

Unlocking the potential of whole-profile carbon sequestration in agricultural soils

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Abstract Agricultural soils have great potential to sequester carbon, mitigating climate change while enhancing soil health. Subsoil layers are particularly promising for long-term carbon storage due to their lower carbon density and slower carbon turnover compared to topsoil. The reduced subsoil carbon density primarily results from limited carbon inputs at depth, while slower turnover is driven by 1) stronger physiochemical constraints on microbial decomposition, and 2) limited availability of high-quality, energy-rich substrates. These factors underscore the opportunities to target management practices that either increase carbon inputs to subsoil layers or reduce carbon turnover rates to enhance subsoil carbon sequestration. Advancing this field requires understanding the vertical distribution of carbon input quality and quantity, as well as the processes driven vertical carbon transport within soil profiles. Additionally, it is critical to elucidate how substrate properties (e.g., energy and nutrient content) and vertical environmental constraints (e.g., hydrothermal regimes and oxygen availability) influence microbial efficiency. Addressing these knowledge gaps will enable the design of effective management practices, unlocking the full potential of whole-profile carbon sequestration in agricultural systems.

Keywords carbon sequestration, carbon turnover, carbon input, agricultural soils, subsoil

1 Introduction

The soil organic carbon (SOC) reservoir is a key component of the global carbon cycle, regulating atmospheric CO₂ levels and supporting soil function (Paustian et al., 2016). Globally, human land use has

caused significant SOC depletion, including an estimated loss of 133 Pg in the top 1 m of soil, with croplands and pastures each contributing approximately half (Sanderman et al., 2017). In Australia, 50 years of land clearing for agriculture has led to SOC losses of 50% in the top 0.1 m and 40% in the top 0.3 m of soil (Luo et al., 2010b). These losses not only exacerbate climate change but also degrade soil health. Restoring SOC or increasing its storage represents a critical nature-based solution for sustainable agriculture and climate change mitigation.

To promote SOC accumulation, various agricultural management practices have been explored, such as cover cropping, residue retention, conservational tillage, and biochar application (Weng et al., 2017; Garland et al., 2021). These practices enhance carbon inputs into the soil or protect SOC from microbial decomposition, thus facilitating SOC accumulation. However, their impact on subsoil carbon remains poorly understood, as most research has focused on surface layers (Button et al., 2022), with significant uncertainties highlighted by both experimental and modeling studies (Button et al., 2022; Gaudaré et al., 2023; Xiao et al., 2024). Subsoil carbon density is only approximately one-third that of topsoil, suggesting untapped potential for subsoil carbon sequestration (Sierra et al., 2024). However, subsoil SOC research is complicated by the high heterogeneity of soil environments, including variations in physiochemical conditions, microbial activity, and root inputs along the soil profile and across spatial scales (Button et al., 2022; Gaudaré et al., 2023; Xiao et al., 2024). Addressing these uncertainties and realizing the subsoil carbon sequestration potential require a holistic understanding of processes and mechanisms underpinning whole-profile SOC dynamics and their response to management interventions.

In this Perspective, we argue that subsoil carbon sequestration potential is both theoretically and

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practically achievable. To support this claim, we first explore the key drivers and processes shaping whole-profile soil carbon dynamics. We then examine the fundamental mechanisms governing the formation of SOC profiles, focusing on carbon turnover – a critical property determining SOC persistence and influenced by vertical variations in physical, chemical, and biological conditions. Finally, we summarize strategies with the potential to enhance subsoil SOC storage and identify critical knowledge gaps to prioritize future research. Our objective is to provide a cohesive framework for understanding the formation and transformation of whole-profile SOC profiles, advancing whole-profile SOC management and addressing both scientific and practical challenges in agricultural soils.

2 The foundation of soil carbon profile formation

SOC stocks at any depth result from the balance between carbon inputs and outputs. The rate of SOC change over time can be expressed as

$$\frac{dSOC}{dt} = \text{Input} - \text{Output}. \quad (1)$$

Inputs predominantly originate from plant-derived organic matter, such as litter, straw, roots, and rhizodeposition, which are the primary carbon sources in most systems, including agroecosystems. Climate pattern largely determines the maximum potential inputs. However, this potential can be significantly modified by local environmental constraints (e.g., nutrient availability, fire, soil acidity and salinity) and land management practices (e.g., residue removal). External organic carbon amendments, such as manure and biochar, can significantly contribute to inputs, particularly in regions where organic amendments are applied regularly. These inputs not only vary in their chemical composition and decomposition rates but also influence the vertical distribution of SOC within the soil profile.

Outputs are primarily driven by microbial decomposition, where organic carbon is mineralized and released as CO₂ through respiration. However, in situ quantification of CO₂ emissions remains a significant challenge, as soil respiration is a combination of microbial heterotrophic respiration and root autotrophic respiration, which are difficult to separate (Werth and Kuzyakov, 2010). Partitioning CO₂ emissions to specific depths, where CO₂ is produced, is even more complex (Wordell-Dietrich et al., 2020). As a result, outputs are commonly estimated as the product of the SOC stock and its average turnover rate (k), representing the fraction of SOC lost per time step. The inverse of k is referred to as turnover time (τ), defining the average residence time of carbon in the soil (Sierra et al., 2017; Luo et al., 2019).

The turnover rate depends on factors such as substrate quality, microbial community composition, temperature, moisture, soil physiochemical properties, and management practices. In addition to respiration, outputs also include carbon losses through runoff, leaching of dissolved organic carbon, and erosion. These non-respiratory outputs are particularly significant in soils with poor structure or those situated in sloping landscapes. The magnitude of these losses depends on location-specific conditions such as soil type, landscape position, and land management practices.

Equation (1) forms the foundation for understanding and predicting SOC profile formation. Changes in SOC at any depth reflect the integrated consequences of varying input sources and turnover rates. Dividing SOC into multiple pools, each with distinct turnover rates and input sources, allows for a more detailed representation of SOC dynamics and can be expressed as special cases of Eq. (1). Along soil profiles, the vertical distribution of SOC is inherently shaped by the vertical patterns of inputs and outputs. Understanding these patterns and their underlying controls is the key to identify agricultural management practices that promote whole-profile SOC sequestration.

3 The vertical pattern of carbon inputs

In all ecosystems, including agroecosystems, plant root debris — comprising dead roots and root exudates — are the primary source of carbon inputs to the mineral soil, complementing the significant contribution of aboveground plant residues to surface soil carbon inputs. Consequently, the depth distribution of plant root biomass plays a central role in shaping soil carbon profiles (Jobbágy and Jackson, 2000). Among ecosystems, root system architectures vary substantially, influenced by plant physiologic characteristics, prevailing environmental conditions, and management practices (Xiao et al., 2023a). These variations result in highly dynamic and spatially heterogeneous patterns of carbon inputs, which can be tailored to local environmental conditions to enhance SOC sequestration (Luo et al., 2024). Globally, root biomass decreases exponentially with depth, with > 50% of root biomass concentrated in the top 0.2 m soil (Xiao et al., 2023a). This pattern closely mirrors the vertical distribution of SOC stocks, as observed across the globe and croplands (Fig. 1(a)).

Carbon inputs to a given soil layer are not solely derived from plant residues within that layer. Adjacent layers also contribute through physical and chemical processes. Dissolved organic carbon, for example, is transported vertically through leaching, diffusion, and advection, contributing to subsoil carbon pools (Schmidt et al., 2011; Kaiser and Kalbitz, 2012). Bioturbation by soil-dwelling organisms such as earthworms, ants, and

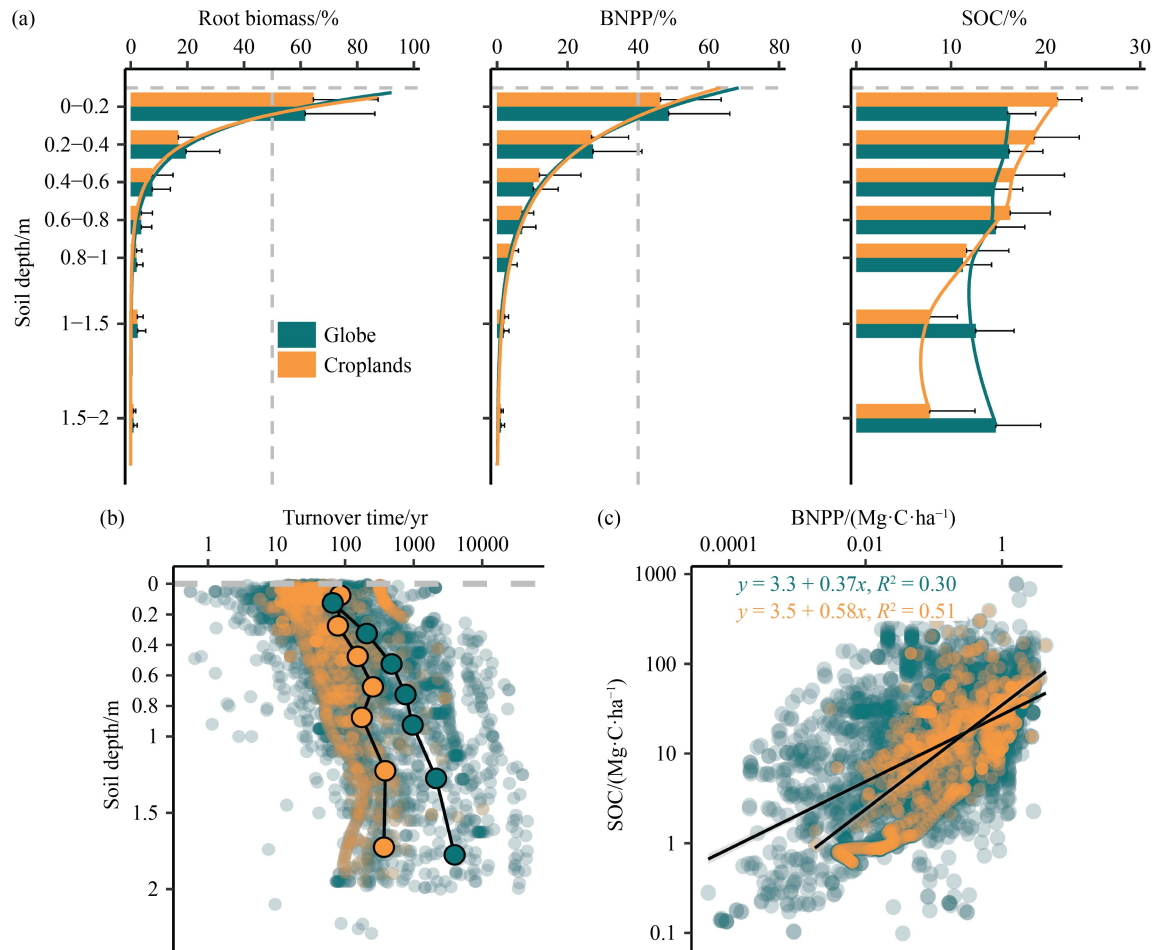


Fig. 1 Depth distribution of carbon inputs and turnover times. (a) The proportional vertical distributions of root biomass, belowground net primary productivity (BNPP), and soil organic carbon (SOC) stocks. The root biomass and BNPP data were adopted from Xiao et al. (2023b). The data for the vertical distribution of SOC were derived from the WoSIS (Batjes et al., 2020) soil profile database. (b) Vertical distribution of turnover times of SOC, which can be accessed from Wang et al. (2024). (c) The relationship between SOC stocks and BNPP. In panel (a), the lines represent the regression relationship of the mean proportional contribution against soil depth; the error bars indicate one standard deviation. In (b), the solid dots with black circles represent the average turnover time in each standard soil depth layer. The black lines in panel (c) are the regression lines, with R^2 denoting the determination coefficient. Please note the log scale of x -axis in (b) and (c).

termites further redistribute organic matter across layers, altering SOC profiles (Tonneijck and Jongmans, 2008; Guidi et al., 2022). Root activity also facilitates vertical carbon movement. As roots grow, die, and decay, they create macropores, form soil aggregates, increase soil hydraulic conductivity, and enhance water infiltration. These processes promote the movement of particulate and dissolved organic carbon into deeper layers. At larger scales, soil erosion and deposition significantly influence SOC distribution across landscapes (Lal, 2005; Doetterl et al., 2016). Erosion removes topsoil carbon, often leading to shallower SOC profiles and substantial carbon losses, particularly in mountainous regions where erosion rates are high (Gregorich et al., 1998; Ritchie et al., 2007). Conversely, sediment deposition in riparian zones or low-lying areas can accumulate organic carbon, contributing to the development of deep soil carbon profiles (Mariappan et al., 2022). These processes

highlight the interconnected nature of SOC dynamics and the need to consider both vertical and lateral carbon movements when evaluating SOC sequestration potential.

4 The vertical pattern of carbon turnover

Globally, the turnover time of organic carbon (i.e., $1/k$) in the 0–0.2 m soil layer is estimated at approximately 50 years (Fig. 1(b)). It increases exponentially with depth, exceeding 4000 years in the 1.5–2.0 m soil layer (Xiao et al., 2022). Radiocarbon dating corroborates this pattern, revealing that subsoil carbon is much older than topsoil carbon (Shi et al., 2020; Wang et al., 2023). As a result, subsoil retains more carbon per unit of input compared to topsoil. Notably, net primary productivity allocated to soil decreases with depth at a faster rate than the decline in SOC stock, highlighting the greater carbon retention

efficiency in subsoil layers (Fig. 1(a)). This has direct implications for carbon management: increasing carbon inputs to deeper soil layers could enhance long-term SOC sequestration due to the prolonged turnover times of subsoil carbon. The longer turnover times in subsoil can be attributed to reduced microbial activity and increased physiochemical protection of SOC against microbial attack.

4.1 Gradients of microbial activity

The exponential increase in SOC turnover times with depth reflects reduced microbial activity, as microbes drive SOC turnover (Dove et al., 2021). Along the soil profile, metabolic and environmental constraints intensify with depth, limiting microbial activity and SOC decomposition in subsoils (Fierer et al., 2003; Sun et al., 2020; Kang et al., 2021). One key indicator of microbial activity is the microbial quotient (MQ), defined as the ratio of microbial biomass to SOC content. MQ consistently decreases with soil depth across ecosystems, reflecting a decline in microbial activity relative to available carbon (Sun et al., 2020).

Metabolically, microbial activity in deeper layers is constrained by limited availability of energy-rich substrates and nutrients, such as sugars, proteins, and inorganic nitrogen. This limitation is evident from observed increase in microbial activity and priming effects upon the addition of fresh carbon or nutrients to deep-layer soils (Fontaine et al., 2007; Karhu et al., 2016). Environmentally, several factors further inhibit microbial activity at depth. For example, O₂ availability generally decreases with depth, especially in poorly aerated soils (Blossfeld et al., 2011; Owens et al., 2016). SOC decomposition in upland soils predominantly relies on O₂ as the primary electron acceptor, and insufficient O₂ supply slows decomposition, particularly for recalcitrant compounds prevalent in subsoils (Li et al., 2022). However, it is noteworthy that O₂ limitations significantly impede SOC decomposition only when O₂ diffusion is severely restricted, such as under water-logged conditions (Noyce et al., 2023).

Another important gradient is that subsoil environments are more stable than topsoil environments. For example, temperature is generally more stable in deeper layers, leading to lower microbial activity (Allison and Martiny, 2008). This phenomenon can be referred as environmental variability priming. It posits that microbial activity increases under fluctuating environmental conditions due to heightened metabolic responses. Under fluctuating conditions, microbes ramp up enzyme production, accelerate resource uptake, or reproduce faster to exploit transient opportunities. Four main hypotheses have been proposed to explain the variability priming: 1) stress-induced responses: fluctuations may act as mild stresses, inducing the production of stress-

response proteins and enzymes that enhance microbial activity to cope with environmental changes (Amarnath et al., 2023); 2) metabolic flexibility: while constant environments streamline microbial metabolism, fluctuating conditions maintain metabolic flexibility, enabling rapid adaptation to changing conditions (Chen et al., 2021; Ortiz et al., 2021); 3) legacy effects: microbes may retain enzymes or metabolic products from previous encounters, allowing rapid responses when resources reappear (Jurburg et al., 2017; Canarini et al., 2021); 4) increased diversity: environmental fluctuations create new ecological niches, disrupting microbial competition and promoting diversity, which enhances SOC decomposition efficiency by expanding microbial functional capacity (Cooper and Lenski, 2000; Zeglin, 2015). However, these mechanisms and their relative importance have been rarely tested in field condition.

4.2 Gradients of physiochemical protection

Minerals and aggregates protect SOC from decomposition, promoting the persistence of carbon in soil (Kleber et al., 2021). Along the soil profile, mineral weathering generally decreases with depth, altering mineral surfaces and reducing their capacity to bind organic matter. However, subsoil minerals are often less saturated with SOC due to low SOC content in these layers. In the topsoil, evidence indicates that mineral-associated organic carbon shows a saturation relationship with total SOC (Cotrufo et al., 2019). This suggests that mineral binding sites in carbon-rich topsoil are closer to saturation, whereas subsoil minerals may have more unoccupied binding sites.

The concept of saturation, determined by the maximum mineral surface area available for binding SOC, is considered a key mechanism regulating SOC sequestration potential (Georgiou et al., 2022). However, the saturation concept has been questioned by observed linear positive relationships between mineral-associated organic carbon (MAOC) and SOC even in carbon-rich systems (Begill et al., 2023; García-Palacios et al., 2024). A proposed mechanism is that MAOC can accumulate on MAOC bonded to minerals, forming a “skyscraper-like” structure (Begill et al., 2023), as supported by micro-scale imaging of clay particles (Schweizer et al., 2021) and organo-organic associations (Kang et al., 2024). Nevertheless, both the saturation and “skyscraper” would be unlikely to occur in subsoil layers due to much lower overall carbon density thereby limited mineral surface occupation by SOC. Additionally, minerals with high charge, such as certain clays and metal oxides, are often more abundant in subsoil due to reduced weathering compared to topsoil and deposition of minerals leached from upper soil layers. These minerals exhibit strong electrostatic attraction to organic matter, enhancing its stabilization and protection. Overall, SOC in deeper soil

layers is generally older, more stable, and more intimately associated with minerals than in surface soils. This reflects a combination of slower turnover rates, protective mechanisms, and selective inputs of carbon to the subsoil.

5 Novel management practices

It is certain that low subsoil carbon density is primarily due to the exponential decrease of carbon inputs with depth (Fig. 1(a)). It is also certain that carbon inputs to subsoil persist longer (Fig. 1(b)) due to stronger protection mechanisms, including mineral associations, physical occlusion, and suppressed microbial activity in subsoil environments. These two facts highlight two general pathways to promote soil carbon accumulation: 1) increasing carbon inputs (Fig. 1(c)), and 2) slowing down SOC turnover. Where agricultural management practices have been extensively studied for their impact on surface soil carbon (Luo et al., 2010b), novel strategies are needed to target whole-profile carbon sequestration, particularly in subsoil (Table 1). By leveraging the unique characteristics of subsoil environments, these practices can unlock their sequestration potential, contributing to long-term carbon storage and sustainable soil management.

5.1 Deep-rooted crops, perennials, and agroforestry

Deep-rooted plants, such as perennial grasses (e.g., switchgrass) and certain crops (e.g., alfalfa, sorghum), channel significant biomass belowground, increasing carbon inputs to subsoil layers (Lynch et al., 2022). Root-derived carbon inputs from these plants include exudates, sloughed-off cells, and decaying roots, all of which

contribute to subsoil SOC accumulation. Advances in crop breeding have further expanded the potential of these species by developing cultivars with deeper, more extensive root systems tailored to site-specific conditions (Busch and Miller, 2022; Eckardt et al., 2023). Mixed cropping systems that combine shallow- and deep-rooted species can further optimize whole-profile carbon sequestration by leveraging complementary rooting depths (Luo et al., 2024). Agroforestry, a prominent example of such system, integrates trees with crops or pastures and is particularly valuable for carbon sequestration and climate change mitigation. Trees in agroforestry systems provide additional carbon inputs while allocating carbon deeper into the soil profile, enhancing long-term storage (Skole et al., 2021; van Noordwijk et al., 2021). However, the successful implementation of these systems requires careful management to balance potential trade-offs, including competition for water and nutrients, which can limit their effectiveness under resource-constrained conditions.

5.2 Full-inversion tillage

Full-inversion tillage (FIT) involves relocating carbon-rich surface soil into deeper layers where stable environments slow microbial decomposition rates. Simultaneously, FIT exposes low-carbon subsoil layers to fresh organic inputs, enhancing overall sequestration when combined with practices like residue retention or cover cropping (Angers and Eriksen-Hamel, 2008; Luo et al., 2010a; Lawrence-Smith et al., 2021). However, careful management is required to mitigate risks, including CO₂ emissions from previously stable subsoil carbon and potential disruption of soil structure post-inversion.

Table 1 Novel management practices for subsoil carbon sequestration, including their mechanisms, associated challenges, and representative references

Practice	Mechanisms	Challenges	References
Deep-rooted crops and perennials	<ol style="list-style-type: none"> 1) Increase subsoil carbon inputs via root biomass and exudates 2) Enhance microbial carbon processing in deeper layers 	<ol style="list-style-type: none"> 1) Requires crop breeding for specific traits 2) Potential competition for water and nutrients 3) Stimulated decomposition of native organic carbon (i.e., the priming effect) 	Luo et al., 2024; Skole et al., 2021; Lynch et al., 2022
Full-inversion tillage	<ol style="list-style-type: none"> 1) Moves carbon-rich surface soil into deeper layers, reducing microbial decomposition in the stable subsoil environment 2) Exposes topsoil to fresh carbon inputs, promoting net sequestration if accompanied by residue retention or cover cropping 	<ol style="list-style-type: none"> 1) Risks disrupting subsoil structure and increasing CO₂ emissions if poorly managed 2) May require complementary practices to maximize sequestration potential 	Lawrence-Smith et al., 2021; Zhu et al., 2022
Soil amendments	<ol style="list-style-type: none"> 1) Stimulate root growth in subsoil layers by targeted nutrient delivery 2) Directly contribute organic matter to subsoil through deep compost or biochar injection 3) Increase carbon stabilization by adding reactive minerals (e.g., iron oxides) or clay-rich materials 4) Enhance mineral binding of organic carbon 	<ol style="list-style-type: none"> 1) High costs of equipment and labor 2) Potential for soil compaction or uneven nutrient distribution 3) Limited research on field-level applications 4) High costs of sourcing and applying materials 	Buss et al., 2024; Weng et al., 2017; Liu et al., 2022
Bioengineering	<ol style="list-style-type: none"> 1) Introduce beneficial microbes or earthworms to enhance organic matter stabilization 2) Promote mineral-organic associations via microbial byproducts 3) Engineering plants producing root exudates with chemically resistant compounds 	<ol style="list-style-type: none"> 1) Effectiveness highly site-specific 2) Potential ecological risks or unintended consequences 	Elnahal et al., 2022; Thomas et al., 2020; Liu et al., 2023

A promising alternative is the ditch-buried straw return system, which combines the advantages of both FIT and no-till. This novel practice buries crop straw into deep ditches, operating on a small fraction of the field at a time while leaving the majority of the land undisturbed (i.e., untilled) (Zhu et al., 2022). By alternating ditching locations over time, this system gradually loosens the soil (which usually benefits good soil structure and porosity) while minimizing disturbance. Furthermore, it significantly reduces the energy requirements for tillage machinery (Yang et al., 2019), improving the practice's overall sustainability.

5.3 Soil amendments

Targeted application of fertilizers and organic amendments to subsoil layers stimulates root proliferation and enhances carbon inputs at depth (Celestina et al., 2019). For example, deep banding of phosphorus and potassium encourages roots to explore deeper horizons, increasing subsoil carbon inputs (Bordoli and Mallarino, 1998; Liu et al., 2022). Similarly, injecting compost, manure, or biochar into deeper layers bypasses the limitations of shallow carbon inputs and directly contributes to subsoil carbon accumulation (Kirschbaum et al., 2021). Biochar application would be especially useful for stabilizing carbon sources and enhancing nutrient retention (Weng et al., 2017). Given that subsoil carbon sequestration is closely tied to the formation of stable mineral-organic associations, which protect organic matter from microbial decomposition, adding reactive minerals, such as iron and aluminum oxides, to subsoil layers can enhance carbon stabilization by increasing binding sites for organic molecules (Buss et al., 2024). Similarly, incorporating clay-rich materials into subsoil horizons can similarly amplify carbon storage potential, particularly in coarse-textured soils. Despite their promise, these practices require specialized equipment and careful monitoring to avoid soil compaction or nutrient inefficiencies. Practical applications of soil amendments are generally still in early stages and require further research to optimize effectiveness and cost-efficiency. Continued innovation in soil amendment practices would play a critical role in advancing subsoil carbon sequestration strategies while maintaining soil health and productivity.

5.4 Bioengineering

Manipulating microbial communities to enhance carbon stabilization is an emerging frontier in soil management. Microbial inoculants, such as mycorrhizal fungi or phosphate-solubilizing bacteria, can promote root growth, increase nutrient cycling, and enhance the formation of mineral-associated organic matter in subsoils (Elnahal et al., 2022). Additionally, introducing deep-burrowing

earthworms (e.g., *Lumbricus terrestris*) has been shown to transport organic residues from surface layers into subsoil, effectively redistributing carbon (Blouin et al., 2013; Thomas et al., 2020). Engineering plants to produce root exudates with chemically resistant compounds (e.g., suberin) has been also proposed as a strategy to enhance soil carbon storage by increasing the persistence of root-derived carbon in soil (Busch and Miller, 2022; Eckardt et al., 2023; Liu et al., 2023). However, the success of these interventions depends on soil type, local microbial communities, and climatic conditions, necessitating further research on scalability and ecological risks.

6 Future vision

Adopting suitable management practices offers the potential to refill past SOC losses and even increase carbon storage beyond historical levels, positioning subsoil carbon sequestration as a major nature-based climate solution for sustainable agriculture. Global change presents both opportunities and challenges for whole-profile SOC dynamics, as evolving cultivars and cropping systems to ensure food security remain underexplored in this context. For instance, recent breeding efforts have produced cultivars with higher root densities in topsoil but shallower rooting depths, potentially reducing carbon input to subsoil layers. Such shifts in root architecture may alter the overall amount and depth distribution of carbon inputs, disrupting the carbon input-output balance across the soil profile. Explicit evaluation of these impacts is urgently needed to better understand how future cropping systems may influence whole-profile carbon storage. Additionally, global change influences crop performance and drives farmers' choice of land management practices. As farmers adapt to evolving climatic conditions, their adoption of novel cultivars and management strategies to mitigate global change impacts could have profound implications for SOC dynamics. These shifts necessitate proactive research to ensure that new agricultural practices not only maintain productivity but also enhance land sustainability represented by carbon sequestration.

Despite the promise of the novel practices to enhance whole-profile carbon sequestration, challenges remain (Table 1). Subsoil environments are difficult to explore and, like topsoil, exhibit substantial heterogeneity in their physical, chemical, and biological properties. This variability complicates the implementation of uniform management strategies and underscores the need for site-specific approaches. Knowledge-guided machine learning is a such approach, which substantially improves model prediction accuracy at the spatiotemporal scale meaningful for land management (Liu et al., 2024; Xiao et al., 2024). Long-term field studies are essential to

assess the persistence of subsoil carbon under diverse climatic and management scenarios. Additionally, economic analyses are critical to ensure the feasibility of these practices for widespread adoption. By integrating innovative management practices into agricultural systems, we can unlock the potential of subsoil carbon sequestration. Such efforts will not only contribute to climate change mitigation but also ensure sustainable agricultural productivity and soil health.

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