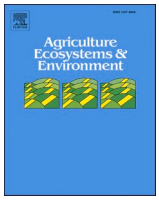
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Cover crop root attributes and their contribution to soil processes and agroecosystem sustainability

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ABSTRACT

Modern agriculture faces growing threats from soil degradation, nutrient loss, and declining biological activity, primarily driven by intensive tillage, monoculture, and the extensive use of agrochemicals. Cover crops hold promises for restoring soil health and resilience. However, their potential is often underutilized due to the limited understanding of cover crop–soil interactions. This review synthesizes the current knowledge on the role of cover crop root systems in shaping soil biological, chemical, and physical functions. The review methodology followed an 'integrative' approach to overview the knowledge base, critically review, reconceptualize, and expand on the theoretical foundation of the broad and interdisciplinary topic of cover crop root functions in agroecosystems. Through structural root traits and exudates, cover crops can influence microbial communities, regulate organic matter decomposition and nutrient cycling, improve soil aggregation and porosity, and promote carbon sequestration. However, the extent of these benefits depends strongly on cropping system design, tillage intensity, species selection, and management practices such as sowing date, seeding rate, and harvest timing. Despite their importance, root traits remain underutilized in cover crop breeding due to limited phenotyping capabilities and insufficient germplasm resources. Advances in biosensors, *in situ* imaging, and genomic techniques, now provide opportunities to identify and select root traits that enhance soil function. We emphasize the importance of root-focused breeding strategies and context-specific management approaches to maximize the agricultural and ecological benefits of cover crops and to advance progress toward more sustainable and regenerative agricultural systems.

1. Introduction

Intensive tillage, monoculture, and extensive use of agrochemicals have disrupted natural soil processes, degrading the physical, chemical, and biological integrity of ecosystems (Allam et al., 2022; Marinari et al., 2022; Nunes et al., 2020). These practices reduce soil aggregate stability, porosity, organic matter, and microbial diversity, driving widespread declines in soil health (Lehman et al., 2015). Globally, an estimated 33% of soils are moderately to severely degraded (FAO, 2015). In the United States, continuous cultivation and erosion have resulted in a 30–50% loss of soil organic carbon in croplands (Cordova et al., 2025; Sanderman et al., 2017; Thaler et al., 2021), with erosion rates in the southeast often 5–10 times faster than the rate of natural soil formation (Blanco-Canqui et al., 2013). These losses reduce water infiltration, increase runoff and erosion, and decrease fertility, thereby threatening both agricultural productivity and environmental sustainability (Blanco-Canqui et al., 2013; Lal, 2015). Soil health is underpinned by four interconnected functions: (i) maintaining soil structure and hydrologic regulation, (ii) nutrient cycling and provisioning, (iii) supporting soil biota, and (iv) regulating climate through carbon storage and greenhouse gas exchange (Hao et al., 2025; Rollett and Williams, 2024). Together, these functions provide essential ecosystem services such as food production, water purification, and climate-change mitigation (Delgado-Baquerizo et al., 2025; Telo da Gama, 2023).

Cover crops are recognized as an effective strategy for restoring soil function and improving agroecosystem sustainability (Delgado and Gantzer, 2015; Franzluebbers et al., 2021; Wang et al., 2025). By maintaining continuous soil cover and reducing fallow periods, they

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protect soil from erosion, maintain biological activity, and enhance the stability of natural ecosystems (Delgado and Gantzer, 2015; Petcu et al., 2023). These conditions support nutrient cycling, microbial activity, and soil stabilization (Bielenberg et al., 2023; Delgado and Gantzer, 2015; Olson et al., 2014). However, cover crop performance is inconsistent and strongly influenced by management decisions, environmental conditions, and species selection. Results from the 2019–2020 National Cover Crop Survey [by the United States Department of Agriculture's Sustainable Agriculture Research and Education (SARE), Conservation Technology Information Center (CTIC), and American Seed Trade Association (ASTA)] illustrate this variability. Among 1172 farmers across diverse production systems, 86% reported long-term soil improvements, yet only 51% observed immediate yield benefits, and nearly 25% experienced yield declines- often linked to poor establishment, drought, or mismanagement of seeding rates, species, or termination timing. Meta-analyses indicate that cover crops improve or maintain subsequent crop yields in approximately two-thirds of evaluated studies, with mean yield gains typically ranging from 5% to 10%, particularly in rainfed temperate systems, maize-based rotations, and low to moderate nitrogen input systems (Poeplau and Don, 2015; Tonitto et al., 2006). Yield benefits are most consistently observed following leguminous cover crops, where biological nitrogen inputs partially substitute for synthetic fertilizer and improve nitrogen availability without yield penalties. In contrast, 20–30% of studies report neutral or negative yield responses, with yield reductions generally being modest (often <10%) and primarily associated with water-limited environments, short-term cover crop adoption, late termination, or high C:N non-legume cover crops that temporarily immobilize nitrogen. Importantly, long-term syntheses indicate that yield penalties are context-dependent rather than systematic, and not an inherent outcome of cover cropping when species selection and management are aligned with pedo-climatic conditions (Poeplau and Don, 2015). These inconsistencies highlight the need to optimize cover crop–soil interactions to local soil and climate conditions. Research has traditionally emphasized aboveground biomass as a proxy for soil health benefits (Blanco-Canqui et al., 2015; Clark, 2007). While residue inputs are important, they do not fully explain the variability in outcomes. Belowground processes, particularly root-mediated interactions with soil microbes, nutrient dynamics, and soil structure, remain comparatively underexplored (Finney et al., 2016; McDaniel et al., 2014; Rosolem and Pivetta, 2017).

This review examines the functional roles of cover crop roots in agroecosystem sustainability. We focus on how root traits interact with soil biotic and abiotic components, their contributions to soil health, and their implications for long-term agricultural sustainability. By advancing understanding of root-mediated processes, we outline strategies to better leverage cover crop root systems for building productive, resilient, and environmentally sound farming systems.

2. Methodology

The manuscript is organized around a focused synthesis of contemporary literature on how cover crop root systems influence soil processes and agroecosystem function. An integrative review approach was followed, consistent with Snyder's (2019) guidelines, that allows for critical synthesis of broad and interdisciplinary topics and conceptual integration, as opposed to a systematic review or meta-analysis, which are typically narrower in scope and focused on a specific research question (Snyder, 2019). The methodology followed in this review involved four phases, as outlined by Snyder (2019), that focused on review design, literature search (inclusion and exclusion), thematic organization, and synthesis and reporting (Fig. 1). In the review design phase, the scope and objective were defined around the role of cover crop roots in shaping soil biological, chemical, and physical processes and their broader implications for agroecosystem sustainability. Based on this core theme, relevant studies were identified through targeted searches of Scopus and Google Scholar using keywords related to cover crops, root traits, rhizosphere processes, soil biological activity, soil physical processes, nutrient cycling, carbon dynamics, and agroecosystem sustainability. Rather than applying a rigid systematic screening protocol, studies were evaluated iteratively and selected based on their relevance to root-mediated biological, physical, and chemical processes. The literature included in this review comprised 263 publications spanning 2000 through 2025 (Fig. 2). Out of the 263 publications, 254 were peer-reviewed articles, and the remaining nine were dissertations, reports, preprints, and extension articles. Though the references spanned over two decades, emphasis was put on those published over the past 15 years. Overall, the literature base was predominantly composed of recent work, while still incorporating earlier studies that provided the conceptual foundation of the topic of interest (Fig. 2). The selected studies were grouped into major thematic areas, including soil physical, chemical, and biological processes, cover crop management practices, cover crop breeding, and emerging technologies. Within each thematic area, the reported information was synthesized to identify recurring patterns, knowledge gaps, implications for agroecosystem management, and future research directions.



Fig. 1. Workflow of the integrative review adapted from Snyder (2019), showing the four main phases of the review process.

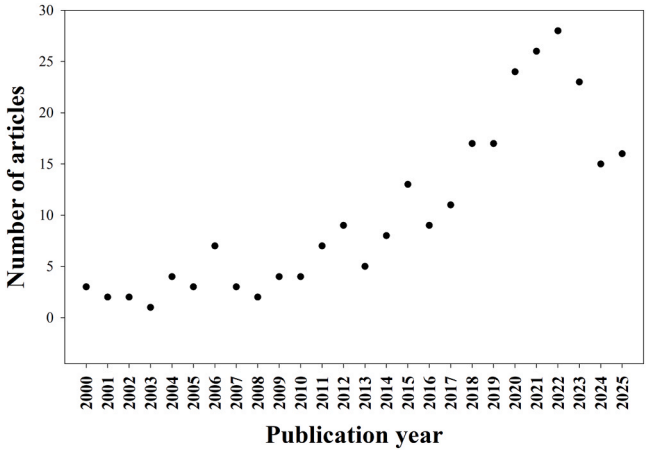


Fig. 2. Distribution of references included in the review by publication year.

3. Functional roles of cover crop roots in soil physical, chemical, and biological processes

3.1. Role of cover crop roots in soil physical processes

Cover crop roots strongly influence soil physical properties by improving aggregation, porosity, and structural stability (Fig. 3). These changes reduce compaction, enhance water infiltration, and lower erosion risk (Hao et al., 2023; Pauletto et al., 2016; Zhang et al., 2022a). Root system architecture plays a central role in this process. For example, tap-rooted species such as forage radish (*Raphanus sativus* var. *longipinnatus*), alfalfa (*Medicago sativa*), and chicory (*Cichorium intybus*) can penetrate compacted subsoils through root swelling and biopore formation (Chen and Weil, 2011; Han et al., 2015). Burr-Hersey et al. (2017) demonstrated the biodrilling potential of tillage radish and black oat (*Avena strigose*), which effectively penetrated sandy loam subsoils. These biopores reduce mechanical resistance and provide low-resistance pathways for subsequent crop roots (Han et al., 2015; Huang et al., 2020; Zhou et al., 2021). Fibrous-rooted species such as rye and annual rye grass create fine pore networks in the upper soil layers, enhancing water retention and gas exchange. Coarse-rooted species with thick taproots or dense fibrous roots, such as tillage radish, disrupt larger soil volumes, increasing macroporosity (Bodner et al., 2014).

Cover crop roots also contribute to aggregate stability. Root exudates act as natural adhesives that bind mineral particles (Naveed et al., 2018; Sedghi and Weil, 2022; Van Deynze et al., 2018; Wang et al., 2012), while hyphal networks of root-associated fungi-particularly arbuscular mycorrhizal fungi (AMF), further reinforce soil cohesion. Thus, different root morphologies contribute to the development of pore networks and structural integrity of the soil (Bodner et al., 2014).

Decomposing cover crop roots also shape soil physical properties. Senesced roots leave behind channels that preserve macroporosity and pore continuity, while releasing organic matter that promotes aggregation (Yang et al., 2019). Root-derived carbon supports soil fauna, particularly earthworms, which create additional macropores through burrowing activity (Marcinkevičienė et al., 2022). These structural improvements have a direct impact on soil water dynamics. Cover crop roots increase the water-holding capacity, infiltration, and plant-available water (Abdollahi and Munkholm, 2017; Basche et al., 2016; Basche and DeLonge, 2019; Blanco-Canqui et al., 2011). Enhanced aggregation and microporosity reduce water loss, allowing soils to retain moisture for longer periods of time (Zhang et al., 2022b). Root channels further increase infiltration and water percolation, which are critical for mitigating drought stress (Pi et al., 2023; Saha et al., 2011; Stanchi et al., 2015; Zhang et al., 2022b; Zhao et al., 2023). Yu et al. (2016) showed that cover crop root length and diameter influence hydraulic conductivity, with coarse-rooted species such as yellow sweet clover (*Melilotus officinalis*), grass pea (*Lathyrus sativus*), and linseed (*Linum usitatissimum*) improving water infiltration and reducing surface runoff by ~17%.

Improvements in the soil physical structure also enhance root exploration and nutrient uptake by subsequent crops. Long-term experiments further demonstrate that root-derived macropores created by deep-rooted pre-crops (including forage or cover crops) can persist across multiple seasons and be reused by subsequent crops, improving rooting depth and yield performance, particularly during dry years (Behrend et al., 2025). For example, under long-term no-till, rainfed management on silt loam soils in the upper midwestern United States, Yin et al. (2025) attributed 7–8% yield gains in soybean to improved rooting associated with biopore legacy effects created through repeated cover cropping. In a primarily rainfed, no-till soybean-corn system on a compacted silt-loam soil of two mid-Atlantic sites in the United States, Williams and Weil (2004) observed that root channels created by forage radish and cereal rye were later colonized by soybean roots, resulting in yield increases of approximately 6–20% relative to no-cover treatments, with the strongest gains occurring under drought stress. In the same

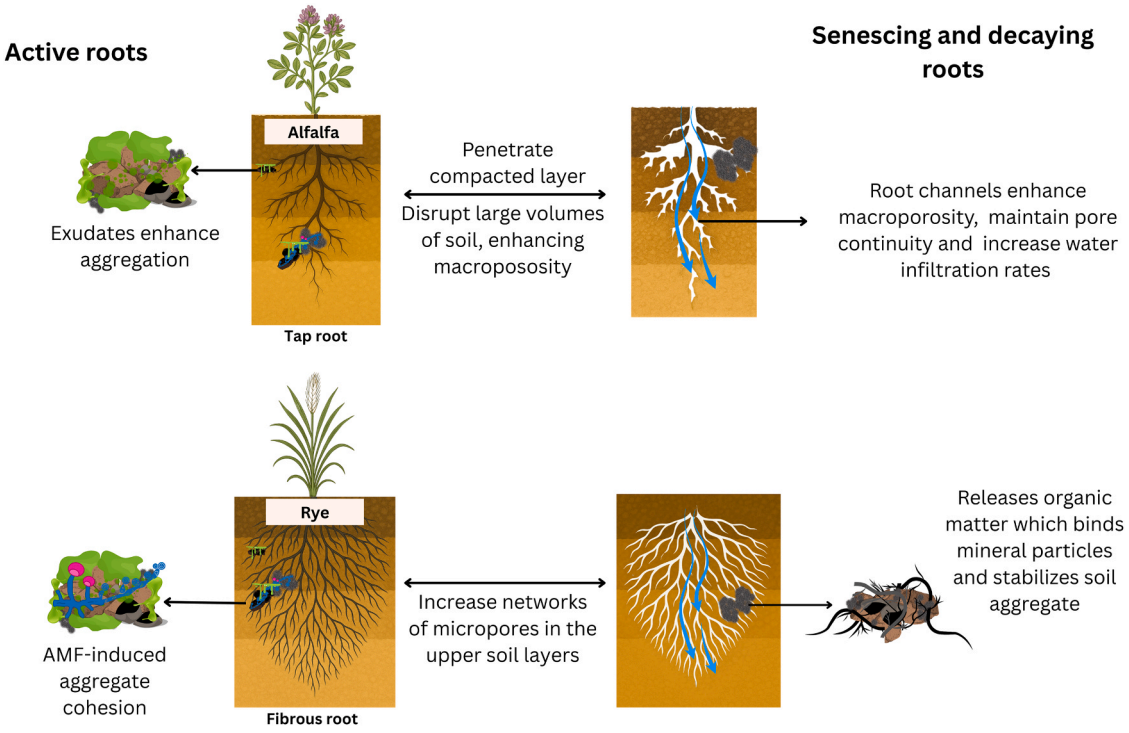


Fig. 3. Effects of active and decaying cover crop roots on soil physical properties. Active roots of tap-rooted species, such as alfalfa, penetrate compacted soil layers and disrupt large soil volumes, enhancing macroporosity. Fibrous-rooted species, such as rye, develop dense networks of micropores in the upper soil layers, improving water retention and gas exchange. Root exudates and arbuscular mycorrhizal fungi (AMF) further promote soil aggregation. As roots senesce, decaying root channels maintain pore continuity, enhance water infiltration, and release organic matter that binds mineral particles, stabilizing soil aggregates, and reinforcing long-term soil structural integrity.

mid-Atlantic region of the United States, Chen and Weil (2011) showed that across increasing levels of soil compaction in rainfed silt-loam soils, brassica cover crops (forage radish/rapeseed) improved biopore continuity and reduced mechanical impedance. These conditions improved maize root growth and maize silage yield by approximately 15–30% compared with no-cover treatments. Similarly, in loamy soils under cereal-based rotations in central Pennsylvania in the United States, autumn rye–oat cover crops increased water-stable aggregation and AMF colonization, enhancing phosphorus uptake and sweet corn yields by approximately 20–40% relative to fallow treatments (Kabir and Koide, 2002). These findings indicate that biopore formation by cover crop roots can reduce soil physical resistance, supporting healthy root growth of subsequent crops, thereby resulting in yield gains and stability. This evidence reinforces the role of cover crop roots in agroecosystem sustainability and reduced reliance on intensive tillage. However, some long-term field studies and syntheses have also reported neutral or negative root-mediated effects on soil physical conditions and subsequent crop yields under certain species choices and management regimes or water-limited environments (Poeplau and Don, 2015; Blanco-Canqui et al., 2015; Finney et al., 2016). For example, in a humid U.S. Coastal Plain no-till corn site at Rocky Mount, North Carolina (fine sandy loam soil), cover crops did not reduce bulk density after three years (e.g., bulk density was 1.52 and 1.47 Mg m^{-3} under wheat and hairy vetch cover crops, respectively while it was 1.44 Mg m^{-3} under no cover crop), indicating a lack of advantage on soil compaction mitigation (Wagger and Denton, 1989). In a review of cover crops' ecosystem services, Blanco-Canqui et al. (2015) concluded that changes in bulk density and soil compaction would be a function of the duration of cover cropping and cover crop management, and effects may be neutral in short term.

3.2. Role of cover crop roots in soil chemical processes

Cover crop roots play a central role in regulating soil chemical processes by reducing nutrient losses, enhancing nutrient cycling, and contributing to carbon sequestration, thereby supporting long-term soil fertility and environmentally sustainable nutrient management (Fig. 4). By actively taking up nutrients, cover crop roots limit nitrogen and phosphorus leaching and runoff, thereby lowering the risk of eutrophication (Daryanto et al., 2017; Dorissant et al., 2022; Dybowski et al., 2020; Fageria et al., 2014; Liang et al., 2025; Nouri et al., 2022). This function is particularly important in the off-season, when no cash crop is present to absorb nutrients. Deep-rooted species, such as rye and radish are "nutrient pumps", scavenging nitrate and other mobile nutrients from deeper horizons and returning them to the surface profile as their residues decompose (Kruse and Nair, 2016; Pi et al., 2023; Saha et al., 2011; Stanchi et al., 2015; Zhang et al., 2022a; Zhao et al., 2023). In addition, improved soil structure and microbial activity associated with cover crop roots enhance organic nitrogen mineralization, increasing plant-available forms and improving nitrogen-use efficiency (Curtright et al., 2024; Kristensen and Thorup-Kristensen, 2004; Murrell et al., 2020; Nicole et al., 2021; Nouri et al., 2022; Smukler et al., 2012; Thapa et al., 2018a).

Cover crops can also alter the rhizosphere chemistry. Protons (H^+ ions) released during nutrient uptake, particularly ammonium, acidify the rhizosphere, improving the solubility of otherwise unavailable nutrients such as phosphorus, iron, and manganese. For example, lupins (*Lupinus spp.*) and crimson clover (*Trifolium incarnatum*) strongly acidify the rhizosphere mobilizing phosphorus and micronutrients in nutrient-depleted soils (Bolan et al., 2025; Lambers et al., 2006; Pearse et al., 2009). Enhanced nutrient retention and cycling ultimately benefit cash crop yields: Spargo et al. (2016) reported that a hairy vetch (*Vicia villosa*) cover crop, planted in autumn and terminated in spring right before corn planting, increased early corn nitrogen uptake by 76% and corn grain yield by 53% compared to fallow treatments in the mid-Atlantic United States on a Codorus silt loam soil. Cover crop roots play a crucial role in soil carbon sequestration by contributing biomass to long-term organic carbon pools (Fig. 4) (Bolan et al., 2025; Dasgupta and Mahanty, 2024; McCauley and Barlow, 2023; Zhang et al., 2023). Root–carbon interactions encompass the processes through which roots deposit,

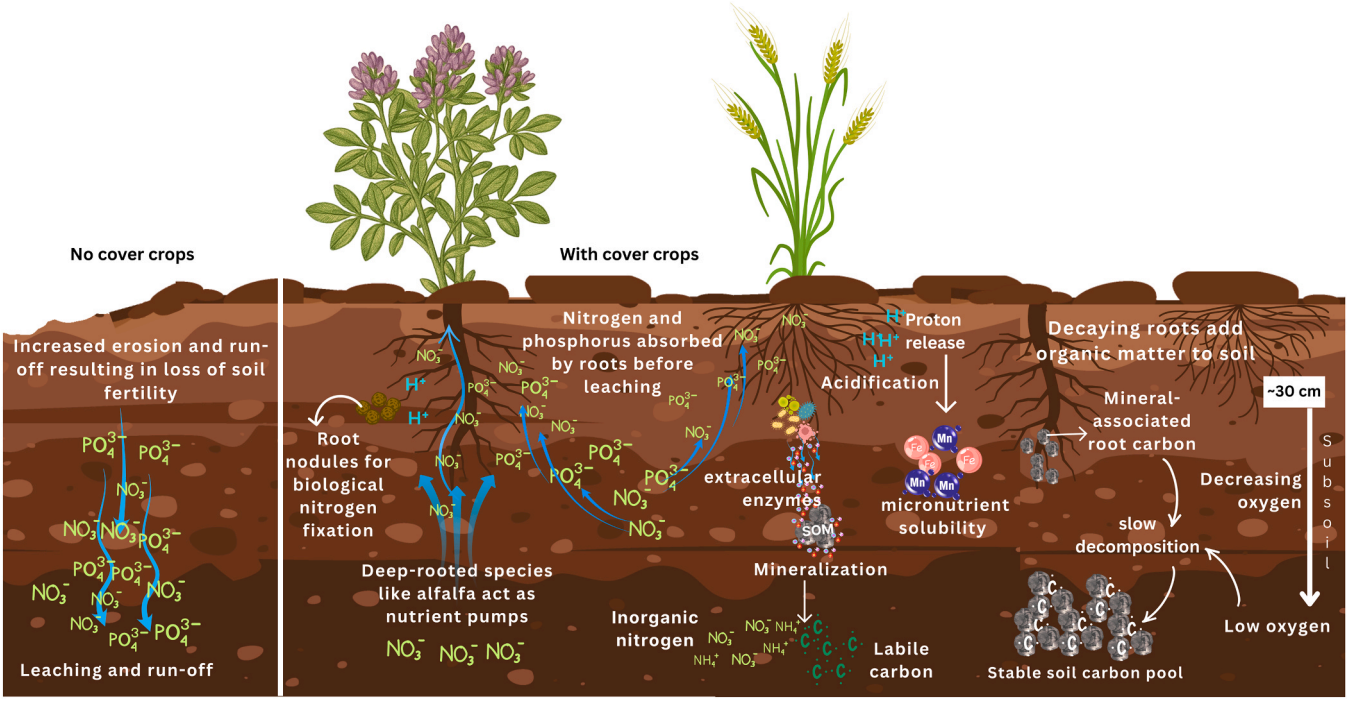


Fig. 4. Schematic representation of the influence of cover crop roots on soil chemical properties. Cover crops reduce nutrient losses through root uptake, biological nitrogen fixation, and deep nutrient scavenging. Root-mediated processes enhance nutrient cycling via enzyme activity, mobilize unavailable nutrients, and increase nutrient use efficiency. Compared with aboveground biomass, root-derived carbon decomposes more slowly due to its high lignin and suberin content, stabilizes in deeper soil and contributes more to long-term carbon sequestration.

transform, and stabilize carbon in the soil, directly influencing soil carbon storage and supporting healthy microbial ecosystems (Poeplau and Don, 2015; Sadeghi and Raeini, 2016; Sokol et al., 2019). Beyond biomass inputs, roots continuously release rhizodeposits- exudates, mucilage, and sloughed cells that serve as immediate microbial substrates and contribute to the formation of mineral-associated organic carbon (Sokol et al., 2019). While these labile inputs cycle rapidly through microbial pathways, root biochemical compounds, such as lignin and suberin, persist longer in the soil, gradually integrating into stable carbon fractions. This slow turnover supports the accumulation of soil organic matter and long-term carbon storage (Amsili and Kaye, 2021; Beillouin et al., 2021; Fulton-Smith and Cotrufo, 2019; Matheus et al., 2020; Spielvogel et al., 2006). Most studies have reported root effects on soil organic carbon within the upper 30 cm of soil (Amsili and Kaye, 2021; Jackson et al., 2003; Sainju et al., 2006), but roots can influence carbon dynamics at greater depths (Kell, 2012; Rasse et al., 2005). Therefore, understanding the distribution of root biomass throughout the soil profile is critical for assessing the potential for deep carbon sequestration (Peixoto et al., 2022; Wong et al., 2024). Traits that enable cover crops to develop persistent root systems are particularly valuable, as they enhance carbon retention and stabilization (Griffiths et al., 2022).

Because roots decompose more slowly, are more stable, and release less CO_2 than aboveground biomass, cover crop root systems often contribute more to the soil organic carbon pool than shoots (Beillouin et al., 2021; Gale et al., 2000; Kong and Six, 2010; Matheus et al., 2020; Wilhelm et al., 2004). Root contributions to soil organic carbon pools can reach up to 75% of the total organic carbon inputs (Gale et al., 2000; Gale and Cambardella, 2000), emphasizing their role in soil carbon sequestration. Species such as cereal rye and hairy vetch are notable for producing extensive root systems with high biomass that persist in the soil (Austin et al., 2017; Pisarčik et al., 2024; Thapa et al., 2018b), whereas sunn hemp (*Crotalaria juncea*), with its deep taproot and high lignin content, is particularly effective at stabilizing carbon in deeper soil layers (Baitsaid et al., 2018; Kell, 2012; Rasse et al., 2005; Srikavi and Mekala, 2023). A high root-to-shoot ratio further enhances soil organic carbon sequestration by allocating more biomass belowground (Redin et al., 2018; Saadat et al., 2025). Belowground decomposition is slower than surface residue decomposition due to lower microbial activity, limited oxygen levels, and greater physical protection within soil aggregates (Qin et al., 2023). However, trade-offs can arise. For example, Peng et al. (2025) reported that combining cover crops with no-tillage increased soil greenhouse gas emissions, primarily due to elevated respiration, despite reducing nitrate leaching in rainfed corn-soybean fields (Blount silt loam soil) near Fort Wayne, Indiana, USA. While aboveground biomass contributes less to soil organic carbon

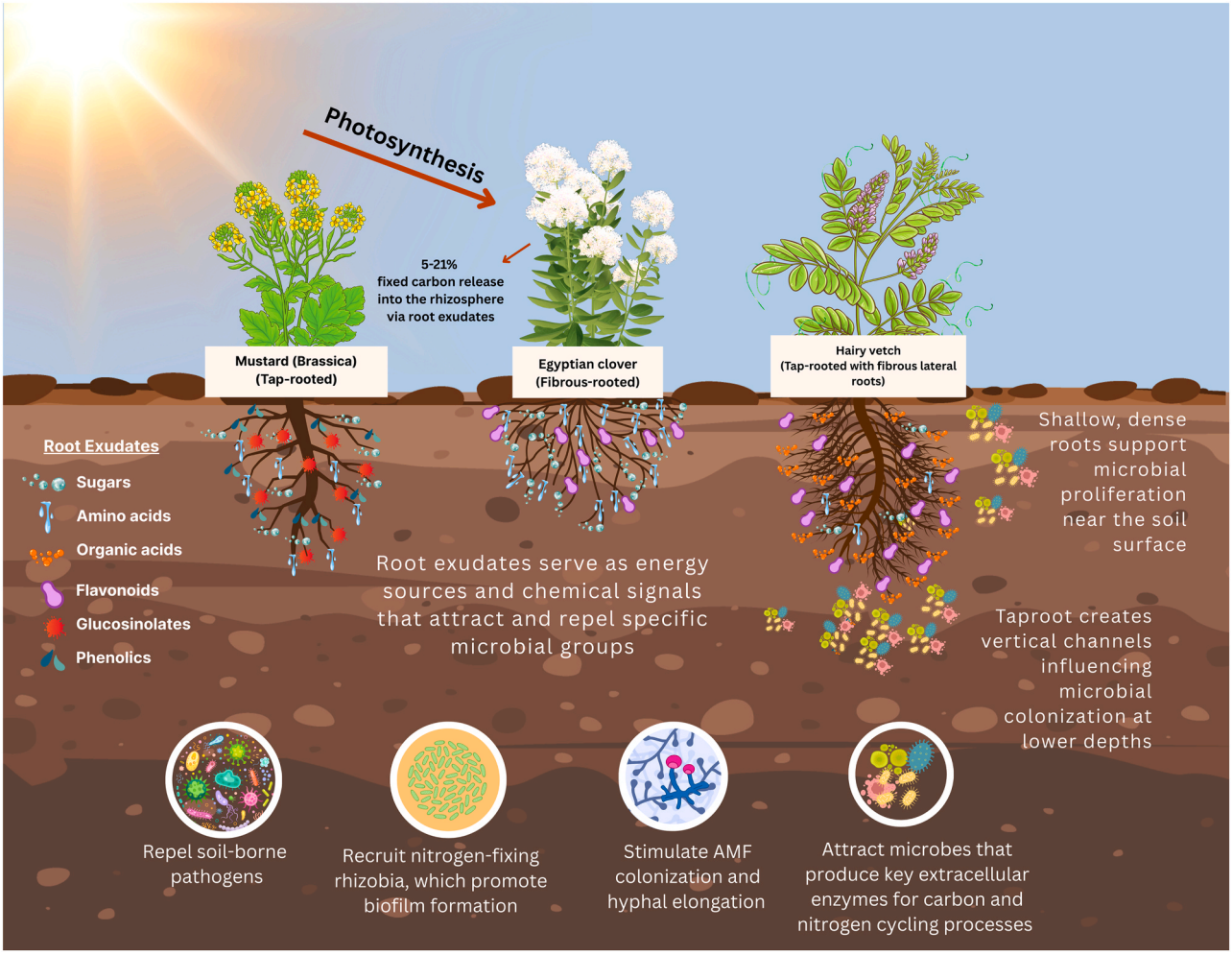


Fig. 5. Root-mediated biological interactions in the rhizosphere of cover crops. Cover crop roots release 5–21% of photosynthetically fixed carbon as exudates, including sugars, amino acids, organic acids, flavonoids, glucosinolates, and phenolics that shape microbial community structure and function. Tap-rooted species, such as mustard and hairy vetch, form vertical biopores, enhancing microbial colonization at depth, whereas fibrous-rooted species, such as Egyptian clover, promote surface-level microbial activity. Exudates act as signals and energy sources that (i) stimulate arbuscular mycorrhizal fungi (AMF) colonization, (ii) promote biofilm formation through nitrogen-fixing rhizobia, (iii) suppress pathogens, and (iv) activate microbial enzymes for carbon and nitrogen cycling.

than roots, it remains essential for functions such as soil surface protection, moisture retention, and weed suppression.

3.3. Role of cover crop roots in soil biological processes

Soil biological processes underpin the long-term sustainability of agroecosystems by regulating nutrient cycling, soil fertility, biological resilience, and ecosystem stability. These processes are primarily regulated by the vitality, abundance, and metabolic activity of microbial communities, nematodes, and earthworms (Angst et al., 2022; Cozim-Melges et al., 2025; Lu et al., 2020). Active microbial populations drive organic matter decomposition, CO_2 release, and nutrient cycling, forming the basis for nitrogen mineralization, biological nitrogen fixation, and suppression of soil-borne pathogens (Blagodatskaya and Kuzyakov, 2013; Wagg et al., 2014). Cover crop traits and root exudates strongly influence microbial dynamics shaping the rhizosphere and driving soil biological processes (Fig. 5).

3.3.1. Cover crop root - microbe interactions

Root exudates, comprising sugars, amino acids, organic acids, phenolics, flavonoids, and other metabolites, are primarily released from root tips, border cells, and lateral root emergence sites (Bais et al., 2006). Between 5% and 21% of a plant's fixed carbon can enter the rhizosphere through exudation (Badri and Vivanco, 2009; Yetgïn, 2023). Exudate composition varies among cover crops. For example, Egyptian clover (*Trifolium alexandrinum*) and white mustard (*Sinapis alba*) release high amounts of simple sugars and amino acids, brassicas exude phenolic acids and glucosinolates, and legumes, such as hairy vetch, produce flavonoids and organic acids (Heuermann et al., 2023; Seitz et al., 2024). These compounds act as energy sources and signaling molecules that selectively recruit specific microbial groups. For instance, sorgoleone from sorghum alters the bacterial community composition by suppressing nitrifiers such as *Nitrosomonas europaea,* while enriching taxa involved in carbon cycling, including *Nocardia* and *Methylophilaceae* (Wang et al., 2021,2021). Wheat exudes phenolic acids in cultivar-specific patterns (Wu et al., 2001), which contribute to the selective recruitment of rhizobacteria such as *Pseudomonas s*pp. (Hu et al., 2018). Chemotaxis—the directed movement of microbes toward or away from chemical stimuli—further facilitates root colonization, with beneficial microbes responding to specific root exudate gradients (Feng et al., 2021). Through these mechanisms, cover crop roots reshape the composition, diversity, and assembly of the microbial community (Cazzaniga et al., 2023; Kim et al., 2020; Thapa et al., 2021; Zhao et al., 2022). For example, oilseed radish (Brassicaceae) promotes Pseudomonadaceae while repressing Microascaceae, and lentil (Fabaceae) broadly stimulates fungal taxa such as Trichocomaceae and Glomerales (Cazzaniga et al., 2023). Recent research has also demonstrated that legume and cereal cover crop roots impose distinct microbial legacies that persist in subsequent maize crops (Shi et al., 2025). Legume roots, through nitrogen-fixing symbioses and organic acid exudation, reduced microbial groups that inhibit maize growth while enriching taxa such as Nonomuraea and Pedomicrobium, which promote maize biomass. In contrast, grass roots stimulated taxa that compete for nitrogen, resulting in significant reductions in maize biomass.

Cover crop roots influence soil microbial communities not only taxonomically but also functionally, as reflected by shifts in functional genes that serve as molecular markers for microbial nutrient-transforming capacity. Long-term field studies have illustrated these effects. In a 36-year, rainfed continuous cotton experiment on a Lexington silt loam soil of Jackson, Tennessee, USA, hairy vetch, grown under both conventional tillage and no-tillage, increased the abundance of key nitrogen-cycling genes, including *nifH* (nitrogen fixation), *amoA* (ammonia oxidation), *nirK* and *nirS* (nitrite reduction/denitrification), and *nosZ* (nitrous oxide reduction), relative to both no-cover and winter wheat treatments (Hu et al., 2021). Similarly, Brtnicky et al. (2021) reported a higher abundance of *phoD* genes (organic phosphorus mineralization) in white clover rhizospheres than in bulk soil under rainfed conditions in Troubsko, Czech Republic on silt to silty-loam Haplic luvisol soils. Li et al. (2024) found that combining white clover with orchard grass increased the abundance of genes linked to carbon fixation and nitrogen metabolism pathways in the rhizosphere in Hefei, Anhui Province, Southeast China. Controlled microcosm studies have further demonstrated that exudates from cereal rye and sorghum can reprogram microbial functional trajectories, enriching nitrite oxidizers, stimulating phytohormone-related pathways, and redirecting nitrogen-cycling activity (Seitz et al., 2024).

Cover crop roots support symbiosis with AMF, which form specialized structures called arbuscules within root cortical cells (Ebbisa, 2023; Qiu et al., 2024). These arbuscules facilitate water and nutrient acquisition, particularly phosphorus and micronutrients, from soil zones otherwise inaccessible to roots, with AMF receiving the carbon fixed by plant photosynthesis (Ebbisa, 2023; Qiu et al., 2024). Root traits influence AMF colonization, and exudates play a critical role in signaling and hyphal stimulation (Ebbisa, 2023; Steinkellner et al., 2007).

Root exudates also provide energy for rhizosphere microbes that produce extracellular enzymes that break down organic residues into forms accessible to both microbes and plants (Elhaddad et al., 2024; Seitz et al., 2023; Wang et al., 2021b). For example, exudates from hairy vetch enhance the activity of key carbon-cycling enzymes such as β-glucosidase and cellulase, which degrade cellulose, hemicellulose, and other plant polymers into glucose and simpler sugars (Elhaddad et al., 2024; Mubvumba and Tyler, 2024). This accelerates carbon turnover in the rhizosphere, promotes residue decomposition, and improves soil health (Pett-Ridge et al., 2021).

Cover crop root traits, such as rooting depth, lateral spread, and branching density, strongly influence microbial colonization patterns and shape oxygen gradients and nutrient distribution within the rhizosphere (Amadou et al., 2021; Hudek et al., 2022; Ogilvie et al., 2021; Wendel et al., 2022). For instance, the taproot of daikon radish (*Raphanus sativus* var. longipinnatus) penetrates deep into the soil, forming vertical channels that promote microbial colonization at lower depths, whereas the shallow, dense root systems of species such as phacelia (*Phacelia tanacetifolia*) enhance microbial proliferation in upper soil layers (Amadou et al., 2021; Hudek et al., 2022; Ogilvie et al., 2021; Seitz et al., 2024). Leguminous cover crops, such as hairy vetch and crimson clover are also effective at supporting dense microbial communities in surface soils (Koudahe et al., 2022; Mubvumba and Tyler, 2024). High fine root density and expanded surface area increase the spatial extent of microbial colonization and the delivery of labile carbon to the rhizosphere (Amadou et al., 2021; Ogilvie et al., 2021; Seitz et al., 2024). Chaparro et al. (2014) reported that microbial community composition shifts dynamically in response to root system development over time, underscoring the influence of root structural traits on rhizosphere microbial dynamics. Functional root traits further determine the effectiveness of cover crops in facilitating decomposition. High root-hair density and extensive lateral root proliferation expand the rhizosphere volume, creating broader zones of microbial activity where residue breakdown can occur (Zhang et al., 2022a). Additionally, root traits improve soil aeration and moisture retention, which are two key factors that sustain microbial and enzymatic activity in decomposition zones (Zhang et al., 2022a).

The diversity and activity of beneficial rhizosphere microbes under cover cropping also strengthen soil suppression of pathogens (Peralta et al., 2018). Root exudates and structural traits help create rhizosphere conditions that favor beneficial microbes over pathogens (Hu et al., 2018). For instance, brassicas such as Indian mustard (*Brassica juncea*) release bioactive compounds, such as isothiocyanates, which suppress pathogens like *Fusarium oxysporum* (Liu et al., 2021,2021), the causal agent of Fusarium wilt. Similarly, Dawadi et al. (2019) found that incorporating a mixture of crimson clover and annual ryegrass (*Lolium multiflorum*) into nursery soils reduced the prevalence of *Rhizoctonia solani*, which causes root rot and damping-off.

3.3.2. Cover crop root- soil macro-biota interactions

Beyond microbes, cover crop roots influence higher trophic levels in the soil food web, notably nematodes and earthworms, which in turn, regulate microbial turnover, nutrient cycling, and soil structure. Diverse root architectures and exudate profiles can shift nematode community composition, often increasing the abundance of bacterial- and fungal-feeding nematodes that accelerate organic matter mineralization, while suppressing populations of plant-parasitic nematodes (Garba et al., 2024; Marquez and Hajihassani, 2023; Wang et al., 2022). For example, brassica cover crops release bioactive compounds with nematicidal properties, reducing root-knot nematode densities and mitigating damage to subsequent crops (Garba et al., 2024; Mcsorley, 2011). Earthworms also respond positively to root-driven increases in organic matter inputs, functioning as ecosystem engineers that directly and indirectly enhance soil biological processes (Akhila and Entoori, 2022; Lemtiri et al., 2014). Burrowing and casting activities improve soil aeration, water infiltration, and aggregate stability, facilitate the incorporation of organic residues into mineral soil to form humus, and redistribute nutrients (Akhila and Entoori, 2022). Nutrient-rich casts act as hotspots for microbial activity, enzyme production, and nutrient cycling, accelerating the decomposition of organic matter and the mineralization of nitrogen and phosphorus (Akhila and Entoori, 2022; Blouin et al., 2013). Cover crop species vary in their capacity to support earthworm populations. Fibrous-rooted grasses and legumes, in particular, provide continuous root-derived carbon and stable pore networks that foster earthworm abundance and activity (Bertrand et al., 2015; Blanco-Canqui, 2022; Pelosi et al., 2020).

3.3.3. Nodulation and biological nitrogen fixation

Leguminous cover crops contribute to biological nitrogen fixation, enriching soil fertility and reducing dependence on synthetic fertilizers. Fixed nitrogen becomes available to subsequent crops upon residue decomposition (Curtright et al., 2024; Murrell et al., 2020; Nicole et al., 2021; Nouri et al., 2022; Smukler et al., 2012; Thapa et al., 2018a). The reported amounts of fixed nitrogen inputs range from ~ 30–200 kg N ha^{-1} per growing season, depending on species and management (Brennan and Boyd, 2012; Maham et al., 2020). Teasdale et al. (2008) reported that hairy vetch, as a single species or in a mixture with rye, accumulated ~200 kg N ha^{-1} in a humid mid-Atlantic U.S. no-till sweet corn system (loamy sand soils) at Beltsville, Maryland. More typically, hairy vetch contributes ~70–80 kg N ha^{-1} under favorable conditions, whereas clovers often contribute ~50–60 kg N ha^{-1} (Kirchmann et al., 2007). Brennan and Boyd (2012) estimated ~57–76 kg N ha^{-1} fixed by legume (purple vetch, faba bean, and field pea)-rye mixtures in an irrigated organic vegetable system with Chualar loamy sandy soil in Central Coast, California, USA.

The nodulation process is initiated and shaped by root-specific chemical signaling. Flavonoids exuded by legume roots induce the expression of nodulation (nod) genes in compatible rhizobia, leading to the synthesis of nod factors. Upon host recognition of nod factors, root hair curling occurs, followed by infection thread formation (Oldroyd et al., 2011; Roy et al., 2020). This signaling highlights the role of flavonoid root exudation in determining infection success and the distribution of nodules across the root system (Oldroyd, 2013). Some legume cover crops exhibit broad or preferential compatibility with indigenous rhizobial populations, partly because their root exudate profiles effectively induce nod gene expression in locally adapted diazotrophs. Species such as clovers (*Trifolium spp.*), vetches (*Vicia spp.*), and peas (*Pisum spp.*) typically nodulate successfully without inoculation in most soils, reflecting compatibility with resident rhizobia and a response to the host plant's flavonoids and isoflavonoids (Fustec et al., 2010; Peoples et al., 2009; Schipanski et al., 2014). Repeated cultivation of these legume cover crops can increase the abundance of symbiotically effective rhizobial populations in soil (Sulieman and Tran, 2016; Mahmud et al., 2020). Enrichment is driven by selective stimulation of compatible rhizobia during successive cycles of root exudation, infection, and nodule turnover. Such enrichment may create a biological legacy, increasing the pool of host-compatible diazotrophs, contributing to more effective nodulation and earlier symbiotic establishment in subsequent legume crops, particularly in soils with historically low rhizobial populations.

4. Maximizing cover crop root benefits through management practices

As outlined above, cover crop root systems provide substantial agronomic and ecological benefits. When effectively managed, they enhance cash crop yield potential and resource use efficiency through improvements in soil biological, physical, and chemical processes. However, consistent success depends on selecting cover cropping systems, species, tillage practices, and management strategies that are suited to local soil, climate, and farm conditions. These choices determine how long roots remain active, how deeply and widely they will grow, and how well they support soil functions such as aggregation, nutrient cycling, water regulation, and microbial activity.

4.1. Choosing the cover crop system

The design of the cover cropping system, whether it be sole cover crops, interseeding, relay cropping, or living mulches (Fig. 6), strongly influences root growth patterns and their contributions to belowground processes. Each system shapes the timing, distribution, and persistence of root activity, thereby affecting the soil structure, organic matter turnover, and microbial dynamics in distinct ways. Sole cover cropping involves planting cover crops independently of cash crops, either as a single species or as a mixture (Clark, 2007; Snapp et al., 2005). In the United States, they are typically sown in autumn following the harvest of the previous summer cash crop or in early spring before summer planting of the next cash crop, depending on regional conditions. Autumn-sown cover crops usually grow for three to six months, producing more root biomass, stimulating greater rhizosphere microbial activity, and improving soil structure more than spring plantings, which persist for only six to ten weeks (Clark, 2007; Snapp et al., 2005). For example, autumn-planted rye has been shown to produce higher root biomass and soil enzyme activity than spring-planted rye (Basche et al., 2016; McDaniel et al., 2014; Mirsky et al., 2011; Mischler et al., 2010; Wagstaff and Thelen, 2011). Similarly, hairy vetch grown across the autumn-spring season accumulated more nitrogen and stimulated greater microbial biomass than spring-planted vetch, due to the longer growth duration and sustained root exudation and residue inputs (Clark, 2007; Mohammadi and Ghobadi, 2010; Wiggins et al., 2017).

Interseeding involves introducing cover crops into a standing cash crop during its early to mid-vegetative stages, allowing both root systems to develop simultaneously. This approach exploits the underutilized niches between crop rows, enhancing resource capture and stimulating soil biological activity (Brooker et al., 2020; Klopp, 2024; Mohammed et al., 2020). For example, interseeding hairy vetch into no-till soybean under rainfed conditions stimulated microbial biomass and increased active carbon pools in the coastal-plain fields (Kempsville fine sandy loam, Suffolk loamy sand, and Atlee silt loam soils) of eastern Virginia, USA (Norris, 2015). Similarly, red clover (*Trifolium pratense*) interseeded with no-till sweet corn contributed biologically fixed nitrogen and elevated residual soil nitrogen in south-central Wisconsin (Plano silt loam soil), USA (Francis, 2020; Gaudin et al., 2013). Cereal rye interseeded into no-till soybean maintained soil cover and enhanced soil health parameters during late-season cash crop growth under rainfed conditions in the midwestern United States (Clarion loam/Webster clay loam soils in Iowa and silty clay loams in Illinois) (Patel, 2020; Ruffatti et al., 2019).

Relay cropping involves sowing cover crops into a standing cash crop before harvest, thereby extending root activity across seasonal transitions (Blanco-Canqui et al., 2015; Lauriault et al., 2018). Early



Fig. 6. Examples of cover cropping systems: (A) Sole cover cropping (crimson clover), (B) Interseeding (buckwheat interseeded into maize. In this system, buckwheat will typically be terminated before maize harvest), (C) Relay cropping (soybean cover crop relayed into maize. In this system, soybeans will typically be terminated after maize harvest, extending root activity beyond the maize season), and (D) Living mulch system (perennial ryegrass as a living mulch in an apple orchard).

establishment supports deeper rooting, greater early biomass, and nutrient capture during periods when soil resources are often underutilized (Griffiths et al., 2022; Homulle et al., 2022). For example, Kaspar et al. (2012) reported an advantage of oat cover crop relayed with no-till corn and soybean on Canisteo and Nicollet soils at Ames, Iowa, USA such that the oat cover reduced nitrate losses by ~26%. However, the success of this approach depends on timing; late cash crop senescence or poor weather may limit cover crop establishment and reduce soil benefits (Lauriault et al., 2018).

Living mulch systems maintain perennial or semi-perennial cover crops as continuous ground cover supporting year-round root activity (Brennan and Smith, 2018; Hartwig and Ammon, 2002). Continuous rooting provides steady carbon inputs, root turnover, and microbial habitats, enhancing long-term soil structure and carbon storage (Tarrant et al., 2020; Woolf and Lehmann, 2012). For instance, a white clover living mulch can increase soil organic matter, improve porosity, and enhance infiltration (Hill et al., 2021). However, without timely management (e.g., mowing, strip-tillage), living mulches may compete with cash crops for water and nutrients, especially in drought-prone or nutrient-limited systems (Hartwig and Ammon, 2002).

Overall, the effectiveness of each system hinges on balancing root-driven benefits—such as biomass production, microbial stimulation, and soil aggregation—against risks like resource competition and management complexity. Strategic coordination of cover crop choice, planting and termination timing, and management practices tailored to system goals is essential. Understanding how different systems influence root architecture, turnover, and rhizosphere processes will enable farmers to better align cover crop systems with soil health, resilience, and agroecosystem services.

4.2. Selecting tillage practice

Tillage practices strongly influence root architecture, root channel persistence, soil porosity, and microbial activity, which determine the effectiveness of cover crop roots in improving soil health and agroecosystem function. Conventional tillage methods, such as moldboard plowing and repeated disking or harrowing, cause substantial mechanical disturbance (Acar et al., 2018; Guo et al., 2016; Villamil et al., 2006). Although they can facilitate field preparation and improve short-term planting conditions, they disrupt soil aggregates, destroy macropores, and accelerate organic matter decomposition (Acar et al., 2018). These disturbances often restrict cover crop roots to shallow layers with limited access to subsoil moisture and nutrients (Guo et al., 2016; Kochiieru et al., 2020). For example, fibrous-rooted species, such as cereal rye and annual ryegrass, typically exhibit reduced root biomass and rooting depth under conventional tillage due to compaction and disrupted pore continuity (Villamil et al., 2006; Wortman et al., 2012).

Conservation tillage reduces soil disturbance and maintains surface residue, creating conditions that support long-term soil health, extended root activity, and beneficial rhizosphere interactions (Guo et al., 2016; Tautges et al., 2019).

Within conservation tillage, several approaches vary in disturbance level and their effects on root processes. Reduced tillage involves moderate soil disturbance, retaining 15–30% of the surface residue (Indiana State Department of Agriculture, 2021; Stichler, 2006). Strip-till disturbs only narrow seed zones, leaving the residue between the rows intact (Haramoto and Brainard, 2012; Jaskulska et al., 2018). Jaskulska et al. (2018) reported a more uniform establishment of winter rapeseed under strip-tillage than under conventional tillage on Cambisol soils under rainfed conditions in a low-rainfall region of northern Poland, potentially due to strip till leading to better rooting and initial plant development. Mulch-till uses full-width tillage but preserves substantial residue, buffering soil conditions and supporting early root development. Mulch-till has been shown to improve soil physical properties, particularly benefiting legumes by promoting lateral and fine root proliferation under warm climates (Blanco-Canqui and Lal, 2009; Dung et al., 2022; Mondal et al., 2019). Ridge-till confines soil disturbance to raised ridges, leaving inter-row soil intact. This stratified approach maintains microbial hotspots and biopores that encourage vertical root expansion in the soil. No-till systems, which leave the soil largely undisturbed, offer the most favorable conditions for root development. For example, Sainju et al. (2005) observed greater root biomass of irrigated sorghum under no-tillage (548 kg ha^{-1}) than under conventional chisel tillage with no ground cover (218 kg ha^{-1}) in central Georgia, USA (Dothan sandy loam soil).

Overall, conservation tillage provides a more favorable environment than conventional tillage for root proliferation, microbial colonization, and biogeochemical cycling. By preserving soil structure, reducing compaction, and maintaining pore networks, conservation tillage systems allow cover crop roots to function more effectively as “biological engineers” ultimately enhancing soil health, resilience, and sustainability.

4.3. Selecting the cover crop

Selecting the appropriate cover crop species is a critical management decision that largely determines the type and extent of soil benefits delivered by the cover crop roots. Cover crops differ in rooting depth, architecture, exudation patterns, and interactions with soil biota, and are often grouped into three broad functional types: legumes, brassicas, and grasses. Legumes (e.g., hairy vetch, crimson clover) develop moderately deep, fine roots with nodules that fix nitrogen. They

stimulate microbial activity through nitrogen-rich exudates but contribute less to long-term carbon storage due to low root C:N ratios (Griffiths et al., 2022; Johnson et al., 2021; Poeplau and Don, 2015; Seitz et al., 2024). Brassicas (e.g., forage radish, mustard) produce large taproots that penetrate compacted subsoils, physically improving soil structure through biodrilling. However, their roots decompose rapidly after termination, limiting their persistence (Bodner et al., 2014; Marcinkevičienė et al., 2022; Rosolem and Pivetta, 2017). Grasses (e.g., rye, annual ryegrass) form dense, fibrous root systems concentrated in the upper soil layers (Wittwer et al., 2017; Wittwer and Van Der Heijden, 2020). These roots stabilize surface aggregates and gradually build organic matter through slower-decomposing residues (Basche and DeLonge, 2019; Poeplau and Don, 2015). Within these groups, species vary widely in function. For instance, hairy vetch develops deep, fine roots with long-lasting rhizobia-rich nodules (Poffenbarger et al., 2015; Sainju et al., 2005), whereas field pea has a shallower root profile and shorter nodulation period, limiting its nitrogen contribution (Boeglin et al., 2022; Johnson et al., 2021; Seitz et al., 2024). Among grasses, cereal rye forms dense, fibrous root mats that strongly stabilize surface aggregates (Crawford et al., 2018; Rai, 2022; Ruis et al., 2020), whereas oat (*Avena sativa*) produces coarser short-lived roots (Basche and DeLonge, 2019; Ruis et al., 2020). Among brassicas, forage radish creates rapid biopores but decomposes quickly (Martinez et al., 2019; Solangi et al., 2024), whereas rapeseed has a more branched system with moderate penetration but greater residue longevity (Johnson et al., 2021; Martinez et al., 2022).

Species mixtures often outperform monocultures by integrating complementary root traits. Beyond increases in total root biomass and root length density (Barel et al., 2019), cover crop mixtures modify soil processes through contrasting root traits of component species that operate simultaneously in space and time (Barel et al., 2019; Thorup-Kristensen et al., 2020). Differences in root diameter, branching density, and vertical penetration depth enhance pore continuity and connectivity, improving both aggregate stability and vertical water and solute movement compared with single-species cover crops (Rillig et al., 2015; Six et al., 2004; Williams and Weil, 2004). Deep-rooted species facilitate subsoil exploration and nutrient uplift, while shallow-rooted species intensify nutrient interception in surface layers, creating synergistic nutrient acquisition across soil horizons (Couëdel et al., 2018; Thorup-Kristensen et al., 2020). In addition, species-specific rhizosphere effects, such as localized pH modification, organic acid release, and different carbon inputs, promote greater microbial diversity and functional heterogeneity (Canarini et al., 2019; Storkey et al., 2019). The strength of these interactions depends on soil and climate conditions, with cover crop mixtures providing the greatest benefits in compacted, nutrient-limited, or water-limited soils where complementary rooting patterns reduce key constraints (Dabney et al., 2001; Finney et al., 2016). Thus, careful selection or mixing of species tailored to management goals is essential to maximize soil improvement and long-term system performance.

4.4. Optimizing cover crop cultural practices

Cultural practices determine not only whether roots establish successfully, but also how long they grow, persist, and interact with soil and microbial communities. Management factors such as planting time and methods, seeding rate, and termination strategies strongly influence the spatial and temporal expression of root traits (Clark, 2007; Murrell et al., 2017). To maximize belowground benefits, cultural management should be tailored to site-specific environmental and agronomic conditions, including climate, soil type, and target cash crops.

Planting time sets the length of the active growth window and shapes root development. In the United States, early seeding—generally 6–10 weeks before the first frost for autumn-planted species or during the early vegetative stages of the cash crop in intercropped systems—promotes greater root biomass, deeper soil penetration, stronger microbial activation, and favorable soil moisture conditions (Clark, 2007; Finney et al., 2017). Late seeding—generally less than four weeks before the first frost for autumn-planted species and during advanced cash crop stages for interseeded cover crops—typically results in poor establishment and root and microbial contributions (Mirsky et al., 2012; Sievers and Cook, 2018). However, the definitions of “early” or “late” planting vary with the cropping strategy. It is also important to note that the first frost is only a practical guideline, as root activity declines when soil temperatures fall below species-specific thresholds, regardless of calendar frost dates (Yang et al., 2021).

Seeding rate affects root system density, distribution, and competition among plants. Higher rates can enhance canopy closure and root biomass, but may intensify intra-specific competition if not aligned with species-specific growth habits, such as rooting depth, lateral spread, and crowding sensitivity (Hadir et al., 2025; Homulle et al., 2022). Deep- or wide-rooted species generally require lower densities to develop fully, while compact- or shallow-rooted species tolerate higher seeding rates without functional compromise (Hadir et al., 2025; Homulle et al., 2022; Kemper, 2024; Wong et al., 2024). Conversely, low seeding rates may reduce competition but risk uneven establishment and patchy root development, particularly under suboptimal germination conditions (Feng et al., 2024).

Termination timing determines whether root systems reach functional maturity. In the United States, autumn-sown cover crops are typically terminated 2–3 weeks before planting the following cash crop (Clark, 2007; Mirsky et al., 2009). Termination outside this window is generally classified as early or late, each with specific agronomic trade-offs (Kaye and Quemada, 2017). Early termination may prevent full root development, thereby limiting biopore formation and long-term soil benefits (Griffiths et al., 2022; Lucas et al., 2022; Wong et al., 2024). Late termination can increase competition for water and nutrients, particularly in regions with erratic spring rainfall (Murrell et al., 2017). For example, late-terminated sorghum can reduce subsequent crop yields by up to 28% in dryland systems due to soil water depletion (Zhang et al., 2023). In interseeded or living mulch systems, cover crops may not be actively terminated but are instead suppressed by environmental factors or competition with cash crop (Ogilvie et al., 2021; Quintarelli et al., 2022).

Termination methods also shape belowground outcomes. Mechanical approaches, such as roller crimping, preserve root systems, slow decomposition, and sustain microbial activity through the gradual nutrient release. Herbicide termination accelerates residue breakdown, creating a short-term nutrient pulse but fewer lasting soil benefits (Price et al., 2019; SARE Outreach, 2020). The effects on root-associated microbes depend on the herbicide type and soil conditions. Frost termination of sensitive species functions similarly to mechanical methods, leaving roots intact and decomposing slowly, thereby improving the soil structure, carbon retention, and microbial habitat.

Overall, optimizing cultural practices is essential for realizing the full potential of cover crops in sustainable agriculture. Aligning management with local conditions ensures that roots support microbial activity, nutrient cycling, and soil structure. In contrast, poorly timed or mismatched practices may reduce these benefits or even lead to competition with the cash crop. Importantly, the effects of cultural practices interact with other management decisions, including cropping system, tillage, and species selection, to determine overall root performance and soil health outcomes (Blanco-Canqui and Ruis, 2018; Tautges et al., 2019). When coordinated effectively, these factors provide substantial benefits; when misaligned, they can undermine system performance.

5. Breeding for cover crop root traits to enhance belowground interactions

Breeding cover crops for root traits is an emerging priority in sustainable agriculture, which has the potential to improve soil health, enhance nutrient-use efficiency, and promote long-term carbon

sequestration. Unlike many commercial cash crops that have undergone decades of intensive breeding, most cover crops remain genetically underexplored, leaving substantial opportunities to harness belowground traits that contribute directly to key agroecosystem services. A major challenge in root-focused breeding is the inherent complexity and plasticity of root traits. Root system architecture, depth, branching patterns, exudate composition, and symbiotic associations vary not only by species but also in response to soil texture, moisture, nutrient availability, and microbial communities. This environmental dependency complicates trait selection and renders traditional phenotypic screening impractical on a large scale.

Genomic selection offers a powerful strategy for accelerating breeding of complex root traits. Integrating whole-genome markers with phenotypic data allows for the early prediction of root biomass, architecture, rhizodeposition, and functional trait expression. Marker-trait associations have been identified for biomass in winter rye, and progress has been made in mapping nodulation and seed dormancy traits in temperate forage legumes (Annicchiarico et al., 2023; Tilhou et al., 2023). In buckwheat, genome-wide association studies across 117 genotypes identified 73 QTLs linked to root surface area, volume, and branching frequency—traits critical for drought tolerance and nutrient acquisition (Singh et al., 2025).

Despite these advances, significant challenges remain. High genotype-by-environment interactions, limited trait heritability, and logistical constraints in phenotyping diverse, multi-species systems complicate the selection for root traits. Root traits are highly plastic and vary temporally with soil conditions, moisture, and planting density. Phenotyping protocols must capture this variability while maintaining throughput and cost efficiency. Standardized, scalable protocols for evaluating root function under field conditions still constrain comparability across studies.

Another major limitation is the scarcity of well-characterized cover crop germplasm collections specifically targeting root traits. Historically, cover crop species have been selected primarily for agronomic traits such as biomass accumulation or nitrogen fixation, with little systematic evaluation of root system diversity. Pre-breeding efforts to assemble and characterize diverse accessions across various environments will be essential for identifying novel alleles and trait combinations relevant to breeding cover crops with enhanced belowground functionality.

6. Emerging technologies

Advances in technology are expanding the capacity to measure root-soil-environmental interactions with greater precision and relevance to field conditions. Tools such as X-ray computed tomography (Zeng et al., 2021), shovelomics combined with 3D modeling, and rhizotron-based platforms allow detailed assessment of root morphology. Tube-based platforms allow for the in-situ monitoring of rooting depth, angle, and growth dynamics under field conditions (Odone and Thorup-Kristensen, 2025). For example, the RadiMax facility—consisting of 40-m-long, V-shaped concrete beds filled with repacked soil—facilitates high-throughput imaging and estimation of rooting depth and spatial distribution through embedded minirhizotron tubes (Odone and Thorup-Kristensen, 2025). Functional indices such as $DeepRoot_{40}$, quantify vertical root distribution and identify zones of the most active root growth, which are critical for traits such as drought tolerance and nitrogen uptake efficiency (Odone et al., 2023). Artificial intelligence-based tools, such as ChronoRoot (Gaggion et al., 2021) and RootNav 2.0 (Yasrab et al., 2019), automate the estimation of root architectural traits with high accuracy and temporal resolution, enabling scalable, high-throughput phenotyping far beyond manual methods.

Advances in 3D root phenotyping from field or simulated field samples have greatly improved the amount of architectural information that can be extracted, in many cases increasing heritability estimates of root system architectural traits (Dowd et al., 2022; Hein et al., 2025; S. Liu et al., 2021; Shao et al., 2021; Wu et al., 2023). X-ray microscopy (XRM) provides non-destructive, three-dimensional imaging of organs at cellular and subcellular resolution, supporting comparative analyses across developmental stages and species (Duncan et al., 2022, 2022, 2019; Jacobsen, 2020). Coupled with spatial transcriptomics, these approaches retain positional context while mapping gene expression within tissues, linking molecular activity to structural features (Cox Jr et al., 2022; Crosetto et al., 2015; Marx, 2021; Sun et al., 2023). Insights from species-level comparisons, such as those in Fig. 7, reveal diversity within single functional groups and illustrate how these methods can be extended to assess functional diversity in cover crops of ecological and agricultural relevance.

Molecular tools have further enhanced root trait assessment by targeting root-microbe interactions rather than architecture alone. Techniques such as quantitative PCR (qPCR), next-generation sequencing, and fluorescence in situ hybridization (FISH) enable the direct quantification of AMF colonization and microbial interactions at the root interface (Corona Ramírez et al., 2023; Wang et al., 2021). Pairing these capabilities with Automatic Mycorrhiza Finder (AMFinder), a convolutional neural network trained to detect AMF structures in stained root images, provides high-throughput and standardized quantification of symbiosis (Evangelisti et al., 2021). When combined with depth-resolved soil core methods and image-based platforms such as Rhizovision Explorer (Seethepalli and York, 2020) or WinRhizo (Regent Instruments), AMFinder links colonization levels with root system placement across soil depths, giving a more complete view of how symbiosis varies among cover crop species and functional groups. In parallel, biosensor-based assays using engineered microbes responsive to root exudates, provide real-time monitoring of rhizosphere signaling (Guyonnet et al., 2018; Rubia et al., 2020). These microbes contain reporter genes (e.g., lux, gfp) that are activated by specific exudate compounds such as sugars, amino acids, or organic acids, producing luminescent or fluorescent signals for non-destructive, temporally resolved detection of root exudation patterns (Neelam and Tabassum, 2023; Porteous et al., 2000; Rubia et al., 2020).

Together, these emerging technologies move root research beyond descriptive studies, enabling mechanistic insights into how roots interact with soil and microbes under realistic field conditions. Their integration across molecular, structural, and environmental scales allows researchers to link trait expression with ecosystem functions such as nutrient cycling, water capture, and stress resilience. Ultimately, this toolbox enables cover crop research to identify and deploy root traits that maximize both agricultural productivity and ecological sustainability.

7. Conclusions and future directions

This detailed review highlights the key point that a paradigm shift is necessary: rather than selecting cover crops primarily for biomass production or nitrogen fixation, root trait diversity should be recognized as a crucial driver of ecosystem function. The evidence synthesized here demonstrates that root architectural diversity, rhizosphere processes, and root-soil-microbe interactions play central roles in regulating soil physical structure, nutrient cycling, and biological activity, which are essential for agroecosystem sustainability. Despite their importance, cover crop root traits remain under-characterized and poorly integrated into selection and management strategies. Bridging this gap is essential to move beyond generalized recommendations toward regionally adapted, trait-informed cover crop systems. Achieving this goal will require interdisciplinary efforts that integrate plant breeding, soil science, and agroecology. Such coordinated efforts will (i) evaluate root-soil interactions under field conditions across diverse environments and cropping systems (e.g., assessing how deep-rooted species or species mixtures perform under reduced tillage or in compacted soils), (ii) identify root traits that confer desirable soil outcomes such as improved

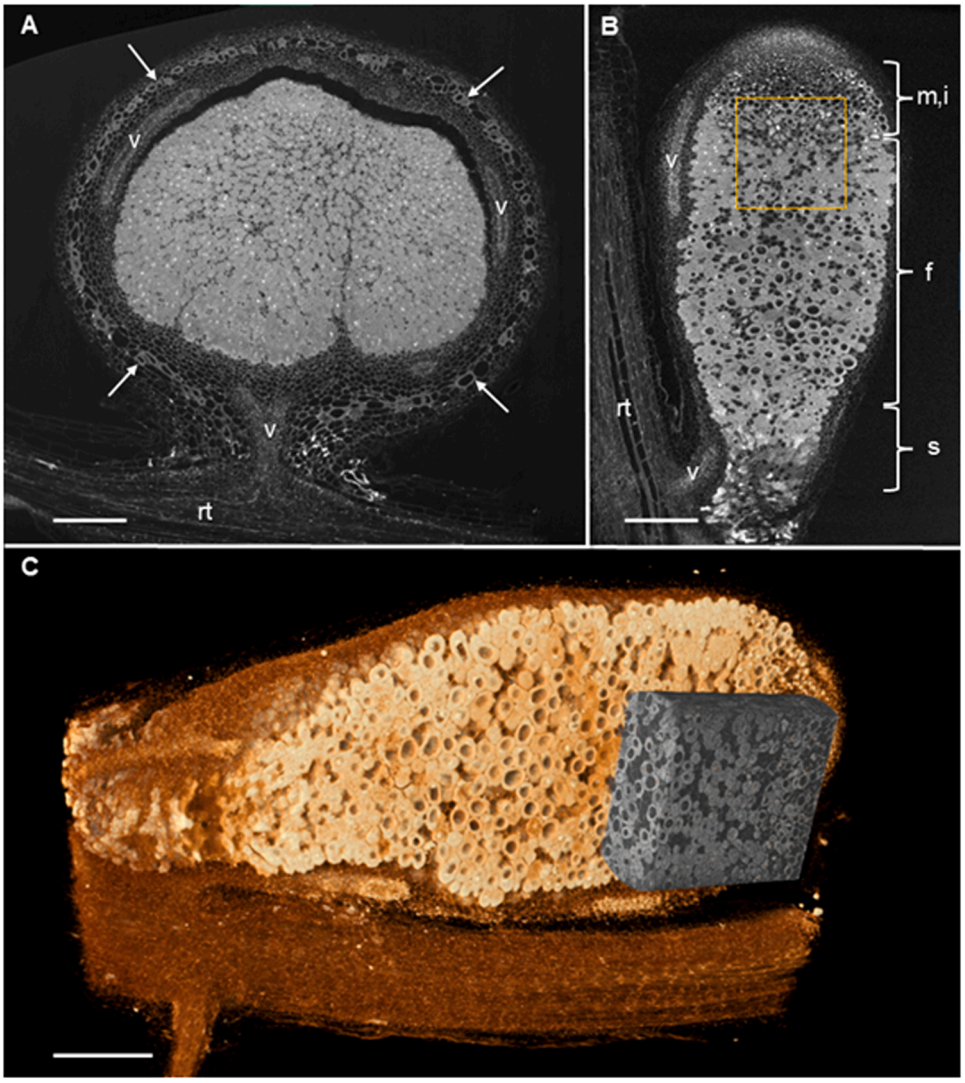


Fig. 7. X-ray microscopy (XRM) imaging of fixed and contrast-enhanced root nodules showing species-level structural diversity within legumes. Panels A&B are both digital sections from XRM scans. (A) Determinate soybean nodule showing a ring of sclerenchyma cells located just below the epidermal cell layer. (B) Indeterminate crimson clover nodule displaying distinct developmental zones of nodulation: meristem (m), infection (i), fixation (f), and senescence (s). (C) Three-dimensional volume rendering of multiscale scans of the crimson clover nodule. The grayscale inset (corresponds to the yellow box in panel B) represents a region-of-interest scan at higher contrast. Samples were prepared as described in Duncan et al. (2022). Scale bars A = 200μm, B = 300μm, C = 500μm. v, vasculature, rt, root. Labels based on Jhu and Oldroyd (2023).

pore connectivity, nutrient capture, and microbial functions, (iii) develop phenotyping tools and datasets to guide species selection, and (iv) enable practitioners to match specific cover crop species or mixtures to soil constraints such as low fertility or poor structure rather than relying on a biomass based cover crop selection.

Harnessing the full potential of cover crop root systems promises a path toward resilient, regenerative agriculture. Aligning root traits with site-specific goals and environmental constraints can enable the design of cover crop systems that deliver consistent, multifunctional benefits. Ultimately, this approach can transform cover cropping from a promising practice into a precision tool for agroecosystem sustainability. Importantly, maximizing these benefits requires careful integration of management practices, as poorly aligned approaches can diminish or negate both soil and agronomic gains.

CRediT authorship contribution statement

Akanksha Sehgal: Writing – review & editing, Writing – original draft. **Rongzhong Ye:** Writing – review & editing, Funding acquisition. **Luvina B. Madrid:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christopher Topp:** Writing – review & editing, Resources. **Sruthi Narayanan:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Kadambot H.M. Siddique:** Writing – review & editing, Resources. **Kirsten Hein:** Writing – review & editing, Writing – original draft.

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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Data Availability

Data will be made available on request.

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