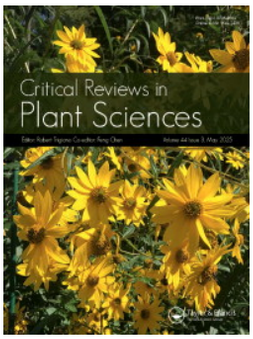

Taylor & Francis
Taylor & Francis Group

Critical Reviews in Plant Sciences

ISSN: 0735-2689 (Print) 1549-7836 (Online) Journal homepage: www.tandfonline.com/journals/bpts20

Exudates of Carboxylates by Roots and Their Implications for Nutrient, Contaminant and Carbon Dynamics in Soil

Nanthi Bolan, Santanu Mukherjee, Shailja Sharma, Shiv Bolan, Jun Yuan, Shengdie Yang, Caroline Peacock, Alba Otero-Fariña, Rasheed Adeleke, Linda Obi, Jiayin Pang & Kadambot H. M. Siddique

To cite this article: Nanthi Bolan, Santanu Mukherjee, Shailja Sharma, Shiv Bolan, Jun Yuan, Shengdie Yang, Caroline Peacock, Alba Otero-Fariña, Rasheed Adeleke, Linda Obi, Jiayin Pang & Kadambot H. M. Siddique (27 Aug 2025): Exudates of Carboxylates by Roots and Their Implications for Nutrient, Contaminant and Carbon Dynamics in Soil, Critical Reviews in Plant Sciences, DOI: 10.1080/07352689.2025.2549655

To link to this article: https://doi.org/10.1080/07352689.2025.2549655

CRITICAL REVIEWS IN PLANT SCIENCES
https://doi.org/10.1080/07352689.2025.2549655

Taylor & Francis
Taylor & Francis Group

Exudates of Carboxylates by Roots and Their Implications for Nutrient, Contaminant and Carbon Dynamics in Soil

Nanthi Bolan[a,b], Santanu Mukherjee[c], Shailja Sharma[d], Shiv Bolan[a,b], Jun Yuan[e], Shengdie Yang[e], Caroline Peacock[f], Alba Otero-Fariña[f], Rasheed Adeleke[g], Linda Obi[g], Jiayin Pang[b,h] and Kadambot H. M. Siddique[b]

[a]UWA School of Agriculture and Environment, The University of Western Australia, Perth, Australia; [b]The UWA Institute of Agriculture, The University of Western Australia, Perth, Australia; [c]School of Agriculture, Shoolini University of Biotechnology and Management Sciences, Solan, India; [d]School of Biological & Environmental Sciences, Shoolini University of Biotechnology and Management Sciences, Solan, India; [e]Jiangsu Provincial Key Lab for Organic Solid Waste Utilization, Jiangsu Collaborative Innovation Center for Solid Organic Wastes, Educational Ministry Engineering Center of Resource-saving fertilizers, Nanjing Agricultural University, Nanjing, China; [f]School of Earth and Environment, University of Leeds, Leeds, UK; [g]Unit for Environment Sciences and Management, North-West University (Potchefstroom Campus), Potchefstroom, South Africa; [h]UWA School of Biological Sciences, The University of Western Australia, Perth, Australia

ABSTRACT

Rhizosheath carboxylates originate from plant root exudates, soil microbial activity, and soil organic matter decomposition. This review provides a comprehensive bibliometric analysis of critical discussions on the role of rhizosheath carboxylates in soil ecosystems by examining factors influencing their release, and their implications for nutrient availability, contaminant behavior, and carbon dynamics. Root exudates comprise numerous compounds, including enzymes, polysaccharides, primary metabolites such as carbohydrates, amino acids, and carboxylates, and secondary metabolites like phenols, glucosinolates, vitamins, and plant hormones. In response to biotic and abiotic stresses, soil microorganisms also release carboxylates as part of their adaptive strategies. Their release, concentration, and persistence in the rhizosheath fluctuate over time, which is influenced by various factors, including soil type, plant species, nutrient availability, microbial activity, and environmental conditions. These carboxylates play a key role in mobilizing carbon, nutrients, and contaminants, thus influencing their bioavailability to plants and microbes. While the dynamic and transient nature of these root exudates allows plants to respond to changing environmental conditions and nutrient demands by adjusting their exudation patterns, it poses significant challenges to the measurement and quantification of root exudates. This challenge can be overcome by developing techniques for the *in situ* measurement of root carboxylate exudation.

Abbreviations: ALMT: Aluminum-activated malate transporter; AMF: Arbuscular mycorrhizal fungi; ATP: Adenosine triphosphate; HMWOA: High-molecular-weight organic acids; LMWOA: Low-molecular-weight organic acids; MATE: Multidrug and toxic compound extrusion; PSB: Phosphate-solubilizing bacteria; RCE: Root carboxylate exudation; SOC: Soil organic carbon; SLAC: Slow anion channel; TCA: Tricarboxylic acid

KEYWORDS

Biotic and abiotic stress; carbon dynamics; carboxylates; contaminant dynamics; root exudation

I. Introduction

Rhizosheath (i.e., a thin layer of soil that adheres strongly to plant roots) carboxylates are derived primarily from plant roots, microbial activity, and organic matter decomposition. Root exudates comprise low (<1000 Da) and high (>1000 Da) molecular weight primary and secondary metabolites. Primary metabolites include carbohydrates (e.g., glucose, sucrose, starch), amino acids (e.g., arginine, aspartate, lysine) and carboxylates (e.g., oxalate, tartrate, malonate, citrate, isocitrate, malate). Secondary metabolites comprise alkaloids, phenolics, terpenoids, flavonoids, glycosides, vitamins, hormones, enzymes, and polysaccharides (Cornelis and de Tombeur 2022). Carboxylates – the anions of low- and high-molecular-weight organic acids (LMWOA and HMWOA) – form the major

CONTACT Nanthi Bolan nanthi.bolan@uwa.edu.au UWA School of Agriculture and Environment, The UWA Institute of Agriculture, M079, Perth WA 6009 Australia; Kadambot H. M. Siddique kadambot.siddique@uwa.edu.au The UWA Institute of Agriculture, The University of Western Australia, Perth, Western Australia 6009, Australia.

Supplemental data for this article can be accessed online at https://doi.org/10.1080/07352689.2025.2549655.

components of root exudates. Soil microbes –particularly bacteria and fungi – also produce and exude carboxylates as part of their adaptative responses to environmental stresses (Mimmo *et al.* 2014; Wang *et al.* 2024). Additionally, plants and microorganisms contribute to organic matter decomposition by releasing extracellular enzymes (i.e., also known as exoenzymes that are synthesized inside a cell and then secreted outside the cell) (Daunoras *et al.* 2024). Various factors influence the type and concentrations of rhizosheath carboxylates, including plant species and genotype, environmental conditions and the presence of biotic or abiotic stressors (Cornelis and de Tombeur 2022).

In the rhizosheath and hyphosphere (i.e., soil adjacent to root-associated fungal hyphal tips) microenvironments, carboxylates are involved in mineral weathering through ligand-promoted complexation and proton-promoted deprotonation processes. These processes, alongside pH buffering and organic matter mineralization, are central to regulating soil nutrient, contaminant, and carbon dynamics, thereby contributing to underpinning ecosystem functioning (Oburger *et al.* 2009; Adeleke *et al.* 2017). Moreover, carboxylate-driven transformations are key to the stabilization and accumulation of soil organic carbon (SOC) (Clarholm *et al.* 2015; Karadihalli Thammaiah *et al.* 2022). Carboxylates are particularly effective in solubilizing nutrients from inorganic sources (Marschner 2012; Lambers and Plaxton 2015). Under conditions of limited nutrient availability – especially phosphorus (P) – plants increase carboxylate exudation to mobilize sparingly soluble inorganic P in soil, often accompanied by phosphatase enzyme activity that facilitates the hydrolysis of organic P compounds from soil organic matter (Jindo *et al.* 2023; Santoro *et al.* 2024). Carboxylates also enhance the mobility and bioavailability of heavy metals such as lead (Pb) and cadmium (Cd) due to their strong chelating properties (Achor *et al.* 2020; Seregin and Kozhevnikova 2024). In addition, P-acquisition strategies that rely on carboxylate exudation can destabilize iron (Fe)- and aluminum (Al)-associated organic matter, increasing its accessibility to microbial degradation and subsequent mineralization. The effect of carboxylate exudation on soil carbon stocks can vary significantly, however, depending on soil type (Ding *et al.* 2021; Ma *et al.* 2022).

In alkaline soils typical of arid and semi-arid regions – where inorganic carbon predominates the C pool, carboxylate-mediated P acquisition promotes the dissolution and release of Ca-bound P. The released Ca^{2+} may precipitate as pedogenic carbonate in the presence of elevated CO_2 levels from root and microbial respiration (Lambers 2022; Gerke 2024). Conversely, in acid soils, where organic carbon dominates, P acquisition involves organic P mineralization, leading to carbon loss through CO_2 emissions (Cornelis and de Tombeur 2022). As a result, carboxylate exudation in alkaline soils may lead to net carbon sequestration, while in acidic soils, it can contribute to carbon loss (Wang and Lambers 2020). In dryland regions, this process may enhance SOC sequestration potential.

While numerous studies have focused on root proton exudation and its role in nutrient mobilization via carboxylates (Cornelis and de Tombeur 2022; Lambers 2022; Gerke 2024), there are limited studies specifically addressing the role of rhizosheath carboxylates in contaminant mobility and carbon cycling (Jones *et al.* 2003; Peña 2022). These studies have focused mostly on the effects of LMWOA exudation on the dissolution and mineralization of P from inorganic and organic sources in the soil. Studies on the role of root exudation on the complexation and immobilization of heavy metals in soil, and the mobilization of SOC, are lacking yet are critical in relation to soil remediation and carbon sequestration. This review provides a bibliometric analysis of critical discussions on the role of rhizosheath carboxylates in soil ecosystems by examining factors influencing their release, and their implications for nutrient availability, contaminant behavior, and carbon dynamics. The specific objectives of this review are to (i) examine the processes involved in the release of rhizosheath carboxylates from plant roots, soil microorganisms, and organic matter decomposition, (ii) evaluate the role of carboxylates in nutrient acquisition and contaminant mobilization, and (iii) elucidate the contributions of rhizosheath carboxylates in SOC dynamics. Ultimately, this review seeks to inform strategies to optimize root carboxylate exudation for improved nutrient cycling, contaminant management and carbon sustainability in soil systems.

II. Methodology

A comprehensive literature search was conducted on March 25, 2025, using the Web of Science Core Collection. The search terms included: “carboxylates” AND “organic anions” OR “metabolites” AND TS Topic search = (“roots” OR “microbes” OR “organic matter decomposition”) AND TS = (“nutrients” OR “contaminants” OR “carbon” OR “phosphorus”) AND TS = (“acquisition” OR “mobilization” OR “dissolution” OR “precipitation”) AND TS = (“respiration” OR “enzyme” OR “nutrient cycling” OR “carbon

sequestration"). This search yielded 3246 results. Supplementary Figures S1 and S2 illustrate the article selection process. Figure S1 presents the PRISMA methodology, outlining the workflow of the bibliometric analysis. Figure S2 shows how the key research topics in the field evolved over the review period, based on data from online databases such as the Web of Science.

III. Processes of carboxylate exudation

Root exudation significantly shapes microbial communities in the soil ecosystem (Canarini *et al.* 2019; Seitz *et al.* 2024). During this process, plants release numerous primary and secondary metabolites that support beneficial plant-microbe interactions and alter soil properties. These metabolites comprise a complex mix of LMW and HMW organic compounds, delivered into the soil through rhizodeposition. Common carboxylates, such as citrate and tartrate, can originate from plant roots, microbial secretions or soil organic matter. These compounds, predominantly exuded by plants, are critical for nutrient mobilization and metal ion chelation (Mitra *et al.* 2022), underscoring their multifunctional role in plant-soil-microbe interactions (Seregin and Kozhevnikova 2024).

Root carboxylate exudation (RCE) – the release of carboxylates into the rhizosheath – is governed by plant physiology, soil conditions and microbial activity (Figure 1 and Table 1). Although plant roots are the main source, contributions from soil organic matter and microorganisms are also significant. The RCE process is a vital nutrient acquisition strategy, especially in nutrient-deficient soils. In response to nutrient limitations, carboxylates released through root exudation influence the biogeochemical cycling of key nutrients such as P and nitrogen (N). The extent and efficiency of this process depend on various environmental and biological factors, including nutrient status, soil type and pH, microbial community composition, plant species, and specific physiological traits (Ma *et al.* 2022).

Plants initiate foraging (scavenging) and mining strategies, producing carboxylates via metabolic pathways such as the tricarboxylic acid (TCA) cycle. These compounds are transported across cell membranes

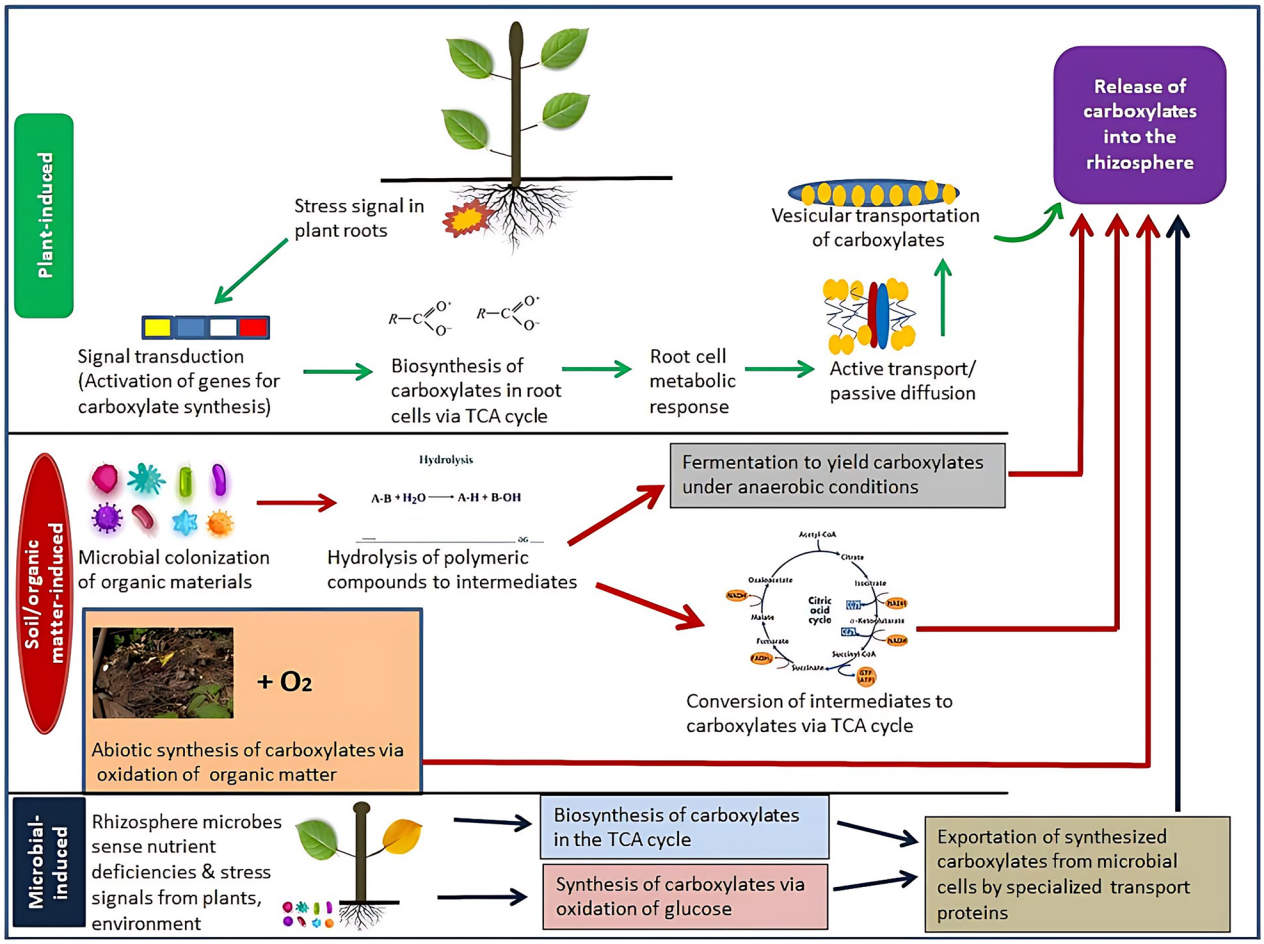

Figure 1. Schematic illustration of the processes involved in carboxylate exudation from plant roots, soil organic matter, and microorganisms.

Table 1. Concentrations of various carboxylates from different sources.

Origin	Source	Carboxylates	Quantity produced	References
Plants	Tall wheatgrass	Citrate; Acetate; Malonate; Trans-aconitate	1 µM; 4.2 µM; 3.8 µM; 1 µM respectively	(Tshewang *et al*. 2020)
	White Lupin	Citrate; Malate	45 µM; 48 µM respectively	(Pearse *et al*. 2006)
	Tomato	Citrate	0.13 µM	(Neumann and Römheld 1999)
	Tall fescue	Citrate; Acetate; Malonate	0.5 µM; 3.1 µM; 2.6 µM respectively	(Tshewang *et al*. 2020)
	Wheat	Malate	1.5–3.5 µM	(Fischer *et al*. 2010)
	Soybean	Citrate	4 µM	(Nwoke *et al*. 2008)
	Veldt grass	Citrate; Acetate; Malonate	0.2 µM; 4.8 µM; 5 µM respectively	(Tshewang *et al*. 2020)
Soil organic matter	Rhizosphere	Citrate; Malate	50 µM	(Jones *et al*. 1996; Adeleke *et al*. 2017)
	Rhizosphere	Citrate	1–5 µM	(Strobel 2001; Adeleke *et al*. 2017)
	Rhizosphere	Citrate; Malate	1 mM–80 mM	(Ström *et al*. 2005; Adeleke *et al*. 2017)
Microbial	*Penicillium oxalicum* PSF-4	Oxalate; Formate; Acetate; Malate; Lactate	~454.5 µM; ~3998.2 µM; ~856 µM; ~1640.8 µM; ~2469.1 µM respectively	(Jiang *et al*. 2020)
	Aspergillus niger	Oxalate; Citrate	86.6–6206.6 µM; 199.5–240.3 µM respectively	(Tian *et al*. 2021)
	Penicillium aurantiogriseum	Oxalate; Citrate	~2841.3 µM; ~1004.7 µM respectively	(Hu *et al*. 2022)

and released into the rhizosheath in response to specific environmental triggers (Dong *et al*. 2021). Microorganisms also play a key role in producing carboxylates as metabolic byproducts during the decomposition of organic substrates in the rhizosheath, including through the TCA cycle and nutrient mineralization processes (Wu *et al*. 2024). Hence, the synergistic interaction between plant roots and soil microbes forms the biological foundation for carboxylate production, influencing soil health and plant productivity (Figure 1; Table 1).

A. Plant-induced root carboxylate exudation processes

Plant roots release a significant portion of the carbon fixed during photosynthesis into the soil as root exudates. These exudates, including carboxylates, alter soil physicochemical conditions, shape microbial communities, and help plants cope with both biotic and abiotic environmental stressors, thereby supporting growth and development (Afridi *et al*. 2024). Environmental cues such as nutrient deficiencies or stress trigger carboxylate exudation (Kruthika *et al*. 2024; Seregin and Kozhevnikova 2024). Detection of low nutrient status activates genes involved in carboxylate biosynthesis, a systemic response to signals originating from nutrient-deprived leaves (Amjad *et al*. 2024). These carboxylates form as intermediates in the Krebs or TCA cycle during carbohydrate metabolism, particularly when the cycle intersects with anaplerotic pathways (Panchal *et al*. 2021).

Root cells release biosynthesized carboxylates either through active transport involving specific proteins or via passive diffusion along concentration gradients (Weston *et al*. 2012). For example, foliar application of magnesium (Mg) enhances citrate and malate exudation, improving wheat growth and development (Kibria *et al*. 2021). Active secretion typically occurs via anion channels driven by proton pumps and this is an energy-dependent process (Kruthika *et al*. 2024). In contrast, passive diffusion involves the movement of LMW compounds without energy input, driven by concentration differences between the root cytoplasm and the rhizosheath (Vurukonda *et al*. 2022; Agarwal *et al*. 2024). Additionally, vesicle-mediated transport releases LMW and HMW exudates to the rhizosheath via anion channels (Ma *et al*. 2022; Kruthika *et al*. 2024).

Some plant species have evolved specialized strategies to exude carboxylates under P deficiency. White lupin (*Lupinus albus* L.), a nonmycorrhizal species, is known for its high carboxylate output under P-deficient conditions (Mimmo *et al*. 2011; Tiziani *et al*. 2020). Members of the Proteaceae family also adjust carbon allocation in response to nutrient stress, producing specialized cluster roots ("proteoid roots") to enhance carboxylate release (Delgado *et al*. 2014). For instance, *Hakea prostrate* allocates about 25% of its biomass to cluster root development under severe P deficiency, leading to intense, short-term carboxylate exudation (Shane and Lambers 2005). Conversely, *Embothrium coccineum* forms fewer cluster roots but exudes carboxylates at a faster rate over a longer period (Funayama-Noguchi *et al*. 2021). In *L. albus*, proteoid

roots also play a pivotal role, enhancing nutrient acquisition and plant survival with their large surface area and substantially greater exudation capacity than nonproteoid roots (Tiziani *et al.* 2020). Nevertheless, noncluster roots can also exude carboxylates, albeit at lower rates (Ortíz *et al.* 2020).

B. Soil-induced root carboxylate exudation processes

Soil-induced RCE refers to processes in which the soil environment indirectly stimulates carboxylate exudation, primarily through organic matter decomposition, including plant litter, aromatic compounds, and animal waste. While plant litter, mainly composed of structural compounds, does not contain carboxylates, they can be produced during microbial decomposition of organic matter (Sheik *et al.* 2020).

The microbial decomposition of carbon-rich plant and animal residues is a complex biochemical process that shapes the rhizosheath and soil chemistry. Microorganisms involved in this decomposition secrete various carboxylates, contributing significantly to soil biochemical processes (Adeleke *et al.* 2017). The process begins with microbial colonization of organic material, where microbes release hydrolytic enzymes such as cellulases, lipases, and proteases to degrade complex carbon-rich polymers like polysaccharides, lipids, and proteins. The resulting intermediate products are then further metabolized into carboxylates – such as acetate, lactate, citrate, malate, and oxalate (Igamberdiev and Eprintsev 2016) – via metabolic pathways like glycolysis and the TCA cycle (Choi *et al.* 2021). The dynamic interaction between microbial communities and soil properties is critical in determining the extent and nature of carboxylate exudation, influencing key soil functions such as nutrient cycling and carbon sequestration (Philippot *et al.* 2024). In addition to aerobic processes, carboxylate production also occurs under anaerobic conditions through microbial fermentation (Arslan *et al.* 2016). During this process, the intermediate products from hydrolysis undergo acidogenesis, acetogenesis, and methanogenesis, driven by specific microbial communities. The acidogenic phase is particularly important, where the fermentation of fatty acids, amino acids, and lactic acid results in the formation of carboxylates, including acetate, butyrate, lactate, and formate (Sikora *et al.* 2019).

Soil weathering further contributes to carboxylate formation by driving the breakdown of organic matter and promoting soil-microbe interactions that release nutrients (Mimmo *et al.* 2014). For example, oxalate can be synthesized during the oxidative degradation of aromatic compounds, such as the breakdown of catechol (a secondary metabolite) during soil weathering (Studenroth *et al.* 2013). Thus, the extent of carboxylate exudation is linked to the degree of soil weathering. Excessive soil weathering can be detrimental, however, potentially reducing soil fertility and impairing nutrient cycling (Drever and Vance 1994).

C. Microbial-induced root carboxylate exudation processes

Microorganisms are central to driving biochemical processes in soil, including carboxylate production through RCE. In addition to their role in organic matter decomposition, rhizosheath microorganisms – collectively referred to as the *rhizomicrobiome* – originate from multiple sources, including the seed microbiome, plant-associated microbial communities (*phytomicrobiome*), the broader soil microbial pool, and environmental vectors such as water, wind, animals, and human activities (Phour *et al.* 2020).

These rhizosheath and plant-associated microbes are key players in RCE, significantly influencing nutrient availability and overall soil health. In response to nutrient deficiencies or environmental stress signals from plants, microbes engage in a range of metabolic processes, including the synthesis of carboxylates. These compounds are produced via the TCA cycle (through anaplerotic pathways) and glycolysis, enabling nutrient mobilization and metal detoxification in the rhizosheath (Fazeli-Nasab *et al.* 2022). Environmental stress often triggers microbial production of carboxylates, and many microbial taxa produce similar types of carboxylates to adapt to these challenges (Guan *et al.* 2017).

A diverse range of microbes is known to secrete carboxylates. Fungi such as *Aspergillus, Trichoderma,* and *Penicillium* produce oxalate, citrate, lactate, and fumarate (Tian *et al.* 2021; Hu *et al.* 2022). Various strains of *Bacillus* generate carboxylates, including gluconate, citrate, lactate, acetate, formate, succinate, and malate (Azaroual *et al.* 2020; Wang *et al.* 2020). Bacterial genera such as *Pseudomonas, Enterobacter, Serratia,* and *Paenibacillus* also contribute by producing compounds like succinate, citrate, malate, oxalate, gluconate, and acetate (Brito *et al.* 2020). Beyond carboxylates production, the rhizomicrobiome enhances plant growth through the secretion of other beneficial molecules, such as phytohormones, antibiotics and hydrolytic enzymes, which contribute to plant development, stress tolerance and soil ecosystem stability (Phour *et al.* 2020).

The nature and concentration of carboxylates released by various root-exudation processes discussed in the above sections are influenced by a number of plant, soil, microbial, and environmental factors (Table 2), which are covered in the following section.

IV. Factors affecting carboxylate exudation

Various factors, including the host plant species, environmental stresses, soil physicochemical properties, and microbial communities, influence rhizosheath carboxylate production (Figure 2 and Table 2). The composition of these exudates – such as dicarboxylic acids like tartaric acid and oxalic acid – varies with the plant species, as seen in rice and tomato (More *et al.* 2020). Environmental stressors, including salinity and plant diseases, can significantly alter exudation profiles (Yang *et al.* 2025). In addition, soil texture, nutrient availability, and moisture levels shape the nature and quantity of carboxylate exudates (Adeniji *et al.*, 2025). Microbial communities, particularly arbuscular mycorrhizal fungi and other root-associated microbes, also play a key role in modulating exudation patterns (Li *et al.* 2022).

Root exudation is modulated by biotic and abiotic factors, and their interactions can produce exudation patterns that may be quite different from the sum of the effects of individual factors (Sharma *et al.* 2023; Robert *et al.* 2025). This complexity results from the fact that plants react to a variety of internal and external stimuli, which frequently have either antagonistic or synergistic effects on exudate profiles. Increased generation of carbohydrates and more substrates for root exudation are the two benefits of enhanced photosynthesis brought on by elevated CO_2. Higher temperatures speed up the metabolism of plants, especially the respiration of roots, which increases root activity and development and, ultimately, carbon release. Organic matter decomposes more quickly at higher temperatures, therefore soil microbial activity is further increased, which in turn improves nutrient cycling and perhaps increases the need for carbon-rich root exudates. For example, it is shown that at high temperatures, N fertilizer application promotes *Pinus tabuliformis* exudation, and suggested that higher temperatures, which increase plant metabolic rates, may also increase the need for N (Yin *et al.* 2013; Xu *et al.* 2025).

Nitrogen satisfies the higher needs of plants when it is easily accessible, promoting improved root development and exudation. Alternately, changes in microbial communities may mediate indirect effects that influence root exudation patterns, which in turn may influence the relationships between temperature and N availability. On the other hand, by reducing the production of osmo protectants (proline, sugars, and organic acids) in favor of antimicrobial chemicals (phenolics, flavonoids, and phytoalexins), pathogens may counteract the exudate response to abiotic stressors such as dehydration and salt. These tradeoffs demonstrate how the plant may optimize its survival strategy in a complex stress environment by prioritizing its metabolic output according to the current stress levels. Further research into the complex relationships between abiotic factors influencing root exudation patterns has occasionally shown contradictory reactions to straightforward nutrient responses (Canarini *et al.* 2019; Freschet *et al.* 2021; Adeniji et al., 2025). A concomitant S or P shortage significantly reduces the enhanced exudation of

Table 2. Factors affecting carboxylates exudation.

Carboxylates	Factors	Host	References
Tartarate	Plant species	Rice	(Yang *et al.* 2020a)
Oxalate, acetate, propionate	Plant species	Tomato	(Yang *et al.* 2016)
Citrate	Plant species	Beans	(Kidd *et al.* 2001)
2-methylbutyrate, stearate, palmitate, palmitoleate, oleate	Salt stress	*Lupinus sinense*	(Xiong *et al.* 2020)
Malate, citrate, succinate	Foliar diseases	*Arabidopsis thaliana*	(Yuan *et al.* 2018)
2-hydroxyvalerate, threonate acid	Soilborne diseases	Cucumber	(Wen *et al.* 2023b)
Citrate	Nutrient availability (phosphorus deficiency)	*Caustis blakei*	(Playsted *et al.* 2006)
Citrate, malate	Nutrient availability (iron deficiency)	Medicago	(M'Sehli *et al.* 2008)
Malate, citrate	Nutrient availability (aluminum toxicity)	*Citrus sinensis*	(Yang *et al.* 2020b)
Oxalate, citrate	Soil texture	–	(Hayakawa *et al.* 2018)
Malate, lactate, acetate, succinate, citrate	Soil moisture	Corn	(Canarini *et al.* 2016)
Oxalate	Microbes	Arbuscular mycorrhizal fungi	(Andrino *et al.* 2021)
Malate	Interactions between plant roots and microbes	*Pteris vittata*	(Yizhu *et al.* 2020)
Succinate, malate, fumarate	Interactions between plant roots and microbes	*V. unguiculata*, *V. radiata*, and *M. atropurpureum*	(Lardi *et al.* 2016; Lardi and Pessi 2018)

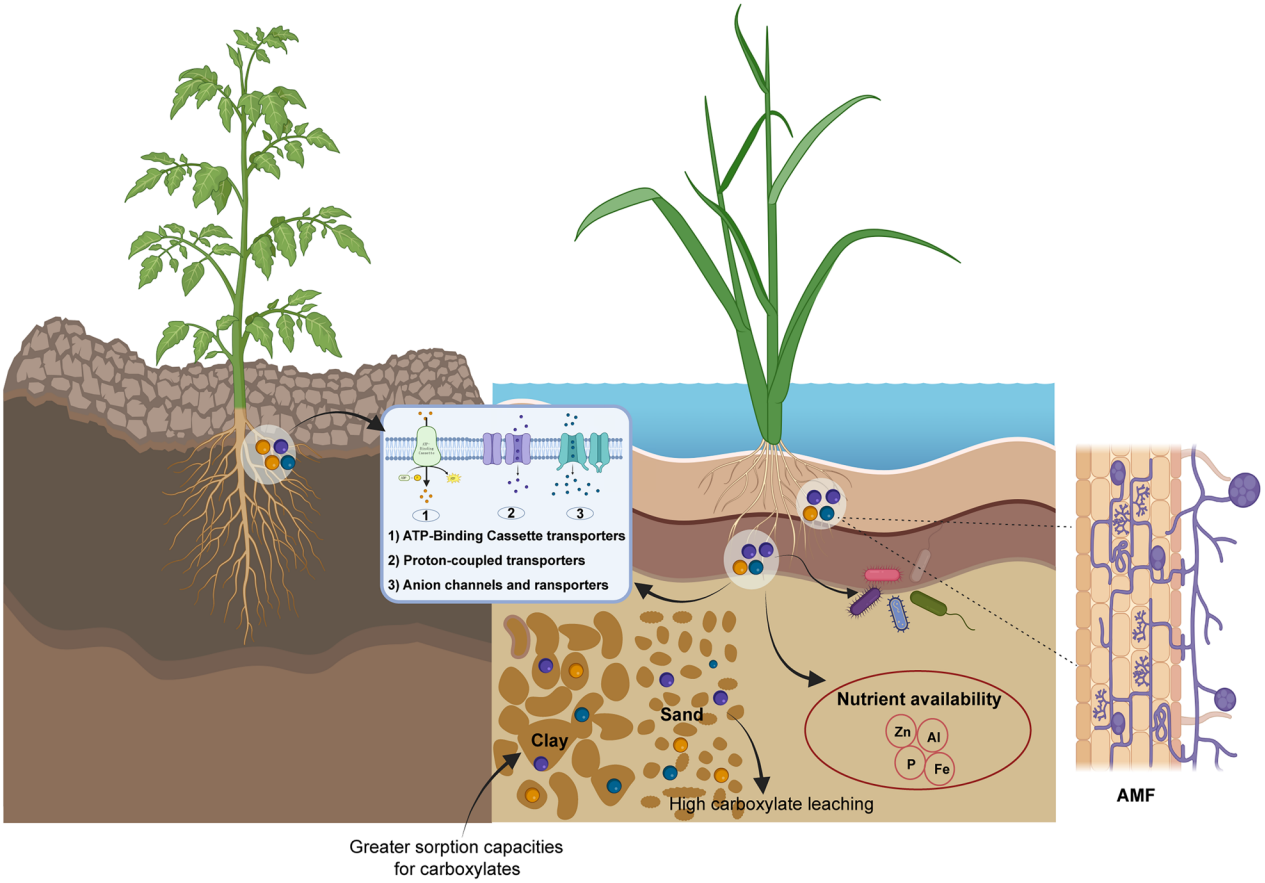

Figure 2. Schematic representation of the factors influencing carboxylate exudation, including plant traits, soil properties (soil type, nutrient availability), and microbial interactions (arbuscular mycorrhizal fungi, AMF).

phytosiderophores and chelators in barley, wheat, and Arabidopsis that is caused by a Fe deficiency, as discussed above (Astolfi *et al.* 2020, 2021). Apple trees increase the exudation of carboxylates, including malate, in response to concurrent shortages in Fe and P (Valentinuzzi *et al.* 2019; Ličina *et al.* 2024). The consequences of Fe deficiency appear to be mitigated by this change in exudation strategy to deal with Fe deficit under further S or P shortages. The P deficiency-induced citrate exudation in barley and legume cultivars varies according to the N (NH_4/NO_3^-) supply and depends on its accessibility (Marschner 2012). While in legume species, citrate exudation is reduced under P shortage with both sources of N present but not with NH_4^+ alone, whereas in barley cultivars, P deficiency enhances citrate efflux with NH_4^+ but does not alter the exudation with balanced NH_4^+/NO_3^- fertilization. This does not greatly change the overall growth of the plants. There are a number of nonexclusive theories that explain why plants respond differently to single vs multiple nutritional challenges in terms of exudation and how these tactics support development and equilibrium (Russ *et al.* 2023; Fujii 2024).

A. Plant factors

Plants exudates carboxylates through their roots, with the quantity and type of carboxylates released regulated by factors such as species type, genetic factors, and environmental conditions (Ryan et al., 2011) (Figure 2).

1. Plant species

Different plant species secrete distinct carboxylates. For instance, rice roots primarily release tartrates (Yang *et al.* 2020a), whereas tomato roots exude oxalate, acetate, and propionate (Imas *et al.* 1997). These differences extend to responses under stress – under Al stress, species like beans, soybean, and maize exhibit increased citrate secretion, while rice and tobacco do not (Abd El-Moneim *et al.* 2022). Even within a species, genotypic differences can result in varying exudation rates. For example, the Al-tolerant *Phaseolus vulgaris* L. genotype 'G19842' secretes citrate at rates 2–3 times higher than the Al-sensitive 'ZPV' genotype (Rangel *et al.* 2007).

2. Genetic regulation

A suite of transport proteins, metabolic pathways, and regulatory mechanisms governs carboxylate secretion.

Genes controlling transporters and enzymes involved in carboxylate metabolism are key to this process (Figure 2). These include: (1) Proton-coupled transporters such as ALMT (aluminum-activated malate transporter) and MATE (multidrug and toxic compound extrusion) (Liu *et al*. 2009; Cardoso *et al*. 2020), which use proton gradients to transport organic anions; (2) Adenosine triphosphate (ATP)-binding cassette transporters, which use ATP to actively move carboxylates across membranes (Kretzschmar *et al*. 2011); and (3) Anion channels and transporters, such as SLAC1 (slow anion channel-associated 1), which regulate anion efflux (Vahisalu *et al*. 2008). The synthesis of carboxylates within cells, facilitated by enzymes like malate dehydrogenase and citrate synthase, also contributes to their availability for secretion.

3. Environmental stress

Environmental factors such as salinity and disease stress strongly influence root exudation (Kumar *et al*. 2023). Under salt stress, *Ligustrum sinense* roots show increased exudation of oleate, palmitate, palmitoleate, stearate, and 2-methylbutyrate (Xiong *et al*. 2020). Pathogens can also trigger exudation; for instance, foliar diseases in *Arabidopsis thaliana* induce the release of malate, citrate, and succinate (Yuan *et al*. 2018). Cucumbers affected by *Fusarium* wilt exude 2-hydroxyvalerate and threonate to recruit beneficial microbes (Wen *et al*. 2023a, 2023b). These processes underscore the adaptive role of carboxylate release in managing stress and mediating plant-microbe interactions.

B. Soil factors

Soil conditions strongly influence the nature and extent of root carboxylate exudation. Key factors include nutrient availability, soil texture, moisture, and soil pH (Szabó *et al*. 2024) (Figure 2).

1. Nutrient availability

Deficiencies in key nutrients, such as P, Fe, and zinc (Zn), drive RCE as plants attempt to mobilize these nutrients from the soil (Wei *et al*. 2010; Valentinuzzi *et al*. 2015). For instance, in P-deficient soils, plants like *Caustis blakei* exude large quantities of citrate to enhance P uptake (Playsted *et al*. 2006), which is crucial in P-deficient soils where direct P uptake is insufficient to meet plant needs. *Medicago* species exposed to lime-induced Fe deficiency increase citrate and malate release to enhance Fe solubility (M'Sehli *et al*. 2008). Soil pH also plays a role in determining nutrient solubility and mobility (Penn and Camberato 2019). Under Al toxicity in acidic soils, *Citrus sinensis* roots release more malate to chelate toxic ions (Yang *et al*. 2020b). Similarly, Zn deficiency stimulates oxalate release to mobilize Zn (Hoffland *et al*. 2006). The type and concentration of carboxylates exuded are often closely aligned with specific nutrient deficiencies, demonstrating the adaptive strategies of plants in response to nutrient limitations.

2. Soil properties

Soil texture, moisture, and pH influence carboxylate retention and mobility (Szabó *et al*. 2024). Carboxylates like citrate and oxalate are more readily sorbed to minerals in clay-rich soils, leading to reduced availability and slower turnover (Hayakawa *et al*. 2018). Increased sorption capacity in these soils can decrease rhizosheath concentrations of carboxylates, resulting in higher secretion rates from roots (Cornelis and de Tombeur 2022). Soil moisture also affects exudation: under drought conditions, rhizosheath carboxylate concentrations may increase to enhance nutrient acquisition and maintain osmotic balance (Canarini *et al*. 2016). Moreover, soil pH can influence the composition of exudates *Lupinus albus*, for example, increases citrate and decreases malate exudation under rising pH (Veneklaas *et al*. 2003).

C. Microbial factors

Microorganisms play a pivotal role in shaping the dynamics of carboxylate exudation within the rhizosheath. Organic acid-producing microbes are typically abundant in this zone, with bacteria such as *Pseudomonas* spp. secreting various organic acids into the surrounding soil. Rhizosheath microbes synthesize a wide range of aliphatic organic acids–including acetic, oxalic, tartaric, and citric acids–which contribute to nutrient mobilization and soil chemical processes (Rovira *et al*. 1974). The microbial production of carboxylates is often stimulated by environmental stress, including biotic stressors like disease (Morrison *et al*. 2017). For instance, *Pseudomonas fluorescens* produces phenazine-1-carboxylic acid in response to root disease pressure, which plays a key role in suppressing take-all disease in wheat caused by *Gaeumannomyces graminis* var. *Tritici* (Thomashow *et al*. 1990).

Fungi, particularly arbuscular mycorrhizal fungi (AMF), are also prominent producers of oxalic acid, which aids in mobilizing P bound to iron (hydr) oxides (Andrino *et al*. 2021). At the interface between the fungal hyphae and soil particles, oxalic acid

secretion can lead to the formation of calcium oxalate crystals (Graustein *et al.* 1977). Moreover, interactions between plant roots and fungi also influence carboxylate quantity and composition. Mycorrhizal associations enhance the exudation of carboxylates, such as citrate and malate (Almario *et al.* 2017), which support nutrient mobilization and uptake. Arbuscular mycorrhizal fungi can increase carboxylate exudation in response to abiotic stress. Under heavy metal stress, AMF can enhance the release of chelating carboxylates that mitigate toxicity (Garg *et al.* 2017). For example, AMF inoculation increases malate exudation in *Pteris vittata* and *Astragalus sinicus* under arsenic (As) stress, helping to alleviate metal toxicity (Yizhu *et al.* 2020). In addition to AMF, N-fixing rhizobia also contribute to carboxylate exudation. These bacteria form nodules on the roots of legumes and are associated with enhanced exudation of organic acids like succinate, malate, and fumarate, which facilitate nutrient acquisition and symbiotic efficiency (Lardi and Pessi 2018).

Carboxylates released from various soil, plant, and microbial processes play a vital role in mobilizing nutrients such as P and contaminants such as heavy metals, and carbon, thereby contributing to strategies for improving plant nutrition, soil remediation, and carbon sequestration. The implications of carboxylates exudation on nutrient, contaminant, and carbon dynamics are covered in the following section.

V. Implications of carboxylates exudation on nutrient, contaminant and carbon dynamics

Carboxylates produced by root and microbial activities are critical for stabilizing SOC, and when concentrated in the rhizosheath, they can significantly influence the bioavailability of nutrients and contaminants.

A. Nutrient mobilization

Carboxylates are pivotal in nutrient and contaminant dynamics, driving soil mineral dissolution and buffering rhizosheath pH. They facilitate mineral dissolution primarily via two mechanisms: acidification and chelation. Acidification enhances the solubility of minerals, increasing the concentration of essential macro- and micronutrients concentrations in soil pore waters. Yet acidification can also mobilize excess metals, which may be beneficial in small amounts but toxic at higher concentrations. Chelation involves the formation of two or more coordinate bonds between a polydentate carboxylate ligand and a central metal atom, similarly, leading to the solubilization of nutrients, such as P, Fe, K, and Mg, and potential contaminants. In the case of P, which is often limited in availability due to its immobility and solid-state forms (Rawat *et al.* 2021), carboxylates are especially important (Figure 3 and Table 3). While phosphatase enzymes release P from organic sources, carboxylates primarily mobilize P from inorganic sources by

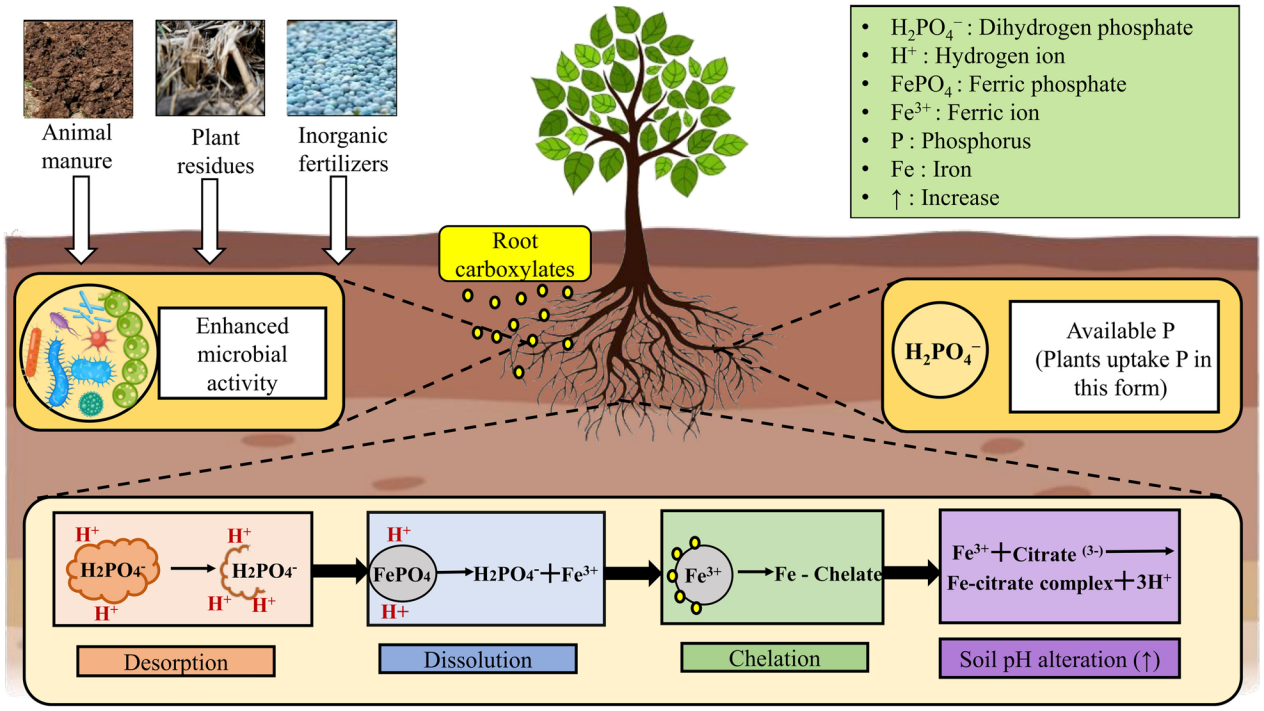

Figure 3. Schematic illustration of the effect of carboxylate exudation on phosphorus mobilization in the rhizosphere.

Table 3. Selected references on the effect of carboxylate exudation on phosphorus (P) mobilization.

Plant species	Carboxylate precursors/ exudates	Soil types	Experimental Approach	Forms of P	Effect on P mobilization	References
Veldt grass, tall wheatgrass, and tall fescue	Citrate, acetate, and malonate	Sand	Pot experiment in a glasshouse (10 weeks)	$Ca(H_2PO_4)_2{\cdot}H_2O$	Higher P supply increased citrate and malonate exudation, enhancing P acquisition, while reducing mycorrhizal colonization.	(Tshewang *et al.* 2020)
12 pasture herbs and legumes, including 4 *Lotus* species and 2 crop legumes (*Cicer arietinum*, *Lupinus albus*)	Oxalate, malate, citrate, citrate, malate, and malonate	Sand	Pot experiment in a glasshouse (6 weeks)	KH_2PO_4	Malate and citrate were found in all species, while citrate and malate, accounting for 10%–82% (total secreted carboxylates), was specific to *Lotus*. *Cicer arietinum* had the highest carboxylate exudation rate, enhancing P mobilization. Citrate and malate may support P uptake when combined with citrate and malate.	(Kidd *et al.* 2018)
Zea mays	Citrate and malate	Sand	Pot experiment in a greenhouse (45 days)	KH_2PO_4	Rhizobium Inoculation treatments showed increased exudation rates of citrate and malate, whereas phosphorus supply had no effect.	(D'Angioli *et al.* 2017)
Maize and alfalfa	Organic anions (Formic, malic, tartaric, lactic, citric, succinic, acetate, and citrate)	Chernozem	Field experiment (3 years)	Organic P	Intercropping maize and alfalfa reduced rhizosphere pH by 0.35 and 0.24 units, respectively, increased total organic anions (28%–30%), and enhanced acid phosphatase activity (21%–41%), leading to higher phosphorus availability. While lateral root volume primarily drove phosphorus uptake in alfalfa (86.6%), rhizosphere P mobilization played a minimal role (0.2%).	(Sun *et al.* 2020)
Lupinus albus L.	Citrate and malate	Acidic soil	Split-root culture (10 weeks)	Mineral-bound P source (Fe–P/ Al–P)	Phosphorus solubility increased at pH 5.5, indirectly influencing citrate accumulation and shoot P uptake. Cluster-root growth was not directly affected by pH but responded (increased) to higher P availability.	(Shane *et al.* 2008)
Chickpea (*Cicer arietinum)*, white lupin (*Lupinus albus* L.), and wheat (*Triticum aestivum* L.)	Citrate, malate, and malonate	Loamy to clayey	Pot experiment in a greenhouse (69 days)	NA*	Carboxylates significantly enhanced P availability, with malate (111%), malonate (134%), and citrate (216%) increasing P extraction compared to water. P uptake correlated with rhizosphere carboxylate concentration, particularly in soils with lower P sorption capacity.	(Veneklaas *et al.* 2003)
Ptilotus macrocephalus, P. polystachyus, and *P. nobilis*	Citrate, lactate, acetate, oxalate, and malate	Sandy loam Karrakatta soil (KS), washed river sand (WRS), and Jarrah forest soil (JFS)	Pot experiment in a glasshouse (6–7 weeks)	KH_2PO_4	Phosphorus release was highest in KS soil (~0.95 mg P kg^{-1}) and lowest in JFS and WRS (~0.13 mg P kg^{-1}). In KS, citrate, oxalate, and their combination enhanced P release, while malate had minimal impact.	(Suriyagoda *et al.* 2016)
Chickpea (*Cicer arietinum* L.)	Malonate, citrate, acetate, and malate	Sand	Pot experiment in Plastic pots (7 weeks)	$FePO_4$	Shoot P content exhibited a strong positive correlation with acetate ($r = 0.52$, $p < 0.001$), malate ($r = 0.35$, $p < 0.001$), and malonate ($r = 0.64$, $p < 0.001$) per plant, while citrate exhibited no significant correlation ($r = 0.14$, $p > 0.05$).	(Pang *et al.* 2018)

*NA: Not available.

dissolving P-enriched minerals like iron and aluminum (hydr)oxides. Carboxylates released by roots and microbes can enhance the bioavailability of P, Fe, and K in nutrient-deficient soils (Bin *et al.* 2008; Nwoke *et al.* 2008; Fischer *et al.* 2010). Their release is often accompanied by proton exudation, which drives anion efflux and contributes to rhizosheath acidification, enhancing inorganic phosphate solubilization (Chai and Schachtman 2022). Carboxylates are also involved in mobilizing other key nutrients like Zn and K, particularly through microbial interactions (Sindhu *et al.* 2022).

Phosphate-solubilizing bacteria (PSB), such as *Pseudomonas*, *Bacillus*, *Serratia*, *Enterobacter,* and *Rhizobium*, produce various carboxylates (e.g., fumarate, malate, citrate, oxalate), which can lower rhizosheath pH and solubilize insoluble phosphate forms like tricalcium phosphate and iron phosphate (Buddhi Charana *et al.* 2022). The type and quantity of carboxylates secreted vary depending on the specific PSB strain and the form of phosphate present (Jiang *et al.* 2020). Generally, mono-carboxylates such as formate, acetate and lactate are less effective at binding phosphate than di- and tri-carboxylates (Efthymiou *et al.* 2018). The presence of Fe-bound phosphate (Fe-P) enhances citrate synthase activity in *Aspergillus niger*, resulting in increased citrate production (Tian *et al.* 2021). This fungus is known to deploy diverse strategies for carboxylate secretion, primarily producing two major carboxylates: oxalate and citrate (Table 3). The potential for robust carboxylate release by phosphate-solubilizing fungi is highlighted, with *Penicillium oxalicum* and *A. niger* reported to secrete oxalate and formate, although *A. niger* produces more carboxylates than *P. oxalicum* and has greater potential adaptability to acidic conditions (Li *et al.* 2016).

B. Contaminant (im)mobilization

Carboxylates also affect the dynamics of contaminants in soils via chelation and complexation. Depending on the specific context, these processes can mobilize or immobilize toxic metals (Figure 4 and Table 4). Complexation may enhance the bioavailability and solubility of contaminants like Cd, potentially adversely affecting plant growth. Yet some plants –known as hyperaccumulators – can absorb and sequester large amounts of toxic metals by exuding carboxylates that facilitate metal uptake. The effectiveness of these processes is closely linked to the number of carboxylic acid groups in the organic molecule, with tri-carboxylic acids generally more effective than di- and mono-carboxylic acids (Gang *et al.* 2012).

Carboxylates are potent chelating agents that bind metal ions or displace anions such as phosphate, facilitating its release into the soil, where P is associated with Fe and Al (hydr)oxides, increasing phosphate availability (Amarasinghe *et al.* 2022). Carboxylates

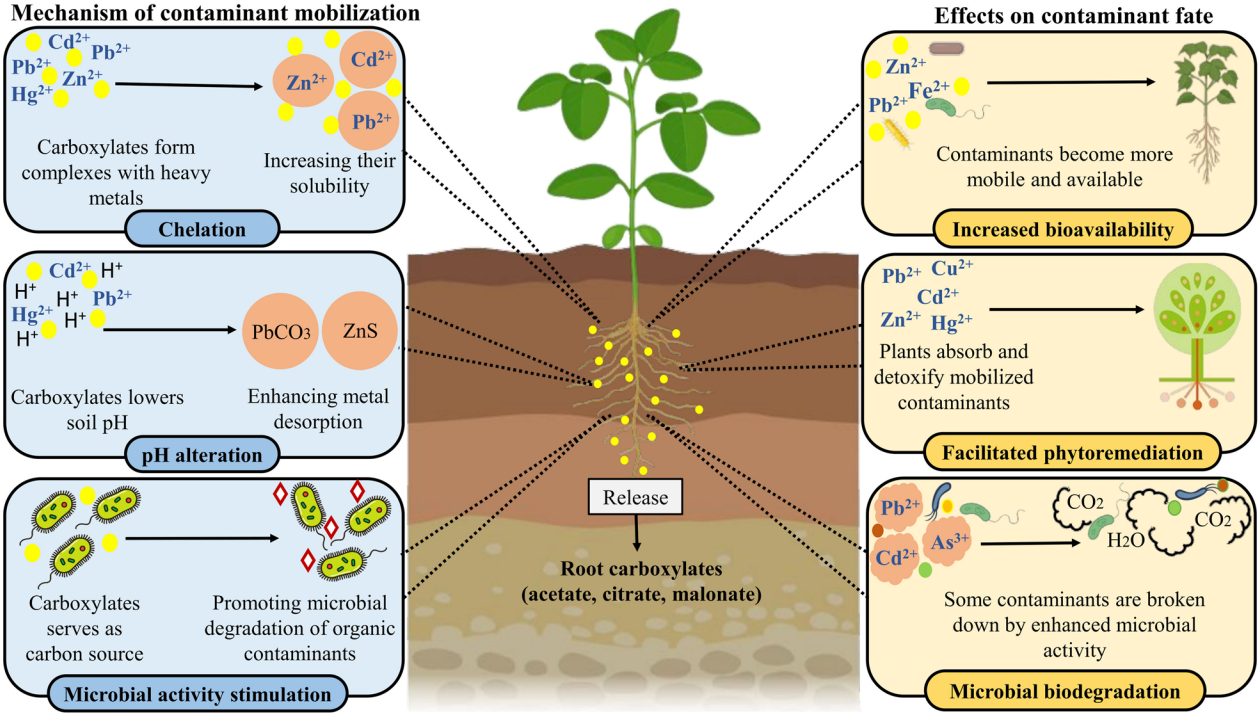

Figure 4. Schematic representation of the effect of carboxylate exudation on contaminants mobilization.

Table 4. Selected references on the effect of carboxylates exudation on contaminants mobilization.

Plant species	Carboxylate/Carboxylic acid precursors (exudates)	Soil types	Contaminants	Analytical methods used (**)	Effects on contaminant mobilization	References
Holcus lanatus and *Cytisus striatus*	Ferulic, pyruvic, fumaric, oxalic, salicylic, citric, malonic, succinic, p-coumaric, and pyruvic acid	Montmorillonite, alumi-umbric Cambisol (A horizon), with humic acid presence	BTEX (toluene, o-xylene, benzene, ethylbenzene, m-xylene, p-xylene), fuel oxygenates (ETBE and MTBE)	HS-GC-MS	In the presence of humic acid, exudates enhanced contaminant mobility, while mixtures in the A horizon and montmorillonite reduced it. Carboxylic acids increased, and phenolic acids decreased mobility. Humic acid showed the highest retention (15%–85%).	(Balseiro-Romero *et al.* 2014)
Holcus lanatus	Natural and artificial (Succinic, citric, methyl-malonic, fumaric, pyruvic, L(+) tartaric, and oxalic acid)	Sandy loam + 5% clay	γ-, α-, δ-, and β-isomers of hexachlorocyclohexane (HCH)	GC/ECD	Natural and artificial exudates both enhanced mobilization of HCH, with α-, β-, and γ-HCH desorption increasing by 23.0%, 26.8%, and 15.5% with natural exudates and 40.1%, 25.9%, and 25.6% with artificial exudates mixture. δ-HCH desorption was <10%.	(Rodríguez-Garrido *et al.* 2020)
NA*	Citrate and malonate	Sandy loam	Petroleum hydrocarbons (PHCs)	GC-MS	BPA addition had no significant effect on carboxylate exudation. Carboxylate addition had minimal impact on hydrocarbon degradation, with only a slight change in the biodegradation biomarker.	(Martin *et al.* 2016)
NA	Acetic, oxalic, and citric acid	Cambisol	As and Pb	ICP-OES	Pb leaching increased due to stable complexes formed with citric acid, unlike other acids. In both surface and subsurface soils, the carboxylate type had a substantial impact on the amount of As and Pb mobilization.	(Ash *et al.* 2016)
Triticum aestivum	Citrate, malonate, fumarate, and malate	Haplic luvisol	Bisphenol A (BPA)	HPLC	Presence of BPA did not have a significant impact on carboxylate exudation.	(Yacoumas *et al.* 2020)
Sunflower (*Helianthus annuus* L.) and Indian mustard (*Brassica juncea*)	Citrate, malonate, fumarate, lactate, oxalate, and tartarate	Acidic and alkaline soils	Cd, Zn, Cu, and Pb	HPLC and ICP-MS	Lactate increased 3–10 fold compared to the control. Elevated rhizosphere DOC at pH > 8 enhanced Cu and Pb solubility via metal DOC complex formation. Soluble Cu rose to 493–524 μg L^{-1} and Pb to 149–148 μg L^{-1} in contaminated alkaline soil.	(Kim *et al.* 2010)
Tomato (*Solanum lycopersicum L.*) and nightshade (*Solanum nigrum L.*)	Tartaric, malic, acetic, oxalic, and citric acid.	Meadow burozem	Cd	FAAS and HPLC	Higher root exudation of carboxylates in *S. nigrum* enhanced Cd availability in soil, leading to increased uptake and translocation compared to *S. lycopersicum*.	(Bao *et al.* 2011)
5 Acacia species: *Acacia ligulate* A. Cunn. ex Benth, *Acacia hilliana* Maiden, *Acacia acradenia* F.Muell, *Acacia chisholmii* F.M.Bailey, and *Acacia holosericea* A. Cunn. ex G. Don.	Citric and fumaric acid	Sand	Cu, Pb and Zn	ICP-OES and HPLC	Elevated root exudates in rhizosphere tailings increased Zn bioavailability, leading to its higher accumulation in *Acacia* shoots (*A. acradenia*: 140 mg kg^{-1}, *A. hilliana*: 230 mg kg^{-1}). Citric acid played a key role in enhancing metal uptake ($p < 0.05$)	(Kabas *et al.* 2017)
Zea mays L. cv. 31P41 (Cd-sensitive) and cv. 3062 (Cd-tolerant)	Glutamic, succinic, acetic, oxalic, citric, formic, and malic acid	NA	Cd	HPLC	Maize root exudates in cv. 3062 experienced acidosis under Cd stress, leading to a substantial rise in organic acid concentrations that affected Cd mobility. The increased exudation of dicarboxylic group likely promoted Cd mobilization while supporting nutrient uptake and antioxidant responses.	(Javed *et al.* 2017)
Festuca arundinacea L.	Stearic, benzoic, palmitic, and ρ-hydroxybenzoic acid.	NA	Total petroleum hydrocarbon (TPH)	FT-IR, GC-MS	Soil amendment with ρ-hydroxybenzoic acid (7.8%), benzoic acid (14.9%), and palmitic acid (19.2%) significantly increased petroleum removal compared to the control.	(Liu *et al.* 2015)

*NA: Not available.

**HS-GC-MS: Headspace Gas Chromatography-Mass Spectrometry; GC/ECD: Gas Chromatography with Electron Capture Detector; GC-MS: Gas Chromatography-Mass Spectrometry; ICP-OES: Inductively Coupled Plasma Optical Emission Spectroscopy.

HPLC: High-Performance Liquid Chromatography; ICP-MS: Inductively Coupled Plasma Mass Spectrometry; FAAS: Flame Atomic Absorption Spectroscopy; FT-IR: Fourier Transform Infrared Spectroscopy.

may also indirectly influence P mobility and fate through rhizosheath engineering, impacting soil structure and stability. By promoting aggregation or disaggregation, carboxylates affect root penetration and the subsequent uptake of water, nutrients, and contaminants. Compounds containing carboxyl groups have high affinity for metal (hydr)oxides (Curti *et al.* 2021), enhancing soil aggregate stability and growth through electrostatic interactions (Otero-Fariña *et al.* 2023).

C. Carbon dynamics

Carboxylates exert positive and negative effects on SOC stabilization and accumulation, making their impact context-specific–a 'double-edged sword' (Dijkstra et al., 2021) (Figures 5 and 6; Table 5). On the one hand, they can promote SOC decomposition through the microbial priming effect, wherein fresh carbon inputs stimulate microbial activity and accelerate the breakdown of more stable organic matter, potentially leading to net carbon loss in acidic soils or increased carbon sequestration in alkaline soils through carbonate formation. According to the soil microbial carbon pump model (Liang *et al.* 2017), microbes convert labile organic carbon into stable forms that can be protected within soil aggregates. Carboxylates contribute to this process by sorbing strongly to Fe (hydr)oxides like ferrihydrite and goethite via carboxyl ligand exchange (Yang *et al.* 2017; Curti *et al.* 2021), especially at higher concentrations, which reduces their desorption back into the microbially accessible soil pore water pool (Curti *et al.* 2021).

Furthermore, carboxylic and amino-rich compounds can undergo polymerization, forming complex aromatic structures that are more resistant to microbial attack. These reactions – often catalyzed by Fe and Mn (hydr)oxides – help transform labile carbon into more persistent mineral-associated organic matter (Longman *et al.* 2022), which plays a vital role in long-term SOC storage and health. The net impact of rhizosheath carboxylate exudation on SOC thus depends on the balance between microbial mineralization and mineral association, both of which are strongly mediated by rhizosheath conditions and soil mineralogy (Liang *et al.* 2023).

VI. Opportunities and challenges

Recognizing the combined and individual contributions of plants and microbes to the rhizosheath carboxylate pool highlights several opportunities for future research. One key direction involves identifying specific root traits that enhance carboxylate exudation, which could enable the development of crop varieties better suited to nutrient-deficient soils. Additionally, research on the role of cover crops in fostering

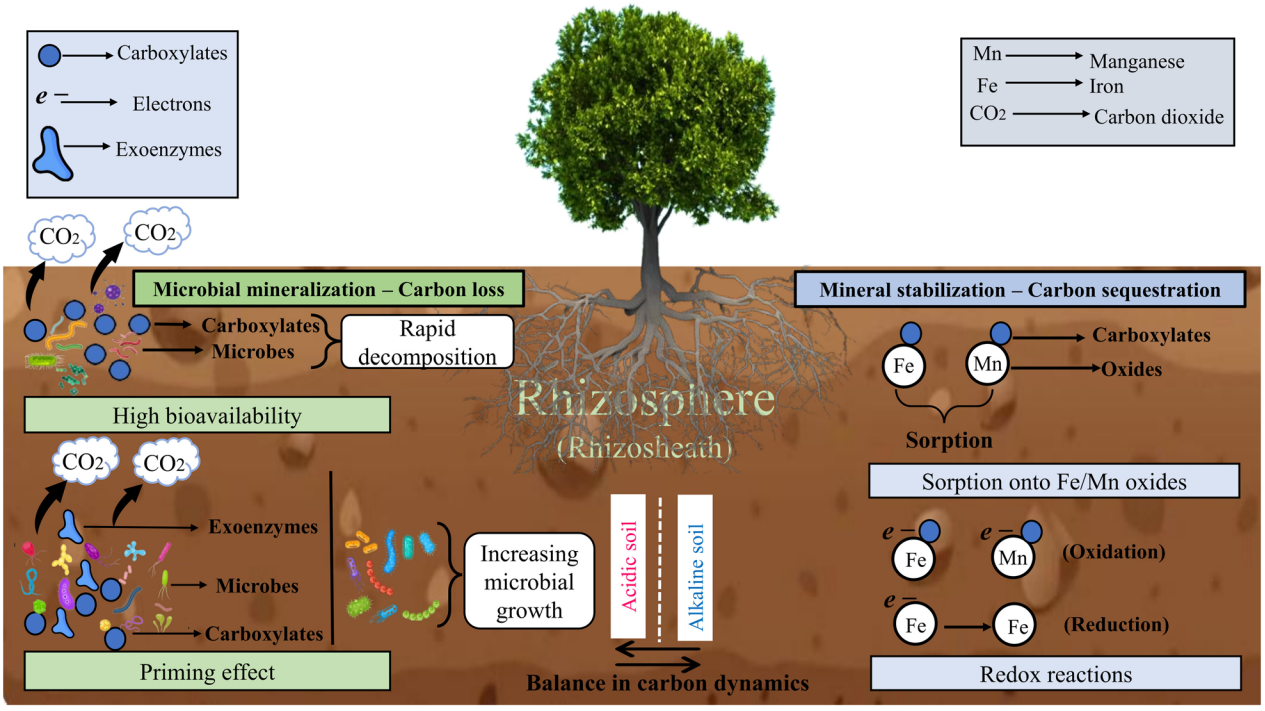

Figure 5. Graphical illustration of the effect of carboxylate exudation on soil carbon dynamics.

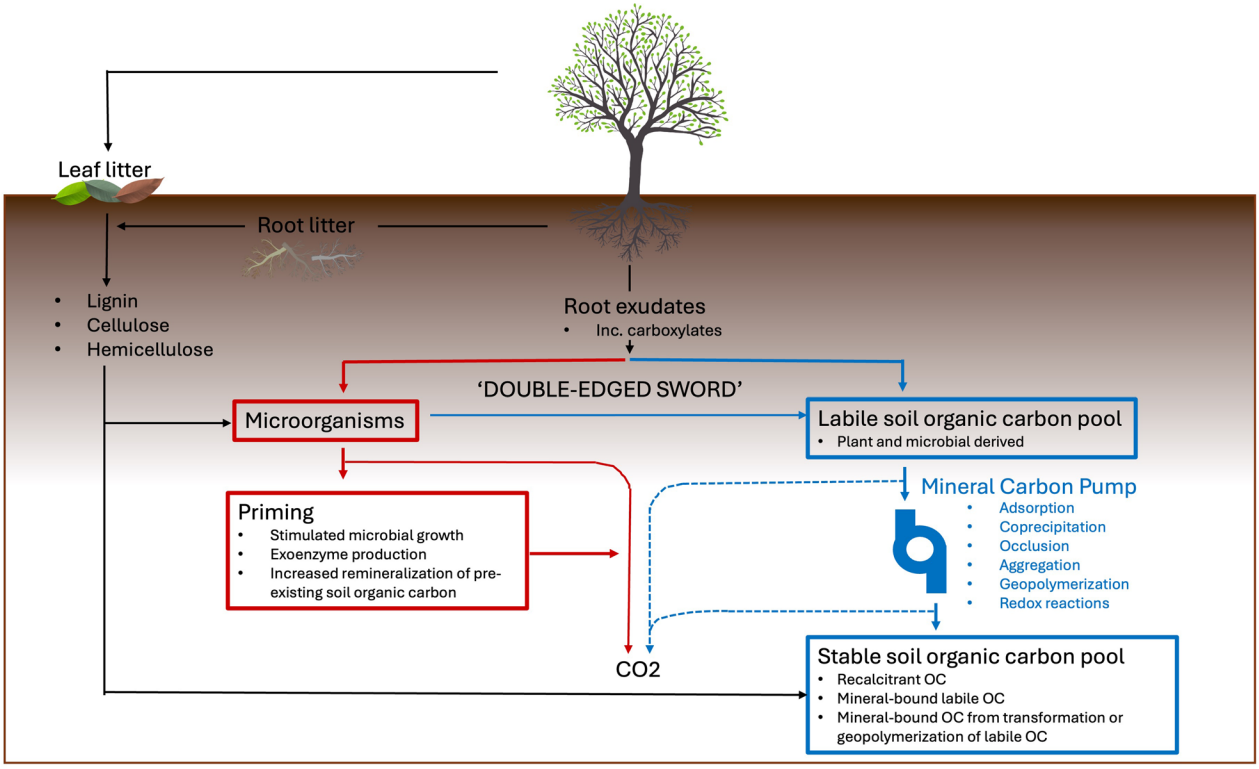

Figure 6. The 'double-edged sword' of rhizosheath carboxylates, where carboxylates either diminish or enhance soil organic carbon(SOC) stabilization and storage. Microbial mineralization and priming effects reduce SOC stabilization and storage (red boxes and arrows), whereas the association of carboxylates with soil minerals via the mineral carbon pump enhances SOC stabilization and long-term storage (blue boxes and arrows) (modified from Xiao et al., 2023).

microbial diversity and boosting carboxylate production may provide strategies to improve soil health and agricultural crop productivity (Chen and Liu 2019). Given our current understanding, the following areas deserve focused investigation:

A. Synthesis and release of carboxylates

Empirical studies are needed to clarify the physiological mechanisms governing rhizodeposition and improve the accuracy of carboxylate release measurements. Sensitivity analyses have concentrated on root exudates, yet other carbon sources – such as mucilage, sloughed-off root cells, and physically protected soil carbon – contribute significantly to microbial activity. Future work should aim to quantify the relative contributions of these carbon sources to improve our understanding of rhizodeposition dynamics.

B. Factors influencing carboxylate exudation

Plants release numerous compounds into the rhizosheath through active and passive mechanisms. These root exudates vary in composition depending on various physical, chemical, and biological factors. Future research should explore the conditions that drive root exudation under stress to expand our understanding of plant-soil interactions in challenging environments.

C. Carboxylates and nutrient mobilization

Further investigation is needed into the factors facilitating nutrient acquisition and species coexistence in biodiverse systems. Special emphasis should be placed on competitive and synergistic interactions mediated by soil microbiota, particularly where plants with high carboxylate-releasing potential (e.g., legumes like chickpea and faba bean) are involved. These species can enhance nutrient remobilization by rapidly depleting and transforming nutrients in the rhizosheath (Lardi and Pessi 2018).

D. Carboxylates and carbon sequestration

As labile sources of SOC, root exudates are central to sustaining microbial activity. Root exudates may contribute to SOC formation and stabilization in ecosystems such as forests and grasslands, supporting long-term carbon sequestration (Bononi *et al.* 2020). Conservation of natural ecosystems and the strategic

Table 5. Selected references on the effect of carboxylates exudation on microbial activity, carbon transformation and priming effect.

Plant species/sample collection	Carboxylate/Carboxylic acid precursors (exudates)	Impacts on microbial activity	Effects on carbon dynamics	Priming effects	References
Alfalfa *(Medicago sativa)*	Tartrate	Tartrate stimulates phosphate-solubilizing bacteria in the rhizosphere under phosphorus deficiency.	Higher tartrate exudation shifts carbon from biomass to root exudates, impacting carbon cycling	More carboxylates are released at a lower phosphorus and higher nitrogen supply.	(He *et al.* 2020)
Triticum spp	Oxalic acid, glucose, and acetic acid	Oxalate addition (0–4 mm from the root) increased *Bacteroides* and *Proteobacteria* abundance while reducing *Verrucomicrobia, Acidobacteria*, and *Firmicutes* ($p < 0.05$).	Oxalate mineralization resulted in higher microbial carbon-use efficiency (CUE) and biochemical oxygen demand (BOD) than glucose, accelerating native soil carbon decomposition more effectively.	Oxalate accelerated microbial carbon mineralization, leading to ~4% native carbon loss.	(Keiluweit *et al.* 2015)
Macaranga (*Macaranga gigantea*), Dipterocarp (*Shorea laevis* and *Dipterocarpus cornutus*)	Acetate, oxalate, malate, and citrate	Malate mineralization by microbes was more active in the rhizosphere of *Dipterocarp* and *Macaranga* trees.	Root exudation carbon flux was highest in *Dipterocarpus cornutus* (11.3 ± 1.6 mol C m^{-2} $month^{-1}$), followed by *Shorea laevis* (4.8 ± 1.2) and *Macaranga gigantea* (2.1 ± 0.5 mol C m^{-2} $month^{-1}$).	Rhizosphere microbial activity and root exudation may enhance malate turnover, influencing carbon fluxes at both soil profile and ecosystem levels.	(Fujii *et al.* 2021)
Soil samples from grassland, coniferous, and hardwood forests	Glucose, glycine, and citric acid	All three substrates significantly influenced microbial community structure, primarily increasing *β-Proteobacteria*, *Actinobacteria, and γ-Proteobacteria*. Citric acid had the strongest impact, elevating *β-Proteobacteria* abundance by 2–5 times.	Respiration increased significantly with all three substrates ($p < 0.01$). The highest CO_2 release was observed with glucose in coniferous soil (555%) and citrate in grassland (391%) and hardwood forest (82%). No substrate showed a uniform effect across all soil types.	All three C substrates induced a positive priming effect, significantly increasing CO_2 production in all soils.	(Eilers *et al.* 2010)
Soil samples from an agriculture field	Amino acids, carboxylic acids, and sugars	Carboxylic acids promoted Actinobacteria growth and enhanced carbon mobilization, while amino acids favored *Proteobacteria*, limiting DOC release.	Short-chain carboxylic acids increased dissolved organic carbon (DOC) and available Fe, whereas amino acids reduced both. Sugars had a moderate effect on DOC and Fe levels.	Short-chain carboxylic acids had a negative priming effect on DOC and Fe release, while amino acids exhibited a positive effect. Sugars showed minimal priming impact.	(Wen *et al.* 2022)
Soil samples from forest, grassland, cropland, Tundra, and wetland.	Amino acids, simple sugars, and low-molecular-weight organic acids	Root exudates enhanced microbial biomass carbon by 26.7% ($p < 0.001$) and elevated fungal and bacterial biomass ($p < 0.05$). Simple sugars exerted a more pronounced influence, increasing microbial biomass carbon 2.3-fold more than organic acids while raising fungal and bacterial by 37.8% and 30.2% respectively.	Application of root exudate increased soil carbon decomposition by an average of 39% across all studies.	Amino acids exhibited the highest positive priming effect (116.1%), surpassing simple sugars (50.5%) and organic acids (18.3%).	(Yan *et al.* 2023)
Soil samples from subalpine woodland	Glucose, glycine, and oxalic acid	Adding glucose and oxalate significantly enhanced microbial biomass and enzyme activities. However, glucose had a stronger impact than oxalate on microbial biomass C (MBC) and microbial biomass N (MBN). Conversely, glycine did not exhibit a significant effect on MBN or MBC but significantly reduced peroxidase (PER) and polyphenol oxidase (PPO) activity.	Compared to the control, glucose and glycine treatments increased total soil carbon by 1.28% and 2.52%, respectively, while oxalate reduced it by 1.12%.	Oxalate stimulated soil C loss by enhancing SOC mineralization, while glycine promoted C accumulation by suppressing microbial degradation.	(Wang *et al.* 2021)
Soil samples from 6 *Panicum virgatum* (switchgrass cultivars)	L-serine, D-fructose, oxalate, L-arginine, succinate, acetate, D-xylose, L-glycine, D-glucose, fumarate, glutamate, and L-proline	Microbial activity in shallow soils increased with synthetic root exudates, accelerating stable SOC decomposition, but this effect was negligible or suppressive at deeper levels	Carbon dynamics were impacted by differences in soil carbon availability and root structure between switchgrass varieties. In shallow soils, increased depth-related fluctuations exacerbated priming, whereas small changes in soil carbon had no effect on exudate-induced priming.	The ratio of root exudate carbon to total soil carbon affects priming magnitude, with greater effects in shallow soils with high labile carbon content. Measuring microbial respiration from ^{13}C-labeled exudates revealed SOC decomposition patterns.	(Graaff *et al.* 2014)

development of artificial grasslands that stimulate root exudation should be prioritized as part of broader climate change mitigation efforts.

E. Carboxylates and contaminant mobilization

A deeper understanding of how carboxylates influence contaminant behavior in soil-plant systems is urgently needed. Such insights would clarify the role of root exudates in mediating contaminant uptake, transformation, and transport. Future research should consider both the synergistic and antagonistic effects of contaminants on plant growth and soil ecology to develop more effective remediation and management strategies.

One of the major challenges in undertaking research on root carboxylate exudation is the dynamic and transient nature of the release of these exudates. Their release, concentration, and persistence in the rhizosheath fluctuate over time, which is influenced by various factors, including soil type, species and age of plants, nutrient availability and microbial activity in the soil, and environmental conditions. While the dynamic and transient nature of these root exudates allows plants to respond to changing environmental conditions and nutrient demands by adjusting their exudation patterns, it poses significant challenges to the measurement and quantification of root exudates. This challenge can be overcome by developing techniques for the *in situ* measurement of root carboxylate exudation.

VII. Conclusions

Root exudates contain a range of primary and secondary plant-derived metabolites, including carbohydrates, amino acids, carboxylates, phenols, glucosinolates, vitamins, plant hormones, plant enzymes, and polysaccharides. In response to biotic and abiotic stressors, soil microorganisms, such as bacteria and fungi, also produce and release carboxylates as part of their adaptative strategies. Both plants and microbes contribute to carboxylate release through the secretion of extracellular enzymes that facilitate the biological decomposition of organic materials. The nature and concentration of root exudate-derived carboxylates is controlled by plant, soil, microbial and environmental factors. Carboxylates released from various soil, plant, and microbial processes play a key role in mobilizing nutrients (e.g., P), contaminants (e.g., heavy metals), and carbon, thereby promoting plant nutrition, soil remediation, and carbon sequestration. Yet the dynamic and transient nature of these root exudates poses significant challenges to their measurement and quantification, indicating are search requirement to develop techniques for the in-situ measurement of root carboxylate exudation.

Acknowledgments

We would like to thank Professor Hans Lambers, The University of Western Australia for this constructive and thorough feedback for this review.

Authors contributors

This review is written by a number of authors, which are leading in their field. Many of them have published in leading journals including *International Materials Reviews*, *Critical Reviews in Plant Science, Critical Reviews in Environmental Science and Technology*, *Chemical Engineering Journal, Journal of Hazardous Materials*, *Water Research*, *Environment International*, *Bioresource Technology, Environmental Pollution, Journal of Cleaner Production* etc.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

The authors declare no funding was received.

Authors' list of publications related to carboxylates and low molecular organic acids

Adeleke K, et al. Origins, roles and fate of organic acid in soils: a review, 2017. South African Journal of Botany, 108, 393–406. https://doi.org/10.1016/j.sajb.2016.09.002

Banwart SA, Nikolaidis NP, Zhu YG, Peacock CL, Sparks DL. (2019) Soil functions: connecting earth's critical zone. *Annu Rev Earth Planet Sci.* 47, 333–359. DOI: 10.1146/annurev-earth-063016-020544.

Bolan, N. S., Naidu, R., Mahimairaja, S., & Baskaran, S. (1994). Influence of low-molecular-weight organic acids on the solubilization of phosphates. *Biology and Fertility of Soils*, *18*(4), 311-319. doi: 10.1007/BF00570634.

Elias, D.M.O., Mason, K.E., Goodall, T., Taylor, A., Zhao, P., Otero-Fariña, A., Chen, H., Peacock, C.L., Ostle, N.J., Griffiths, R., Chapman, P.J., Holden, J., Banwart,S.A., McNamara, N.P., Whitaker, J. (2024) Microbial and mineral interactions decouple litter quality from soil organic matter formation. *Nat. Commun*., 15, 10063. https://doi.org/10.1038/s41467-024-54446-0

Pang J, Bansal R, Zhao H, Bohuon E, Lambers H, Ryan MH, Ranathunge K, Siddique KHM. 2018. The carboxylate-releasing phosphorus-mobilizing strategy can be proxied by foliar manganese concentration in a large set of chickpea germplasm under low phosphorus supply. New Phytol. 219(2):518-529. doi: 10.1111/nph.15200.

Tshewang, S.; Rengel, Z.; Siddique, K.H.M.; Solaiman, Z.M. 2020. Growth, Rhizosphere Carboxylate Exudation, and Arbuscular Mycorrhizal Colonization in Temperate Perennial Pasture Grasses Varied with Phosphorus Application. Agronomy 2020, 10, 2017. https://doi.org/10.3390/agronomy10122017

Curti, L., Moore, O.W., Babakhani, P., Xiao, K-Q., Woulds, C., Bray, A.W., Fisher, B.J., Kazemian, M., Kaulich, B., Peacock, C.L. (2021) Carboxyl-richness controls organic carbon preservation during coprecipitation with iron (oxyhydr)oxides in the natural environment. *Commun. Earth Environ*, 2, 229. DOI: 10.1038/s43247-021-00301-9.

Johnson, K., Purvis, G., Lopez-Capel, E., Peacock, C.L., Gray, N., Wagner, T., Marz, C., Bowen, L., Ojeda, J., Finlay, N., Robertson, S., Worrall, F., Greenwell, C. (2015) Toward a mechanistic understanding of carbon stabilization in manganese oxides. Nat. Commun. 6, 7628. https://doi.org/10.1038/ncomms8628

Moore, O.W., Curti, L., Woulds, C., Bradley, J.A., Babakhani, P., Mills, B.J.W., Homoky, W.B., Xiao, K-Q., Bray, A.W., Fisher, B.J., Kazemian, M., Kaulich, B., Dale, A.W., Peacock, C.L. (2023) Long-term carbon preservation enhanced by iron and manganese. *Nature* 621, 312-317. DOI: 10.1038/s41586-023-06325-9.

Otero-Fariña, A., Janot, N., Marsac, R., Catrouillet, C., Groenenberg, J. E., Rare earth elements binding humic acids: NICA–Donnan modeling. *Environmental Chemistry* 21, (2024) EN23049.https://doi.org/10.1071/EN23049

Otero Fariña, A., Peacock, C.L., Fiol, S., Antelo, J., Carvin,B., A universal adsorption behavior for Cu uptake by iron (hydr) oxide organo-mineral composites,Chemical Geology479 (2018). https://doi.org/10.1016/j.chemgeo.2017.12.022.

Otero-Fariña, A., Fiol, S., Arce, F., Antelo, J., Effects of natural organic matter on the binding of arsenate and copper onto goethite,Chemical Geology 459 (2017). https://doi.org/10.1016/j.chemgeo.2017.04.012.

Wen, T., Ding, Z., Thomashow, L.S., Hale, L., Yang, S., Xie, P., Liu, X., Wang, H., Shen, Q., and Yuan, J. 2023b. Deciphering the mechanism of fungal pathogen-induced disease-suppressive soil. *New Phytol.*238: 2634–2650.

Wen, T., Xie, P., Liu, H., Liu, T., Zhao, M., Yang, S., Niu, G., Hale, L., Singh, B.K., Kowalchuk, G.A., et al. 2023a. Tapping the rhizosphere metabolites for the prebiotic control of soil-borne bacterial wilt disease. *Nat. Commun.*14: 4497.

Wen, T., Xie, P., Penton, C.R., Hale, L., Thomashow, L.S., Yang, S., Ding, Z., Su, Y., Yuan, J., and Shen, Q. 2022. Specific metabolites drive the deterministic assembly of diseased rhizosphere microbiome through weakening microbial degradation of autotoxin. *Microbiome*10: 177.

Yuan, J., Zhao, J., Wen, T., et al. 2018. Root exudates drive the soil-borne legacy of aboveground pathogen infection. Microbiome, 6, 1-12.

Wen, T., Zhao, M., Yuan, et al. 2021. Root exudates mediate plant defense against foliar pathogens by recruiting beneficial microbes. Soil Ecology Letters, 3, 42-51.

Wen, T., Yuan, J., He, X., et al. 2020. Enrichment of beneficial cucumber rhizosphere microbes mediated by organic acid secretion. Horticulture research, 7.

Xiao, K-Q., Zhao, Y., Liang, C., Zhao, M., Moore, O.W., Otero-Fariña, A., Zhu, Y-G., Johnso, K., Peacock, C.L. (2023) Introducing the soil mineral carbon pump. *Nat. Rev. Earth Environ.* 4, 135-136. DOI: 10.1038/s43017-023-00396-y.

Zhao Y., Moore O.W., Xiao K-Q., Curti L., Otero-Fariña A., Banwart, S.A., Peacock, C.L. (2022) The role and fate of organic carbon during aging of ferrihydrite. *Geochim. Cosmochim. Acta* 335, 339-355. DOI: 10.1016/j.gca.2022.07.003.

Zhao Y., Otero-Fariña, A., Xiao, K.Q., Moore, O.W., Banwart, S.A., Ma, F.J., Gu, Q.B., Peacock, C.L. (2023) The mobility and fate of Cr during aging of ferrihydrite and ferrihydrite organominerals. *Geochim. Cosmochim. Acta* 347, 58-71. https://doi.org/10.1016/j.gca.2023.02.021

Zhao, Y., Moore, O.W., Xiao, K.Q., Otero-Fariña, A., Banwart, S.A., Wu, F.C., Peacock, C.L. (2023) Behavior and Fate of Chromium and Carbon during Fe(II)-Induced Transformation of Ferrihydrite Organominerals. *Environmental Science & Technology 57* (45), 17501-17510. DOI: 10.1021/acs.est.3c05487.

ORCID

Nanthi Bolan http://orcid.org/0000-0003-2056-1692
Santanu Mukherjee http://orcid.org/0000-0002-3698-0448
Shailja Sharma http://orcid.org/0009-0002-2342-7659
Caroline Peacock http://orcid.org/0000-0003-3754-9294
Alba Otero-Fariña http://orcid.org/0000-0002-0053-9482
Rasheed Adeleke http://orcid.org/0000-0002-8974-422X
Linda Obi http://orcid.org/0000-0003-2600-2525
Jiayin Pang http://orcid.org/0000-0002-8127-645X
Kadambot H. M. Siddique http://orcid.org/0000-0001-6097-4235

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

References

Abd El-Moneim D, Contreras R, Silva-Navas J, Gallego FJ, Figueiras AM, Benito C. 2022. Repression of mitochondrial citrate synthase genes by aluminum stress in roots of *Secale cereale* and *Brachypodium distachyon*. Front Plant Sci. 13:832981. doi: 10.3389/FPLS.2022.832981/BIBTEX. [InsertedFromOnline

Achor S, Aravis C, Heaney N, Odion E, Lin C. 2020. Response of organic acid-mobilized heavy metals in soils to biochar application. Geoderma. 378:114628. doi: 10.1016/j.geoderma.2020.114628.

Adeleke R, Nwangburuka C, Oboirien B. 2017. Origins, roles and fate of organic acids in soils: A review. South Afr J. Bot. 108:393–406. doi: 10.1016/j.sajb.2016.09.002.

Adeniji A, Huang J, Li S, Lu X, Guo R. 2025. Hot viewpoint on how soil texture, soil nutrient availability, and root exudates interact to shape microbial dynamics and plant health. Plant Soil. 511(1-2):69–90. doi: 10.1007/s11104-024-07020-y.

Afridi MS, Kumar A, Javed MA, Dubey A, Medeiros F d, Santoyo G. 2024. Harnessing root exudates for plant mi-

crobiome engineering and stress resistance in plants. Microbiol Res. 279:127564. doi: 10.1016/j.micres.2023.127564.
Agarwal P, Vibhandik R, Agrahari R, Daverey A, Rani R. 2024. Role of root exudates on the soil microbial diversity and biogeochemistry of heavy metals. Appl Biochem Biotechnol. 196(5):2673–2693. doi: 10.1007/s12010-023-04465-2.
Almario J, Jeena G, Wunder J, Langen G, Zuccaro A, Coupland G, Bucher M. 2017. Root-associated fungal microbiota of nonmycorrhizal *Arabis alpina* and its contribution to plant phosphorus nutrition. Proc Natl Acad Sci U S A. 114(44):E9403–E9412. doi: 10.1073/pnas.1710455114.
Amarasinghe T, Madhusha C, Munaweera I, Kottegoda N. 2022. Review on mechanisms of phosphate solubilization in rock phosphate fertilizer. Commun Soil Sci Plant Anal. 53(8):944–960. doi: 10.1080/00103624.2022.2034849.
Amjad E, Sokouti B, Asnaashari S, Dastmalchi S. 2024. A systematic review on the role of SnRK2 gene in *Arabidopsis thaliana* growth stages under abiotic stresses. OBM Genet. 08(04):1–26. doi: 10.21926/obm.genet.2404275.
Andrino A, Guggenberger G, Kernchen S, Mikutta R, Sauheitl L, Boy J. 2021. Production of organic acids by arbuscular mycorrhizal fungi and their contribution in the mobilization of phosphorus bound to iron oxides. Front Plant Sci. 12:661842. doi: 10.3389/fpls.2021.661842.
Arslan D, Steinbusch KJJ, Diels L, Hamelers HVM, Strik D, Buisman CJN, Wever HD. 2016. Selective short-chain carboxylates production: a review of control mechanisms to direct mixed culture fermentations. Crit Rev Environ Sci Technol. 46(6):592–634. doi: 10.1080/10643389.2016.1145959.
Ash C, Tejnecký V, Borůvka L, Drábek O. 2016. Different low-molecular-mass organic acids specifically control leaching of arsenic and lead from contaminated soil. J Contam Hydrol. 187:18–30. doi: 10.1016/j.jconhyd.2016.01.009.
Astolfi S, Celletti S, Vigani G, Mimmo T, Cesco S. 2021. Interaction between sulfur and iron in plants. Front Plant Sci. 12:670308. doi: 10.3389/fpls.2021.670308.
Astolfi S, Pii Y, Mimmo T, Lucini L, Miras-Moreno MB, Coppa E, Violino S, Celletti S, Cesco S. 2020. Single and combined Fe and S deficiency differentially modulate root exudate composition in tomato: a double strategy for Fe acquisition? Int J Mol Sci. 21(11):4038. doi: 10.3390/ijms21114038.
Azaroual SE, Hazzoumi Z, Mernissi NE, Aasfar A, Meftah Kadmiri I, Bouizgarne B. 2020. Role of Inorganic phosphate solubilizing *bacilli* isolated from Moroccan phosphate rock mine and rhizosphere soils in wheat (*Triticum aestivum* L) phosphorus uptake. Curr Microbiol. 77(9):2391–2404. doi: 10.1007/s00284-020-02046-8.
Balseiro-Romero M, Kidd PS, Monterroso C. 2014. Influence of plant root exudates on the mobility of fuel volatile compounds in contaminated soils. Int J Phytoremed. 16(7-12):824–839. doi: 10.1080/15226514.2013.856851.
Bao T, Sun T, Sun L. 2011. Low molecular weight organic acids in root exudates and cadmium accumulation in cadmium hyperaccumulator *Solanum nigrum* L. and non-hyperaccumulator *Solanum lycopersicum* L. African J Biotechnol. 10:17180–17185. doi: 10.5897/AJB11.1617.
Bin L, Ye C, Lijun ZHU, Ruidong Y. 2008. Effect of microbial weathering on carbonate rocks. Earth Sci Front. 15:90–99. doi: 10.1016/S1872-5791(09)60009-9.
Bononi L, Chiaramonte JB, Pansa CC, Moitinho MA, Melo IS. 2020. Phosphorus-solubilizing *Trichoderma* spp. from Amazon soils improve soybean plant growth. Sci Rep. 10(1):2858. doi: 10.1038/s41598-020-59793-8.
Brito LF, López MG, Straube L, Passaglia LMP, Wendisch VF. 2020. Inorganic phosphate solubilization by rhizosphere *Bacterium Paenibacillus* sonchi: Gene expression and physiological functions. Front Microbiol. 11:588605. doi: 10.3389/fmicb.2020.588605.
Buddhi Charana W, Kodithuwakku Kankanange Indika Upali A, Min Ho Y. 2022. Phosphate solubilization by phosphate solubilizing microorganisms: insight into the mechanisms. Korean J Agric Sci. 49:463–481. doi: 10.7744/kjoas.20220041.
Canarini A, Kaiser C, Merchant A, Richter A, Wanek W. 2019. Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. Front Plant Sci. 10:157. doi: 10.3389/fpls.2019.00157.
Canarini A, Merchant A, Dijkstra FA. 2016. Drought effects on *Helianthus annuus* and *Glycine max* metabolites: from phloem to root exudates. Rhizosphere. 2:85–97. doi: 10.1016/j.rhisph.2016.06.003.
Cardoso TB, Pinto RT, Paiva LV. 2020. Comprehensive characterization of the ALMT and MATE families on *Populus trichocarpa* and gene co-expression network analysis of its members during aluminium toxicity and phosphate starvation stresses. 3 Biotech. 10(12):525. doi: 10.1007/s13205-020-02528-3.
Chai YN, Schachtman DP. 2022. Root exudates impact plant performance under abiotic stress. Trends Plant Sci. 27(1):80–91. doi: 10.1016/J.TPLANTS.2021.08.003/ASSET/851CB756-3272-491A-94BE-435A9F6B918D/MAIN.ASSETS/GR3.SML.
Chen Q, Liu S. 2019. Identification and characterization of the phosphate-solubilizing bacterium *Pantoea* sp. S32 in reclamation soil in Shanxi, China. Front Microbiol. 10:2171. doi: 10.3389/fmicb.2019.02171.
Choi I, Son H, Baek J-H. 2021. Tricarboxylic acid (TCA) cycle intermediates: regulators of immune responses. Life. 11(1):69. doi: 10.3390/life11010069.
Clarholm M, Skyllberg U, Rosling A. 2015. Organic acid induced release of nutrients from metal-stabilized soil organic matter – The unbutton model. Soil Biol Biochem. 84:168–176. doi: 10.1016/j.soilbio.2015.02.019.
Cornelis J-T, de tombeur F. 2022. Soil controls on carboxylate-driven processes and opportunities. Plant Soil. 476(1-2):239–250. doi: 10.1007/s11104-022-05549-4.
Curti L, Moore OW, Babakhani P, Xiao K-Q, Woulds C, Bray AW, Fisher BJ, Kazemian M, Kaulich B, Peacock CL. 2021. Carboxyl-richness controls organic carbon preservation during coprecipitation with iron (oxyhydr)oxides in the natural environment. Commun Earth Environ. 2:229. doi: 10.1038/s43247-021-00301-9.
D'Angioli AM, Viani RAG, Lambers H, Sawaya ACHF, Oliveira RS. 2017. Inoculation with *Azospirillum brasilense* (Ab-V4, Ab-V5) increases Zea mays root carboxylate-exudation rates, dependent on soil phosphorus supply. Plant Soil. 410(1-2):499–507. doi: 10.1007/s11104-016-3044-5.
Daunoras J, Kačergius A, Gudiukaitė R. 2024. Role of soil microbiota enzymes in soil health and activity changes depending on climate change and the type of soil ecosystem. Biology. 13(2):85. doi: 10.3390/biology13020085.

Delgado M, Suriyagoda L, Zúñiga-Feest A, Borie F, Lambers H. 2014. Divergent functioning of Proteaceae species: the South American *Embothrium coccineum* displays a combination of adaptive traits to survive in high-phosphorus soils*Funct*. Ecol. 28(6):1356–1366. doi: 10.1111/1365-2435.12303.

Dijkstra FA, Zhu B, Cheng W. 2021. Root effects on soil organic carbon: a double-edged sword. New Phytol. 230(1):60–65. doi: 10.1111/nph.17082.

Ding W, Cong W-F, Lambers H. 2021. Plant phosphorus-acquisition and -use strategies affect soil carbon cycling. Trends Ecol Evol. 36(10):899–906. doi: 10.1016/j.tree.2021.06.005.

Dong J, Hunt J, Delhaize E, Zheng SJ, Jin CW, Tang C. 2021. Impacts of elevated CO_2 on plant resistance to nutrient deficiency and toxic ions via root exudates: a review. Sci Total Environ. 754:142434. doi: 10.1016/j.scitotenv.2020.142434.

Drever JI, Vance GF. 1994. Role of soil organic acids in mineral weathering processes. In: Organic acids in geological processes. Berlin: Springer Berlin Heidelberg; pp. 138–161.

Efthymiou A, Grønlund M, Müller-Stöver DS, Jakobsen I. 2018. Augmentation of the phosphorus fertilizer value of biochar by inoculation of wheat with selected *Penicillium* strains. Soil Biol Biochem. 116:139–147. doi: 10.1016/j.soilbio.2017.10.006.

Eilers KG, Lauber CL, Knight R, Fierer N. 2010. Shifts in bacterial community structure associated with inputs of low molecular weight carbon compounds to soil. Soil Biol Biochem. 42(6):896–903. doi: 10.1016/j.soilbio.2010.02.003.

Fazeli-Nasab B, Piri R, Farid Rahmani A. 2022. Assessment of the role of rhizosphere in soil and its relationship with microorganisms and element absorption. Plant Prot. 225:9783110771558-010. doi: 10.1515/9783110771558-010.

Fischer H, Eckhardt K, Meyer A, Neumann G, Leinweber P, Fischer K, Kuzyakov Y. 2010. Rhizodeposition of maize: short-term carbon budget and composition. Z Pflanzenernähr Bodenk. 173(1):67–79. doi: 10.1002/jpln.200800293.

Freschet GT, Roumet C, Comas LH, Weemstra M, Bengough AG, Rewald B, Bardgett RD, Deyn GBD, Johnson D, Klimešová J, et al. 2021. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. New Phytol. 232(3):1123–1158. doi: 10.1111/nph.17072.

Fujii K. 2024. Plant strategy of root system architecture and exudates for acquiring soil nutrients. Ecol Res. 39(5):623–633. doi: 10.1111/1440-1703.12477.

Fujii, Kazumichi, Hayakawa, Chie, Sukartiningsih, 2021. Root exudation and biodegradation of organic acids in a tropical forest soil under dipterocarp and pioneer trees. Plant Soil. 469: 213–226. doi: 10.1007/s11104-021-05132-3.

Funayama-Noguchi S, Shibata M, Noguchi K, Terashima I. 2021. Effects of root morphology, respiration and carboxylate exudation on carbon economy in two non-mycorrhizal lupines under phosphorus deficiency. Plant Cell Environ. 44(2):598–612. doi: 10.1111/pce.13925.

Gang XU, Hongbo S, Nie Y, Pei Y, Sun Z, Blackwell MSA. 2012. The role of root-released organic acids and anions in phosphorus transformations in a sandy loam soil from Yantai, China. African J Microbiol Res. 6(3):674–679, 23 doi: 10.5897/AJMR11.1296.

Garg, N., Singh, S., Kashyap, L. 2017. Arbuscular Mycorrhizal Fungi and Heavy Metal Tolerance in Plants: An Insight into Physiological and Molecular Mechanisms. In: Varma, A., Prasad, R., Tuteja, N. (eds) Mycorrhiza – Nutrient Uptake, Biocontrol, Ecorestoration. Springer, Cham. https://doi.org/10.1007/978-3-319-68867-1_4

Gerke J. 2024. Improving phosphate acquisition from soil via higher plants while approaching peak phosphorus worldwide: A critical review of current concepts and misconceptions. Plants (Basel). 13(24):3478. doi: 10.3390/plants13243478.

Graaff M-A, de Jastrow JD, Gillette S, Johns A, Wullschleger SD. 2014. Differential priming of soil carbon driven by soil depth and root impacts on carbon availability. Soil Biol. Biochem. 69:147–156. doi: 10.1016/j.soilbio.2013.10.047.

Graustein WC, Cromack K, Sollins P. 1977. Calcium oxalate: Occurrence in soils and effect on nutrient and geochemical cycles. Science. 198(4323):1252–1254. doi: 10.1126/science.198.4323.1252.

Guan N, Li J, Shin HD, Du G, Chen J, Liu L. 2017. Microbial response to environmental stresses: from fundamental mechanisms to practical applications. Appl Microbiol Biotechnol. 101(10):3991–4008. doi: 10.1007/s00253-017-8264-y.

Hayakawa C, Fujii K, Funakawa S, Kosaki T. 2018. Effects of sorption on biodegradation of low-molecular-weight organic acids in highly-weathered tropical soils. Geoderma. 324:109–118. doi: 10.1016/j.geoderma.2018.03.014.

He H, Wu M, Guo L, Fan C, Zhang Z, Su R, Peng Q, Pang J, Lambers H. 2020. Release of tartrate as a major carboxylate by alfalfa (*Medicago sativa* L.) under phosphorus deficiency and the effect of soil nitrogen supply. Plant Soil. 449(1-2):169–178. doi: 10.1007/s11104-020-04481-9.

Hoffland E, Wei C, Wissuwa M. 2006. Organic anion exudation by lowland rice (*Oryza sativa* L.) at zinc and phosphorus deficiency. Plant Soil. 283(1-2):155–162. doi: 10.1007/s11104-005-3937-1.

Hu J, Wang L, Zhang L, Gao H, Tian D. 2022. A study of phosphate solubilizing capacity by *Penicillium Aurantiogriseum* under different carbon and nitrogen resources. E3S Web Conf. 350:03002. doi: 10.1051/e3sconf/202235003002.

Igamberdiev AU, Eprintsev AT. 2016. Organic acids: the pools of fixed carbon involved in redox regulation and energy balance in higher plants. Front Plant Sci. 7:1042. doi: 10.3389/fpls.2016.01042.

Imas P, Bar-Yosef B, Kafkafi U, Ganmore-Neumann R. 1997. Phosphate induced carboxylate and proton release by tomato roots. Plant Soil. 191(1):35–39. www.jstor.org/stable/42948027. doi: 10.1023/A:1004262730434.

Javed MT, Akram MS, Tanwir K, Javed Chaudhary H, Ali Q, Stoltz E, Lindberg S. 2017. Cadmium spiked soil modulates root organic acids exudation and ionic contents of two differentially Cd tolerant maize (*Zea mays* L.) cultivars. Ecotoxicol Environ Saf. 141:216–225. doi: 10.1016/j.ecoenv.2017.03.027.

Jiang Y, Tian J, Ge F. 2020. New insight into carboxylic acid metabolisms and pH regulations during insoluble phosphate solubilisation process by *Penicillium*

*oxalicum*PSF-4. Curr Microbiol. 77(12):4095–4103. doi: 10.1007/s00284-020-02238-2.

Jindo K, Audette Y, Olivares FL, Canellas LP, Smith DS, Paul Voroney R. 2023. Biotic and abiotic effects of soil organic matter on the phytoavailable phosphorus in soils: a review. Chem Biol Technol Agric. 10(1):29. doi: 10.1186/s40538-023-00401-y.

Jones DL, Darah PR, Kochian LV. 1996. Critical evaluation of organic acid mediated iron dissolution in the rhizosphere and its potential role in root iron uptake. Plant Soil. 180(1):57–66. doi: 10.1007/BF00015411.

Jones DL, Dennis PG, Owen AG, Hees, PAW van. 2003. Organic acid behavior in soils – misconceptions and knowledge gaps. Plant Soil. 248(1-2):31–41. doi: 10.1023/A:1022304332313.

Kabas S, Saavedra-Mella F, Huynh T, Kopittke PM, Carter S, Huang L. 2017. Metal uptake and organic acid exudation of native Acacia species in mine tailings. Aust J Bot. 65(4):357. doi: 10.1071/BT16189.

Karadihalli Thammaiah M, Pandey RN, Purakayastha TJ, Chobhe KA, Vashisth A, Chandra S, Pawar AB, Trivedi A. 2022. Impact of low molecular weight organic acids on soil phosphorus release and availability to wheat. Commun Soil Sci Plant Anal. 53(18):2497–2508. doi: 10.1080/00103624.2022.2071935.

Keiluweit M, Bougoure JJ, Nico PS, Pett-Ridge J, Weber PK, Kleber M. 2015. Mineral protection of soil carbon counteracted by root exudates. Nature Clim Change. 5(6):588–595. doi: 10.1038/nclimate2580.

Kibria MG, Barton L, Rengel Z. 2021. Applying foliar magnesium enhances wheat growth in acidic soil by stimulating exudation of malate and citrate. Plant Soil. 464(1-2):621–634. doi: 10.1007/s11104-021-04984-z.

Kidd DR, Ryan MH, Hahne D, Haling RE, Lambers H, Sandral GA, Simpson RJ, Cawthray GR. 2018. The carboxylate composition of rhizosheath and root exudates from twelve species of grassland and crop legumes with special reference to the occurrence of citramalate. Plant Soil. 424(1-2):389–403. doi: 10.1007/s11104-017-3534-0.

Kidd PS, Llugany M, Poschenrieder C, Gunsé B, Barceló J. 2001. The role of root exudates in aluminium resistance and silicon-induced amelioration of aluminium toxicity in three varieties of maize (*Zea mays* L.). J Exp Bot. 52(359):1339–1352. doi: 10.1093/jexbot/52.359.1339.

Kim K-R, Owens G, Naidu R, Kwon S. 2010. Influence of plant roots on rhizosphere soil solution composition of long-term contaminated soils. Geoderma. 155(1-2):86–92. doi: 10.1016/j.geoderma.2009.11.028.

Kretzschmar T, Burla B, Lee Y, Martinoia E, Nagy R. 2011. Functions of ABC transporters in plants. Essays Biochem. 50(1):145–160. doi: 10.1042/bse0500145.

Kruthika S, Ashu A, Anand A, Sammi Reddy K, Vara Prasad PV, Gurumurthy S. 2024. Unveiling the role of root exudates in plant adaptation to drought and heat stress. J Crop Heal. 76(5):941–955. doi: 10.1007/s10343-024-01013-8.

Kumar N, Haldar S, Saikia R. 2023. Root exudation as a strategy for plants to deal with salt stress: An updated review. Environ Exp Bot. 216:105518. doi: 10.1016/j.envexpbot.2023.105518.

Lambers H, Plaxton WC. 2015. Phosphorus: back to the roots. Annu. Plant Rev. 48:1–22. doi: 10.1002/9781118958841.ch1.

Lambers H. 2022. Phosphorus acquisition and utilization in plants. Annu Rev Plant Biol. 73(1):17–42. doi: 10.1146/annurev-arplant-102720-125738.

Lardi M, Murset V, Fischer H-M, Mesa S, Ahrens CH, Zamboni N, Pessi G. 2016. Metabolomic profiling of *Bradyrhizobium diazoefficiens*-induced root nodules reveals both host plant-specific and developmental signatures. Int J Mol Sci. 17(6):815. doi: 10.3390/ijms17060815.

Lardi M, Pessi G. 2018. Functional genomics approaches to studying symbioses between legumes and nitrogen-fixing rhizobia. High Throughput. 7(2):15. doi: 10.3390/ht7020015.

Li M, Song Z, Li Z, Qiao R, Zhang P, Ding C, Xie J, Chen Y, Guo H. 2022. Populus root exudates are associated with rhizosphere microbial communities and symbiotic patterns. Front Microbiol. 13:1042944. doi: 10.3389/fmicb.2022.1042944.

Li Z, Bai T, Dai L, Wang F, Tao J, Meng S, Hu Y, Wang S, Hu S. 2016. A study of organic acid production in contrasts between two phosphate solubilizing fungi: *Penicillium oxalicum* and *Aspergillus niger*. Sci Rep. 6(1):25313. doi: 10.1038/srep25313.

Liang C, Schimel JP, Jastrow JD. 2017. The importance of anabolism in microbial control over soil carbon storage. Nat Microbiol. 2(8):17105. doi: 10.1038/nmicrobiol.2017.105.

Liang G, Stark J, Waring BG. 2023. Mineral reactivity determines root effects on soil organic carbon. Nat Commun. 14(1):4962. doi: 10.1038/s41467-023-40768-y.

Ličina V, Krogstad T, Fotirić Akšić M, Meland M. 2024. Apple growing in Norway—Ecologic factors, current fertilization practices and fruit quality: a case study. Horticulturae. 10(3):233. doi: 10.3390/horticulturae10030233.

Liu J, Magalhaes JV, Shaff J, Kochian LV. 2009. Aluminum-activated citrate and malate transporters from the MATE and ALMT families function independently to confer Arabidopsis aluminum tolerance. Plant J. 57(3):389–399. doi: 10.1111/j.1365-313x.2008.03696.x.

Liu W, Hou J, Wang Q, Yang H, Luo Y, Christie P. 2015. Collection and analysis of root exudates of *Festuca arundinacea* L. and their role in facilitating the phytoremediation of petroleum-contaminated soil. Plant Soil. 389(1-2):109–119. doi: 10.1007/s11104-014-2345-9.

Longman J, Faust J, Bryce C, Homoky WB, März C. 2022. Organic carbon burial with reactive iron across global environments. Biogeochem Cycles. 36(11). e2022GB007447. doi: 10.1002/essoar.10511279.1.

M'Sehli W, Youssfi S, Donnini S, Dell'Orto M, Nisi PD, Zocchi G, Abdelly C, Gharsalli M. 2008. Root exudation and rhizosphere acidification by two lines of *Medicago ciliaris* in response to lime-induced iron deficiency. Plant Soil. 312(1-2):151–162. doi: 10.1007/s11104-008-9638-9.

Ma W, Tang S, Dengzeng Z, Zhang D, Zhang T, Ma X. 2022. Root exudates contribute to belowground ecosystem hotspots: a review. Front Microbiol. 13:937940. doi: 10.3389/fmicb.2022.937940.

Marschner H. 2012. Marschner's mineral nutrition of higher plants. Amsterdam: Academic Press.

Martin BC, George SJ, Price CA, Shahsavari E, Ball AS, Tibbett M, Ryan MH. 2016. Citrate and malonate increase microbial activity and alter microbial community com-

position in uncontaminated and diesel-contaminated soil microcosms. Soil. 2(3):487–498. doi: 10.5194/soil-2-487-2016.

Mimmo T, Buono D, Del Terzano R, Tomasi N, Vigani G, Crecchio C, Pinton R, Zocchi G, Cesco S. 2014. Rhizospheric organic compounds in the soil–microorganism–plant system: their role in iron availability. Eur J Soil Sci. 65(5):629–642. doi: 10.1111/ejss.12158.

Mimmo T, Hann S, Jaitz L, Cesco S, Gessa CE, Puschenreiter M. 2011. Time and substrate dependent exudation of carboxylates by *Lupinus albus* L. and *Brassica napus* L. Plant Physiol Biochem. 49(11):1272–1278. doi: 10.1016/j.plaphy.2011.08.012.

Mitra R, Yadav P, Usha K, Singh B. 2022. Regulatory role of organic acids and phytochelators in influencing the rhizospheric availability of phosphorus and iron and their uptake by plants. Plant Physiol Rep. 27(2):193–206. doi: 10.1007/s40502-022-00650-3.

More SS, Shinde SE, Kasture MC. 2020. Root exudates a key factor for soil and plant: an overview. Pharma Innov J. 8:449–459.

Morrison CK, Arseneault T, Novinscak A, Filion M. 2017. Phenazine-1-carboxylic acid production by *Pseudomonas fluorescens* LBUM636 alters *Phytophthora infestans* growth and late blight development. Phytopathology. 107(3):273–279. doi: 10.1094/phyto-06-16-0247-r.

Neumann G, Römheld V. 1999. Root excretion of carboxylic acids and protons in phosphorus-deficient plants. Plant Soil. 211(1):121–130. doi: 10.1023/A:1004380832118.

Nwoke OC, Diels J, Abaidoo R, Nziguheba G, Merckx R. 2008. Organic acids in the rhizosphere and root characteristics of soybean (*Glycine max*) and cowpea (*Vigna unguiculata*) in relation to phosphorus uptake in poor savanna soils. Afr J Biotechnol. 7(20):3620–3627.

Oburger E, Kirk GJD, Wenzel WW, Puschenreiter M, Jones DL. 2009. Interactive effects of organic acids in the rhizosphere. Soil Biol Biochem. 41(3):449–457. doi: 10.1016/j.soilbio.2008.10.034.

Ortíz J, Sanhueza C, Romero-Munar A, Hidalgo-Castellanos J, Castro C, Bascuñán-Godoy L, Coba de la Peña T, López-Gómez M, Florez-Sarasa I, Del-Saz NF. 2020. In vivo metabolic regulation of alternative oxidase under nutrient deficiency-interaction with arbuscular mycorrhizal fungi and rhizobium bacteria. Int J Mol Sci. 21(12):4201. doi: 10.3390/ijms21124201.

Otero-Fariña A, Brown H, Xiao K-Q, Antelo J, Fiol S, Chapman P, Holden J, Banwart S, Peacock C. 2023. Carbon preservation in soils: the role of carbon chemistry in soil aggregate formation. EGU23, the 25th EGU General Assembly, held 23-28 April, 2023 in Vienna, Austria and Online. doi: 10.5194/egusphere-egu23-1525.

Panchal P, Miller AJ, Giri J. 2021. Organic acids: versatile stress-response roles in plants. J Exp Bot. 72(11):4038–4052. doi: 10.1093/jxb/erab019.

Pang J, Bansal R, Zhao H, Bohuon E, Lambers H, Ryan MH, Ranathunge K, Siddique KHM. 2018. The carboxylate-releasing phosphorus-mobilizing strategy can be proxied by foliar manganese concentration in a large set of chickpea germplasm under low phosphorus supply. New Phytol. 219(2):518–529. doi: 10.1111/nph.15200.

Pearse SJ, Veneklaas EJ, Cawthray GR, Bolland MDA, Lambers H. 2006. Carboxylate release of wheat, canola and 11 grain legume species as affected by phosphorus status. Plant Soil. 288(1-2):127–139. doi: 10.1007/s11104-006-9099-y.

Peña A. 2022. A comprehensive review of recent research concerning the role of low molecular weight organic acids on the fate of organic pollutants in soil. J Hazard Mater. 434:128875. doi: 10.1016/j.jhazmat.2022.128875.

Penn C, Camberato J. 2019. A critical review on soil chemical processes that control how soil pH affects phosphorus availability to plants. Agriculture. 9(6):120. doi: 10.3390/agriculture9060120.

Philippot L, Chenu C, Kappler A, Rillig MC, Fierer N. 2024. The interplay between microbial communities and soil properties. Nat Rev Microbiol. 22(4):226–239. doi: 10.1038/s41579-023-00980-5.

Phour M, Sehrawat A, Sindhu SS, Glick BR. 2020. Interkingdom signaling in plant-rhizomicrobiome interactions for sustainable agriculture. Microbiol Res. 241:126589. doi: 10.1016/j.micres.2020.126589.

Playsted CWS, Johnston ME, Ramage CM, Edwards DG, Cawthray GR, Lambers H. 2006. Functional significance of dauciform roots: exudation of carboxylates and acid phosphatase under phosphorus deficiency in *Caustis blakei* (Cyperaceae). New Phytol. 170(3):491–500. doi: 10.1111/j.1469-8137.2006.01697.x.

Rangel AF, Rao IM, Horst WJ. 2007. Spatial aluminium sensitivity of root apices of two common bean (*Phaseolus vulgaris* L.) genotypes with contrasting aluminium resistance. J Exp Bot. 58(14):3895–3904. doi: 10.1093/JXB/ERM241.

Rawat P, Das S, Shankhdhar D, Shankhdhar SC. 2021. Phosphate-solubilizing microorganisms: Mechanism and their role in phosphate solubilization and uptake. J Soil Sci Plant Nutr. 21(1):49–68. doi: 10.1007/s42729-020-00342-7.

Robert CAM, Himmighofen P, McLaughlin S, Cofer TM, Khan SA, Siffert A, Sasse J. 2025. Environmental and biological drivers of root exudation. Annu Rev Plant Biol. 76(1):317–339. doi: 10.1146/annurev-arplant-083123-082752.

Rodríguez-Garrido B, Balseiro-Romero M, Kidd PS, Monterroso C. 2020. Effect of plant root exudates on the desorption of hexachlorocyclohexane isomers from contaminated soils. Chemosphere. 241:124920. doi: 10.1016/j.chemosphere.2019.124920.

Rovira AD, Davey CB, Carson EW. 1974. The plant root and its environment. Charlottesville: Univ. Press Virginia; p. VA153.

Russ D, Fitzpatrick CR, Teixeira PJPL, Dangl JL. 2023. Deep discovery informs difficult deployment in plant microbiome science. Cell. 186(21):4496–4513. doi: 10.1016/j.cell.2023.08.035.

Ryan PR, Tyerman SD, Sasaki T, Furuichi T, Yamamoto Y, Zhang WH, Delhaize E. 2011. The identification of aluminium-resistance genes provides opportunities for enhancing crop production on acid soils. J Exp Bot. 62(1):9–20. doi: 10.1093/jxb/erq272.

Santoro V, Schiavon M, Celi L. 2024. Role of soil abiotic processes on phosphorus availability and plant responses with a focus on strigolactones in tomato plants. Plant Soil. 494(1-2):1–49. doi: 10.1007/s11104-023-06266-2.

Seitz VA, McGivern BB, Borton MA, Chaparro JM, Schipanski ME, Prenni JE, Wrighton KC. 2024. Cover crop root exudates impact soil microbiome functional

trajectories in agricultural soils. Microbiome. 12(1):183. doi: 10.1186/s40168-024-01886-x.
Seregin IV, Kozhevnikova AD. 2024. The role of low-molecular-weight organic acids in metal homeostasis in plants. Int J Mol Sci. 25(17):9542. doi: 10.3390/ijms25179542.
Shane MW, Lambers H, Cawthray GR, Kuhn AJ, Schurr U. 2008. Impact of phosphorus mineral source (Al–P or Fe–P) and pH on cluster-root formation and carboxylate exudation in Lupinus albus L. Plant Soil. 304(1-2):169–178. doi: 10.1007/s11104-007-9535-7.
Shane MW, Lambers H. 2005. Cluster roots: a curiosity in context. Plant Soil. 274(1-2):101–125. doi: 10.1007/s11104-004-2725-7.
Sharma I, Kashyap S, Agarwala N. 2023. Biotic stress-induced changes in root exudation confer plant stress tolerance by altering rhizospheric microbial community. Front Plant Sci. 14:1132824. doi: 10.3389/FPLS.2023.1132824/XML.
Sheik CS, Cleaves HJ, Johnson-Finn K, Giovannelli D, Kieft TL, Papineau D, Schrenk MO, Tumiati S. 2020. Abiotic and biotic processes that drive carboxylation and decarboxylation reactions. Am. Mineral. 105(5):609–615. doi: 10.2138/am-2020-7166CCBYNCND.
Sikora A, Detman A, Mielecki D, Chojnacka A, Błaszczyk M. 2019. Searching for metabolic pathways of anaerobic digestion: a useful list of the key enzymes. In: Banu JR, Ravi YK, editors. Anaerob Dig. doi: 10.5772/intechopen.81256.
Sindhu SS, Sehrawat A, Glick BR. 2022. The involvement of organic acids in soil fertility, plant health and environment sustainability. Arch Microbiol. 204(12):720. doi: 10.1007/s00203-022-03321-x.
Strobel BW. 2001. Influence of vegetation on low-molecular-weight carboxylic acids in soil solution—A review. Geoderma. 99(3-4):169–198. doi: 10.1016/s0016-7061(00)00102-6.
Ström L, Owen AG, Godbold DL, Jones DL. 2005. Organic acid behaviour in a calcareous soil implications for rhizosphere nutrient cycling. Soil Biol Biochem. 37(11):2046–2054. doi: 10.1016/j.soilbio.2005.03.009.
Studenroth S, Huber SG, Kotte K, Schöler HF. 2013. Natural abiotic formation of oxalic acid in soils: results from aromatic model compounds and soil samples. Environ Sci Technol. 47(3):1323–1329. doi: 10.1021/es304208a.
Sun B, Gao Y, Wu X, Ma H, Zheng C, Wang X, Zhang H, Li Z, Yang H. 2020. The relative contributions of pH, organic anions, and phosphatase to rhizosphere soil phosphorus mobilization and crop phosphorus uptake in maize/alfalfa polyculture. Plant Soil. 447(1-2):117–133. doi: 10.1007/s11104-019-04110-0.
Suriyagoda LBD, Tibbett M, Edmonds-Tibbett T, Cawthray GR, Ryan MH. 2016. Poor regulation of phosphorus uptake and rhizosphere carboxylates in three phosphorus-hyperaccumulating species of Ptilotus. Plant Soil. 402(1-2):145–158. doi: 10.1007/s11104-015-2784-y.
Szabó L, Vancsik A, Bauer L, Jakab G, Király C, Hatvani IG, Kondor AC, Szalai Z. 2024. Effects of root-derived organic acids on sorption of pharmaceutically active compounds in sandy topsoil. Chemosphere. 355:141759. doi: 10.1016/j.chemosphere.2024.141759.
Thomashow LS, Weller DM, Bonsall RF, Pierson LS. 1990. Production of the antibiotic phenazine-1-carboxylic Acid by fluorescent pseudomonas species in the rhizosphere of wheat. Appl Environ Microbiol. 56(4):908–912. doi: 10.1128/aem.56.4.908-912.1990.
Tian D, Wang L, Hu J, Zhang L, Zhou N, Xia J, Xu M, Yusef KK, Wang S, Li Z, et al. 2021. A study of P release from Fe-P and Ca-P via the organic acids secreted by *Aspergillus niger*. J Microbiol. 59(9):819–826. doi: 10.1007/s12275-021-1178-5.
Tiziani R, Mimmo T, Valentinuzzi F, Pii Y, Celletti S, Cesco S. 2020. Root handling affects carboxylates exudation and phosphate uptake of white lupin roots. Front Plant Sci. 11:584568. doi: 10.3389/fpls.2020.584568.
Tshewang S, Rengel Z, Siddique KHM, Solaiman ZM. 2020. Growth, rhizosphere carboxylate exudation, and arbuscular mycorrhizal colonisation in temperate perennial pasture grasses varied with phosphorus application. Agronomy. 10(12):2017. doi: 10.3390/agronomy10122017.
Vahisalu T, Kollist H, Wang Y-F, Nishimura N, Chan W-Y, Valerio G, Lamminmäki A, Brosché M, Moldau H, Desikan R, et al. 2008. SLAC1 is required for plant guard cell S-type anion channel function in stomatal signalling. Nature. 452(7186):487–491. doi: 10.1038/nature06608.
Valentinuzzi F, Pii Y, Vigani G, Lehmann M, Cesco S, Mimmo T. 2015. Phosphorus and iron deficiencies induce a metabolic reprogramming and affect the exudation traits of the woody plant *Fragaria×ananassa*. J Exp Bot. 66(20):6483–6495. doi: 10.1093/jxb/erv364.
Valentinuzzi F, Venuti S, Pii Y, Marroni F, Cesco S, Hartmann F, Mimmo T, Morgante M, Pinton R, Tomasi N, et al. 2019. Common and specific responses to iron and phosphorus deficiencies in roots of apple tree (Malus × domestica). Plant Mol Biol. 101(1-2):129–148. doi: 10.1007/s11103-019-00896-w.
Veneklaas EJ, Stevens J, Cawthray GR, Turner S, Grigg AM, Lambers H. 2003. Chickpea and white lupin rhizosphere carboxylates vary with soil properties and enhance phosphorus uptake. Plant Soil. 248(1-2):187–197. doi: 10.1023/A:1022367312851.
Vurukonda SSKP, Chaudhary S, Bodhankar S. 2022. An overview: interaction between microbial endophytes and root exudates. IJPSS. 34:25–38. doi: 10.9734/ijpss/2022/v34i2131236.
Wang Q, Yuan Y, Zhang Z, Liu D, Xiao J, Yin H. 2021. Exudate components mediate soil C dynamic through different priming mechanisms in forest soils. Appl Soil Ecol. 160:103855. doi: 10.1016/j.apsoil.2020.103855.
Wang W, Sarpong CK, Song C, Zhang X, Gan Y, Wang X, Yong T, Chang X, Wang Y, Yang W. 2020. Screening, identification and growth promotion ability of phosphate solubilizing bacteria from soybean rhizosphere under maize-soybean intercropping systems. *BioRxiv*.
Wang X, Chi Y, Song S. 2024. Important soil microbiota's effects on plants and soils: a comprehensive 30-year systematic literature review. Front Microbiol. 15:1347745. doi: 10.3389/fmicb.2024.1347745.
Wang Y, Lambers H. 2020. Root-released organic anions in response to low phosphorus availability: recent progress, challenges and future perspectives. Plant Soil. 447(1-2):135–156. doi: 10.1007/s11104-019-03972-8.
Wei L, Chen C, Xu Z. 2010. Citric acid enhances the mobilization of organic phosphorus in subtropical and tropical forest soils. Biol Fertil Soils. 46(7):765–769. doi: 10.1007/s00374-010-0464-x.

Wen T, Ding Z, Thomashow LS, Hale L, Yang S, Xie P, Liu X, Wang H, Shen Q, Yuan J. 2023a. Deciphering the mechanism of fungal pathogen-induced disease-suppressive soil. New Phytol. 238(6):2634–2650. doi: 10.1111/nph.18886.

Wen T, Xie P, Liu H, Liu T, Zhao M, Yang S, Niu G, Hale L, Singh BK, Kowalchuk GA, et al. 2023b. Tapping the rhizosphere metabolites for the prebiotic control of soil-borne bacterial wilt disease. Nat Commun. 14(1):4497. doi: 10.1038/s41467-023-40184-2.

Wen T, Yu G-H, Hong W-D, Yuan J, Niu G-Q, Xie P-H, Sun F-S, Guo L-D, Kuzyakov Y, Shen Q-R. 2022. Root exudate chemistry affects soil carbon mobilization via microbial community reassembly. Fundam Res. 2(5):697–707. doi: 10.1016/j.fmre.2021.12.016.

Weston LA, Ryan PR, Watt M. 2012. Mechanisms for cellular transport and release of allelochemicals from plant roots into the rhizosphere. J Exp Bot. 63(9):3445–3454. doi: 10.1093/jxb/ers054.

Wu H, Cui H, Fu C, Li R, Qi F, Liu Z, Yang G, Xiao K, Qiao M. 2024. Unveiling the crucial role of soil microorganisms in carbon cycling: a review. Sci Total Environ. 909:168627. doi: 10.1016/j.scitotenv.2023.168627.

Xiao K-Q, Zhao Y, Liang C, Zhao M, Moore OW, Otero-Fariña A, Zhu Y-G, Johnson K, Peacock CL. 2023. Introducing the soil mineral carbon pump. Nat Rev Earth Environ. 4(3):135–136. doi: 10.1038/s43017-023-00396-y.

Xiong Y-W, Li X-W, Wang T-T, Gong Y, Zhang C-M, Xing K, Qin S. 2020. Root exudates-driven rhizosphere recruitment of the plant growth-promoting rhizobacterium *Bacillus flexus* KLBMP 4941 and its growth-promoting effect on the coastal halophyte *Limonium sinense* under salt stress. Ecotoxicol Environ Saf. 194:110374. doi: 10.1016/j.ecoenv.2020.110374.

Xu L, Li Y, Dai X, Jin X, Zhao Q, Tian B, Zhou Y. 2025. Symbiotic fungal inoculation promotes the growth of *Pinus tabuliformis* seedlings in relation to the applied nitrogen form. BMC Plant Biol. 25(1):10. doi: 10.1186/s12870-024-05883-y.

Yacoumas A, Honvault N, Houben D, Fontaine J, Meglouli H, Laruelle F, Tisserant B, Faucon M-P, Sahraoui AL-H, Firmin S. 2020. Contrasting response of nutrient acquisition traits in wheat grown on bisphenol A-contaminated soils. Water Air Soil Pollut. 231:23. doi: 10.1007/s11270-019-4383-7.

Yan S, Yin L, Dijkstra FA, Wang P, Cheng W. 2023. Priming effect on soil carbon decomposition by root exudate surrogates: A meta-analysis. Soil Biol Biochem. 178:108955. doi: 10.1016/j.soilbio.2023.108955.

Yang CX, Chen SJ, Hong XY, Wang LZ, Wu HM, Tang YY, Gao YY, Hao GF. 2025. Plant exudates-driven microbiome recruitment and assembly facilitates plant health management. FEMS Microbiol Rev. 49:fuaf008. doi: 10.1093/femsre/fuaf008.

Yang J, Li M-R, Qin L, Feng S-H, Zhan F-D, Li Y, He Y-M. 2020a. The effects of enhanced UV-B radiation on root morphology and secretion content of rice (*Oryza sativa* Linn.). IOP Conf Ser Earth Environ Sci. 446(3):032073. doi: 10.1088/1755-1315/446/3/032073.

Yang J, Liu J, Hu Y, Rumpel C, Bolan N, Sparks D. 2017. Molecular-level understanding of malic acid retention mechanisms in ternary kaolinite-Fe(III)-malic acid systems: The importance of Fe speciation. Chem Geol. 464:69–75. doi: 10.1016/j.chemgeo.2017.02.018.

Yang T-Y, Qi Y-P, Huang H-Y, Wu F-L, Huang W-T, Deng C-L, Yang L-T, Chen L-S. 2020b. Interactive effects of pH and aluminum on the secretion of organic acid anions by roots and related metabolic factors in *Citrus sinensis* roots and leaves. Environ Pollut. 262:114303. doi: 10.1016/j.envpol.2020.114303.

Yang Z, Li Y, Li P, Zhang F, Thomas BW. 2016. Effect of difference between day and night temperature on tomato (*Lycopersicon esculentum* Mill.) root activity and low molecular weight organic acid secretion. Soil Sci Plant Nutr. 62(5-6):423–431. doi: 10.1080/00380768.2016.1224449.

Yin H, Li Y, Xiao J, Xu Z, Cheng X, Liu Q. 2013. Enhanced root exudation stimulates soil nitrogen transformations in a subalpine coniferous forest under experimental warming. Glob Chang Biol. 19(7):2158–2167. doi: 10.1111/gcb.12161.

Yizhu L, Imtiaz M, Ditta A, Rizwan MS, Ashraf M, Mehmood S, Aziz O, Mubeen F, Ali M, Elahi NN, et al. 2020. Response of growth, antioxidant enzymes and root exudates production towards As stress in *Pteris vittata* and in *Astragalus sinicus* colonized by arbuscular mycorrhizal fungi. Environ Sci Pollut Res Int. 27(2):2340–2352. doi: 10.1007/s11356-019-06785-5.

Yuan J, Zhao J, Wen T, Zhao M, Li R, Goossens P, Huang Q, Bai Y, Vivanco JM, Kowalchuk GA, et al. 2018. Root exudates drive the soil-borne legacy of aboveground pathogen infection. Microbiome. 6(1):156. doi: 10.1186/s40168-018-0537-x.