land use. Haaf et al. (2021) found that climate was not the dominant control over the temperature sensitivity of soil respiration, especially in temperate ecosystems. Rather, a wide variety of environmental characteristics explained the temperature sensitivity, such as soil solution chemistry, plant growth conditions, texture, clay, and weathering. In particular, the temperature sensitivity of organic compound decomposition depends on soil to resist microbial decomposition is depending on the mechanisms that control their stabilization with minerals, rather than their chemical composition (von Lützow and Kögel-Knabner, 2009; Moinet et al., 2018, 2020). However, climate also has a strong influence on the temperature sensitivity of decomposition in extreme environments, such as cold and dry regions. Thus, using large datasets to assess SOC turnover should always be combined with field and laboratory experiments aiming to disentangle relevant stabilization mechanisms. In doing so we will be able to better understand the major factors controlling temperature sensitivity of SOC turnover in different regions of the world, and their interaction with moisture availability as main controls of SOC sequestration and loss.

3.1.2 Moisture effects on soil organic carbon cycling

Water is the main driver of weathering, mobilization of nutrients, leaching, microbial activity, and redox potentials in soils. The effects of changes in soil water levels can depend on soil texture, porosity, bulk density, and drainage, and often effects are nonlinear and strongly interact with temperature (Xu et al., 2004). Many model representations of soil moisture and SOC loss assume that soil-water relations follow an optimum curve, with specific soil moisture values for which SOC loss is maximized (Moyano et al., 2013). At other moisture conditions, SOC loss from heterotrophic respiration may be lower, either due to anaerobic conditions at high moisture levels (Skopp et al., 1990), or a decrease in effective substrate availability due to low diffusion rates and pore connectivity under dry conditions (Kleber et al., 2021; Peyton Smith et al., 2017).

Experiments that manipulate soil water are often difficult to compare due to the numerous types of manipulations that are conducted (e.g. amount and frequency of watering). A recent review of more than 500 drought studies found that only a third of the studies explicitly reported how 'drought' was defined, and there were many different types of definitions, ranging from reduced rainfall, low water depth, plant stress, soil moisture, natural occurrence of the dry season, or a difference from ambient conditions (Slette et al., 2019). Nevertheless, field and laboratory experiments that manipulate soil moisture have provided many insights into the biological and chemical effects of soil water.

Drought and rewetting experiments are often observed to affect SOC cycling indirectly via changes to plant growth and subsequent C allocation belowground (Bredemeier et al., 1998; Ingrisch et al., 2020). However, direct effects of soil moisture conditions on SOC cycling have also been observed. For example, dry conditions were shown to affect soil enzyme activity (Sanaullah et al., 2011) and directly suppress CO₂ emission from soils in seasonally dry climates such as the Mediterranean forests (Asensio et al., 2007; Hicks Pries et al., 2017) or well-drained temperate soils (Borken et al., 2006). However, in moist soils, drying and draining may increase the aerobic pore space in the soil, which may both increase CO₂ emissions and decrease CH₄ emissions, respectively increasing CH₄ uptake. This is commonly observed in both cool moist soils such as peatlands (Qiu et al., 2021; Huang et al., 2021) and in warm moist soils such as tropical soils (Wood and Silver, 2012; Cleveland et al., 2010). Therefore, the overall effect of the moisture regime on SOC sequestration depends on the balance of CO₂, CH₄, and N₂O emissions, SOC accumulation via plant inputs and microbial transformation, and DOC leaching.

3.1.3 Integrating biosphere responses to human-induced climate change

Anthropogenic GHG emissions are causing rapid increases in soil temperature and changes to precipitation regimes (IPCC, 2021). Under climate change, the effects of temperature and moisture on SOC cycling are becoming increasingly important, but the magnitude of their effects and internal feedbacks remain uncertain across different regions and scales (Wiesmeier et al., 2019). While temperatures are expected to warm globally, predicted changes in precipitation are much more variable. Both, the frequency and intensity of heavy precipitation and droughts have increased since the 1950s and are predicted to continue to increase in the future (IPCC, 2021). These indirect disturbances of ecosystems may interact with direct disturbances to soil such as those related to land cover change, which can alter local and regional temperature and moisture regimes.

While the effects of typical climatic trends on vegetation patterns and carbon cycling have been well-described, it is important to note that our rapidly changing climate has introduced unprecedented and unpredictable climatic events, of which the complex environmental consequences are just beginning to be examined. Intense shifts in precipitation have resulted in simultaneous flooding and droughts, with drastically fluctuating temperatures further exacerbating these changing conditions (Seneviratne et al., 2021). For example, although wildfires are considered typical environmental disturbances that have been recorded both historically and contemporarily, both the frequency, intensity, and even regions of fire occurrence have changed dramatically over the past decades (Westerling et al., 2006; Canadell et al., 2021). Such drastic

changes are estimated to affect not only vegetation dynamics, but the global carbon cycle as well. For example, it was shown that the global average of soil C and N contents from fire-affected ecosystems decreased by 12.1% and 10.4%, respectively, with savanna grasslands and broadleaf forests showing the highest decreases (Pellegrini et al., 2018). Such significant changes are hypothesized to limit future plant growth and thus further exacerbate the carbon losses predicted from such events (Pellegrini et al., 2018). Furthermore, changes in fire regime have also been shown to change the actual structure and composition of vegetation species over time, with more herbaceous and grass species becoming dominant in fire-prone areas compared to woody species (Reich et al., 2001) and appearing in ecosystems where they were formerly less frequent or even unknown (Hu et al., 2015; Bowman et al., 2020). As forests have been shown to sequester more C than any other ecosystem type (IPCC, 2022), it is likely that reducing global forest cover in such a way will significantly reduce the capacity for terrestrial C storage as we know it.

In addition, legacy SOC stored in organic soils under boreal soil is likely to be affected by increasing fire return intervals thereby turning boreal forests from a small sink into a C source (Walker et al., 2020). One changing climatic factor undoubtedly contributing to these more frequent fire events is the increasingly widespread occurrence of prolonged droughts brought about by increasing temperatures and outcompeting evapotranspiration rates relative to water recharge (Westerling et al., 2006; IPCC, 2013). Not only are such extreme droughts becoming more frequent in the past decades, they are also more widely spread than previously recorded, a trend which is predicted to increase even further in the coming years (IPCC, 2013). Such changes in temperature and water availability have been shown to significantly shape plant species distribution at both local and regional scales through mechanisms such as niche differentiation (Engelbrecht et al., 2007) as well as through changes in the spatial distribution of soil nutrient availability (John et al., 2007). Together, these direct changes in both plant species composition as well as soil nutrient composition impact rates of organic matter decomposition, which in turn influence the amount of nutrients available for plant uptake, SOC sequestration onto soil minerals, and release into the atmosphere through microbial respiration (Davidson and Janssens, 2006).

However, one key factor which must not be overlooked is the strong change in precipitation patterns that have occurred in the past decades. For example, in addition to droughts, flooding has also become more frequent in recent years (Doocy et al., 2013). Such events can lead to soil erosion and landslides, which have a clear and direct impact on vegetation patterns and thus subsequently SOC dynamics. Yet even mild flooding can increase the soil water content to the extent that oxygen diffusion into the soil system is drastically reduced, inducing changes in the soil redox potential with effects on electron transfer and organo-mineral complexes (Keiluweit et al., 2017) and thus decreasing potential

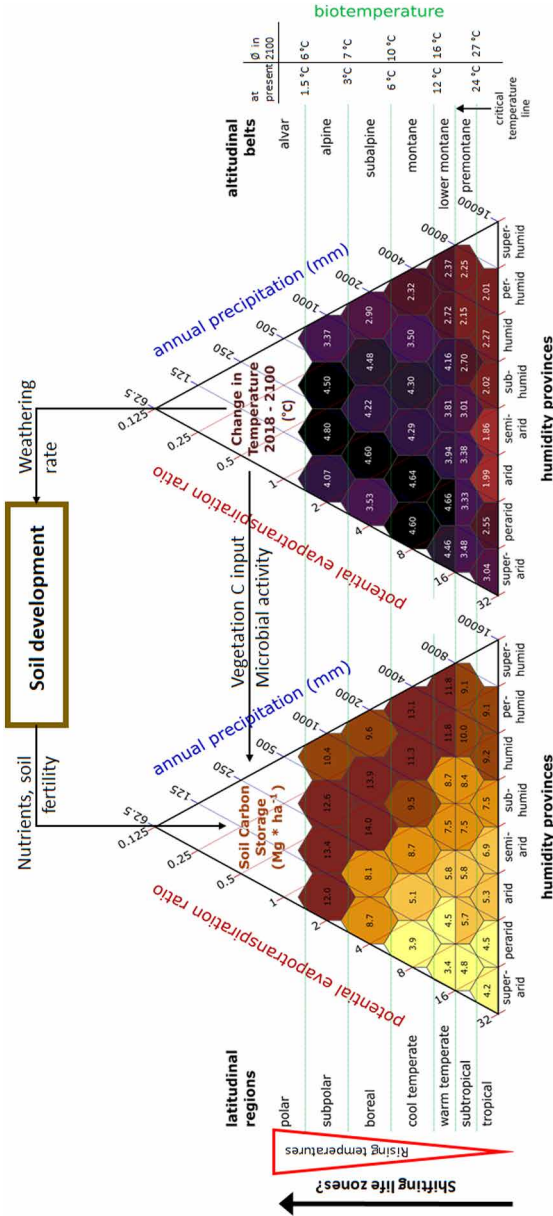


Figure 4 Holdridge life zones (HLZ) represented in hexagons for vegetated climatic regions of the world. Eight humidity provinces based on the mean annual precipitation are distinguished and plotted against annual mean precipitation and potential evapotranspiration leading to distinct bioclimatic (life) zones. Left panel: current SOC stocks following Jungkunst et al. (2021). Right panel: potential temperature increase in each HLZ according to the CMIP6 SSP3 RCP7.0 scenario following IPCC (2014). As a consequence of global warming, short- and long-term responses of biological processes (vegetation and soil microbial activity) as well as of soil weathering rates are to be expected with unknown consequences for the global SOC budget.

metabolic processes leading to a slowdown of decomposition rates (Davidson and Janssens, 2006). While it is estimated that such changes in climate will decrease land carbon uptake and SOC sequestration in future years, the exact magnitude of such changes is difficult to accurately predict due to the complex interconnected factors influencing these biogeochemical processes (Canadell et al., 2021). A way to illustrate the potential effects of changing climates on global SOC stocks and potential feedback to soil development among Holdridge life zones (Holdridge, 1947) is given below, modified following Jungkunst et al. (2021) (Fig. 4). In this study, Holdridge life zones system as a global bioclimatic scheme for the classification of land areas are used to map distinct soil and (climax) vegetation patterns as important factors for assessing SOC stocks.

3.2 The historic and modern role of global land use change on biogeochemical cycling and soil organic carbon sequestration⁶

3.2.1 Human impact on soil organic carbon dynamics through land use change and intensive agriculture

Among the active C reservoirs, especially soils and the living above- and belowground biomass show distinct regional variations in the amounts of C stored, with both components being highly vulnerable to human-induced disturbances. For example, boreal forests currently store about 559 Gt of C globally, of which 84% is found in soils, whereas tropical forests store about 428 Gt of C with 50% in soils (Janzen, 2004). On the lower end of the spectrum are cropland agro-ecosystems that contain about 131 Gt of C with more than 90% of the C found in soil (Janzen, 2004). Both soil and biomass store C mainly as organic C that can be lost directly to the atmosphere in the form of CO₂ or CH₄ or to aquatic ecosystems in various organic or inorganic forms. Such losses are accelerated and magnified by anthropogenically induced disturbances of intact terrestrial ecosystems by, for example, destroying, removing, or degrading the above ground vegetation and using the soil for agricultural production. The intensity and rate of such disturbances, expressed as area disturbed per unit time is thereby directly related to the increasing demand of a growing global population for food and other commodities. Over the last centuries, the human population expanded globally from about 253 million in 500 AD to about 7.3 billion in 2015 (Klein Goldewijk et al., 2017). This growth resulted in an intensified and increased rate of land use to provide food, feed, energy, fiber, construction materials, consumer products, space for infrastructure and urbanization, as well as resources and raw materials for industrial production.

⁶ This section was written by Michael Kaiser, Gina Garland and Sarah van den Broek.

From 500 to 2015, the areas globally used as cropland and grassland (pasture and rangeland), for example, increased from 133 to 1591 million hectares and from 249 to 3241 million hectare (Klein Goldewijk et al., 2017; see also Fig. 5), respectively. This increase came mainly at the cost of primary or intact terrestrial ecosystems (Hurtt et al., 2020).

Studies dealing with temporal aspects of global land use change patterns consider the majority of terrestrial ecosystems to prevail in their primary undisturbed conditions until 1800–1850 (e.g. Sanderman et al., 2017; Friedlingstein et al., 2020) suggesting that the majority of SOC lost due to system transformations appeared in the last 150–200 years. Based on Hurtt et al. (2020), global trends in the distribution of major land use classes between 850 and 2015 can be summarized as a decrease in the areas covered by primary non-forest and primary forest and an increase in the areas covered by secondary forest as well as managed pasture and rangeland, crop land (annual

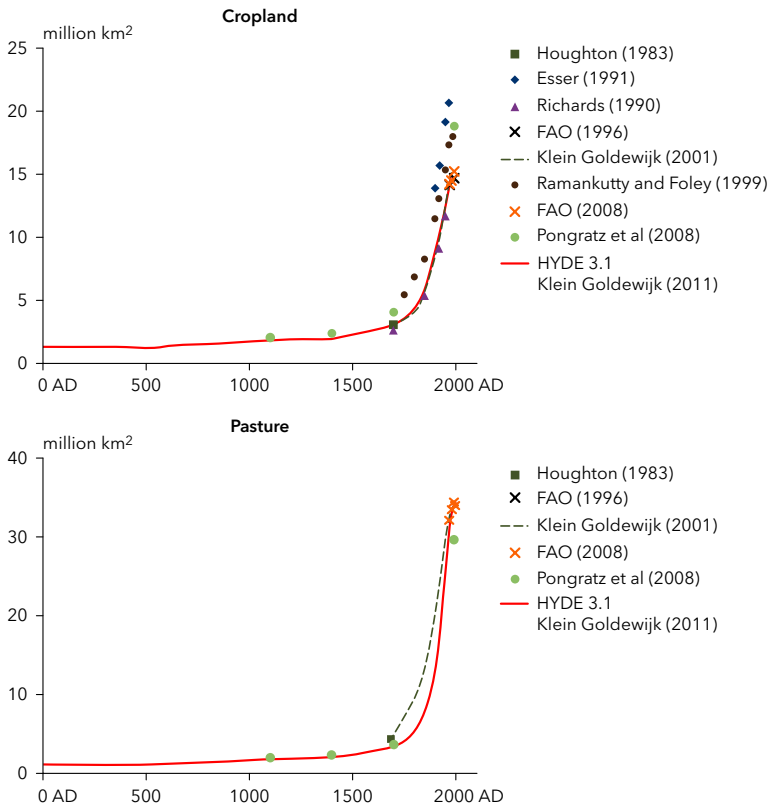


Figure 5 Overview of historical changes in global agricultural land area, divided in cropland and pastures. Published in Klein Goldewijk et al. (2011).

C3 and C4, perennial C3 and C4, C3 legumes), and urban land. The percentage of agricultural land (crop land and grazing-pasture/rangeland) increased from 2.9% of the total land area in 500 to 37.1% in 2015 (Klein Goldewijk et al., 2017). For estimating historical and actual losses of C from terrestrial ecosystems to the atmosphere due to land use change, both compartments biomass-C (living and dead) and SOC need to be considered.

As summarized by Friedlingstein et al. (2020; see also Fig. 6), land use change-induced CO₂ emissions and uptake fluxes are calculated based on

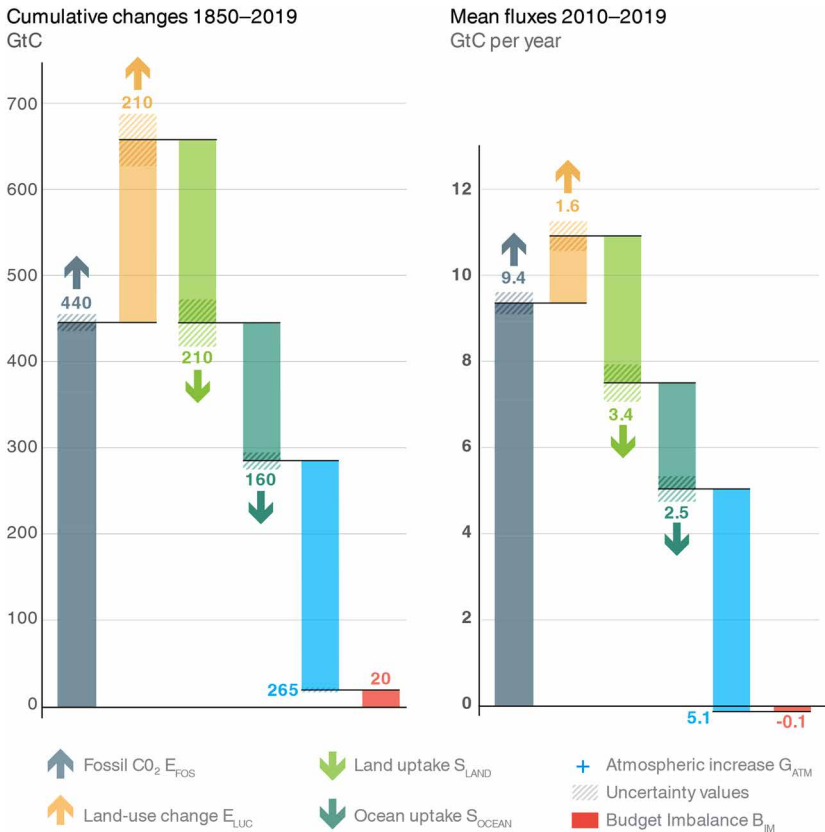


Figure 6 Cumulative changes during 1850–2019 and mean fluxes during 2010–2019 for the atmospheric perturbation as defined in the legend. The components of the CO₂ budget that are reported annually include the following separate estimates for the CO₂ emissions: (1) fossil fuel combustion and oxidation from all energy and industrial processes, also including cement production and carbonation (EFOS); (2) the emissions resulting from deliberate human activities on land, including those leading to land-use change (ELUC); (3) their partitioning among the growth rate of atmospheric CO₂ concentration (GATM; Gt C year⁻¹); (4) the sink of CO₂ in the ocean (SOCEAN); and (5) the sink of CO₂ on land (SLAND). Published in Friedlingstein et al. (2020).

bookkeeping models, which go back to the original bookkeeping approach of Houghton (2003) that includes C stored in vegetation and soils before and after land use change expressed as the transitions between various natural vegetation types to cropland and pasture. Land use change related CO₂ emissions have also been estimated using dynamic global vegetation models (DGVMs) that account for deforestation and regrowth but do not represent all processes resulting directly from human activities on land such as peat fires and fires as a management tool, N fertilization, or irrigation (Friedlingstein et al., 2020). Based on calculated yearly emissions, Gasser et al. (2020) estimated a cumulative total loss of 206 ± 57 Pg C due to land cover change for the period from 1750 to 2018. A comparison to the cumulative losses of 235 ± 75 Pg C for the period of 1750–2018 and of 205 ± 60 Pg C for the period of 1850–2018 as calculated by Friedlingstein et al. (2020) highlights that the majority of C losses resulting from land use change took place over the last 150 years. The land use change over the last 250 years therefore transformed vegetation types that can provide a large carbon sink per area unit (i.e. forests, native grasslands) into less efficient land use types such as cropland or degraded grassland. Gasser et al. (2020) accounted for a land use change-induced global 'loss of additional sink capacity' of 0.68 ± 0.57 Pg C per year (2009–2018) and 32 ± 23 Pg C in total (1750–2018), which is excluded from the calculated emissions.

Gasser et al. (2020) provided a breakdown into different model based C pools, which revealed mean annual C fluxes from and to the atmosphere over the last decade of -3.66 ± 0.96 Pg C year⁻¹ for vegetation C due to biomass regrowth, 2.84 ± 0.85 Pg C year⁻¹ for SOC mainly derived from heterotrophic respiration of SOC and dead biomass, and 2.18 ± 0.65 Pg C year⁻¹ emitted from oxidation of harvest wood products (HWP). For the period of 1750–2018, these pool-specific annual fluxes summed to -443 ± 155 Pg C for vegetation, 373 ± 137 Pg C for soil, and 276 ± 84 Pg C for HWP. Using a different approach, Sanderman et al. (2017) modeled the loss of SOC due to land use and land cover change during the last 12 000 years (Fig. 7) based on a machine learning model that was fitted using a global compilation of SOC data and the History Database of the Global Environment (HYDE) for land use data in combination with climatic, landform, and lithology covariates. In their study, Sanderman et al. (2017, 2018) reported a lower C emission from soil due to land use change than previously assumed. The model results indicated a cumulative loss of SOC with about 116 Pg C from the top 2 m due to agricultural activities over the last 12 000 years with a strongly increased loss rate over the last 200 years. The modeled data thereby compared well with global datasets from paired sites where each site had one plot with undisturbed native vegetation and one adjacent plot under agricultural land use but with similar soil conditions for both plots per specific site (Sanderman et al., 2017). The authors showed that regions with the highest losses of SOC are often associated with major

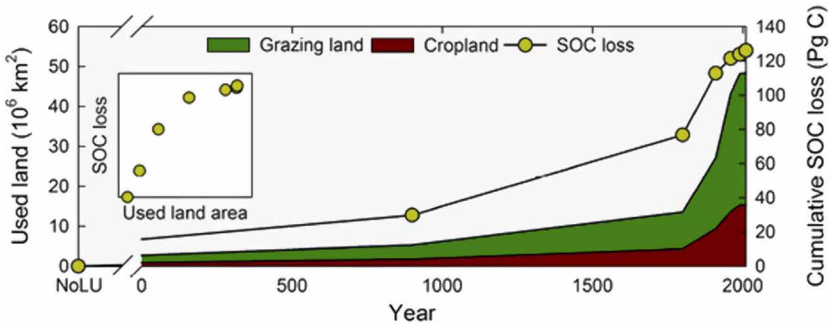


Figure 7 Historic reconstruction of loss in soil organic C (SOC) relative to 10 000 BC (assumed no land use [NoLU]). Temporal evolution of cropland and grazing land is given in stacked area plots. (Inset) Biplot of SOC loss (Pg C) v. total used land area (10^6 km^2) for each predicted time interval. Published in Sanderman et al. (2017).

cropping regions of intensified agriculture and degraded grazing lands. These regions are also the most likely ones to respond positively with increased SOC sequestration when managed differently (Paustian et al., 2019), which should in turn be targeted first for restoration efforts rebuilding SOC stocks as a means to develop strategies for climate change mitigation by using well-known sustainable and emerging technologies and practices.

3.2.2 Impacts of agricultural management practices on soil microbial communities and plant productivity

Soil fauna and microbial communities transform nutrients (Van Groenigen et al., 2015), provide plant nutrition (Bossolani et al., 2020) and maintain soil fertility by contribute to soil structure (Lehmann and Kleber, 2015) and cycling carbon and nitrogen (Cotrufo et al., 2013; Schmidt et al., 2019). Beneficial bacteria in these communities can inhibit plant pathogens (De Tender et al., 2019; Lupatini et al., 2017), promote plant growth (Aasfar et al., 2021), protect against plant parasitic weeds (Masteling et al., 2019), and help to suppress disease in soils (Jayaraman et al., 2021). Changes in microbial activity affect plant nutrient uptake (Leite et al., 2017) but also the interactions between soil microbes that determine microbial community functioning (Cordero and Datta, 2016), affecting nutrient turnover and plant productivity (Andreote and Pereira e Silva, 2017).

However, the increasing demand for food security due to a rising world population leads to an intensification of agriculture to improve plant productivity. Farmers often reach to inorganic fertilization because it is readily available and easy to apply. Although the number of organic farms is on the rise, the majority of agriculture is conventional with continuous cropping systems (Willer et al., 2021). Continuous cropping increases pest prevalence

(Thomine et al., 2022) and often relies on the use of pesticides (Cernava et al., 2019). While inorganic fertilization practices affect soil microbial communities more indirectly (for example through changing soil pH) (Pan et al., 2014), the use of pesticides can affect soil carbon and nitrogen cycling directly by altering microbial communities (Ullah and Dijkstra, 2019). Additionally, farming practices largely determine whether the soil and plant microbiome benefit or harm plant productivity (Bakker et al., 2012). Inorganic fertilization practices hinder the plants' ability to recruit beneficial microorganisms (Reid et al., 2021) which increase plant productivity (Jones et al., 2019; Schulz-Bohm et al., 2018). Contrarily, using organic amendments increases soil microbial diversity (Hartmann et al., 2015) and can increase the abundance of plant growth promoting bacteria (de Carvalho et al., 2021).

While intensification of agricultural systems has undoubtedly contributed to the vast increases in worldwide crop production over the past decades, it has unfortunately also furthered numerous negative environmental impacts such as GHG emissions, eutrophication of waterways, and reduction of biodiversity (Tilman et al., 2011). For example, the use of crop protection products (i.e. fungicides, herbicides, and insecticides) has increased exponentially in the past decades and it is currently estimated that four million tons of pesticides are applied to agricultural systems globally (FAO Stat). As only a fraction of these chemicals actually reach the target plants, this practice is known to cause significant direct and indirect pollution of air, water, and soils (Sharma et al., 2019). As soils are known to harbor some of the most diverse communities of microorganisms on earth (Bardgett and van der Putten, 2014), such pollution has potentially severe consequences for soil biodiversity. For example, application of pesticides has been shown to reduce the diversity and activity of certain microbial populations (Bünemann et al., 2006; Al-Ani et al., 2019), which in turn impacts soil nutrient and carbon cycling (Pelosi et al., 2014), and even can inhibit nitrogen-fixing and phosphorus-solubilizing bacteria (Hussain et al., 2009). They may thus affect soil health and ultimately also SOC sequestration. Even more alarming, pesticide residues have been found in soils of organic agricultural systems (Riedo et al., 2021), showing the strong persistence of such chemicals in the environment even after decades of discontinued use.

Similarly, fertilization of agricultural systems has also increased greatly in the past decades, from as estimated 11.3 Tg N year⁻¹ in 1961 to 107.6 Tg N year⁻¹ in 2013 (Lu and Tian, 2017). Such inputs have also been shown to impact soil microbial communities, although the general trends are difficult to predict as it seems to depend on the fertilizer type (i.e. organic or mineral), specific amount applied, duration of application, soil type, climate, and cropping system (Geisseler and Scow, 2014). For example, while some studies have shown that increasing N fertilization decreases soil microbial diversity and

biomass (Lu et al., 2011), others have shown that the application of mineral fertilizers actually increases soil microbial biomass and SOC content (Geisseler and Scow, 2014; Geisseler et al., 2017). Similarly, while it has been shown that organic fertilization can increase SOC stocks, it may also stimulate soil microbial communities responsible for N₂O emissions (Lazcano et al., 2021), and thus site-specific best management practices must be determined prior to fertilization regime in order to balance tradeoffs between increased crop production and C storage with other negative environmental impacts.

Soil emissions strongly depend on the type of farming practices, because some practices increase these emissions (Lourenço et al., 2021), while others mitigate them (Shu et al., 2021). The soil microbial community structure can help predict these GHG emissions (Morales et al., 2010). Thus, increased understanding of the soil microbial communities helps to lay hold of how changes in these communities affect SOC sequestration and release (de Bruijn et al., 2015; Fierer, 2017). It is essential to increase our research efforts to unravel how novel fertilization practices affect soil emissions and plant productivity to increase agricultural sustainability while increasing or maintaining the SOC pool.

3.3 The consequences and dimension of lateral soil (and soil organic carbon) movement through human activity⁷

3.3.1 Human-induced redistribution of soil within landscapes

What is often ignored in assessments of land cover and land use change-induced alterations of the C cycle and SOC stocks (Fig. 7; Section 2.2) is the fact that considerable amounts of soil and SOC are redistributed laterally across landscape units. The lateral movement of soil driven by water and wind erosion is a natural process that can drastically alter biogeochemical cycling in the plant-soil-atmosphere continuum. Soil redistribution is in part responsible for the small-scale variability of soil properties, often following typical patterns along slope profiles (Fig. 8). Naturally occurring erosion is most pronounced in environments with minimal soil cover, e.g. arid to semiarid areas, higher altitudes or very steep slopes limiting plant growth, and those exposed to high wind speeds or heavy rainfall events in combination with steep slopes. However, human activities substantially accelerated erosion processes and hence lateral soil movement. By far the most important change in land use affecting soil erosion is a shift toward arable use, as soil tillage introduces periods of more or less bare soils. Since the beginning of soil cultivation during the Neolithic Revolution (Weisdorf, 2005), not only water and wind erosion dramatically

⁷ This section was written by Peter Fierer.

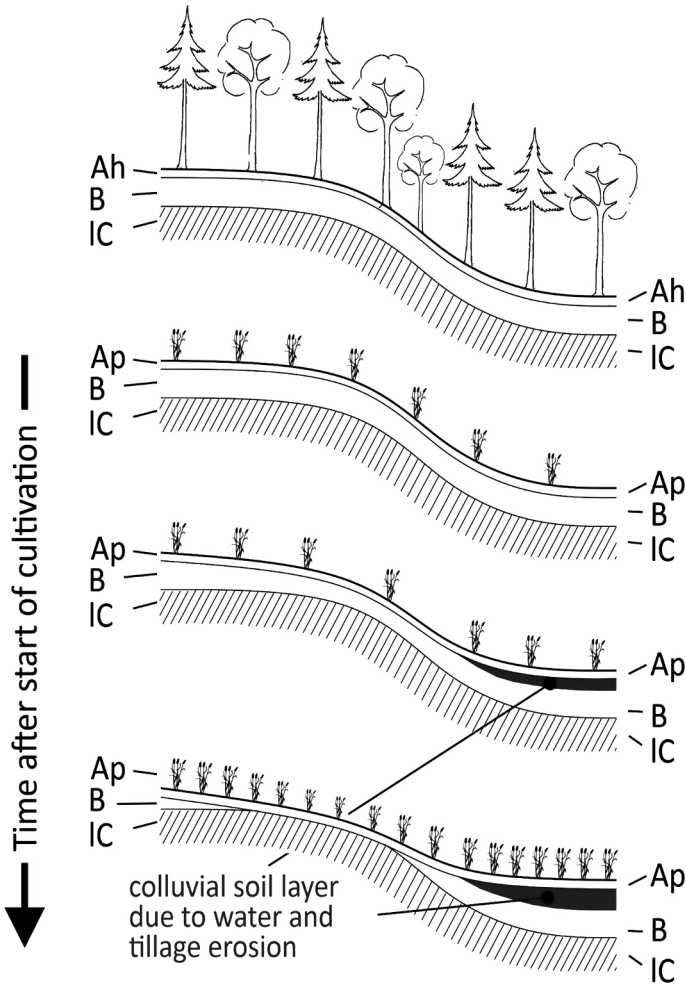


Figure 8 Schematic change in soil profiles at different landscape positions due to a long phase of erosion typically found on arable land in hilly landscapes. Note: In this figure, water and tillage erosion lead to a colluviation at the toe slope. This is not always the case, as e.g. the areas of most pronounced water erosion along thalwegs is often the area of most pronounced tillage deposition.

increased, but also other erosion processes came into play. Namely, tillage erosion, moving soils from slope convexities to concavities (Govers et al., 1994), and harvest erosion, removing soil attached to root crops (Ruysschaert et al., 2007). Furthermore, anthropogenic modifications of landscapes are often associated with forest burning and/or clearing for different purposes (hunting, cultivation, etc.), and declines in soil cover for increasingly large areas (Kaplan et al., 2009). In consequence, today large areas are globally

affected by erosion processes, which under natural conditions would hardly be affected at all. Therefore, in order to prevent organic matter loss and enhance SOC sequestration, one of the principal measures is to reduce soil loss through erosion by establishing permanent soil cover (see, for example, Chenu et al., 2019).

Recent global estimates regarding the importance of different erosion types suggest that water erosion is the dominant process, while tillage erosion moves roughly a fifth of the amount of mass compared to water erosion, but over twice the amount moved by wind erosion (Quinton et al., 2010). Whether water and wind erosion increased or decreased from historic to modern agriculture is open to debate. Estimates of global soil erosion rates under recent land use are challenging and associated with large uncertainties (Table 1), and our knowledge regarding the long-term dimension of global lateral soil redistribution and loss and its effects on soils and their SOC sequestration potential is very limited, and mostly based on small to regional scale case studies. Especially if soil cultivation takes place for centuries or even millennia, detailed, spatially distributed data regarding land use and management over such long periods of time are hardly available.

Table 1 Estimates of global soil erosion

Global soil erosion (Pg year ⁻¹)	Method	Processes	Source
74	Extrapolated for plot measurements	Interill and rill erosion (no deposition)	Pimentel et al. (1995)
120			Hooke (2000)
24–65	Estimated from sediment fluxes in large rivers and storage in lakes and reservoirs	All erosion and deposition processes are estimated from sediment delivery	Stallard (1998)
75			Lal (2003)
60			Wilkinson and McElroy (2007)
75			Berhe et al. (2007)
81	Modeling with universal soil loss equation-based model types (only Van Oost et al. (2007) include tillage erosion modeling)	Interill and rill erosion (no deposition)	Yang et al. (2003)
140			Ito (2007)
20.5 ± 10.3			Doetterl et al. (2012)
47.6 ± 10			Naipal et al. (2018)
34.9			Guerra et al. (2020)
43 ± 9/7			Borrelli et al. (2020)
30–40			Interill and rill erosion (no deposition) and tillage erosion

Depending on literature information, ranges or variability of means (standard deviation) are given. Note: all plot and modeling approaches focus on human-induced erosion (mostly on arable land), while the estimates from sediment fluxes in rivers and lakes and reservoirs also include natural erosion.

Clearly, tillage erosion increased since cultivation started as rates of soil movement from hand tools and plows pulled by animals are much lower than those associated with mechanized agriculture and these rates have especially accelerated in recent decades as agriculture has intensified and machinery has increased in size and power (Schjønning et al., 2015). In consequence, the following evaluation of human-induced lateral soil movement is mostly dedicated to water and tillage erosion. In this context, it is important to note that tillage erosion solely redistributes soils within arable land, while in the case of water erosion, soil (and associated C) is at least partly moved into other ecosystems, mostly inland waters.

3.3.2 Effects of lateral soil redistribution on soil organic carbon cycling

In (agricultural) landscapes with severe erosion and soil degradation, soil profiles exhibit a large variability in soil properties (Fig. 9) resulting from the removal of topsoil at erosional sites and burial of these soils at depositional sites. With the loss and gain of soil at different landscape positions, large amounts of SOC are also redistributed (Van Oost et al., 2007; Doetterl et al., 2016). However, the effects of soil redistribution on soil C cycling are complex, as redistribution may also affect SOC sequestration and its mineralization through their impact on soil physical properties and microbial communities. Effects can change with (1) severity of erosion, (2) the time since cultivation began, or (3) the amount of soil that is deposited and buried in colluvial and alluvial valleys and floodplains (Wang et al., 2017; Schrumpf et al., 2021).

Briefly, soil redistribution with regard to SOC can be structured into several compartments. First, at the beginning of erosional processes (see 1A and 3A in Fig. 9), the most important process affecting landscape scale C balance is the transport of SOC-rich topsoil from slopes to valleys and the partial SOC loss to adjacent ecosystems, mostly inland waters. In this context, it is important to note that SOC is often preferentially transported and hence lost to other ecosystems since it is tied to smaller, easily transportable particles (clay sized) or transported as particulate or dissolved organic matter of low density. This enrichment of SOC in general and in particular its labile and low density compounds in sediments was shown numerous times in many experimental studies (Jacinthe et al., 2004; Rumpel et al., 2006; Schiettecatte et al., 2008b; Juarez et al., 2011). However, it is difficult to generalize for larger areas (e.g. catchments), where soil redistribution takes place through a wide mix of selective and nonselective erosion and deposition processes (Kuhn et al., 2012; Schiettecatte et al., 2008a). Second, during erosional transport and shortly after deposition of soil, mineralization of SOC might occur following aggregate breakdown (Six et al., 2000a, 2001) (see 2A and 2B in Fig. 9). The breakdown of aggregates and the

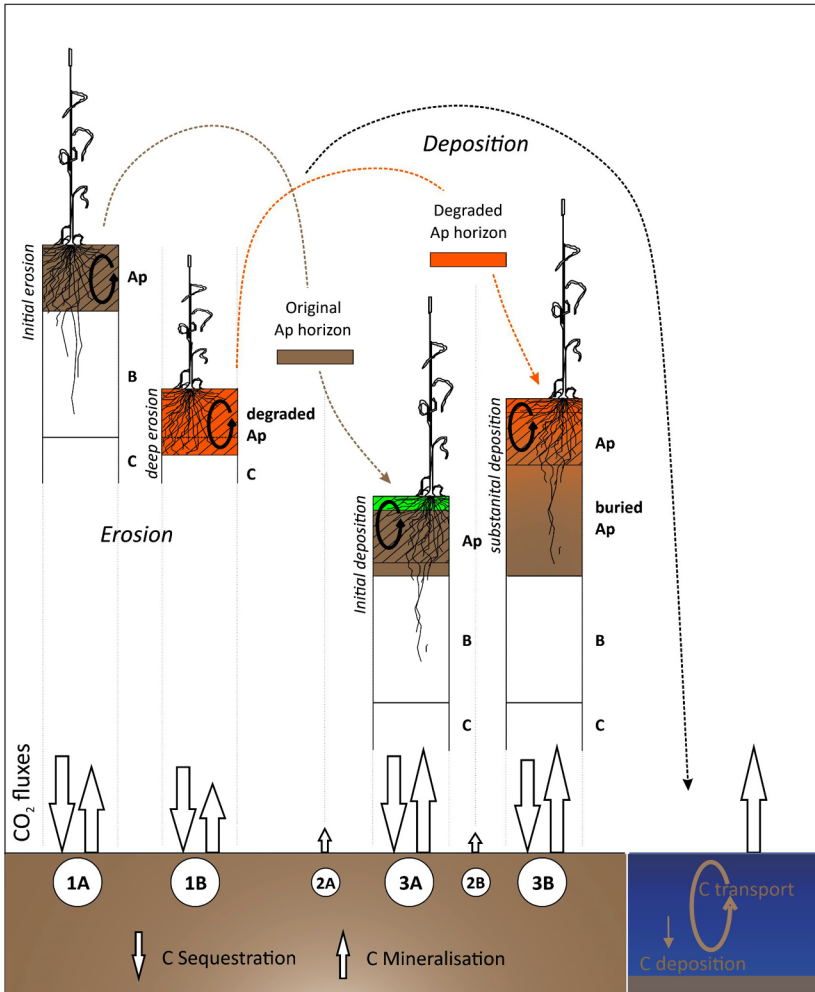


Figure 9 Schematic overview of soil and C redistribution and its effect on C sequestration and mineralization at different landscape positions. 1A–B and 3A–B refer to fluxes in case of different erosion and deposition intensity. 2A–B refers to C mineralization during transport.

associated CO₂ effluxes from mobilized SOC hereby depends predominantly on the kinetic energy of raindrop impact. Several studies have demonstrated this relationship and quantified an increase in SOC mineralization under laboratory (Jacinthe et al., 2004; Polyakov and Lal, 2008) or field conditions (Van Hemelryck et al., 2011). However, the increase in CO₂ fluxes is short lived and only recognizable for several days after an erosion event (Bremenfeld et al., 2013; Jacinthe et al., 2002; Van Hemelryck et al., 2010). Third, with increasing

changes in soil horization other processes than the above are becoming increasingly important for erosion-induced changes of SOC cycling (see 1B and 3B in Fig. 9). At eroding landscape positions, two contrasting processes need to be considered: (1) plant productivity and hence C input tends to decrease if soils are getting thinner due to prolonged erosion (Öttl et al., 2021), because degraded soils often show a reduced water storage capacity and lower nutrient availability. Soil surface removal experiments show that the effect of soil loss upon biomass production is significantly more pronounced in case of zero or low fertilizer inputs (Bakker et al., 2004). (2) The eroded SOC is replaced by new C inputs via new photosynthates, which was first termed 'dynamic replacement' by Harden et al. (1999). This replacement is driven by a number of processes: surface soil at eroded sites is mixed with subsurface soil via tillage. As long as C inputs from agricultural crops are not substantially reduced, SOC can be replaced to reach the previous equilibrium between C inputs and outputs. Additionally, chemical weathering of former subsoils may lead to the formation of new organo-mineral complexes when minerals stabilize newly sequestered SOC at reactive surfaces that are not yet saturated with sorbed SOC (Harden et al., 1999; Van Oost et al., 2007; Remus et al., 2018;). These processes are very site specific, as they depend strongly on the biogeochemical properties of mineral soil and the environmental conditions under which weathering occurs.

At depositional landscape positions (Fig. 9, see 3B), soil-eroded upslope accumulates leading to the burial of transported and in-situ sequestered SOC. At the same time, deposition of fertile, former topsoil can increase plant productivity at depositional landscape positions (Bouchoms et al., 2018; Öttl et al., 2021). Overall our knowledge regarding the scale of SOC burial in depositional sites is still very limited (Rumpel and Kögel-Knabner, 2011; Wang et al., 2017) as well as our knowledge regarding the stability of buried SOC (Zhang et al., 2021) and its stability under changing climatic and environmental conditions (Soong et al., 2021; Zosso et al., 2021). On average, it is estimated that only between 10% and 30% of topsoil material redistributed due to agricultural (water) erosion is subsequently transported into lakes and oceans via major rivers (de Vente et al., 2007; Walling, 1996). The rest is deposited in different soil environments, ranging from footslope and colluvial deposits to alluvial flood plains. In conclusion, the effects of soil redistribution can lead to both SOC losses and SOC gains depending on the overall ability of soils affected by erosion to sustain plant growth, and the amount of SOC buried over time in depositional sites. The efficiency at which SOC can be conserved at depositional sites largely depends on the rate of burial, the time since burial, the quality of the buried SOC and very importantly the environmental conditions, where SOC is buried (Doetterl et al., 2016). In well-aerated colluvial soils, often strong depth gradients in SOC concentrations can be found with lower SOC

concentrations in the deepest and therefore oldest layers, whereas in alluvial soils under oxygen limited conditions soils can be stored for centuries without substantial changes (Hoffmann et al., 2009, 2013a,b; Steger et al., 2019). River regulation and the associated drainage of alluvial plains can pose therefore a serious risk of increased mineralization of buried SOC when soils become increasingly aerated (e.g. for the areas, exposing alluvial soil SOC to better aerated conditions).

3.3.3 Global consequences and dimensions of lateral soil redistribution on soil organic carbon cycling

The approaches used to estimate the global effects of erosion on SOC cycling can be roughly subdivided in two subgroups: (1) soil-centered approaches upscaling results from plot to small catchment scale while using parsimonious modeling approaches (Naipal et al., 2018; Van Oost et al., 2007; Wang et al., 2017) and (2) sediment-centered approaches estimating the importance of soil redistribution on SOC cycling from sediment in globally important river systems (Smith et al., 2001; Lal, 2001). While the first appropriately address the catchment internal erosion and deposition and its effect on SOC fluxes, the latter integrate more processes such as erosion, deposition, transport, and mineralization on land as well as mineralization and burial in inland waters, but lack detail in catchment internal dynamics. Thus, at the local to regional scale, the SOC sink or source effect of this redistribution is well determined. However, we still lack data, methods, and process understanding to appropriately analyze the global C cycle effect of SOC, which is moving through landscapes into oceans. Global estimates of the dimensions of lateral soil redistribution on SOC cycling are challenging and associated with large uncertainty, as briefly illustrated while describing the different processes involved. A recent study in Australia (Chappell et al., 2016) indicates that SOC loss from arable land via erosion is often incorrectly attributed to a loss via soil respiration. In the case of the Australian National Greenhouse Gas inventory, this incorrect attribution leads to an overestimation of the net C flux from cropland by up to 40% and an overestimation of the potential (100 year) C sink (if erosion is reduced) by up to 17% (Chappell et al., 2016). Overall, common approaches used to estimate the global effects of soil erosion on SOC cycling result in contradicting estimates, which were widely discussed within the last two decades (for reviews, see Doetterl et al., 2016; Kirkels et al., 2014). These global estimates range roughly from a net source of 1 Pg SOC year⁻¹ to a net sink of 1 Pg SOC year⁻¹, whereas later studies indicate more moderate effects, mostly assuming a slight global C sink introduced via erosion processes (Van Oost et al., 2007; Quinton et al., 2010) (Fig. 10).

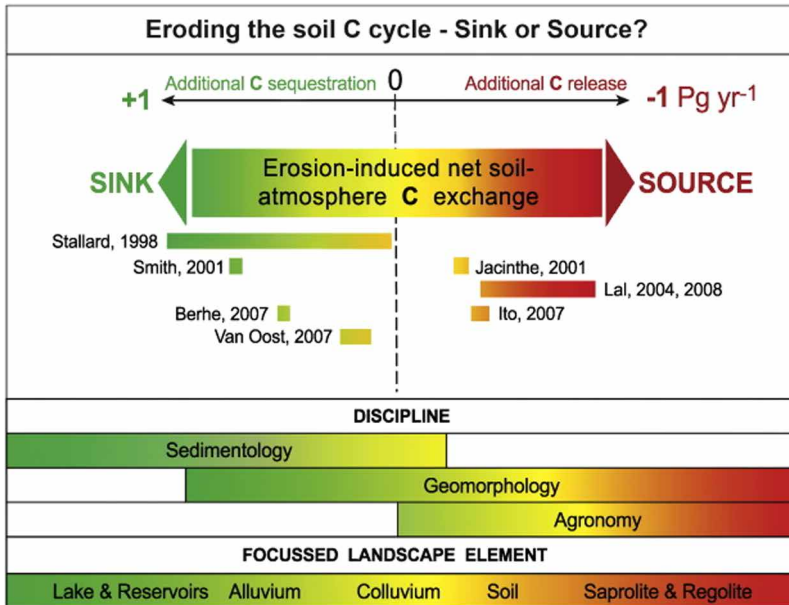


Figure 10 Net effect of soil redistribution on SOC cycling as determined by current global-scale studies. Colors and position along the X-axis show the relationship between the disciplines and landscape elements focused on in these studies. Republished from Doetterl et al. (2016).

3.4 The soil organic carbon sequestration (and loss) potential of human-modified landscapes and land use systems⁸

3.4.1 Recovery of soil organic carbon stocks at global scales

The literature on the connection between human management and SOC provides global estimates on the average efficiency of sequestering SOC by different management, mostly by meta-analyses. Present global SOC stock estimates help to put sequestration into perspective. The amount of SOC stored until 2 m soil depth was estimated as 2400 Pg C (Batjes, 1996; Minasny et al., 2017). With a global land surface area of 149 million km², an average of about 100 t SOC ha⁻¹ can be found in the first meter of soil. Tang et al. (2019) reported in their meta-analysis that the global average loss of SOC stocks to 60 cm depth after conversion of grassland to arable land was about 18% of initial stocks. Wei et al. (2014) reported globally differentiated SOC losses following conversion of forest to agricultural land: about 50% for temperate forest, 40% for tropical and 30% for boreal forests. Historical losses in SOC have been highest, where land was under cultivation for many centuries. Global estimates state that in

⁸ This section was written by Moritz Laub and Sebastian Doetterl.

cultivated soils overall, between 40% and 60% of initial SOC stocks have been lost due to agriculture (Lal, 2004; Wei et al., 2014). These historic losses are the theoretical maximum potential for SOC sequestration when soils are put out of management to approach their natural state. In practice, land available to be given up for this purpose is strongly constrained by the human need for food and biomass. The fact that gains in SOC occur much slower than losses (Attard et al., 2016) also limits the sequestration potential in the near future, indicating that maintenance of intact ecosystems should be a priority. However, despite many uncertainties and limitations (e.g. Poulton et al., 2018), improved management of soils by, for example, reducing SOC losses through measures limiting erosion, reducing tilling depths and frequencies, the use of deep rooting or perennial crops as well as the active addition of stable organic C compounds to soils (biochar) are discussed as possible ways for soils to remain under agricultural land use while continuously sequestering SOC (Minasny et al., 2017; Paustian et al., 2019; Chapters 16–24 of this book).

Despite the SOC sequestration potential of (agricultural) soils, rebuilding historic stocks is tedious and the effects of improved management practices on the reversal some of these losses at decadal time scales are uncertain. For example, soil tillage disrupts soil aggregates and speeds up soil C turnover (Six et al., 2000a,b). The difference between plowing and a no-till management has been estimated to be about 0–0.2 t C ha⁻¹ year⁻¹ under humid climate conditions (Six et al., 2004; Virto et al., 2012), and very little potential for additional SOC sequestration in dry conditions. Exception may be highly weathered soils in tropical regions (Chapter 22 of this book). In addition, it was noted that due to an increase in N₂O emissions in the first 10 years, a net benefit for the reduction of GHG-related global warming potential would only be possible if no-till is maintained for at least two decades. Similarly, mineral N application on previously unfertilized agricultural land also shows potential to increase SOC stocks between 5% and 10%, mostly by increasing plant biomass inputs into the soil (Han et al., 2016; Yue et al., 2016). Yet, to fully assess the influence of such measures on global warming, tradeoffs such as increased N₂O emissions must be accounted for (Chapter 6 of this book), at best normalized per unit of crop yield (Clark and Tilman, 2017). Others have provided estimates of global average SOC sequestration for a number of management practices (Freibauer et al., 2004; Smith, 2004) such as no-tillage, 0.4 t C ha⁻¹ year⁻¹; application of animal manure, 0.4 t C ha⁻¹ year⁻¹; planting of permanent or deep rooting crops, 0.6 t C ha⁻¹ year⁻¹; extensification or organic farming, 0.5 t C ha⁻¹ year⁻¹, and conversion of cropland to woodland, 0.6 t C ha⁻¹ year⁻¹; or to grassland, 1.5 t C ha⁻¹ year⁻¹. As part of the 4 per 1000 initiative, Minasny et al. (2017) estimated that a targeted annual sequestration of 0.4% of current stocks would be possible for a few decades on agricultural soils, offsetting 20–35% of global GHG emissions. They assumed the largest potential for SOC accumulation for afforestation

(+0.6 t C ha⁻¹ year⁻¹), pasture implementation (+0.5 t C ha⁻¹ year⁻¹), residue incorporation (+0.35 t C ha⁻¹ year⁻¹), and reduced tillage (+0.3 t C ha⁻¹ year⁻¹) but acknowledge that initial SOC stocks determine the locally achievable potential. Also in the context of 4 per 1000, Poulton et al. (2018) compared several long-term experiments in United Kingdom and concluded that by adding about 3 t C ha⁻¹ year⁻¹ of manure, it is theoretically possible to sequester between 0.1 and 0.4 t C ha⁻¹ year⁻¹, with a decrease in sequestration rates to zero after around 150 years. At the same time, several practical limitations such as sourcing such high amounts of manure, economic and food security tradeoffs arise that need to be taken into consideration when optimizing land use for SOC sequestration.

Similar to these examples from temperate regions, small effects of higher C inputs to soil to increase SOC stocks can also be confirmed in tropical environments, where turnover of soil C is high due to higher temperatures and more heavily weathered soils with limited capacity to stabilize C by association with minerals (Doetterl et al., 2021, Chapter 22 of this book). In recent studies, the strongest influences of improved management on SOC stocks were related to the amount of C inputs (0.45 ± 0.14 t C ha⁻¹ year⁻¹), while type of management practices (0.32 ± 0.06 t C ha⁻¹ year⁻¹), such as reduced tillage and residue retention, was less important (Fujisaki et al., 2018). Fujisaki et al. (2018) also reported that on average, only 8% of carbon inputs into the soil were translated into SOC. Another meta-analysis in the sub-Saharan Africa context looking at relative SOC sequestration rates, found that the implementation of agroforestry or conservation agriculture applying a combination of reduced tillage, mulching and crop rotation/intercropping could help to achieve the goal of the 4 per 1000 initiative of an annual rate of 0.4% C increase of SOC stocks (Corbeels et al., 2019).

It is also important to note that the land use history of a site determines its future potential to sequester SOC by improved management. For example, if cultivation of a site has started relatively recently, with the status of soils still being similar to their natural equivalent, the introduction of an improved management scheme may slow SOC losses, but not sequester SOC. In contrast, if a site has been under long-term cultivation and is close to reach the new steady state for low SOC input, improved management shows potential to sequester SOC (Fig. 11). This concept also shows why heavily eroded soils may sequester SOC (Wang et al., 2017), as SOC stocks of the new topsoil are below the level of steady state. In the long run, regardless of the current state of soil, a specific balance between C inputs and outputs to soil after agricultural land use has stopped should, in theory, lead to the same levels of SOC before conversion, if soil fertility (and the resulting plant productivity) remains similar. Yet, the timescale to reach this is expected to be in the order of centuries to millennia and is thus several magnitudes slower than the loss of SOC. Furthermore, many soils under agricultural land use are formed from parent

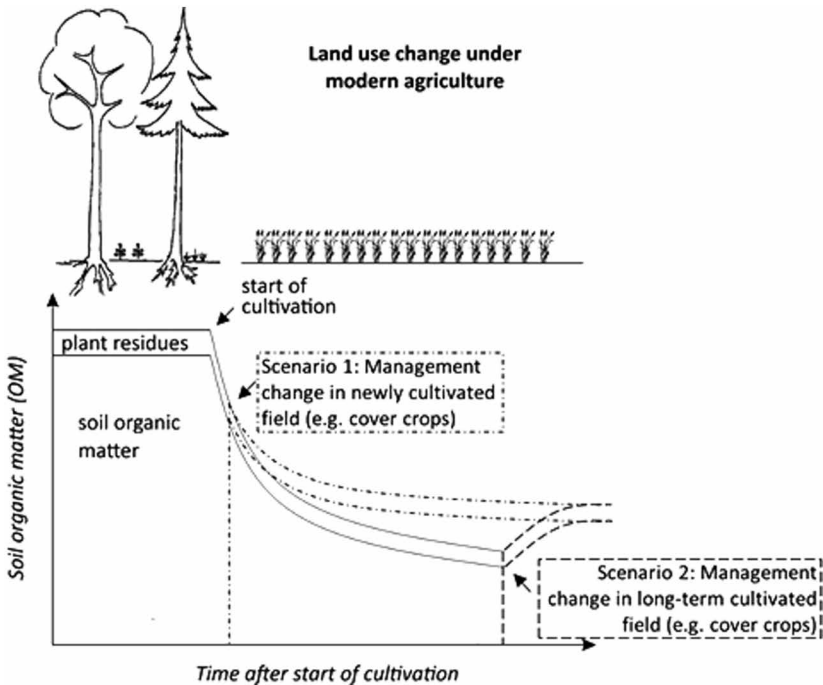


Figure 11 Schematic figure of potential changes in different C pools following the change to improved management. The time passed since the transformation of the natural to an agricultural ecosystem determines how close the system is to a new low input steady state. This determines whether improved management can only reduce soil C losses (Scenario 1) or lead to soil C sequestration (Scenario 2).

material with limited availability and no active mechanism for replacement. For example, some of the most fertile soils across the northern hemisphere are formed from aeolian late periglacial deposits (loess) with often only a few cm to several meters thickness (IUSS Working Group WRB, 2015; Kögel-Knabner and Amelung, 2014; Rejman et al., 2014). Once this resource has been eroded, underlying material (often bedrock or tertiary, deeply weathered sediments) does often have less suitable properties to form productive and fertile soils. With the recovery of loess resources being tied to stadial/interstadial cycles, the recovery of loess-derived soils is therefore practically not possible even at millennial timescales (Roberts et al., 2013).

An exception to the slow recovery of SOC stocks with immediate effects of increasing SOC sequestration is the management of peatland and wetland soils by ending and reversing draining measures (Chapter 21 of this book). Being comparatively small in their spatial extent and rich in SOC, drained peatlands experience yearly CO_2 losses of a factor of 20 and more compared to mineral soils. For example, a significant correlation between depth of the water

table and yearly peat SOC losses was found in meta-analysis for Southeast Asia (Carlson et al., 2015), estimating yearly losses of 20 t SOC ha⁻¹ year⁻¹ at a water table depth of 70 cm, losses being reduced by 0.2 t SOC ha⁻¹ year⁻¹ with each cm of increased water table. Equally important is therefore the conservation of remaining peatlands. Peatland soils, while making up less than 3% of global soil covered land (Leifeld and Menichetti, 2018), can annually lose as much SOC, as several optimistic scenarios promise to sequester in all mineral soils combined.

3.4.2 Synthesis of the potential soil organic carbon sequestration potential on a human dominated planet Earth

Due to the heterogeneity of global soils and a lack of high-resolution soil data in many areas, estimates of global SOC losses and sequestration potential are yet rather rough and uncertainties are high. However, as more than 40% of the earth surface is covered by croplands and pastures combined (Foley et al., 2005), the potential for SOC sequestration by improved management, while being slow and in parts hard to implement, is still substantial. For example, Doetterl et al. (2012) and Sanderman et al. (2017) compared natural sites to agricultural sites globally and created maps of estimated SOC losses due to agricultural activity. They estimate that as a result of agriculture, ~116-150 Pg SOC have been lost in the last 12 000 years, globally. Recovering and rebuilding only a fraction of this C mass through SOC sequestration can buy important time for transforming the world's leading industrial nations into carbon neutral economies (Rogelj et al., 2018).

Studies on the global potential of SOC sequestration are still scarce and based on simplified global assumptions, such as that all soils could additionally sequester a certain percentage of their current SOC stocks. Yet, region and land use-specific estimates provide an initial basis of where to focus. Due to the land-use history effect, it will be important to target the most promising sites for SOC sequestration - sites with depleted SOC and poor management at the moment (Rumpel et al., 2020). Spatially diversified strategies that acknowledge difference in storage potentials and availability of C inputs for the soil will therefore be needed in the future (Amelung et al., 2020). These strategies should ideally be based on measured soil properties, as recent evidence suggests the human influence on SOC could be overestimated by global models, finding a mismatch between global soil carbon model outputs and observed global soil profiles data (Georgiou et al., 2021). For example, the work by Chen et al. (2018) provided spatially explicit estimates of SOC sequestration potential across France, based on the difference between measured SOC and SOC at an assumed, texture-related saturation level. While they estimated total sequestration potential to be 2.4 Pg SOC for top- and subsoils overall,

huge variations in saturation deficits existed for all land types, highlighting the importance for spatially resolved maps (Chapter 12 of this book). Such spatially explicit approaches can also recognize the potential of pedogenetic drivers of SOC storage potential, which can in some cases explain more variation in SOC than the land use (von Fromm et al., 2021). Therefore, a better global coverage of soil and land use data will be highly relevant to better estimate local SOC sequestration potential and thereby improve the global estimates.

4 Future trends in research

4.1 Climate change and a biogeochemical perspective on soil properties to store carbon

Part of this chapter illustrates that the effects of climate change on soil C cycling and SOC sequestration are not yet fully understood. They will vary across regions and scales and are dependent on other factors like soil mineralogy and plant community dynamics. Among the soil properties controlling carbon storage, future research from a geochemical perspective should better constrain the influence of the ongoing climate change on soil water dynamics and their controls on organo-mineral interactions. To move this field forward, analysis of large data sets should always be combined with (long-term) field and laboratory experiments to understand the mechanisms behind observed patterns and improve our understanding of the main factors controlling the temperature sensitivity and the effect of moisture and drought on SOC sequestration in different regions of the world. In particular, it is important to consider regional differences rather than trying to find universal, global-scale relationships. Being able to quantitatively assess the local impact of this shift on carbon storage would be a major step forward to improve predictions of the capacity of soil to store carbon by Earth System Models. As climate change accelerates, it will also become important to make newly collected measurements and existing data available under FAIR (Findable, Accessible, Interoperable, Reusable) principles so that researchers, stakeholders, and policymakers have access to the information needed for climate mitigation and adaptation.

4.2 Soil microbial community responses and functions

The link between soil microbial diversity and functions (i.e. who is doing what?) has been a central theme of investigation for a long time, yet much remains unclear. However, recently developed molecular techniques, such as metagenomics and metatranscriptomics, can help to shed light on this important question. With the introduction of next generation sequencing, there has been

an increasing number of studies characterizing the soil microbial communities in various settings using meta-omics methods. Combined with well-designed experiments, these techniques might also help to understand the impact of the environmental factors on the microbial carbon use efficiency and the functioning of microbial communities at local to global scales. Furthermore, these studies help to disentangle these complex soil microbial communities and their response to climate change as well as changes in agricultural management and its consequences for soil carbon dynamics. To be able to better include soil microbial community responses in climate models, it is also essential to fill spatial gaps by measuring soil microbial communities and plant productivity in previously uncharacterized soils that are representative for more remote areas. Closing these gaps and integrating the knowledge gained from existing studies has the potential to enable us to determine drivers of changes to carbon dynamics and investigate how to utilize agricultural management to create climate-smart soil microbial communities (for instance to stimulate soil carbon sequestration).

4.3 Future soil carbon-sequestration potential in anthropogenically modified landscapes

As described in this chapter, the interactions between soil organic carbon mineralization and sequestration and soil redistribution driven by human activities that modify agricultural and natural landscapes for millennia through a wide range of processes are not yet fully understood. Gaps in knowledge range from detailed process understanding regarding erosion-affected carbon fluxes, e.g. changes in crop yields and crop root-to-shoot ratios following severe erosion, to landscape-scale effects on erosion-affected C balance taking several erosion processes into account. As soil and soil organic carbon redistribution is mostly associated with short extreme events occurring in local scales, upscaling to regional or even global assessments is still challenging. Furthermore, for targeting modern farming techniques and management practices to achieve additional C sequestration in soil, further research on the site-specific limitations and potentially achievable C increases are needed. A second concern is what rates are realistic under real farming conditions to reach C increase in soils in a specific timeframe. This information then will help to assess the best techniques and practices to achieve fast gains in soil C while not jeopardizing other important soil functions (soil health, biodiversity, crop yields, water storage, etc.).

Finally, with new data collected and studies being published everyday at an increasing rate, it will be of growing importance that the knowledge gained from these efforts is shared and analyzed in a more synergistic way than currently done. One way to achieve this is to motivate researchers (and create the

infrastructure and conditions for them) to store data in open-access databases, promote open science, and in general decrease the barriers for knowledge transfer between fields to stimulate interdisciplinary and transdisciplinary systems research. One way to deal with the sometimes contrasting results that new studies deliver on 'hot' subjects in relation to soil C research or studies from remote regions is to increase our efforts to conduct meta-analyses. Lastly, it is important to remember that global model predictions on C release and sequestration potential fundamentally rely on good data. This involves not only current-day observations at fine resolution at a global scale but also a solid understanding of past processes and changes and the fact that soils change and develop at different time scales than most of the changes to the C cycle that we would like to gain knowledge on. Estimates of C emissions from land use change can be compromised by poor quality of historical land-cover and land-use change maps, the rudimentary representation of management processes in most models, and the confusion in methodologies and boundary conditions used across methods. For example, the very coarse land-use categories used in the different upscaling approaches do not represent specific soil management strategies that might reduce or even reverse the emission of C from agricultural soils. Consequently, improved model parametrization is recognized as a major factor to lower uncertainties in estimates of land use change derived C emissions. Improving future land use scenarios and related C dynamics also desperately need better links to socioeconomic models that include the effects of global trade, consumer behavior, and population growth on agricultural production and the expansion of agricultural land into natural landscapes (especially in the Tropics). Together with climatic change, land degradation, and the overuse of soils that typically lowers the capacity of soils for cropping, economic and societally driven short-term and globally variable developments are ultimately the factors that will define future land-use patterns and the exchange and storage of C in soils.

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