



Review

The Case for Digging Deeper: Soil Organic Carbon Storage, Dynamics, and Controls in Our Changing World [†]

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Abstract: Most of our terrestrial carbon (C) storage occurs in soils as organic C derived from living organisms. Therefore, the fate of soil organic C (SOC) in response to changes in climate, land use, and management is of great concern. Here we provide a unified conceptual model for SOC cycling by gathering the available information on SOC sources, dissolved organic C (DOC) dynamics, and soil biogeochemical processes. The evidence suggests that belowground C inputs (from roots and microorganisms) are the dominant source of both SOC and DOC in most ecosystems. Considering our emerging understanding of SOC protection mechanisms and long-term storage, we highlight the present need to sample (often ignored) deeper soil layers. Contrary to long-held biases, deep SOC—which contains most of the global amount and is often hundreds to thousands of years old—is susceptible to decomposition on decadal timescales when the environmental conditions under which it accumulated change. Finally, we discuss the vulnerability of SOC in different soil types and ecosystems globally, as well as identify the need for methodological standardization of SOC quality and quantity analyses. Further study of SOC protection mechanisms and the deep soil biogeochemical environment will provide valuable information about controls on SOC cycling, which in turn may help prioritize C sequestration initiatives and provide key insights into climate-carbon feedbacks.

Keywords: soil organic carbon; deep SOC protection; microbial processing; biogeochemical processes; dissolved OC; C sources; C sequestration; climate change; land use; management

1. Introduction

Soils have the unique ability to sequester and store large amounts of carbon (C). They are estimated to contain about two to three times the amount of C stored in the atmosphere and vegetation combined [1,2]. Most soil C is in the form of organic C derived from living organisms and has been stored for hundreds to thousands of years in deeper soil layers (below ~20 cm) [3,4]. Therefore, the loss of even relatively small amounts of this soil organic C (SOC) could exacerbate global climate change by releasing substantial amounts of greenhouse gases, such as carbon dioxide (CO₂) and methane (CH₄), to the atmosphere. Various components of the soil environment interact to protect SOC from loss or, alternatively, enhance the microbial decomposition of organic C compounds. Changes in environmental constraints affect SOC cycling by altering soil properties and C inputs, which in

turn alter soil microbial communities and processes, as well as their access to organic matter and other nutrients.

Our shifting understanding of SOC “stability” and the interactions of organic C with the soil environment have resulted in the proposal of numerous conceptual and mechanistic SOC models [2,5,6]. Here we provide a unified conceptual model for SOC cycling by gathering the available information on SOC sources, dissolved organic C (DOC) dynamics, and deep soil biogeochemical processes. Emphasis is placed on how our emerging understanding of SOC protection mechanisms translates into a pressing need to sample deeper soil layers. We also discuss SOC vulnerability on a global scale in different soil types and ecosystems. Finally, we identify additional common practices that may affect SOC quality and quantity analyses and their comparability, such as the use of different soil sampling methods [7], the exclusion of the coarse soil (>2 mm) fraction [8], and the use of varying SOC fractionation techniques [9–11].

2. Vertical Distribution and Storage: Our Shifting Understanding of Soil Organic Carbon “Stability”

Soil depth plays an important role in SOC distribution. Although SOC concentrations decrease rather linearly with increasing depth, total SOC storage is greater in deeper soil layers than at the surface. In fact, due to increased mass in deeper soil layers, well over 50% of the global SOC stock is stored in deeper soil layers (below ~20 cm) [12,13]. Radiocarbon ages of SOC also increase with depth, with deep SOC commonly being as old as 1000 to more than 10,000 years [3,4,14,15]. The sharp increase in SOC age from surface to deeper soil suggests that SOC is stored longer in deeper soil layers.

2.1. “Humus” Versus a Decomposition Continuum

Historically, long-term storage (or preservation) of SOC was thought to occur via the formation of complex and “stable” SOC compounds, generally referred to as “humus”. While this theory of “humification” is based on alkaline extraction of SOC in the laboratory (which Lehmann and Kleber [2] describe as “incomplete, selective, and prone to creating artifacts”), contemporary, in situ spectromicroscopic techniques have revealed the presence of much smaller, more chemically simple organic C compounds in the soil environment [3]. Moreover, no modern analytic techniques have observed “humic substances” in the soil [2], and alkaline extraction is unable to confirm the existence of these substances [16]. The emerging concept of SOC storage as an ecosystem property, rather than simply the result of chemical “recalcitrance” or “stability,” is well-supported in the literature over the past few decades [2,3,5,17]. This concept is based on the premise that organic matter in the soil decomposes along a continuum. Microbial processing increases the solubility and potential for protection of organic C compounds [2,18,19]. Protection of these compounds is provided by the interaction of the physical, chemical, and biological properties of the soil environment, which reduce the probability (and thus rate) of decomposition, creating the capacity of soil to sequester C [2,3].

2.2. Physical Protection and Mineral Sorption

In most mineral soils, SOC protection occurs primarily through abiotic mechanisms involving physical protection and mineral sorption [2]. Physical protection takes place in the fine pores of soil microaggregates ($0.053 \text{ mm} < \text{diameter } (\varnothing) < 0.25 \text{ mm}$) in which anoxic conditions prevail or which are inaccessible to, or spatially separated from, microbial decomposers [20,21]. Microaggregates are often formed and stabilized within macroaggregates ($\varnothing > 0.25 \text{ mm}$), the formation of which is fostered primarily by roots [21,22]. Microorganisms, particularly root-associated microorganisms, and organic matter also play key roles in fostering aggregate formation [21–23]. The sorption of dissolved organic C (DOC) compounds to minerals occurs in large part with the clay fraction [24,25]. The iron and aluminum hydrous oxides (secondary minerals containing iron and aluminum, respectively, hydroxides $[\text{OH}^-]$, and weakly bound H_2O) of some clay separates are especially effective sorbents of SOC [5,24,26–29]. Mineral sorption is likely the primary means of SOC protection [2,30–36] and is particularly important in deeper soil layers [2,5,26,37,38]. The fraction of SOC sorbed to minerals has

been shown to increase with depth and comprise the majority of organic C stored in soils [25,26,39–41]. While the age of SOC in the surface soil is primarily dependent on climate and land use variables, deep SOC age is more strongly related to soil type, highlighting the importance of soil texture and mineralogy—specifically the clay fraction—in promoting long-term SOC storage [42,43].

2.3. Vertical Movement and Cycling

Major mechanisms contributing to deep SOC include C inputs from roots and root-associated-microorganisms [25,44–50], as well as the translocation of DOC to deeper soil layers [5,6,26,27,30,51]. Rain events and new inputs of organic matter are important drivers of DOC flux [44,52]. Waterflow or the saturation of mineral sorption sites in surface soil layers by organic matter inputs preferentially releases less-strongly-sorbed DOC from sorption sites [52,53]. Dissolved organic C released into the soil solution is susceptible to further microbial processing and transport to deeper soil layers, where minerals often have greater surface area (higher clay content and greater abundance of iron and aluminum hydrous oxides) and mineral surfaces are not yet saturated with C [21,53,54]. As DOC is transported vertically down the soil profile, certain organic C compounds are preferentially sorbed to mineral surfaces. Preferential sorption appears to occur with smaller, microbial-derived, highly-oxidized, hydrophobic, and nitrogenous organic C compounds [2,5,18,24,27,55–59], likely due to the stronger affinity for mineral surfaces of proteinaceous microbial residues versus less proteinaceous plant residues [29,60–62]. Therefore, the quality (i.e., composition) of organic C compounds plays a role in long-term SOC storage [63] in relation to soil mineralogy and mineral associations, particularly at depth [64].

Dissolved organic C fluxes contribute indirectly and directly to SOC storage by supporting microorganisms and sorbing to the mineral fraction, respectively. In fact, nearly one-third of deep soil microbial activity may be supported by DOC fluxes [44]. Similar to SOC concentrations, DOC concentrations decrease with increasing soil depth [27,52,54,65]. However, this decrease appears to be primarily due to sorption rather than respiration losses [54,66]. Dissolved organic C age has been found to increase with depth [52] and to approximate the age of SOC at the same depth [67,68], supporting the framework of a continuum of organic matter decomposition and protection and release processes.

3. Inputs and Sources: A Deeper Look at Shoot Litter, Roots, and Microorganisms

Quantifying organic matter inputs to soil from various sources and their relative and total contributions to SOC can provide key insights into processes related to SOC protection and cycling [18]. Organic matter inputs to soil include shoot litter, roots (including root death and a wide variety of rhizodeposition processes, such as passive and active secretion of exudates and the sloughing of root tissues), and microbial biomass [69–71]. Relative contributions to SOC from these three sources, and the complex dynamics of their interactions with the soil environment, are largely debated.

Shoot-derived C is incorporated into the bulk SOC through the transport of DOC from the litter layer [5,6,30,65], as well as through the mixing of particulate organic matter into superficial soil layers via soil fauna (i.e., bioturbation). Bioturbation can play an important role in SOC cycling in some ecosystems [26]. However, the abundance and effect (particularly long-term) of bioturbation agents usually declines sharply with depth [72], and their contributions to deep SOC may be negligible compared to DOC transport [73]. Because root- and microbial-derived C are input belowground, incorporation into the DOC pool and bulk SOC may be more direct. Nonetheless, most belowground C inputs undergo stages of decomposition via repeated microbial processing, protection, and release into the DOC pool.

Studies that reviewed or modeled DOC dynamics in forest ecosystems estimated that DOC-derived SOC represented ~20%–89% of total SOC [44,74–76]. Unfortunately, only shoot-derived C contributions to the DOC pool were considered in these reviews and models, leaving gaps in our knowledge of DOC dynamics [70,77] and the relative contributions of different sources to SOC [78].

Here we review the evidence regarding SOC and DOC sources and provide a unified conceptual model for SOC cycling (Figure 1).

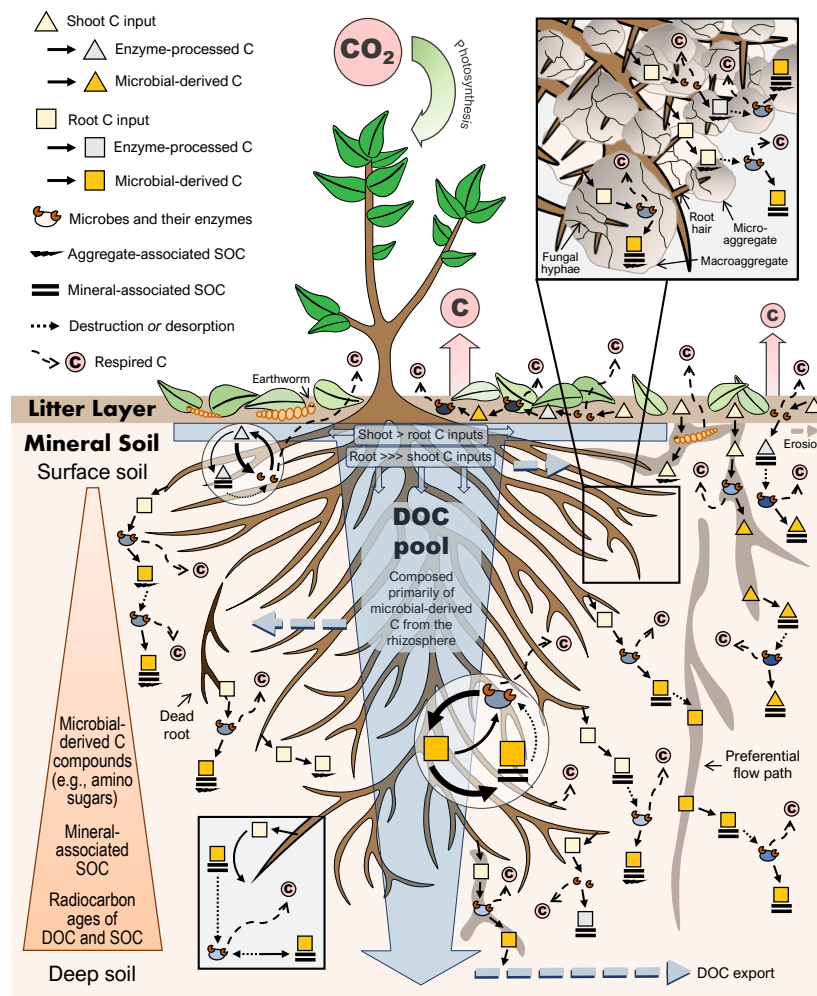


Figure 1. Proposed model for soil organic carbon (SOC) cycling showing root carbon (C) inputs as the primary source of both SOC and dissolved organic C (DOC) in most ecosystems. Root-derived C is shown undergoing multiple stages of microbial processing, protection, and release into the DOC pool as it is transported vertically down the soil profile. Unlike shoot C inputs—which are often mineralized in the litter layer or undergo partial oxidation via microbial extracellular enzymes—most root C inputs will undergo microbial assimilation, biosynthesis, and turnover prior to SOC incorporation. Microbial processing increases the solubility and potential for protection of organic C compounds, which are protected primarily through abiotic mechanisms involving physical protection within soil micro- and macro-aggregates (upper right inset) and mineral sorption of DOC compounds. Microbial activities, and thus SOC decomposition, can be stimulated by multiple mechanisms, and the protection of SOC can be counteracted by physical or biochemical mechanisms, such as by certain root exudates fostering the release of organic C compounds from protective mineral associations (lower left inset). Soil fauna (e.g., detritivores) are represented by earthworms, which contribute to bioturbation. Respired C is shown for the whole soil (in relative amounts), as well as for individual processes. Differences in microbial communities between the litter layer, rhizosphere (i.e., the portion of soil in the immediate vicinity of roots), bulk soil, and with depth are indicated by color. Within the circles illustrating DOC cycling, thicker lines indicate more rapid rates. The size of the ends of wedges represents a relative increase or decrease. Controls on the processes shown include temperature, moisture, the flora and fauna present, and other ecosystem and soil properties (e.g., parent materials, texture, mineralogy, and pH).

3.1. Root Versus Shoot Contributions

About 40–50% of all C fixed by plants via photosynthesis is allocated belowground, and about one-fourth of this C is released into the soil environment by growing roots via rhizodeposition [69,71,79,80]. Compared to aboveground contributions to mineral SOC, root-derived C contributions are approximately 1.5–10 times greater, and they may make up as much as 75% of total SOC [25,44–50]. In a recent review, Jackson et al. [37] found that average root-derived C contributions to SOC in agricultural systems were 45%, compared to just 8% for aboveground C inputs. Several direct and indirect mechanisms are responsible for the incorporation of root C into the bulk SOC. Direct mechanisms include exudate sorption to mineral surfaces and root litter protection in aggregate interiors, while indirect mechanisms include processing or assimilation by root-associated microorganisms or mycorrhizae [19,21,81]. For example, ectomycorrhizal fungi appear to obtain all their C from tree roots, thus acting primarily as a transfer of root C to the surrounding soil environment [82]. In a chronosequence of boreal forested islands, ¹⁴C bomb-carbon modeling revealed that 50–70% of the SOC was root- or root-associated-microbial-derived [83]. Similarly, in a poplar plantation, mycorrhizal fungal external mycelium were found to contribute ~60% of new SOC over three growing seasons, a larger contribution than fine root turnover inputs and over twice that of shoot litter inputs [84].

Shoot litter and root manipulation experiments have provided mixed results as to whether aboveground or belowground C inputs are more important for maintaining SOC stocks [85–87]. Recolonization of roots in “root exclusion” plots [86], potential changes in bulk density between plots over time [86,88], and confounding variables, such as microbial biomass [89], can complicate the interpretation of results. For example, shoot litter manipulations affected SOC concentrations (at 0–10 cm in depth) after only two years in a wet tropical forest; however, changes in fine root biomass, surface DOC fluxes, microbial biomass, nutrient fluxes, and soil moisture accompanied the SOC changes [89]. Therefore, the effects of shoot litter manipulation on SOC concentrations may have been indirect and more related to modifications in fine root biomass and root C inputs, which in turn may have driven changes in microbial activity and microbial biomass turnover [89]. Although some studies have shown the importance of shoot C inputs to maintaining SOC stocks [85,87,90], changes in SOC quantity from shoot litter manipulations have not resulted in similar changes in SOC quality [86,89]. In a temperate deciduous forest, SOC composition and microbial biomass (at ~0–10 cm in depth) were strongly influenced by root manipulations over 20 years, while shoot litter manipulations had no effect on either [91]. This indicates that SOC stocks are primarily derived from underground sources. However, modifications in aboveground C inputs may rapidly affect SOC quantity to varying degrees in different ecosystems, likely due to changes in both particulate organic C [87] and complex biogeochemical interactions in the soil environment [86,90].

3.2. Microbial Processing and Turnover

Incubation and in situ root growth experiments have shown that the mean transit time of root-derived C in soils is over twice that of shoot-derived C [21], which is often mineralized in the litter layer [3,52]. The creation of micrometer-scale pores and aggregates by mycorrhiza and root-hair activities enhance the physical protection of root-derived C from microorganisms [18,21,92], as does the fact that C input belowground has more opportunities for interactions with the mineral soil and sorption to the clay fraction than does shoot-derived C. Nonetheless, due to organic matter inputs by roots, the portion of soil in the immediate vicinity of roots (i.e., the rhizosphere) has higher concentrations of SOC and other nutrients, and thus enhanced microbial activity compared to the bulk soil [21,93]. Therefore, a substantial portion of rhizodeposits undergoes microbial processing and bio-transformation into other microbial-derived C compounds prior to SOC incorporation [6,25,79,81]. For example, root exudates—which are the primary form of rhizodeposits [69]—have been found to rapidly approach the signature of microbial sugars, while rhizospheric sugars as a whole were found to rapidly approach the chemical composition of the bulk SOC [79]. This suggests that a substantial portion of root exudates, following microbial processing, is ultimately incorporated into the bulk SOC.

Microbial necromass and products may make up as much as 80% of SOC [94]. Isotopic and biomarker analyses confirm that root-derived C is the primary source of C for soil microorganisms [95,96]. Most root C inputs undergo microbial assimilation, biosynthesis, and turnover [6]. In contrast, aboveground C inputs may evade passing through a living microbial body, rather undergoing partial oxidation via microbial extracellular enzymes [6]. Repeated microbial processing of root C inputs and interrelated SOC protection mechanisms (i.e., mineral sorption) are particularly important in contributing to SOC storage in deeper soil layers [51,97]. In fact, microbial-derived C compounds (amino sugars) associated with root C inputs have been found to increase in abundance (amino sugars per g C) in the rhizosphere and with increasing soil depth [25,98]. Additionally, soils with higher initial microbial biomass and clay fractions result in greater incorporation of C inputs into microbial biomass and SOC [99,100], illustrating the key role soil texture plays in SOC storage. By modelling root mass, amino sugars, the clay fraction, and the particulate organic C fraction, Angst et al. [25] were able to account for >90% of variability in SOC stocks [35,101].

3.3. Dissolved Organic Carbon Pool

A larger clay fraction leads to increased opportunities for SOC protection via mineral sorption of DOC [25,27,32], the primary protection mechanism promoting long-term SOC storage [2,30–36]. At the same time, because preferential sorption to mineral surfaces occurs with proteinaceous microbial residues [29,60–62], SOC stored long-term is enriched in microbial-derived C compounds [63,98]. The strong relationships between root C inputs, microbial-derived C, the clay fraction, and SOC storage indicate that the DOC pool is likely comprised primarily of root-associated-microbial-derived C. Multiple studies reveal a sharp contrast between litter layer and mineral soil DOC sources and fluxes. For example, in a meta-analysis of shoot litter manipulation experiments in temperate forests, DOC differed only in the litter layer in response to aboveground C input changes, while there was no response in the mineral soil [90]. Similarly, although isotopically-labelled shoot-derived C contributed to ~70% of DOC leached from the litter layer in two deciduous forests, this fraction decreased to 8% and 5% at 5 and 10 cm in depth, respectively [65], indicating that the majority of DOC in the soil profile was derived from other sources. This is consistent with the lack of relationship found between mineral soil DOC fluxes and environmental conditions in temperate forests, despite DOC fluxes from the litter layer generally increasing with annual precipitation [102]. The evidence suggests that the sources and drivers of DOC flux in mineral soil may be largely unrelated to the litter layer.

Root biomass and the DOC pool follow similar distribution patterns, with the majority of root biomass across all terrestrial biomes in the upper 30 cm of soil [103] and the majority of DOC emanating from the surface soil (above ~20 cm) in most ecosystems and decreasing with increasing soil depth [44]. In a temperate forest, mean microbial biomass and DOC concentration were two times higher in rhizosphere compared to bulk soils, and the size of these organic C pools was positively related to exudation rates [104]. Similarly, DOC concentrations in a temperate coastal prairie were highest directly below the main rooting zone and the DOC was similar in magnitude and chemical characteristics to DOC collected from a nearby forest [52]. Although there was some seasonal variation in surface DOC concentration and composition in these contrasting grassland and forest ecosystems, the fluctuations declined steeply with depth [52]. This indicates that fresh shoot C inputs are only a minor component of DOC pools, limited primarily to the surface soil and fluxes following rain events after long dry periods [52].

Isotopic and spectroscopic evidence have revealed that the DOC pool is comprised primarily of smaller, more soluble, highly-oxidized organic C compounds released from the bulk SOC following microbial processing [52]. In the deeper soil layers (below ~20 cm) of a temperate forest, Ahrens et al. [51] determined that the DOC pool was comprised of 50–60% microbial-derived C. Microbial diversity and DOC chemistry are both strongly associated with soil depth. In fact, microbial population composition and the chemical character of DOC are interdependent and vary more with soil depth than with landscape position or local vegetation [105]. Compared to shoot-derived C,

root-derived C has a much greater influence on soil microbial community composition [106] and biomass [91]. Similarly, SOC composition is strongly associated with soil depth, root C inputs, and microbial biomass [86,89,91]. On the other hand, manipulations in aboveground C inputs have resulted in only minor or no changes in SOC composition in the mineral soil, even after up to 20 years of shoot litter manipulations [86,89,91].

3.4. Synthesis

The evidence suggests that, in most ecosystems, both SOC and DOC are primarily derived from belowground sources (i.e., roots and microorganisms). Because shoot litter leachate may contribute more substantially to bulk SOC as opposed to rhizosphere SOC [6], the ratio of rhizosphere to bulk soil is an important factor in determining the relative contribution to SOC of aboveground versus belowground sources [81]. Additionally, the litter layer likely plays an important indirect role in maintaining SOC stocks in some forest ecosystems [89]. Our review indicates that microbial-derived C, primarily from microbial-processed and bio-transformed root C inputs [25,95,96], comprises the majority of SOC in most ecosystems [6,25,51,79,83,94] and is protected via the sorption of DOC to minerals [27,52,79,104], particularly to clay [24,25,35]. As shown in Figure 1, root-derived C undergoes multiple stages of microbial processing, protection, and release into the DOC pool as it is transported vertically down the soil profile—helping resolve the argument that the phenomenon of SOC radiocarbon ages increasing with depth is not well explained if roots are considered the primary source of SOC [5,21,107].

4. Deep and Dynamic: Old Soil Organic Carbon is Susceptible to Abrupt Decomposition

Despite organic C in deeper soil layers having longer transit times than in more superficial layers [108], SOC traditionally considered as “stabilized” is vulnerable to abrupt decomposition [3,109]. Numerous studies have indicated that deep and old SOC may be more susceptible than superficial SOC to substantial and potentially rapid decomposition resulting from changes in environmental conditions [33,109–117]. Important knowledge gaps exist regarding deep soil biogeochemical processes, as well as the global amount of SOC and its vertical and spatial distribution [118–121]. Common bias against sampling deeper soil layers not only contributes to uncertainty in global SOC estimates and climate models, but it also limits our understanding of SOC cycling and protection mechanisms. Here we highlight the need to sample deeper soil layers considering our emerging understanding of SOC cycling and the growing body of evidence revealing changes in deep SOC over relatively modest periods of time in response to changes in climate, land use, and management.

4.1. Global Stocks and Sampling Bias

Global SOC stocks from 0–100 cm in depth are estimated to range from 1220–1576 Pg C (1 Pg = 10^{15} g) [12,13,122–126]. In a comparison of 27 studies over the past several decades, Scharlemann et al. [118] found the median across all estimates for the global SOC stock was roughly 1500 Pg C in the upper 100 cm. Estimates for global SOC stocks from 0–200 cm in depth range from ~2000–2500 Pg C [12,13], while the 200–300 cm stock was estimated at 351 Pg C [13]. Far fewer observations exist of the size of SOC stocks in soil below ~20 cm, causing substantial uncertainty in global SOC estimates [12,13,18,25,109,119]. Using a compilation of 86 published soil profiles, Jandl et al. [119] found that about half were sampled to 20 cm or less and ~90% were sampled to 30 cm or less.

Ignoring the component of an ecosystem that often contains the most organic C (i.e., deep soil) can lead to drastic misinterpretations of C cycling and changes over time [109]. For example, following 20 years of shoot litter manipulations in a temperate deciduous forest, Bowden et al. [86] found that most of the SOC loss (compared to the control) in plots with no aboveground C inputs occurred between 10 and 50 cm in depth. However, in shoot litter manipulation experiments across five ecosystems and totaling 70 publications used for a meta-analysis, the majority of sampling was conducted in the top

10 cm of mineral soil [90], which may have led to substantial underestimations of SOC changes. Land use conversion and climate change studies have also illustrated the need to account for deeper soil layers when assessing SOC changes over time, wherein incorrect conclusions about the direction or magnitude of SOC change can be drawn by shallow sampling [43,114,127]. Future progress toward understanding the effects of climate, land use, and management change on global C cycling will come from recognizing that deep SOC can (and does) change on decadal timescales.

4.2. Climate Change

Global surface temperature change by the end of the 21st century is projected to be in the range of +2–4 °C, with greater mean warming over land masses than over the ocean and with the most warming occurring in the Arctic region [128]. Although considerable variation in temperature can occur in the surface soil and even in deeper soil layers, the soil profile as a whole approximates the mean annual air temperature [129,130]. Therefore, soils will warm at roughly the same rate as surface temperatures over the next century. Recent studies underscore the importance of the deep SOC response to global warming. For example, in permafrost soils experiencing thaw, old deeper SOC contributions to ecosystem respiration flux increased with soil temperature and ecosystem respiration flux [113]. While in a temperate forest ecosystem, subjecting the mineral soil profile to 100 cm in depth to 4 °C warming increased CO₂ production at all depths and increased total soil respiration by 34–37% [114]. About 50% and 40% of soil respiration and the warming response, respectively, occurred below 15 cm [114]. Unfortunately, most studies do not report the warming response below 20 cm [114], leaving additional uncertainty in climate models.

Climate change also may have drastic implications for DOC flux. By the end of this century, extreme precipitation events are expected to become more intense and more frequent over mid-latitude and wet tropical terrestrial ecosystems [128]. These extreme precipitation events could transport to deeper soil layers large amounts of DOC comprised primarily of recently-fixed C, especially after prolonged periods without rain events where fresh C compounds have accrued in the surface soil [44,52]. While this could lead to enhanced potential for mineral associations at depth, and thus longer-term SOC storage, rapid fluxes of DOC can also result in increased DOC export [67,131]. Moreover, increased and continuing fresh C inputs to deeper soil layers can enhance bulk SOC decomposition for years to decades [115,117,132,133] by providing deep microbial communities with the energy to synthesize extracellular enzymes for SOC decomposition [4,133–135]. That is, the introduction of fresh organic C compounds to deeper soil layers can stimulate, or prime, microbial activities, alleviating potential energetic barriers to SOC decomposition that may have existed.

Similarly, fresh root C inputs can enhance microbial activity and SOC decomposition, a phenomenon referred to as (positive) rhizosphere priming [136,137]. Under changing environmental conditions, wherein deep soil microbial communities are suddenly exposed to additional root C inputs, increased bulk SOC decomposition can occur. For example, elevated atmospheric CO₂ concentrations and increased aboveground and belowground plant growth have resulted in losses of old SOC that exceeded the formation of new SOC, potentially due to increases in rooting depth and root C inputs [138–141]. In some cases, root exudates may drive increases in bulk SOC decomposition without associated increases in microbial biomass, indicating that the microorganisms are allocating the energy provided by fresh root C exudates to mineralization activities rather than to growth [133].

Interactions between root exudates and the soil mineral matrix can enhance the availability of SOC. For example, the common root exudate, oxalic acid, fosters the release of organic C compounds from protective mineral associations, thereby promoting SOC loss via microbial decomposition or export [33]. This may be why soils with finer texture experience greater rhizosphere priming effects than soils with coarser texture [132]. In other words, rhizosphere priming appears to impact mineral-associated SOC—that potentially has been stored long-term—more than particulate SOC [132]. According to a recent meta-analysis, rhizosphere priming increases SOC decomposition rates by an average of 59% [132], a phenomenon likely driven by root exudates rather than root litter [133].

Compared to surface soil, deeper soil layers appear to be as sensitive or more sensitive to rhizosphere priming [116,135]. In addition to possible rhizosphere priming effects, the introduction of roots to deeper soil layers increases soil moisture variability and aeration through transpiration, exposing soil microorganisms to potentially more favorable metabolic conditions [115].

Projected increases in hot temperature extremes over most land areas during the next century, especially on seasonal timescales [128], could promote the loss of deep SOC by modifying fine root distribution and corresponding rhizodeposits in the soil. In a study that modeled root allocation in temperate forest ecosystems, increased soil temperatures, reductions in soil moisture, and subsequent increases in soil strength led to fine root colonization of deeper soil layers [49]. Compared to coarse roots, fine roots likely release more exudates that travel further from the root surface [142], and they have faster turnover rates [143], both of which can induce rhizosphere priming effects in the surrounding bulk soil. On the other hand, root litter appears to decompose slower in deeper soil layers, likely due to shifts in microbial communities and decreased microbial biomass and available nitrogen [130,144]. In the absence of rhizosphere priming effects, this slowly decomposing root litter could increase SOC stocks and long-term storage under climate-change-induced increases in primary production and rooting depth [130].

Despite multiple soil biogeochemical models projecting reductions in SOC stocks and increases in CO₂ emissions from soils under warming, a substantial fraction of experiments diverge with these modeled results [145]. Additionally, some studies have shown varying priming effects with fresh C inputs depending on soil properties or nutrition, plant nutrient contents, C sources, or relative amounts of C inputs to soil [146–152]. Although additional shoot litter may be unlikely to increase SOC stocks [86,87,90], roots and root-associated microorganisms contribute more substantially to SOC storage, particularly in deeper soil layers. Therefore, climate-change-induced increases in root biomass and rooting depth would likely increase SOC stocks eventually [153]. However, such increases in SOC stocks could take decades to manifest and may be preceded by priming-induced deep and old SOC losses.

4.3. Land Use Change and Management

Land use change and management have been observed to impact deep SOC on decadal timescales [154]. In a meta-analysis, conversion from forest to pasture was found to increase SOC stocks by 7–13% above 100 cm, with similar increases for all depths sampled (<30, 30–50, and 50–100 cm) [155], whereas conversion from forest to crop decreased SOC stocks by ~50% above 60 cm, with similar decreases for the depths sampled (<30 and 30–60 cm) [155]. Conversion from crop to secondary forest increased SOC stocks by 53% [155]; however, sampling depth was not noted in the analysis. When deeper soil layers were sampled following conversion from crop to forest, SOC losses from >15 cm in depth were found to offset surface SOC gains for at least 40 years after conversion [50,115]. Forest harvest also has been shown to affect deep soil, reducing SOC from 60–100+ cm in depth by an average of ~18%, according to a recent meta-analysis [156]. Compared to harvest, thinning resulted in even greater (+9%) SOC reductions in the mineral soil [156]. Deep SOC seems to be especially sensitive to thinning practices [115]. For example, in a temperate forest, thinning reduced SOC stocks by 25% compared to the control over ~11 years of treatments, with most of the loss occurring below ~20 cm [157].

Reductions in deep SOC following land use change and management practices likely result from a combination of effects and complex interactions in the soil environment that enhance microbial activity, SOC decomposition, and DOC export. Land use change and management can affect soil temperature, moisture, and DOC flux, among other soil properties and processes [158]. For example, mean soil temperature and mean daily soil temperature flux at 100 cm in depth have been observed to increase by ~2–4 °C and ~4–6 °C, respectively, in the first two years following harvest compared to an unharvested reference in a temperate forest ecosystem [159]. Soils compacted by harvest treatments experienced greater temperature increases than soils not compacted by the same treatments [159], probably due

to the higher thermal conductivity of compacted soils [129]. These increases in soil temperature can substantially hasten rates of SOC decomposition by enhancing microbial metabolism [129]. Similarly, DOC flux is an important driver of soil biogeochemical processes. Increases in DOC flux from surface soil layers due to land use change or management practices can introduce substantial quantities of fresh C compounds to deeper soil layers, potentially enhancing old SOC decomposition and DOC export [67,68,131,160].

Disturbance or changes in the litter layer in response to land use or management can also affect deeper soil layers. For example, the exclusion of aboveground C inputs over 20 years in a temperate deciduous forest resulted in reductions (−24%) in SOC stocks to at least 50 cm in depth, with much of this loss occurring below 10 cm [86]. On the other hand, increased aboveground C inputs, which could result from enhanced forest productivity, have shown mixed promise toward increasing SOC stocks [86,87,90]. Although few shoot litter manipulation experiments have sampled deeper soil layers [90], a recent incubation experiment revealed that deep SOC as opposed to surface SOC would be more susceptible to priming induced by increased aboveground C inputs [117]. Fresh C from shoot litter could potentially reach deeper soil layers via preferential pathways of interconnected large soil pores. Preferential pathways, which can persist for decades in forest ecosystems [161], represent means for recently-fixed superficial C to enter deeper soil layers without substantial abiotic and biotic interactions with the soil environment along the way [54]. Because decomposition rates in preferential flow paths are likely enhanced [161] due to increased SOC concentrations (+10–70%) and microbial biomass (+9–92%) compared to nearby bulk soil [27,162], these pathways can enhance SOC decomposition in the surrounding soil.

Deep SOC losses observed following reforestation of formerly cultivated land may be primarily due to rhizosphere priming effects induced by changes in root biomass and surface area, rooting depth, and rhizodeposits [50,115]. That is, when relatively shallow-rooted agricultural ecosystems are converted to deep-rooted forests, root C inputs are introduced to deeper soil layers and can enhance or promote the decomposition of older SOC that was formerly protected under the agricultural ecosystem [115,138]. Forest management practices such as fertilization also have been observed to increase soil rooting depth [163], and the added nitrogen could enhance the potential rhizosphere priming response in deeper soil layers [116,144]. On the other hand, increased live fine root length, and thus increased activity and exudation, is considered the likely explanation for gains in SOC storage following conversion from forest to pasture [153]. As noted previously, practices or environmental conditions that increase root C inputs to soil are likely to also increase microbial biomass, which in turn could eventually increase SOC stocks and long-term storage. Nonetheless, in the case of conversion from crop to forest, SOC stocks took nearly 50 years to stabilize, resulting in deep and old SOC losses before potential gains could manifest [50,115].

5. Vulnerability on a Global Scale: Permafrost, Peatland, Wetland, and Forest Soils

Our ability to increase SOC storage and decrease greenhouse gas emissions from soils on a large scale is partially dependent on our gaining a deeper understanding of the mechanisms and controls responsible for the protection of SOC [145,164]. Assessing the vulnerability of both shallow and deep SOC in various soil types and ecosystems is essential to prioritize C sequestration initiatives and constrain climate models. Not only is SOC distributed unequally in the vertical profile, with the majority of SOC stored below ~20 cm [13], but it is also distributed unequally on global and spatial scales, varying substantially across biomes and landscapes [35]. As the magnitude of SOC loss due to both warming and priming increases with the size of the initial stock, soils with larger standing SOC stocks are especially at risk in our changing world [163,165].

5.1. Permafrost Soils

Organic C is stored in soil wherever primary production rates and organic matter inputs are greater than decomposition rates. This relationship of production versus decomposition is highly

dependent on microbial controls, which in turn are highly dependent on climate. In general, maximum decomposition rates occur in warm, humid environments. Therefore, the northern hemisphere stores more SOC than does the southern hemisphere [126]. Soils in the northern permafrost (i.e., any subsurface materials that remain below 0 °C for two or more consecutive years) region are estimated to contain ~1700 Pg C to 300+ cm in depth [166], which is more than the global SOC stock estimated for the upper 100 cm [118]. Nearly 90% of this ~1700 Pg C occurs in perennially frozen soils and deposits [166].

Permafrost SOC is especially vulnerable to abrupt and potentially rapid decomposition due to global warming [164]. While SOC in most mineral soils is protected in aggregate interiors or through adsorption to mineral surfaces [2], protection from microbial decomposition in permafrost soils is primarily dependent on the frozen conditions of the soil [164,167]. The thawing of permafrost thus enables the decomposition of ancient SOC. Unfortunately, the Arctic region is likely to warm more rapidly than the global mean [128], which is expected to increase seasonal permafrost thaw depths by at least 30–50% by 2050 [168]. Substantial reductions, ranging from 37–81% by 2100, in the upper 3.5 m of permafrost in the northern hemisphere have been projected by numerous climate models [128]. During and after permafrost thaw, protection and long-term storage of unfrozen SOC resulting from soil processes, such as the development of soil structure or mineral sorption, is possible [3]. However, thawed permafrost is also susceptible to erosion and mass movement by mudslides [129].

5.2. Peatland and Wetland Soils

Similar to permafrost soils, peatland and wetland soils are more vulnerable than most mineral soils to rapid change because the protection of SOC in these systems is primarily dependent on the anaerobic conditions under which the soils formed [164,167]. Peatlands and wetlands are estimated to contain ~500 Pg C [169,170], or about one-third of the global SOC stock estimated for the upper 100 cm [118]. While peatlands occupy only 3% of the terrestrial global surface [171], they contain over 80% of this estimated 500 Pg C [169]. Expected decreases in soil moisture during the summertime in continental areas [128,172] could potentially dry out surface layers of peat, thus making substantial amounts of SOC available for aerobic decomposition [167]. While additional C sequestration in vegetation and reduced CH₄ emissions may offset increases in CO₂ emissions from peatlands under aerobic conditions, increases in peat fire frequency and severity expected due to higher temperatures and peat drying would rapidly release large amounts of C to the atmosphere [167].

5.3. Forest Soils

Forest ecosystems are estimated to contain over half the global SOC stock [12,13,18], and soils not affected by land use change have been acting as a global C sink for centuries [1,173]. Between 1990 and 2007, the world's forests sequestered as much as 30% of annual global anthropogenic CO₂ emissions [174,175]. However, differences between the two large fluxes of forest soil C inputs and soil respiratory C losses are small [176,177]. Therefore, even minor changes in C inputs or losses from forest soils can potentially affect the global C cycle [176,178]. In our warming world, it is unclear if forest soils will continue to act as a global C sink. Hastened microbial metabolic processes due to warming are projected to result in net global reductions in SOC storage [179]. Moreover, in some forest ecosystems, warming-induced increases in primary production and rhizodeposition could result in priming effects, further decreasing SOC stocks for decades, particularly in deeper soil layers [33,110–112,132,138–140,180]. On the other hand, given the pivotal role that microorganisms play in SOC cycling—that is, increasing the solubility and potential for protection of organic C compounds [2,18,19]—warming and increased belowground C inputs could potentially lead toward greater opportunities for SOC protection and long-term storage [164].

5.4. Models

Current soil models used for climate change projections do not reflect our emerging understanding of SOC cycling, protection, and long-term storage mechanisms [164]. A recently developed SOC model—Carbon, Organisms, Rhizosphere, and Protection in the Soil Environment (CORPSE)—revealed that priming effects, when accounted for, resulted in net SOC storage losses in most terrestrial ecosystems under elevated CO₂, counteracting SOC gains from increased primary production and C inputs [181]. However, priming effects are generally unaccounted for in global models [138]. In fact, standard models used to predict SOC dynamics do not incorporate direct microbial controls on the vertical and spatial distribution of SOC stocks [126]. By modelling microbial processes, Wieder et al. [126] were able to explain 50% of the variation in global SOC observations in the upper 100 cm of soil compared to traditional models that explained only 28–30% of the variation. These results underscore the importance of including microbial controls on SOC dynamics in global models, as well as the need for further study of deep soil microbial processes, SOC protection mechanisms, and their interactions [78,141,145,164]. Much uncertainty remains in controls on SOC cycling, particularly in the deep soil environment. Long-term studies focused on changes in C inputs to soil—and resulting shifts in superficial and deeper soil microbial communities and activity, DOC fluxes and chemistry, SOC fractions, and greenhouse gas fluxes—are needed to help constrain soil biogeochemical models and, by extension, climate models [145].

6. Sampling and Processing: The Need for Methodological Standardization

To understand the effects of climate, land use, and management change on C cycling in soils, our ability to accurately quantify and compare SOC stocks over time is critical. Unfortunately, all soil sampling and processing methods are not equally accurate, precise, or comparable. The inaccuracy or incompatibility of SOC quality and quantity results obtained with different techniques presents additional challenges toward understanding soil biogeochemical processes and SOC protection mechanisms. Identifying these actual or potential issues and developing standards will move us closer to creating more reliable global SOC databases and models.

6.1. Sampling Methods

Numerous soil sampling tools and methods exist. Of the three most common methods—which include core, clod, and excavation methods—the core method is by far the most commonly used [7]. Despite being the most used method, the core method frequently has been found to underestimate soil mass and bulk density compared with other soil sampling methods, which can lead to substantial underestimations of SOC stocks [7,182–186]. Therefore, it is recommended that the accuracy of the core method for measuring these parameters be assessed for a given soil and adjusted appropriately using a more reliable method, such as the excavation method [7]. Additional incompatibility issues arise due to whether soil is sampled by depth or horizon and how (or if) bulk density is used as the parameter to calculate SOC stocks [7,187,188]. In general, sampling by horizon is recommended for studying pedogenic controls on soil properties, while sampling by depth is recommended for nutrition-based studies because it requires a smaller sampling size for a given error limit [189,190]. Calculating SOC stocks using the mass-based approach is commonly recommended to avoid confounding effects caused by land-use- or management-related changes in bulk density over time [88,191–195].

6.2. Coarse Fraction

Many studies exclude the coarse soil (>2 mm) fraction of SOC, which may contain a substantial portion of organic C content [8,109,196]. The coarse soil fraction has been found to contain as much as 75% of total SOC in rocky forest soils [184]. Zabowski et al. [8] concluded that soils with a coarse fraction greater than 20% (by weight) were likely to have substantial (>10% of total SOC) organic C content in the coarse fraction. Within the 48 conterminous United States alone, skeletal ($\geq 35\%$ by volume

rock content) soils comprise ~33% of the area [188]. Therefore, the common practice of discarding the coarse fraction of soils could result in substantial underestimations of the SOC stocks of rocky soils if the volume of soil occupied by coarse fragments is considered void (i.e., coarse fragment mass but not volume is subtracted from SOC estimates, as suggested by Throop et al. [188]) [8,109,196]. Although the coarse fraction of SOC has been historically ignored and considered chemically inert [196], Koele and Hildebrand [197] concluded that nutrient exchange mechanisms were essentially the same for both free and stone-protected fine soil (<2 mm) and that the coarse fraction contribution to short-term nutritional dynamics was substantial. This evidence suggests that we cannot assume coarse fraction SOC is inactive on decadal timescales. While it would be more labor-intensive, determining the contribution of the coarse soil fraction to SOC in rocky soils would improve the accuracy of regional and global SOC stock estimates [8,109,196].

6.3. Processing and Analysis

Soil can be processed field moist, wet, air-dried, oven-dried, or rewetted after drying. These different methods, understandably, can yield very different results. For example, air-drying soil increases the quantity or strength of organic C interactions with minerals, aggregate stability, and DOC, while decreasing microbial biomass C and altering microbial community structure [9,198,199]. Similarly, the common practice of oven-drying soil prior to analysis was shown to increase DOC concentrations [200]. Such effects should be considered and air- or oven-drying should be strictly avoided when microorganisms [201], DOC, or SOC fractions are measured or analyzed. Sieving with mesh sizes smaller than 5–6 mm can also alter soil microbial biomass and activity, as well as DOC concentrations [201–203]. Dissolved organic C quality and quantity analyses are further complicated by the different techniques available, including in situ and laboratory collection techniques [44,200,204] and the use of various extraction methods (e.g., cold or hot with water or a CaCl₂, K₂SO₄, or KCl solution) [11,198,205,206], filter types [11], and pore sizes [207], all of which can lead to different results or potential artefacts.

In general, DOC extracted with different salts is more similar than DOC extracted with water, and the amount of DOC released from mineral soil is greatest for K₂SO₄, similar for KCl and water, and slightly lower for CaCl₂ [205]. Chantigny et al. [206] and Gabor et al. [205] recommend using CaCl₂ extraction in the laboratory for mineral soils to potentially limit organic matter desorption from mineral surfaces or to reduce possible artifacts and interference for fluorescence analysis. Although DOC extracted in the laboratory is not equivalent to DOC in soil solution extracted in the field by lysimeters [205], soil pore water DOC also is not perfectly represented by lysimeters [208,209]. Concerning filter type, Chantigny et al. [206] and Zsolnay [11] recommend polycarbonate filters. Unlike cellulose and acetate filters, polycarbonate filters do not appear to adsorb or release DOC [11]. Dissolved organic C is commonly extracted with a filter pore size of 0.45 µm. However, most DOC compounds are smaller than 0.025 µm, and thus pore sizes between 0.4 and 1.2 µm have resulted in DOC filtrates with similar properties [11,207]. To provide DOC properties that are more homogeneous and to reduce possible interference for fluorescence analysis, Chow et al. [207] recommend a filter pore size of 0.1 µm or smaller.

6.4. Fractionation Methods

Finally, varying methods used for physical fractionation of SOC [10]—to isolate organic C contained in differently sized aggregates, density fractions, and mineral-associations—add ambiguity to meta-analyses and limit our ability to draw overall conclusions about organic C protection mechanisms in the soil environment and in different soil types, ecosystems, and biomes. Not only can SOC fractionation provide insight into mechanisms of C cycling in soils and controls on long-term storage, but it can also reveal changes in SOC fractions over time that may not be evident in the SOC stock as a whole [100]. Although there are many viable and useful SOC fractionation techniques [10], given the essential roles that both mineral sorption [2,25,26,30–36,40,41] and aggregate

formation [36,41,151,152,210,211] play in SOC cycling and protection, methods that include aggregate, density, and particle-size fractionation [210] will provide the most robust data, moving us toward a better understanding of SOC dynamics [145].

7. Synthesis and Future Directions

Any changes in microbial controls, root biomass and surface area, organic matter, or soil properties (e.g., temperature and moisture) can affect SOC accumulation, decomposition, and transit time—even in deeper soil layers. Unfortunately, available data on SOC in the literature is often confined to surface soil layers (above ~20 cm), which store less than half of the global SOC stock [12,13,18,25,109,119]. Deep SOC is not intrinsically “stable” and is vulnerable to potentially rapid decomposition when the environmental conditions under which it accumulated change, as the studies reviewed herein have revealed. With biological activity (and associated SOC cycling processes) often extending to at least 100 cm in depth [212,213], and with half the variation in global SOC observations to 100 cm in depth explained by modeling microbial processes [126], sampling soil to 100 cm in depth should be the standard rather than the exception. However, sampling even deeper may be necessary in certain cases, with some soils containing substantial SOC and microbial activity well below 100 cm [214–217].

The increased accuracy and precision of data gained by sampling deeper soil layers and by following a standardized methodology for SOC quality and quantity analyses would enhance our knowledge of SOC cycling and assist in reducing uncertainty in climate change projections [119]. Due to increasing SOC radiocarbon ages with depth, losses of deeper SOC result in additions of relatively long-sequestered C to the atmosphere and to a comparably short-term C cycle [3,14,15]. Further study of SOC sources and biogeochemical processes in the deep soil environment will contribute substantially to our emerging understanding of SOC protection mechanisms and vulnerability, which can provide us with key insights into climate-carbon feedbacks, as well as help us to prioritize C sequestration initiatives. Importantly, the evidence suggests that belowground C inputs (from roots and microorganisms) are the dominant source of both SOC and DOC in most ecosystems. However, the litter layer likely plays an important indirect role in maintaining SOC stocks in some forest ecosystems. Our shifting understanding of SOC “stability” has important implications for future research and for our understanding of the effects of climate, land use, and management change on SOC cycling.

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