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Invited Perspective

Interactions between small molecules and carbon-engine microbes: Key mechanisms driving soil carbon accumulation

Synergistic interactions between small molecules (SMs) and carbon-engine microbes (CEMs) play key roles in soil organic carbon (SOC) accumulation. The SMs (typically $<$ 1 000 Da), primarily derived from root exudates and polymer degradation, enhance CEM functions by fueling microbial metabolism *via* rapid uptake, elevating carbon use efficiency for persistent necromass formation, and enriching mineral-binding and aggregate-forming taxa. Tailored SMs stimulate CEMs to build macroaggregates and mineral-associated organic carbon while suppressing the positive priming effect. Precision SOC management requires optimized SM inputs (*e.g.*, blended organics and compost-converted recalcitrant carbon), microbial community engineering (*e.g.*, CEM inoculants and synthetic communities), and artificial intelligence (AI)-integrated monitoring (*e.g.*, sensor networks and predictive SM-CEM models) to maximize carbon sequestration and avoid native carbon loss.

The accumulation of soil organic carbon (SOC) improves soil fertility and productivity, promotes agricultural sustainability, and sustains subterranean biological networks (Zhang, 2023). As the largest terrestrial carbon reservoir, soil stores an estimated 1 500–2 400 Pg of carbon within the top meter, surpassing the combined carbon stocks of the atmosphere and vegetation by 1.5- to 2-fold (Balesdent *et al.*, 2018; Friedlingstein *et al.*, 2023). The stability of this SOC pool governs progress toward carbon neutrality goals. Consequently, SOC accumulation is critical for ensuring food security, maintaining ecosystem health, mitigating climate change, and safeguarding sustainable human development.

Small molecules (SMs), characterized by low molecular weight (typically $<$ 1 000 Da), high water solubility, and relatively simple structure, primarily originate from plant root exudates and biochemical degradation of macromolecular polymers (Li *et al.*, 2024a). Common SMs include simple sugars, organic acids, amino acids, and phenols. Due to their structural simplicity, SMs require minimal enzymatic investment for microbial uptake and utilization. In soil environments, SMs are the most reactive fraction of dissolved organic matter and serve dual roles: as immediate "metabolic fuel" for microbial assimilation and as "signaling switches" regulating microbial communities and their carbon use efficiency (CUE) (Marschner and Kalbitz, 2003; Jiao *et al.*, 2010). Microbial CUE depends on the type and C availability of SMs. Using a microdialysis technique, Koyama *et al.* (2025) observed higher microbial CUE for sugars (glucose and sucrose) and an organic acid (acetic acid) than for amino acids (alanine and aspartic acid). Recent studies have revealed that specific SMs (*e.g.*, glutamine and purines) act as "signaling switches" to influence microbial community structure and functions at the molecular level. Root vasculature-derived glutamine provides a strong chemotactic signal to upregulate the expression of bacterial genes related to amino acid transport and thus drive the community assembly and colonization of microbes (*e.g.*, *Pseudomonas*) (Tsai *et al.*, 2025). Linalool activates jasmonate signaling in maize plants, promotes root exudation of benzoxazinoids, and alters the community composition of microbes (*e.g.*, *Bacillus*) in the rhizosphere (Guo *et al.*, 2025). The root exudate purines can recruit beneficial *Pseudomonas via* upregulation of motility-associated genes, mainly chemotaxis and flagellar assembly (Zheng *et al.*, 2024).

Carbon-engine microbes (CEMs), specifically referring to core functional taxa that drive efficient SOC formation and stabilization, play critical roles in SOC accumulation (Liang *et al.*, 2017). These microbes operate through three primary mechanisms. First, as efficient carbon transformers, taxa such as *Actinomycetes* and *Bacillus* with high CUE convert exogenous carbon into persistent necromass (*e.g.*, chitin and peptidoglycan). Second, as mineral-binding engineers, microbes such as acid-producing bacteria and myxobacteria secrete organic acids or extracellular polymeric substances (EPSs) to form chemical bonds between carbon and reactive minerals. Third, as aggregate architects, taxa such as saprophytic fungi, mycorrhizal fungi, and *Pseudomonas* construct soil aggregates *via* hyphae or adhesive substances, physically protecting carbon from decomposition (Six *et al.*, 2006; Keiluweit *et al.*, 2015; Kallenbach *et al.*, 2016). Thus, CEMs comprise three functional groups: high-CUE decomposers enabling biochemically persistent carbon storage, mineral-associated microbes facilitating chemical protection, and aggregate-forming taxa conferring physical shielding.

Interactions between SMs and CEMs drive SOC accumulation through three synergistic mechanisms (Fig. 1): i) rapid membrane transport fueling instantaneous CEM metabolism; ii) enhanced CEM CUE diverting carbon toward persistent necromass; and iii) selective enrichment of CEMs with high carbon stabilization capacity (Wang *et al.*, 2019; Marschmann *et al.*, 2024). Mounting evidence has demonstrated that SM-CEM interactions facilitate SOC

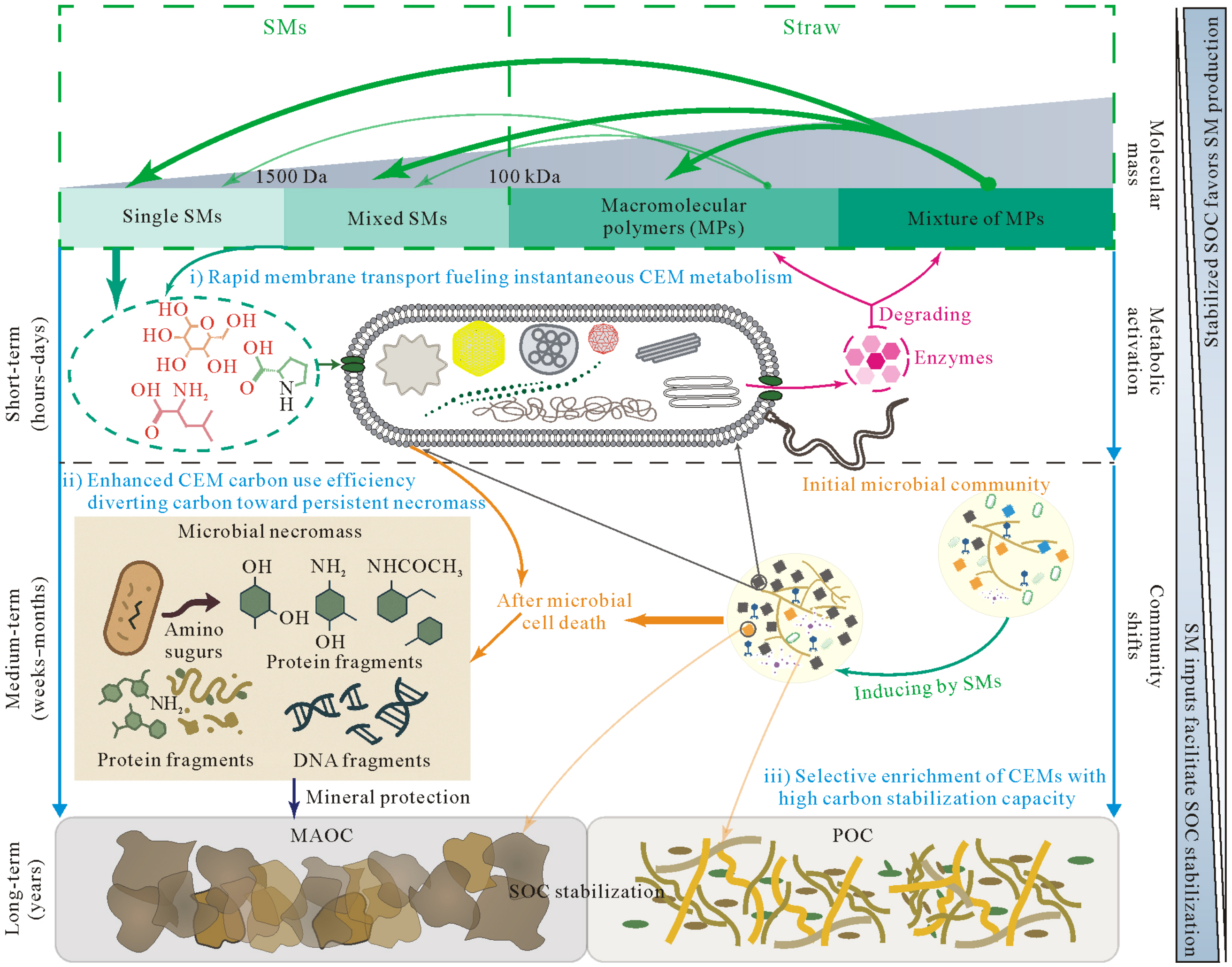

Fig. 1 Diagram illustrating interactions between small molecules (SMs) and carbon-engine microbes (CEMs) driving the stabilization and accumulation of soil organic carbon (SOC), mineral-associated organic carbon (MAOC), and particulate organic carbon (POC). The SM inputs can rapidly activate CEM metabolism and shift the CEM community within a few months, or even within several weeks, ultimately enhancing SOC stabilization in the long term. The stabilized SOC in turn favors SM production by improving soil fertility and productivity.

accumulation, particularly in soils with constraint factors (*e.g.*, poor structure, acidity, and salinity). In poorly-aggregated soils, root-exuded SMs stimulate bacteria (*e.g.*, *Pseudomonas*) to secrete EPSs. These EPSs, alongside glomalin-related soil proteins from arbuscular mycorrhizal fungi, act as binding agents that catalyze stable macroaggregate (> 250 μm) formation (Rillig and Mummey, 2006). The resulting physical occlusion reduces microbial access to organic substrates within aggregates, boosting soil carbon sequestration (Lehmann *et al.*, 2020). In acidic soils, stress-alleviating SMs (*e.g.*, citrate) enrich CEM populations, notably *Actinomycetes* (Jones, 1998), which efficiently convert exogenous carbon into persistent microbial necromass (Liang and Balser, 2011). Saline-alkali soils serve as a key reserve for agricultural expansion, crucial for ensuring food security and mitigating climate change, owing partially to their significant carbon sequestration capacity (Cao *et al.*, 2021; Chen *et al.*, 2024). We have found that lignin-, humus-, and vetch-derived SMs promote trophic interactions between predatory protists and primary decomposers (*e.g.*, *Bacillus* and *Chaetomium*) in saline-alkali soils, accelerating transformation of above- and belowground carbon into SOC, especially mineral-associated organic carbon (Han *et al.*, 2025; Li *et al.*, 2024a, 2025). The SM inputs generally facilitate SOC stabilization and accumulation. However, inappropriate SM inputs may accelerate the decomposition of existing soil organic matter. This releases immobilized nutrients, stimulates microbial growth, and triggers a positive priming effect (Kuzyakov *et al.*, 2000). Thus, SM inputs constitute a “double-edged sword”: excessive or ill-timed application risks both intensifying the mineralization of native SOC and potentially causing soil carbon loss.

Harnessing interactions between SMs and CEMs requires precision strategies. Organic inputs should be optimized by blending diverse amendments (*e.g.*, straw +

green manure + animal manure co-application) and applying partial composting or biological treatment to convert recalcitrant carbon into functional SMs (*e.g*., organic acids and phenols), thereby suppressing the positive priming effect (Koyama *et al*., 2025). Dynamic agronomic management should be implemented by synchronizing SM inputs with crop nutrient demand (*e.g*., base fertilizer + liquid organic fertilizer co-application), utilizing precision drip irrigation for targeted delivery, selecting deep-rooted cultivars, and deploying intercropping/cover crops to enrich beneficial SM diversity in the rhizosphere. We can engineer microbial communities by screening/breeding CEM strains that efficiently convert carbon into persistent necromass or enhance mineral binding and developing functional inoculants or synthetic communities (SynComs) to maximize sequestration. The SynComs have great application potential for soil carbon accumulation and aggregate formation (Coban *et al*., 2022; Zhang *et al*., 2025). We should consider the following principles when designing CEM SynComs, including cooperative key species, biodiversity of SynComs, and interactions between SynCom members (Li *et al*., 2024b). We can integrate technology through real-time monitoring of SM dynamics and CEM activity *via in situ* spectroscopy/sensors, building predictive SM-CEM models, and leveraging artificial intelligence (AI)/big data to generate soil- and climate-specific application protocols.

In summary, interactions between SMs and CEMs substantially drive SOC accumulation. The SM inputs activate carbon-stabilizing functions of CEMs by enhancing microbial CUE, promoting mineral binding, and improving physical protection through aggregate formation. Appropriately-managed SM combinations prevent native SOC mineralization and enable net carbon accrual. Future SOC management strategies must therefore prioritize precision application of SMs through intelligent design.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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