Pedosphere **36**(2): 442–459, 2026
doi: 10.1016/j.pedsph.2025.09.017
ISSN 1002-0160/CN 32-1315/P

Published by Elsevier B.V. and Science Press

PEDOSPHERE

www.elsevier.com/locate/pedosphere

Unveiling root exudates: Composition, characterization, dynamics and collection strategies

Sonia MALIK[1,*], Morteza YOUSEFZADI[2], Oksana SYTAR[3,†], Rambod ABIRI[4], Pooja SHARMA[1], Narges ATABAKI[4], Aakanchha JAIN[5], Siddheshwar CHAUTHE[5] and Mansour GHORBANPOUR[6]

[1]*Department of Biotechnology, Baba Farid College, Bathinda 151002 (India)*
[2]*Department of Biology, Faculty of Science, University of Qom, Qom 3716146611 (Iran)*
[3]*Educational and Scientific Center, Institute of Biology and Medicine, Department of Plant Biology, Taras Shevchenko National University of Kyiv, Volodymyrska 60, Kyiv 01033 (Ukraine)*
[4]*Department of Plant Agriculture, University of Guelph, Guelph N1G 2W1 (Canada)*
[5]*National Institute of Pharmaceutical Education and Research (NIPER) Ahmedabad Palaj, Opp Air Force Station, Gandhinagar 382355 (India)*
[6]*Department of Medicinal Plants, Faculty of Agriculture and Natural Resources, Arak University, Arak 38156-8-8349 (Iran)*

(Received March 26, 2025; revised August 2, 2025; accepted September 10, 2025)

ABSTRACT

Root exudates (REs) represent a promising yet under-explored source of bioactive compounds that could serve as valuable agents in various sectors, including food, medicine, and agriculture. These bioactive compounds, also known as specialized metabolites, vary in nature depending on plant species, environmental factors, and other conditions. They possess diverse biological characteristics and play a vital role in how plants respond to stress. This rapidly evolving area of research has explored a range of applications. However, significant challenges persist regarding practical implementation. These challenges include the collection, identification, and development of appropriate culture systems for REs. Understanding the mechanisms that govern the synthesis and release of REs is essential for utilizing them in a sustainable and environmentally friendly manner. This review examines the current state of knowledge on the composition of REs, their production mechanisms, separation methods, and hydroponic-based collection systems. Ultimately, the choice of methodology and system design is highly dependent on specific research objectives. Future research should focus on developing advanced, non-invasive techniques for monitoring REs, investigating the molecular mechanisms that regulate their production and scaling up controlled environments or soilless culture systems for industrial applications. To fully harness the potential of REs, an interdisciplinary approach that integrates plant physiology, analytical chemistry, microbiology, and genetics is crucial.

Key Words: bioactive molecule, controlled environment agriculture, culture system, plant natural compound, soilless culture, specialized metabolite

Citation: Malik S, Yousefzadi M, Sytar O, Abiri R, Sharma P, Atabaki N, Jain A, Chauthe S, Ghorbanpour M. 2026. Unveiling root exudates: Composition, characterization, dynamics and collection strategies. *Pedosphere*. **36**(2): 442–459.

INTRODUCTION

The global population is expected to continue rising at a rapid pace over the next 50 to 60 years, reaching a peak of 10.3 billion in the mid-2080s, up from 8.2 billion in 2024 (United Nations, 2024). To adequately feed these 10.3 billion people, food production must be increased by 50%–70%, as recommended by the World Health Organization and the United Nations (Hunter *et al*., 2017; Falcon *et al*., 2022; Upadhyay *et al*., 2022; Roy *et al*., 2024). Root exudates (REs) present a promising avenue for obtaining bioactive substances that could be beneficial in the food and pharmaceutical industries, as well as for enhancing agricultural productivity.

Roots play a vital role in the growth and development of vascular plants. They are essential for the overall health of the plant, as they absorb water and nutrients from the soil and transport them to the stem. Additionally, roots help anchor the plant securely to the ground. In response to various biotic and abiotic challenges, as well as attacks from soil microorganisms, roots secrete a wide array of chemical substances into the rhizosphere (Balyan and Pandey, 2024; Ma *et al*., 2024; Malik *et al*., 2024; Zhang *et al*., 2024). To protect themselves, plants continuously release a diverse range of biologically active compounds through their roots. This process is known as root exudation, and the substances released are referred to as REs (Shi *et al*., 2024). Root exudates comprise a mixture of plant-derived compounds, both high and low molecular weight, which can be either liquid or gaseous. These compounds may include sugars, amino acids, vitamins, organic acids, phenolics, enzymes, and mucilages, constituting 5%–21% of the photosynthetic matter (Balyan

---

[*] Corresponding author. E-mail: soniamalik@babafaridgroup.edu.in.
[†] Present address: Agronomic and Agri-food Center of the Province of Hainaut (CARAH), Ath, Belgium.

and Pandey, 2024). Root exudation is part of a broader process called rhizodeposition, where compounds derived from roots are released during plant growth (Guerrieri *et al*., 2019). The quantity of REs and the rate of exudation can vary significantly depending on the plant species, cultivar, age, developmental stage, and the presence of different biotic or abiotic stresses (Badri and Vivanco, 2009). For example, over 500 compounds have been identified in the REs of *Arabidopsis thaliana* during various growth stages and with natural intraspecific variability (Mönchgesang *et al*., 2016; Zhao *et al*., 2021).

Root exudates serve multiple functions, ranging from ecological interactions to biological activities, which can have economic or industrial value for humans. For example, artemisinin, produced and exuded by the roots of sweet wormwood, has been commercially utilized as an anti-malarial drug (Al-Khayri *et al*., 2022; Sharma G *et al*., 2023). Therefore, large-scale production of this compound could aid in the development of novel and cost-effective technologies, offering an alternative to the tedious processes currently used for extracting specialized metabolites from plants. Additionally, REs are a source of novel phytochemicals, including both constitutively secreted and inducible compounds. Consequently, root exudation is increasingly being recognized as an effective and unique form of "phyto-manufacturing", facilitating the production of plant-derived specialized metabolites (Cai *et al*., 2012).

Exudates are continuously released into the medium or rhizosphere, making root exudation a cost-effective approach. Root exudates from wild crop relatives can also enhance agricultural output, potentially reducing our reliance on fertilizers and pesticides (Preece and Peñuelas, 2020). These exudates have been shown to increase nutrient availability by directly mobilizing compounds essential for the uptake of phosphorus (P), nitrogen (N), and iron by plants (Dakora and Phillips, 2002; Tsai and Schmidt, 2017). Fungi and bacteria obtain their carbon (C) from REs. Additionally, REs selectively influence microbial chemotaxis by attracting beneficial microorganisms, such as N-fixing bacteria, while deterring pathogenic species (Walker *et al*., 2003). Root exudates can be collected in three ways: artificially (using hydroponics), semi-naturally (through leachate collection techniques on whole-root systems), or in-field (by planting saplings in rhizotrons for *in situ* exudate collection), which can also involve extracting a root segment from its soil matrix. Distinguishing specific metabolites within the soil can be challenging due to the complex soil matrix, which can hinder RE recovery and contains active microbial communities that rapidly degrade these compounds (Williams *et al*., 2021). Understanding root exudation is crucial for enhancing our knowledge of plant-soil interactions, particularly in response to common factors and increasing stressors. Gaining a thorough understanding of root exudation may provide a new approach to boost global food production sustainably and eco-friendlily, addressing the needs of the world's growing population and evaluating the future functioning of our agricultural and natural ecosystems.

Root exudates have been widely studied over the past decade, primarily their connection with microbial communities in the rhizosphere, particularly plant growth-promoting rhizobacteria (PGPR) (Badri and Vivanco, 2009; Deshpande *et al*., 2011; Doornbos *et al*., 2012; Ulrich *et al*., 2022; Upadhyay *et al*., 2022). Chen and Liu (2024) have thoroughly described the role of REs in the colonization of beneficial rhizobacteria. Several research and review articles have highlighted the therapeutic potential of exudates released from various herbaceous plants and a few tree species, such as jujube, apple, and peach (Zhang *et al*., 2007). A review of the literature indicates that plant REs possess significant therapeutic potential, demonstrating bioactivity against various diseases while exhibiting low cytotoxicity (Licá *et al*., 2018, 2021; Ninković *et al*., 2024). However, there has not been a comprehensive evaluation focusing on their components, collection, and analysis processes, or factors that influence their quantity. Thus, the present review aims to highlight these aspects and discuss the associated challenges. It provides an overview of the origins, chemical nature, and effects of REs, as well as an in-depth discussion on their composition, production mechanisms, and various separation techniques. Additionally, the use of hydroponics for RE production is reviewed.

RE COMPOSITION

In plants, the process of root exudation plays a significant role in C sequestration, which can account for up to 21% of the total C fixed *via* photosynthesis. This percentage varies depending on the type of crop or plant, its growth phase, and the availability of nutrients (Elbasiouny *et al*., 2022). Plant REs often contain substantial amounts of high-molecular-weight substances such as proteins, polysaccharides, organic acids, and mucilage, and a diverse low-molecular-weight and inorganic components, including hydrogen, hydroxide, and bicarbonate ions (Dakora and Phillips, 2002; Walker *et al*., 2003). Low-molecular-weight compounds encompass a variety of primary metabolites, including sugars, amino acids, and carboxylates, as well as specialized metabolites like flavonoids, sorgoleone, coumarin, and terpenes (Mondal and Nag, 2023; Balyan and Pandey, 2024). Table I offers a comprehensive overview of the components of REs and their roles in plant growth, as previously investigated by researchers. It is reported that RE composition varies under different conditions. Additionally, Yang *et al*. (2025) highlighted the relationship between RE composition and classical root traits related to resource acquisition across an environmental gradient.

TABLE I

Root exudate categories, specific compounds, and their functions in plants

Category	Representative examples	Function(s)	Plant species example(s)	Reference(s)
Inorganic ion and gaseous molecule	HCO_3^-, OH^-, H^+, CO_2, H_2	Chemoattractants for microbes	*Brassica napus*, *Solanum lycopersicum*	Vranova *et al.*, 2013; Haichar *et al.*, 2014
Amino acid	All 20 proteinogenic amino acids, homoserine, γ-aminobutyric acid, L-hydroxyproline, α-aminoadipic acid	Nutrient source, chemoattractants, chelators, soil acidifiers, Al detoxifiers, *nod* gene inducers, antifungal agents	*Arabidopsis thaliana*, *Phytolacca americana*, *Avena barbata*	Jones *et al.*, 2004; Strehmel *et al.*, 2014; Dhungana *et al.*, 2023
Fatty acid	Linoleic acid, oleic acid, palmitic acid, stearic acid	Inducers of local and systemic resistance against phytopathogens	*A. thaliana*, *Glycine Max*, *Glycyrrhiza glabra*, *Solanum tuberosum*	Narasimhan *et al.*, 2003; Vranova *et al.*, 2013; Strehmel *et al.*, 2014
Phenolic acid and coumarin	Cinnamic acid, ferulic acid, syringic acid, vanillic acid, umbelliferone, coumarin	Nutrient source, chemoattractants, detoxifiers, inducers and inhibitors of the rhizobial *nod* gene, promoters of microbial growth, inducers of resistance against phytoalexins	*Hordeum vulgare*, *Alnus glutinosa*, *Myricaceae* spp., *Casuarina glauca*, *Nicotiana tabacum*, *Zea mays*, *Centaurea maculosa*	Hayat *et al.*, 2017; Iqbal *et al.*, 2020; Zhang *et al.*, 2020; Preece *et al.*, 2022
Other organic acids	Phthalic acid, L-aspartic acid, citric acid, L-glutamic acid, oxalic acid, malic acid, fumaric acid, succinic acid, acetic acid, butyric acid, valeric acid, glycolic acid, shikimic acid, isocitric acid, chorismic acid, sinapic acid, piscidic acid, formic acid, aconitic acid, caffeic acid, lactic acid, tetronic acid, salicylic acid, pyruvic acid	Nutrient source, chemoattractants, chelators of poorly soluble mineral nutrients	*Lotus corniculatus*, *Pisum sativum*, *Medicago sativa*, *Lactuca sativa*, *Brassica juncea*, *Z. mays*, *Pinus sylvestris*, *Quercus robur*, *Picea abies*, *Betula pendula*, *Fagus sylvatica*, *Abies alba*	Vranova *et al.*, 2013; Haichar *et al.*, 2014; Feng *et al.*, 2018; Dhungana *et al.*, 2023
Terpenoid and flavonoid	Caryophyllene, geijerene, solanoeclepin, α-ginsenosides, strigolactones, β-myrcene, d-limonene, rhizathalene A, kaempferol, apigenin-7-O-glucoside, eriodictyol	Defense substances, antimicrobial agents against pathogens, *nod* gene inducers, nodule development regulators	*Oryza sativa*, *Z. mays*, *Glycine max*, *A. thaliana*, *Medicago truncatula*, *Capsicum annuum*, *Foeniculum vulgare*, *Pisum sativum*, *Citrus* spp.	Begum *et al.*, 2001; Rasmann *et al.*, 2005; Ali *et al.*, 2010; Yang *et al.*, 2022
Enzyme	Amylase, protease, alkaline/acid phosphatase, invertase, lipase, hydroxylase	Catalysts for nutrient transformation	*Sorghum bicolor*, *Pennisetum glaucum*, *Arachis hypogaea*	Upadhyay *et al.*, 2022
Purine, nucleoside	Adenine, guanine, cytidine, uridine	Nutrient source	*Brachiaria humidicola* (Rendle) Schweick., *Brachiaria decumbens*	Badri and Vivanco, 2009; Strehmel *et al.*, 2014; Iqbal *et al.*, 2020
Vitamin	Niacin, pantothenic acid, riboflavin, biotin, thiamine	Promoters of plant and microbial growth, anti-microbial agents against phytopathogens	*Hyoscyamus albus*, *Gossypium hirsutum*, *Picea abies*	Vranova *et al.*, 2013; López-Moral *et al.*, 2023
Anthocyanin	Cyanidin, delphinidin, pelargonidin	Mitigators of oxidative stress	*A. thaliana*	Narasimhan *et al.*, 2003; Li and Ahammed, 2023
Indole compound	Indole-3-acetic acid, brassitin, sinalexin, brassilexin, methyl indole carboxylate, camalexin glucoside	Inducers of broad-spectrum resistance to fungal pathogens	*O. sativa*, *Z. mays*, *Triticum aestivum*, *Hordeum vulgare*	Bednarek *et al.*, 2009; Haichar *et al.*, 2014; Feng *et al.*, 2018
Sterol	Campesterol, sitosterol, stigmasterol	Activators of signaling cascades, promoters of plant growth, enhancers of microbial growth	*Sophora flavescens*, *Taxus chinensis*, *Vitis vinifera*	Narasimhan *et al.*, 2003; Der *et al.*, 2024
Allomone	Juglone, sorgoleone, 5,7,4′-trihydroxy-3′,5′-dimethoxyflavone, 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one, 2,4-dihydroxy-1,4-benzoxazin-3-one	Antibacterial, antifungal, insecticidal, antifeedant, phytotoxic agents	*Brachiaria humidicola*, *Leymus racemosus*, *Z. mays*	Narasimhan *et al.*, 2003; Adedeji and Babalola, 2020
Sugar	Glucose, sucrose, galactose, maltose, ribose, xylose, rhamnose, arabinose, raffinose, deoxyribose,	Nutrient source, promoters of plant growth, enhancers of microbial growth	*Avena barbata*, *Triticum aestivum*, *Salix phylicifolia*, *Alnus incana*, *Betula pubescens*, *Picea abies*, *Quercus robur*, *Fagus sylvatica*	Vranova *et al.*, 2013; Haichar *et al.*, 2014; Yang *et al.*, 2021, 2022

Specialized metabolites found in REs primarily include phenolics, flavonoids, and terpenoids, which function as stimulants, inhibitors, or signaling molecules (Fiorilli *et al.*, 2019; Pang *et al.*, 2021). Begum *et al.* (2001) reported that flavonoids, such as apigenin-7-O-glucoside and eriodictyol, derived from pea REs, play a significant role in inducing *nod* gene expression. Under drought stress conditions, the REs of holm oak were found to contain 71% specialized metabolites, which are associated with the plant response to drought stress. Conversely, when conditions improve and recovery occurs, the composition of these metabolites shifts towards a dominance of primary metabolites. This indicates that the RE composition changed reversibly based on water conditions. In holm oak, it was observed that myricetin, quinic acid, vanillic acid, and epigallocatechin were activated and deactivated in response to drought stress (Preece *et al.*, 2022). Additionally, research on tobacco demonstrated that tartaric acid, ferulic acid, and lauric acid serve as defense substances in REs as part of a pre-infection prevention strategy (Zhang *et al.*, 2020).

Terpenes, a component of REs, exhibit a diverse range based on plant species (Huang and Osbourn, 2019). For example, the terpene (E)-β-caryophyllene, found in maize roots, has been shown to attract the entomopathogenic nematode *Diabrotica virgifera virgifera*, highlighting its potential for biological control against root pests (Rasmann *et al.*, 2005; Bergman and Dudareva, 2024). In another instance, geijerene, which is induced by the presence of root weevil larvae (*e.g.*, *Diaprepes abbreviatus*) on Swingle citrus roots, has been observed to recruit the entomopathogenic nematode *Steinernema diaprepesi* (Ali *et al.*, 2010). Additionally, the terpene solanoeclepin A has been identified as a hatching factor for cyst nematodes affecting potato and tomato plants, as reported by Schenk *et al.* (1999). Moreover, ginsenosides from the REs of notoginseng have been demonstrated to exhibit autotoxic and allelopathic effects, resulting in poor growth and reduced defense in plants (Yang *et al.*, 2015). Lastly, strigolactones from cotton REs have been found to serve as germination stimulants for witchweed and can induce hyphal branching in arbuscular mycorrhizal fungi, as demonstrated in various studies (Cook *et al.*, 1966; Akiyama *et al.*, 2005).

Key terpene compounds found in fennel REs, such as anethole, D-limonene, estragole, γ-terpenes, and β-myrcene, are reported to play a role in the interactions between fennel roots and pathogens. These compounds, particularly anethole, have been shown to induce the accumulation of reactive oxygen species in fungal hyphae as a mechanism of antimicrobial action (Yang *et al.*, 2022). Additionally, the REs of maize contain nitrogenous compounds, fatty acids, organic acids, steroids, and terpenoid derivatives, as confirmed by gas chromatography (GC)-mass spectrometry (MS) and proton nuclear magnetic resonance (^{1}H NMR) analyses. Notably, maize REs treated with *Herbaspirillum seropedicae* exhibited an increased level of terpenoid derivatives, such as kaurenoic acids, which are precursors to gibberellic acids (da Silva Lima *et al.*, 2014).

Numerous studies have demonstrated that REs are involved in various rhizosphere processes. They play well-established roles in the mobilization and acquisition of nutrients, attraction and repulsion of specific microbial species, inhibition of competing plant species, and stimulation of parasite seed germination (Strehmel *et al.*, 2014). Their quantitative and qualitative composition is undoubtedly influenced by factors such as the type of plant, the growth stage, and both biotic and abiotic environmental variables (Dhungana *et al.*, 2023).

MECHANISMS OF ROOT EXUDATION

The exudation of primary metabolites from roots is facilitated by diffusion. Both microbes and plants influence the concentration gradients, and as a result, the rate of diffusion into the soil is directly related to their nutritional status. The concentrations of exuded metabolites are highest at the root tip, where signaling molecules play a role in modifying root architecture (Canarini *et al.*, 2019). Overviews of the root exudation process in plants have also highlighted several mechanisms that enable the secretion of metabolites into the rhizosphere. These mechanisms can be categorized into passive and active transports (Fig. 1). Passive transport is the most common method, which occurs through several means such as simple diffusion, facilitated diffusion, and vesicle-mediated exocytosis (Baetz and Martinoia, 2014).

Plants primarily use simple diffusion to release low-molecular-weight chemicals such as sugars, amino acids, phenolics, and carboxylic acids. This process contributes to soil health by providing organic acids for acidification and chelation, ultimately improving the nutritional status of the soil (Ma *et al.*, 2022). Simple diffusion occurs due to the concentration gradient between the rhizosphere and the cytoplasm of root cells. Factors such as the polarity of the compounds, the integrity of root cells, and the permeability of root membranes can influence this process (Badri and Vivanco, 2009). In facilitated diffusion, ionic channels facilitate the secretion of specific carboxylates, including oxalate and malate, along with carbohydrates, which are often exuded in large quantities through the membranes. Two types of anionic channels play significant roles in the transportation and secretion of these chemicals: quick and slow anion channels. The primary difference between these channels is their activation time. The former, also referred to as rapid type, activates within a few milliseconds, while the latter, known as slow type, takes several seconds to activate (Dreyer *et al.*, 2012).

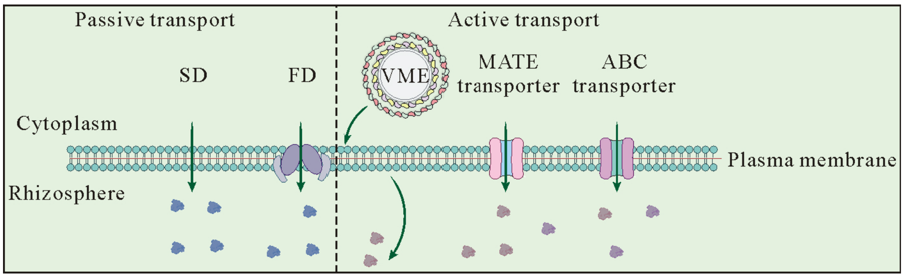

Fig. 1 Schematic diagram showing the mechanisms of root exudation across the plasma membrane, which are categorized into passive transport and active transport. Passive transport includes simple diffusion (SD) and facilitated diffusion (FD) through channels, whereas active transport occurs *via* vesicular carriers or through transporters such as those from the multidrug and toxic compound extrusion (MATE) and adenosine triphosphate-binding cassette (ABC) families. VME = vesicle-mediated exocytosis.

The aluminum (Al)-activated malate transporter (ALMT) has been extensively studied. It is responsible for the exudation of organic acids, primarily malate, and the toxic Al^{3+} ions found in soil. Research has shown that the secretion of organic acids can inactivate and chelate toxic Al^{3+} ions, with ionic channels facilitating the mechanism of Al tolerance, particularly under conditions of Al accumulation (Sharma *et al*., 2016). The ALMT family of organic acid transporters in cellular membranes has been categorized into five separate clades, comprising eight members in *Oryza sativa*, twelve in *Vitis vinifera*, and several in *Arabidopsis thaliana* (Sharma *et al*., 2016).

In addition to the significant role of ALMT in Al tolerance and its high activity in the presence of Al, other protein families, such as the multidrug and toxic compound extrusion (MATE) family of membrane transporters, are also involved in plant Al tolerance mechanisms and are responsible for citrate exudation (Liu *et al*., 2009, 2015). Furthermore, the Al-activated malate transporter 3 (AtALMT3) in *Arabidopsis thaliana* has been shown to play an active role in malate secretion, which is important under P-deficient stress (Maruyama *et al*., 2019). Moreover, the overexpression of *AtALMT1* in the presence of Al leads to increased malate secretion and contributes to the recruitment of rhizobacteria that enhance plant resistance (Kobayashi *et al*., 2013). Additionally, root plasmatic membrane proteins, such as adenosine triphosphate (ATP)-binding cassette (ABC) transporters and MATE proteins, aid in the secretion of root metabolites into the soil through active transport mechanisms (Kang *et al*., 2011; Baetz and Martinoia, 2014).

The root exudation mechanism is generally understood to operate through three distinct conceptual layers defined by their specificity: compounds (released by specific transporters), transporters (which exude various metabolites), and metabolites (the substances ultimately secreted into the rhizosphere). The ABC transporters are considered primary transporters (Jones and George, 2002), as they utilize energy derived from ATP hydrolysis to translocate a diverse range of solutes (Orelle *et al*., 2018).

RE COLLECTION METHODS

Root exudates are essential signaling molecules that facilitate communication between plant roots and the soil ecosystem. They play a significant role in influencing microbial interactions and enhancing nutrient availability in the rhizosphere (Walker *et al*., 2003; Luo *et al*., 2017; Feng *et al*., 2018; Pantigoso *et al*., 2022). Standard methods for collecting and analyzing REs are often limited by their complexity. This has driven the development of several modified approaches. While these methods may not perfectly replicate natural conditions, they still yield exudates that represent their composition and quantity reasonably well. However, there are currently few ideal methods or conditions that accurately reflect the soil environment.

Root exudates can be collected artificially *via* hydroponic systems, semi-naturally using leachate collection techniques on whole-root systems, in field by planting saplings in rhizotrons, and by extracting a root segment directly from the soil matrix (Fig. 2). Distinguishing certain metabolites within a soil matrix can be challenging because the matrix can obstruct root access and contain chemicals that are unlikely to persist in environments where microorganisms may metabolize them (Michalet *et al*., 2013; Zhang *et al*., 2014). To ensure ecologically sound collection of REs, researchers recommend washing the roots prior to collection (Williams *et al*., 2021).

Hydroponics and hybrid approaches

Research indicates that the development of hydroponics significantly affects the morphology of roots (Kawasaki *et al*., 2018), their physiological functions (Sgherri *et al*., 2010), and the overall response of the plant to environmental stress (Chen *et al*., 2018). One potential solution to address these issues is the use of hybrid RE collection techniques. These methods involve covering plants with soil, cleaning them afterward, and then transitioning to a hydroponic solution for the collection of exudates (Canarini *et al*., 2016; Oburger and Jones, 2018). An enhanced hybrid

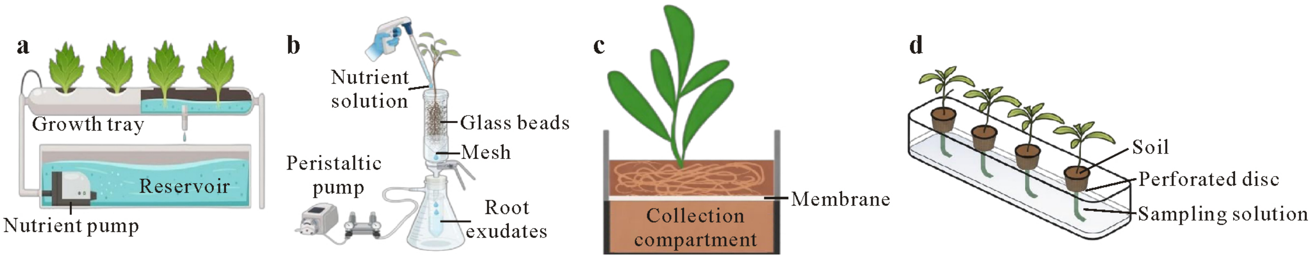

Fig. 2 Schematic diagrams showing four methods commonly used to collect root exudates: hydroponics method (a), soil column-leaching method (b), rhizotron method (c), and soil-hydroponics hybrid method (d) (partly adopted and modified from Yee *et al*. (2021) and Kumar *et al*. (2023)).

approach proposed by Williams *et al*. (2021) allows for accurate measurements of both the quantity and composition of exudates, enabling the identification of metabolite specificity among different species. Since roots grow and develop in soil, hybrid techniques facilitate a physiologically relevant assessment of REs. However, there are limitations associated with hydroponic collection, including microbial breakdown of metabolites, soil impedance, and signals from dissolved organic C. Hybrid strategies have been employed to study changes in exudate production over the growth cycles of various plants, such as rice (Aulakh *et al*., 2001) and lupine (Lucas García *et al*., 2001).

Hybrid techniques enable the application of treatments that are not possible in purely hydroponic systems. Environmental factors, such as the dry season, have been shown to alter exudation rate in sunflower and affect exudate composition in soybean (Canarini *et al*., 2016). Additionally, exudates obtained through a hybrid approach have been reintroduced into the soil to assess their impact on the respiration of soil microorganisms. This highlights that the technique is able to clarify the specific roles that certain root-released substances play in the rhizosphere (de Vries *et al*., 2019). However, despite these advantages, hybrid strategies are susceptible to issues since washing the roots can cause inevitable pressure and damage to the root system (Oburger and Jones, 2018). The extent to which this damage affects exudate composition and production is still not well understood. Many researchers have collected exudates immediately after cleaning, with little to no recovery period, and they have not examined how potential damage might influence the secretion of REs.

Soil column-leaching method

Controlled climate and sterile propagation methods are advanced techniques used to gather REs. An ideal technique allows novel *in vitro* models to provide roots with actual micro or macro-particles, while maintaining similar chemical compositions and microbial populations to mimic soil conditions and components. Although these methods have been utilized since the mid-1900s, researchers still encounter a range of challenges in the collection of REs (Curl and Truelove, 1986). In an effort to improve the reproducibility of plant habitat, Harmsen and Jager (1962) developed a clean artificial soil mix consisting of sand, kaolinite, and potassium-feldspar suspended in a liquid medium. In their studies, this artificially created soil served as a medium through which REs adhered, facilitating the release of soil components. This soil was specifically used to study the deposited N and C contents in wheat, spinach, and vetch plants (Pantigoso *et al*., 2022). Over the years, these artificial soils have been modified and improved, shifting between silica sands, quartz-based sands, and glass beads (Curl and Truelove, 1986). Utilizing these materials as a substrate provides plant models with a more natural growth system, despite the challenges of varying fluid suspension compositions. These substances possess some water-holding properties and can even be sterilized to create microbe-free soil (Curl and Truelove, 1986).

In vitro collection method

The *in situ* collection systems have several limitations, which have led many researchers to develop newer *in vitro* techniques for the extraction REs in liquid media. To address the issue of altered root morphology, researchers have suggested introducing glass beads into liquid media. This simulates the mechanical forces that roots encounter, mimicking the presence of adjacent soil particles (Vranova *et al*., 2013). Additionally, to better replicate a realistic *in vitro* “soil climate”, microorganisms have also been incorporated into these systems. Various strategies are being employed to effectively mimic the conditions needed for cultivating a wide range of plants through *in vitro* cultivation systems for the extraction of REs (Badri *et al*., 2013; Ray *et al*., 2018). Although the procedure commonly recommended for *Arabidopsis* has been detailed by various researchers, it can be adapted with slight modifications for different plant species (Nguyen and Kozai, 2001; Badri *et al*., 2013).

Recent reports indicate that exudation profiles can vary depending on the growth stage of plants and their environmental conditions. Therefore, it is important to identify the ideal plant growth stage for collecting REs and to modify the atmospheric conditions and other factors before collection (Pantigoso *et al*., 2022). The following steps should be followed for the effective collection of exudates: i) carefully remove the plants from their growth media, ii) rinse the plants thoroughly to eliminate any adhering chemicals or particles, and iii) transfer the plants from the fresh culture medium to sterile water. Badri *et al.* (2013) demonstrated the collection of REs from *Arabidopsis thaliana* at intervals of 18–21 d using this method, followed by allowing the plants to grow in sterile water for the next three days (or according to their growth rate). It is crucial to conduct sufficient trials that replicate this process to obtain an adequate volume of exudate for further analytical investigations. Once collected, the exudate should be filtered to remove root sheath and boundary cells using a 0.45-µm nylon filter. For MS and liquid chromatography (LC)-MS analyses, lyophilization (freeze-drying) is commonly employed to concentrate the samples into a solid form. After removing excess water and converting the liquid to solid through lyophilization, the solids can be crushed into a powder and suspended in appropriate solvents.

Limitations of current RE collection methods

Liquid culture plant development offers scientists and researchers several key insights but also presents limitations. Firstly, because roots are not exposed to natural soil particles, bacteria, and other attributes typically found in natural environments, plants grown in sterile conditions often differ from those grown in soil regarding their morphology and physiology (Vranova *et al.*, 2013). Secondly, the absence of chemically based soil gradients, which are primarily formed through diffusion, osmosis, and microbial growth in nature, poses another challenge to the growth of soilless plants. Additionally, the lack of rhizosphere created by plant roots influences the composition of exudates (Pinto *et al.*, 2008). As noted by Miller *et al.* (2020), *in vitro* simulations may struggle to accurately replicate the natural metabolic environment of plants. For the extraction of RE where aseptic conditions are not required, techniques have been developed to collect leachate from plants grown in greenhouse environments or using filter papers applied to specific root regions (Zhu *et al.*, 2016). Haase *et al.* (2007) reported that *in situ* collection of RE is feasible by employing filter papers on root surfaces, which act as artificial sorption media for plant growth. Mini-rhizotrons, or rhizobox microcosms, are used to grow plants and gather their REs (Haase *et al.*, 2007; Neumann, 2007). While collecting RE through filter papers is one approach, Zhu *et al.* (2016) proposed a simpler method involving leachate collection from soil-grown plants in pots located in nurseries or greenhouses. Accurately capturing the chemical complexity of REs under natural rhizosphere conditions remains a significant methodological challenge.

The selection of solvents is crucial for the efficiency of metabolite extraction and for maintaining their chemical stability. Water and aqueous buffers are typically used to extract hydrophilic compounds while preserving near-physiological conditions. Methanol and ethanol are commonly employed to extract a wide range of polar to moderately nonpolar compounds. More nonpolar solvents, such as acetone and acetonitrile, are particularly effective for isolating specialized metabolites, including phenolic acids and terpenoids. Some protocols use mixtures of solvents to balance polarity and enhance recovery across various chemical classes. The choice of solvent not only affects metabolite solubility and stability but also impacts the sensitivity and resolution of downstream analytical detection. For example, in addition to water-soluble metabolites, plant roots also release a variety of lipid-based compounds, such as triacylglycerols, highlighting the need for tailored extraction strategies (Couvillion *et al.*, 2025).

The choice of solvent is crucial for targeting specific classes of metabolites. Hydrophilic and charged compounds, such as amino acids, sugars, and organic acids, are best extracted using water or aqueous buffers at a controlled pH. This approach helps to preserve their ionic forms and chemical stability (Escolà Casas and Matamoros, 2021). In contrast, hydrophobic or uncharged compounds, like lipids, terpenoids, and phenolics, require organic solvents such as methanol, ethanol, acetone, and acetonitrile. To enhance extraction efficiency for various polarities, solvent mixtures are often employed (Lee *et al.*, 2024). Lipidic exudates, including triacylglycerols, phospholipids, and sterol derivatives, are particularly important and require nonpolar solvents or biphasic partitioning systems for effective extraction (Couvillion *et al.*, 2025). The methods used to collect REs must align with specific experimental objectives. Sterile hydroponic systems are frequently utilized to obtain uncontaminated exudates for studying plant-specific metabolite production. Conversely, soil-based collection techniques or the exogenous application of RE substances allow researchers to explore the ecological impacts of these compounds, especially regarding their influence on soil microbial communities (Badri *et al.*, 2013). Additionally, environmental factors and agricultural practices, such as intercropping, play significant roles in modulating the composition and dynamics of REs, further complicating their analysis and interpretation.

RE IDENTIFICATION AND QUANTIFICATION METHODS

Roots release a diverse range of compounds, which can be broadly categorized as primary and specialized metabolites based on their functions in plants (Escolà Casas and Matamoros, 2021). To effectively separate, identify, and quantify compounds in REs, it is essential to have prior knowledge of their presence. This knowledge helps in selecting the appropriate analytical methods. Chromatography is a technique commonly used to separate and analyze biomolecules from complex mixtures. Typically, chromatography is followed by spectroscopy, forming a standard sequence for analyzing compounds in REs.

The high-performance LC (HPLC) method combined with ultraviolet (UV) or photodiode array detection is commonly used for the separation, qualitative, and quantitative analysis of REs that contain known small molecules. The identification of these compounds usually relies on comparisons with authentic standards. A reversed-phase HPLC method has been employed to analyze low-molecular-weight organic acids found in plant REs. This method allows for the separation and quantification of various organic acids, including lactic acid, citric acid, *cis*-aconitic acid, maleic acid, succinic acid, fumaric acid, malic acid, trans-aconitic acid, malonic acid, and acetic acid. Additionally, the proposed method has been utilized to characterize REs from plants such as *Banksia attenuate*, white lupin, and chickpea. The ability to resolve certain well-known organic acids is advantageous, and this method can be applied to various other samples. It is important to note that both the standards and the samples must be acidified to a pH of 4 or lower (Cawthray, 2003). In another study, researchers aimed to separate and quantify low-molecular-weight organic acids in the REs of the chromium-hyperaccumulator *Leersia hexandra* Swartz using HPLC. They analyzed several organic acids, including citric acid, maleic acid, lactic acid, oxalic acid, tartaric acid, malic acid, acetic acid, and formic acid (Wu *et al*., 2018).

The LC-MS technique combines the physical separation capability of LC with the mass analysis capability of MS. Researchers have developed a novel ultra-high-performance LC-tandem MS (MS/MS) method for the direct determination of strigolactones in REs and extracts in less than 11 min. This method allows for the simultaneous quantification of compounds such as fabacyl acetate, 5-deoxystrigol, orobanchyl acetate, strigol, orobanchol, solanacol, and 7-oxoorobanchyl acetate (Rial *et al*., 2019). Recently, researchers described the development of an LC-MS/MS method for quantifying strigolactones in REs and extracts using GR24 (a synthetic analog of strigolactones) as an internal standard (Rial *et al*., 2020). Additionally, a team of scientists evaluated and quantified natural strigolactones from REs using LC-MS/MS (Xie *et al*., 2021). Furthermore, the quantification of six low-molecular-weight organic acids in REs at sub-micromolar detection limits has been achieved using targeted ultra-performance LC combined with high-resolution MS/MS. They employed targeted and matrix-assisted laser desorption/ionization mass spectrometry imaging to detect the spatial location of malic acid and citric acid with high specificity in roots and exudates. The analysis time was reported to be less than 5 min per sample (Gomez-Zepeda *et al*., 2021).

The GC and GC-MS methods are commonly used for analyzing metabolites like amino acids, fatty acids, sugars, and organic acids found in various plant extracts and REs. Before analysis, samples are treated with appropriate derivatizing agents to convert the metabolites into a volatile form. A study by Sun *et al*. (2016) quantified fatty acid amides, such as erucamide and oleamide, in duckweed plant extracts. In another research effort, Bacilio-Jiménez *et al*. (2003) conducted a chemical characterization of REs from rice using GC with a flame ionization detector. Researchers also performed GC-MS analysis of rice REs in aseptic conditions, detecting several metabolites, including sugars (glucose and fructose), organic acids, fatty acids, and amino acids (aspartic acid and L-isoleucine). This was achieved after derivatization with N-methyl-N-trifluoroacetamide and methoxyamine hydrochloride (Suzuki *et al*., 2009). Similarly, Bowsher *et al*. (2015) employed GC-MS to analyze the temporal dynamics of wild sunflower REs, detecting over 60 metabolites, including amino acids, sugar alcohols, phosphates, sugars, and organic acids in significant quantities.

The NMR and GC-MS techniques can be used for a comprehensive analysis of organic ligands in whole REs. The composition of the exudates can be analyzed using ^{1}H and ^{13}C multidimensional NMR and silylation GC-MS. These techniques require minimal sample preparation, and they can achieve negligible loss of unidentified components, simultaneous characterization of constituents in a complex mixture, and reduced overall analysis time. Researcher reported the analysis of various organic and amino acids, including mugineic acid-family phytosiderophores such as 3-epihydroxymugineic acid (Fan *et al*., 1997). In addition, the researchers carried out a thorough chemical profiling of REs from gramineous plants, employing two-dimensional NMR along with GC-MS and high-resolution MS. Using these analytical techniques, they achieved *de novo* identification of a wide range of compounds directly in the crude REs of different plants. The components were quantified utilizing GC-MS, followed by ^{1}H NMR (Fan *et al*., 2001).

The ion-exclusion chromatography (IEC) technique is primarily used for the separation of ionizable molecules, including carboxylic acids, inorganic weak acid anions, weak organic bases, and water. When coupled with MS, it allows for accurate determination of the masses of individual ions (Robards *et al*., 2004). Researchers have successfully confirmed and quantified carboxylic acids derived from plant raw extracts using IEC in combination with electrospray ionization (ESI)-MS (IEC-ESI-MS). This combination enhances both specificity and sensitivity in detection. The separation of nine carboxylic acids, namely maleic acid, oxalic acid, lactic acid, aconitic acid, malonic acid, succinic acid, tartaric acid, pyruvic acid, and citric acid, can be achieved within eight minutes using the IEC-ESI-MS method. In this setup, the ESI generates signals from negative ions in the negative ionization mode. Under optimized MS conditions, a linear relationship between peak area and carboxylic acid concentration was observed in the range of 50–25 000 μg L^{-1} for

MS detection. Thus, the ESI-MS method is effective for analyzing and quantifying carboxylic acids in raw extracts (Chen *et al*., 2008).

The thin-layer chromatography (TLC) is a quick, affordable, simple, and versatile method for RE separation. In one study, the analysis of cotton REs using TLC involved a mobile phase made up of ethyl acetate, n-propanol, acetic acid, and water in a ratio of 4:2:2:1. The developed retention factor (Rf) values were compared to standard values for individual components. Similarly, the analysis of amino acids was conducted using two different mobile phases. One mobile phase, consisting of n-butanol, acetic acid, and water in a ratio of 4:1:1, demonstrated higher resolution than another phase with a composition of n-butanol, acetic acid, and water in a ratio of 3:1:1. The Rf values of the obtained spots were compared to standard values (Rathod and Channarayappa, 2020). Additionally, guava extracts were analyzed using TLC on silica-coated Al plates, which featured a 250 μm-thick layer of fluorescent indicator. This approach facilitated the separation of major components (Souza *et al*., 2023).

Calorimetry is an important technique for investigating the energetics of biomolecules. Two widely used methods in this field are differential scanning calorimetry and isothermal titration calorimetry (ITC), both of which are employed to identify the compounds responsible for chemotaxis in rhizobacteria and their corresponding sensing chemoreceptors in plants. A team of scientists conducted ITC analysis on the PGPR *Bacillus amyloliquefaciens* SQR9 to understand the interaction of its methyl-accepting chemotaxis proteins (MCP) with REs. The study found that McpA was primarily responsible for sensing organic acids and amino acids, while McpC primarily detected amino acids (Feng *et al*., 2018). In a related study, researchers used ITC to confirm the binding of the antibacterial agent formic acid to Atu0526, a Cache-type chemoreceptor from *Agrobacterium fabrum* C58 (Wang *et al*., 2021). Another investigation reported the use of ITC to analyze the chemotactic response of the McpS chemoreceptor from *Pseudomonas putida* to the tricarboxylic acid cycle intermediates. The results indicated that ITC could differentiate between strong attractants (such as malate, succinate, fumarate, and oxaloacetate) and weak attractants (like citrate and iso-citrate) (Lacal *et al*., 2010, 2011).

Researchers conducted a characterization of the secondary metabolites of REs in two cultivars of *Gladiolus* using Fourier-transform Raman, Fourier-transform infrared spectroscopy, ^{1}H NMR, and differential scanning calorimetry. The two cultivars exhibited different levels of resistance and susceptibility to the pathogen strain *Fusarium oxysporum* f. sp. *gladioli*. Spectroscopic analysis revealed differences in the concentrations of aromatic-phenolic compounds, sugar-like components, carbonyls, and aliphatic compounds, while calorimetry was employed for confirmation (Taddei *et al*., 2002). In another study, Huang *et al*. (2017) utilized nano-ITC to examine the role of secondary metabolites in the behavior of engineered nanomaterials from a thermodynamic perspective, which provided essential thermodynamic insights into the interactions between nanomaterials and plant REs.

RE-RHIZOSPHERE INTERACTIONS AND IMPACTS

The rhizosphere effect refers to the various processes occurring at the interface between plant roots and the soil. These processes include gradient diffusion, nutrient transformation, genetic exchange, microbial activity, and root exudation (Starkey, 1983). However, when plant roots heavily absorb organic C compounds, it can limit the availability of other nutrients in the rhizosphere (Kuzyakov, 2002). While it is less commonly discussed, roots can also uptake certain C compounds, such as sugars and organic acids, under specific environmental conditions (Singh *et al*., 2025). This reuptake affects nutrient dynamics in the rhizosphere. It is estimated that about one-third to one-half of the total fixed C (assimilated C) is allocated below ground. Notably, 15%–25% of these organic compounds are secreted from plant roots into the soil, promoting rapid C turnover in the rhizosphere (Kuzyakov, 2002). Nonetheless, the intensive uptake of C by plant roots can lead to the depletion of other nutrients in the rhizosphere (Breland and Bakken, 1991; Haldar and Sengupta, 2015). In contrast, in root-free sections of soil, C levels are limited, while the availability of other nutrients remains relatively high (Haldar and Sengupta, 2015). This disparity creates a significant difference in nutrient dynamics between the rhizosphere and the root-free zones.

Plants primarily communicate with their biotic environment through REs, which facilitate various processes and interactions, including nutrient absorption, resource competition, signaling between species, and the attraction of microorganisms. Different plant species maintain unique microbial communities in their rhizosphere by providing a diverse and C-rich environment (Pantigoso *et al*., 2022). This microbial community benefits the host plant by offering various fitness advantages, influencing community structure, and enhancing beneficial traits. Additionally, compounds in REs play a vital role in developing stress-resistant microbiota in plants, helping to mitigate the impacts of abiotic and biotic stresses such as disease, drought, and nutrient deficiency (Trivedi *et al*., 2020).

RE-microbe interactions

Roots play a crucial role in controlling the local soil microbial ecosystem. They help defend against herbivores, promote advantageous symbiosis, alter the chemical and physical compositions of the soil, and prevent the growth of competing plant species by exuding a diverse range of chemicals (Lamichhane *et al.*, 2024). In addition to providing an environment rich in C and energy, plants can identify and interact with various microorganisms present in the rhizosphere (Dhungana *et al.*, 2023). They establish communication with soil microbial populations by generating signals that regulate colonization. Through their REs, plants mediate both positive and negative interactions in the rhizosphere. Beneficial symbiotic relationships, such as those with rhizobia, mycorrhizae, and PGPR, are examples of positive interactions. Conversely, interactions with pathogenic bacteria, invertebrate herbivores, and parasitic plants represent negative interactions (Haichar *et al.*, 2014). Researchers have demonstrated that sweet basil roots infected with *Pseudomonas aeruginosa* produce rosmarinic acid, a multipurpose caffeic acid ester that exhibits antibacterial properties against *P. aeruginosa in vitro* (Walker *et al.*, 2004; Rolfe*et al.*, 2019). Genomic data indicate that natural compounds such as flavonoids, terpenoids, benzoxazinones, and antibacterial indoles can be produced by species like rice, maize, soybean, *Arabidopsis thaliana*, and *Medicago truncatula* during stress conditions (Bais *et al.*, 2006; Chai and Schachtman, 2022).

A special area of study focuses on plant roots and microorganism interactions, with a particular focus on the effects of co-cultivation on the production and release of REs. Leoni *et al.* (2021) reported that legumes responded positively to co-cultivation with wheat by promoting nodulation and increasing the exudation of allelopathic flavonoid compounds. It was observed that changes in flavonoid concentration involved substances such as daidzein, formononetin, genistein, and medicarpin, which play a role in regulating plant-plant interactions. The intentional release of REs as signaling molecules can help assess plant stress status in relation to rhizospheric microorganisms and neighboring plants (Sharma I *et al.*, 2023). Rhizospheric microorganisms utilize REs as organic C sources, and their composition varies depending on whether plants interact with pathogens or other plants above or below ground. Under biotic stress conditions, certain exudates are secreted, altering the structure of the rhizospheric microbial community and enhancing plant health. Therefore, plant stress can be regulated by manipulating the secretion of REs, which may be commercially utilized as a sustainable method for maintaining healthy crops and agricultural systems.

Relations between REs and root system architecture (RSA)

The RSA is primarily influenced by plant REs (Badri and Vivanco, 2009). Although various regions within the root system are involved in REs, the area just behind the root tip is recognized as the most crucial zone for secretion across different plant species (Haldar and Sengupta, 2015; Ma *et al.*, 2016). Notably, different parts of the root system release distinct chemical compounds. For example, the entire root excretes aspartic acid, while root hairs secrete phenylalanine, leucine, valine, and glutamic acid. Additionally, the root elongation and meristem zones are known to exude threonine and asparagine (Harris, 2015). Moreover, non-diffusible materials are secreted from the lateral and primary root tips of wheat, while diffusible compounds are secreted along the entire length of wheat roots (Haldar and Sengupta, 2015). The apical meristem zone of plant roots is protected by the root cap, which sheds border cells as the root penetrates the soil. Research has indicated that the number of border cells can vary, and these cells are capable of producing polysaccharide mucilages, contributing roughly 10% of the total C and 2%–12% of the total rhizodeposition released by roots (Eshel and Beeckman, 2013).

Evidence suggests that REs are one of the most significant mediators of interactions between plant species, which lead to changes in RSA (Zhang *et al.*, 2022). For instance, kin plants and stranger populations exhibited significantly fewer lateral roots than solo controls (single plants), and this difference was directly influenced by REs acting as cues (Palmer *et al.*, 2016). In contrast to closely related plants or their REs, rice seedlings exposed to distantly related plants or their REs developed larger root systems. Sodium orthovanadate, an inhibitor of root secretion, further supports the role of REs in stimulating changes in RSA (Yang *et al.*, 2018). These findings may have agricultural applications for manipulating plant systems. Root exudates can be utilized to engineer a resilient plant microbiome, thereby enhancing plant health and stress resilience in agriculture (Afridi *et al.*, 2024).

RE MODULATION UNDER VARIOUS STRESS CONDITIONS

The composition and quantity of REs are influenced by various abiotic and biotic factors, particularly the position of roots. Abiotic factors include anthropogenic activities, grazing patterns, and other environmental conditions. In contrast, biotic factors are related to plant characteristics, such as its age and genotype (Darwent *et al.*, 2003; Philippot *et al.*, 2013). Environmental conditions that affect root exudation encompass humidity, light, moisture content, pH, and soil texture. High soil moisture can lead to hypoxia, resulting in the accumulation of alanine, lactic acid, and ethanol, along with an increase in anaerobic respiration within the rhizosphere (Li *et al.*, 2010). Importantly, genotype has been identified as a crucial factor influencing REs. For instance, eight different accessions of *A. thaliana* exhibited distinct secretions of chemical compounds under uniform environmental conditions (Micallef *et al.*, 2009).

Plant age

As mentioned earlier, plant age and the phase of vegetation are important factors that influence REs. The lowest levels of REs have been recorded during the transition from seedling to flowering stages, while REs tend to decrease during the plant maturity phase (Williams *et al.*, 2022). Generally, a positive correlation exists between root growth and root exudation patterns (Aulakh *et al.*, 2001). Similarly, research has shown a positive correlation between age-related resistance in plants and the levels of defense-related proteins and phenolic compounds in the roots of *Arabidopsis* (De-la-Peña *et al.*, 2010).

Heavy metals

The presence or absence of toxic metals and specific nutrients is one of the important factors influencing soil composition. In the presence of cadmium, copper, and zinc, the REs (mainly oxalic acid) of potential hyperaccumulators such as *Poa annua* and *Malva sylvestris* decreased (Montiel-Rozas *et al.*, 2016). However, in the rhizosphere, a common homeostatic ecosystem response to heavy metal stress includes synergistic interactions between bacteria and plants (Barra and Terenzi, 2021). Root exudates may act as electron donors, and certain specialized metabolites can be utilized by metal-reducing bacteria to detoxify heavy metals (Simón Solá *et al.*, 2019). A study on REs from the lead (Pb) accumulator *Sedum alfredii* under Pb stress demonstrated that oxalic acid, galactonic acid, and glyceric acid were effective in removing Pb from the soil (Luo *et al.*, 2017; Xu *et al.*, 2024). Histidine in REs may function as a nickel-detoxifying agent (Salt *et al.*, 2000), while organic acids contribute to Al tolerance (Ma *et al.*, 1997). Differences in the responses of two cultivars of *Dianthus caryophyllus* under cadmium stress revealed differences in RE composition. The free amino acid and organic acid contents in the REs of both cultivars were reportedly reduced. In contrast, the soluble sugar content in the REs of one cultivar increased, while it decreased in the other (Wu *et al.*, 2021).

Drought and heat

Two major issues we are currently facing are the reduction of water availability and the increase in global temperature, which lead to significant agronomic and economic losses worldwide (IPCC, 2022). Over the years, extensive research has been conducted on the impacts of individual abiotic stressors on plants. However, plants typically experience a combination of various stressors rather than a single one. Numerous studies have shown that responses to coupled stresses can result in antagonistic or synergistic effects instead of simply additive ones (Tiziani *et al.*, 2022). Therefore, investigating a single stressor alone cannot adequately predict outcomes. It is crucial to understand how plants respond to different types of abiotic stresses. One study found that levels of certain reactive exudates, such as proline, threonine, and asparagine, increased during drought stress (Zhang *et al.*, 2010). Malic acid, a known reactive exudate, functions as a chemoattractant for *Bacillus subtilis* in the rhizosphere of soybean and sorghum plants under drought stress (Henry *et al.*, 2007; Santana *et al.*, 2020). Additionally, in maize plants, the levels of aconitic acid, total phenols, and flavonoids are higher under heat stress than under drought stress, highlighting that the combined effects of heat and drought might influence exudation differently than each stress does alone. Interestingly, flavonoids are not present in plants subjected to combined stress. In response to drought stress, metabolites such as protocatechuic acid and mellein are down-exuded, while resveratrol, peonidin 3-O-(6$''$-acetyl-galactoside), and luteolin 7-O-(2-apiosyl-glucoside) are up-exuded. Under combined heat and drought stress, researchers reported an increase in different phenolic and flavonoid compounds, including down-exuded metabolites like α-aminoadipic acid, sorgolactone, and 6-geranylnaringenin, as well as up-exuded compounds like lutein, palmitic acid, luteolin 7-O-rutinoside, hesperidin, naringin, 6$'$-malonate, luteolin 7-O-malonyl-glucoside, and L-tryptophan (Tiziani *et al.*, 2022). For example, phenolic compounds are exuded in P-deficient soils, where the secretion of oxalic, malic, and citric acids increases to help detoxify Al (Wang *et al.*, 2007). It has been demonstrated that overexpressing genes involved in organic acid secretion led to organic acid exudation in *Arabidopsis* seedlings in response to P shortage and Al toxicity (Gomez-Zepeda *et al.*, 2021). Moreover, different signaling molecules, such as flavones and flavanones, were exuded in N-deficient soils (Abdel-Lateif *et al.*, 2012). A recent study by Hou *et al.* (2025) showed how drought affected the rate of root exudation in various plant species. They reported that drought-induced changes in root exudation led to increased specific respiration rates in plants, which is one of the strategies plants use to cope with drought conditions.

Phytopathogens

Over time, host-specific phytopathogens can accumulate in the soil surrounding terrestrial plants, negatively affecting plant performance. Various functions in the rhizosphere, such as the development of beneficial plant species, are influenced by REs, which act as substrates and signaling molecules for soil microbes (Bais *et al.*, 2006). Recent studies show that plants respond to biotic stressors, such as pathogens or herbivores, by altering the chemistry of their REs to promote the establishment of beneficial bacteria that help defend the plant. This strategy is referred to as the "cry-for-help" method (Rolfe *et al.*, 2019; Zhou *et al.*, 2023).

Research indicates that plants infected by fungi increase their production of phenolic compounds, which enhances their resistance to specific fungal diseases (Pratyusha, 2022).

For instance, elicitors from *Fusarium oxysporum* f. sp. *cubense* lead to the accumulation of soluble and wall-bound phenolics and phenolic polymers in the roots of *Musa acuminata*. In contrast, infection by the white mold fungus *Sclerotium rolfsii* in *Arachis hypogea* resulted in a reduction of total soluble phenolic content (Cardoza *et al*., 2003). Additionally, non-infected *Arabidopsis thaliana* roots were found to continuously produce and release the diterpene rhizathalene A, suggesting that it plays a role in the root defense mechanism. Plants lacking rhizathalene A were shown to be more susceptible to insect herbivory (Vaughan *et al*., 2013). Numerous studies have demonstrated how different components of REs influence phytopathogens and herbivores in various crop and grass species, highlighting their potential as environmentally friendly biocontrol agents.

As noted, REs play a crucial role in managing both biotic and abiotic stressors. Their diverse biochemical properties provide strong evidence that they can serve as accessible and environmentally sustainable biocontrol agents in agriculture (Tiziani *et al*., 2022). Moreover, by chelating toxic ions, REs help reduce heavy metal pollution and protect agricultural plants from toxic buildup (Vaidya *et al*., 2022). They also enhance plant resistance to heat stress and drought by modulating water absorption and stress-responsive pathways, either individually or in combination (Vives-Peris *et al*., 2018; Sharma I *et al*., 2023). The adaptability and ecological benefits of REs extend beyond agriculture. They have potential applications in industrial biotransformations and bioremediation (Eze and Amuji, 2024). This dual purpose underscores their significance in promoting sustainable farming practices and offering innovative solutions for industrial and environmental applications.

HYDROPONIC SYSTEMS FOR RES AND AUTO-TOXICITY ALLVIATION

Many studies have explored plant systems for the purpose of collecting RE. However, these systems are often limited because they require uprooting the plant to collect the exudate. To address this issue, controlled environment agriculture, including hydroponics, was developed. The root exudation process and the effects of environmental factors in soilless culture systems have recently been reviewed by de Haas *et al*. (2025). Horticultural crops can be grown under controlled conditions in hydroponic systems, with and without the use of a substrate (Lopez-Guerrero *et al*., 2022). Camli-Saunders and Villouta (2025) examined the composition, functions, and influences of vegetable REs within controlled environment agriculture systems. The advantages of hydroponic systems include independence from soil quality, controlled growth, energy savings, and higher plant production per unit area (van Os, 1999). Hydroponic systems are typically classified into closed and open systems. In an open hydroponic system, which is used in areas without environmental hazards, nutrient solutions flow through the system once and are then discarded (Nederhoff and Stanghellini, 2010). In contrast, a closed hydroponic system recycles nutrient solutions without releasing them into the environment, making it a useful tool for plant cultivation in sensitive areas (Ruijs, 1992; van Os, 1994). Despite the advantages of closed hydroponic systems, they also face significant challenges. One notable issue is auto-toxicity, which can occur when certain REs, particularly toxic compounds or excess nutrients, accumulate in the nutrient solution. While some REs are indeed toxic and may require degradation (Asaduzzaman and Asao, 2020), others are not. For example, an inhibitory effect was observed in tomato plants grown in hydroponic systems due to the acidity of the nutrient solution resulting from the accumulation of aromatic acids (Asaduzzaman *et al*., 2022). Moreover, fruit yield reductions have been reported in the late reproductive phase of cucumber plants as a result of toxic chemical exudation, specifically 2, 4-dichlorobenzoic acid, into the nutrient solution (Asao *et al*., 1998, 1999). The growth and yield of *Cryptotaenia japonica* were also negatively affected by acidified REs in hydroponic systems (Koda *et al*., 1977). Furthermore, research indicated that lettuce cultured in a closed hydroponic system with continuously recycled tap water containing moderate to high alkalinity levels experienced nutrient deficiencies, reduced shoot growth, and increased electrical conductivity (Miller *et al*., 2020). As acids and toxins accumulate in closed systems, it is essential to identify and clarify these harmful chemicals.

Auto-toxicity significantly limits plant growth and productivity in closed hydroponic systems. Various methods, including photocatalytic treatment, electro-degradation, and the use of activated C (AC), have been employed to remove accumulated toxic compounds from these systems (Hosseinzadeh *et al*., 2017). However, it is essential to consider that these treatments may also impact the structure or availability of beneficial REs, potentially altering the overall chemistry of the rhizosphere and the interactions between plants and microbes.

Over the last two decades, semiconductor photocatalysis has emerged as an efficient and intriguing method for water purification. While there are various types of semiconductors, sulfides, and metal oxides, such as iron trioxide, cadmium sulfide, tungsten trioxide, zinc sulfide, zinc oxide, and titanium dioxide (TiO_2), have gained more attention in hydroponic systems (Bekbölet *et al*., 1996; Keller *et al*., 2003). Among these, TiO_2 is particularly notable as a semiconductor photocatalyst due to its low production cost, as well as its biological and chemical inertness (Mills and Le Hunte, 1997). It is capable of absorbing UV light with a wavelength of approximately 380 nm or shorter, which corresponds to photons with energy higher than its band gap. This absorption leads to strong oxidation effects that decompose organic compounds adsorbed on its surface into carbon dioxide (Daels *et al*., 2015). Furthermore, significant degradation of phytotoxic substances in hydroponic systems has been observed when treated with immobilized nano-TiO_2 (Qiu *et al*., 2013). Notably, the application of a nano-TiO_2 photocatalyst has been found to increase asparagus yields by approximately 1.6 times in a hydroponic system (Sunada *et al*., 2008). Similarly, the growth and yield of rose plants improved when TiO_2 photocatalyst was utilized in a closed hydroponic system (Miyama *et al*., 2012).

Electrochemical degradation (ED) has been employed to oxidize and degrade phytotoxic substances and phenols from organic pollutants or waste in closed hydroponic systems. The ED compounds are rapidly oxidized at the anode side, resulting in their decomposition into carbon dioxide. Consequently, ED can decompose allelochemicals such as benzoic acid. The decomposition products released into the nutrient solution could thereby effectively reduce autotoxicity in the hydroponic system (Hosseinzadeh *et al*., 2017). Research has shown that treating the closed hydroponic systems of strawberry plantlets with ED leads to an increase in their growth. In a previous study, the benzoic acid in the nutrient solution decomposed when titanium was used as the cathode, and a ferrite rod was utilized as the anode (Asao *et al*., 2008).

The AC is an affordable, amorphous, organic adsorbent made from C-rich materials. It is treated to develop a highly porous structure with a large surface area (Alhamed, 2006). Biologically activated C has been used to remove phytotoxic substances from plant cultures, particularly *in vitro* systems rich in specialized metabolites. For instance, toxic chemicals from REs can be eliminated by adding AC to the hydroponic solution (Koda *et al*., 1977; Asao *et al*., 1998, 1999; Sato, 2004). The use of biologically activated C has several advantages, including low energy and operating costs, low molecular weight, and a high affinity for hydrophobic substances (Ying and Weber, 1979). Among various removal techniques, the AC method is the most common and straightforward for eliminating REs in closed hydroponic systems. For example, the addition of AC to a closed hydroponic system with tomato plants resulted in increased fruit yield and plant dry weight, while reducing C concentration in the nutrient solution (Yu and Matsui, 1993; Yu *et al*., 1993). Notably, the shoot dry weight and leaf count of taro plants were lower in a closed hydroponic system without AC compared to those with AC (Asao *et al*., 2003). Similarly, bean plants grown in a closed hydroponic system without AC showed reduced seed fresh mass, seed and pod quantity, and pod fresh mass compared to those grown in non-renewed systems with AC (Asaduzzaman and Asao, 2012).

Addressing challenges in closed hydroponic systems necessitates effectively separating nutrients and exudates from impurities. Techniques such as electrodialysis, AC filtering, and photocatalysis have been shown to be beneficial. Unlike electrodialysis, which uses electrical currents to decompose pollutants while preserving nutrient integrity, photocatalysis employs light to activate a catalyst that catalyzes the breakdown of organic impurities. For the AC filtering method, AC purifies the nutrient solution by absorbing contaminants. When integrated, these methods enhance the system's efficiency by preventing toxic material accumulation, promoting healthier plant growth, and ensuring the long-term sustainability of hydroponic systems. Combining these techniques results in a more reliable and productive closed hydroponic system. Further research is essential to improve hydroponics for supporting horticultural crops and utilizing REs in both industrial and food applications without harmful substances. To boost crop yield through the use of the RE-PGPR alliance, it is crucial to conduct focused analyses and research on harnessing the beneficial characteristics of REs.

CONCLUSIONS

Exudates secreted by plant roots have significant potential to enhance agricultural productivity and serve as sources of bioactive compounds for the food and pharmaceutical industries. These exudates consist of a complex array of primary and specialized metabolites that play vital roles in nutrient cycling, plant defense, and the development of soil microbial communities. Specialized metabolites, such as phenolic acids and terpenes, are particularly important, as they contribute substantially to plant defense mechanisms. Despite progress in characterizing these compounds, the complex processes that regulate exudate synthesis, transport, and persistence in the soil environment are not yet fully understood. Moreover, optimizing extraction techniques to accurately capture the natural conditions of the rhizosphere presents ongoing challenges. Environmental factors and agricultural practices, such as intercropping, further influence the composition and behavior of REs, adding to the complexity of their study. Future research that employs integrated multi-omics, real-time monitoring, and ecological modeling approaches will be crucial in addressing these complexities, especially in light of the growing pressures from global population growth and climate change. To effectively utilize REs for agricultural and industrial purposes, it is essential to employ diverse sampling methods, ranging from hydroponics and rhizotrons to soil-based systems, along with sophisticated analytical tools for detailed metabolite profiling. While hydroponic cultivation has its advantages, it also presents technical challenges that need to be addressed. Ongoing research and advancements in technology are vital for developing sustainable methods that balance industrial applicability with environmental stewardship. Ultimately, this will enable the practical deployment of REs across various sectors.

DECLARATION OF COMPETING INTEREST

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

REFERENCES

Abdel-Lateif K, Bogusz D, Hocher V. 2012. The role of flavonoids in the establishment of plant roots endosymbioses with arbuscular mycorrhiza fungi, rhizobia and Frankia bacteria. *Plant Signal Behav*. **7**: 636–641.

Adedeji A A, Babalola O O. 2020. Secondary metabolites as plant defensive strategy: A large role for small molecules in the near root region. *Planta*. **252**: 61.

Afridi M S, Kumar A, Javed M A, Dubey A, de Medeiros F H V, Santoyo S. 2024. Harnessing root exudates for plant microbiome engineering and stress resistance in plants. *Microbiol Res*. **279**: 127564.

Akiyama K, Matsuzaki K I, Hayashi H. 2005. Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature*. **435**: 824–827.

Al-Khayri J M, Sudheer W N, Lakshmaiah V V, Mukherjee E, Nizam A, Thiruvengadam M, Nagella P, Alessa F M, Al-Mssallem M Q, Rezk A A, Shehata W F, Attimarad M. 2022. Biotechnological approaches for production of artemisinin, an anti-malarial drug from *Artemisia annua* L. *Molecules*. **27**: 3040.

Alhamed Y A. 2006. Activated carbon from dates' stone by $ZnCl_2$ activation. *J King Abdulaziz Univ Eng Sci*. **17**: 75–100.

Ali J G, Alborn H T, Stelinski L L. 2010. Subterranean herbivore-induced volatiles released by citrus roots upon feeding by *Diaprepes abbreviatus* recruit entomopathogenic nematodes. *J Chem Ecol*. **36**: 361–368.

Asaduzzaman M, Asao T. 2012. Autotoxicity in beans and their allelochemicals. *Sci Hortic*. **134**: 26–31.

Asaduzzaman M, Asao T. 2020. Autotoxicity in strawberry under recycled hydroponics and its mitigation methods. *Hort J*. **89**: 124–137.

Asaduzzaman M, Niu G H, Asao T. 2022. Nutrients recycling in hydroponics: Opportunities and challenges toward sustainable crop production under controlled environment agriculture. *Front Plant Sci*. **13**: 845472.

Asao T, Hasegawa K, Sueda Y, Tomita K, Taniguchi K, Hosoki T, Pramanik M H R, Matsui Y. 2003. Autotoxicity of root exudates from taro. *Sci Hortic*. **97**: 389–396.

Asao T, Kitazawa H, Ban T, Pramanik M H R, Tokumasa K. 2008. Electrodegradation of root exudates to mitigate autotoxicity in hydroponically grown strawberry (*Fragaria* × *ananassa* Duch.) plants. *HortScience*. **43**: 2034–2038.

Asao T, Pramanik M H R, Tomita K, Ohba Y, Ohta K, Hosoki T, Matsui Y. 1999. Influences of phenolics isolated from the nutrient solution nourishing growing cucumber (*Cucumis sativus* L.) plants on fruit yield. *J Jpn Soc Hortic Sci*. **68**: 847–853.

Asao T, Umeyama M, Ohta K, Hosoki T, Ito N, Ueda H. 1998. Decrease of yield of cucumber by non-renewal of the nutrient hydroponic solution and its reversal by supplementation of activated charcoal. *J Jpn Soc Hortic Sci*. **67**: 99–105.

Aulakh M S, Wassmann R, Bueno C, Kreuzwieser J, Rennenberg H. 2001. Characterization of root exudates at different growth stages of ten rice (*Oryza sativa* L.) cultivars. *Plant Biol*. **3**: 139–148.

Bacilio-Jiménez M, Aguilar-Flores S, Ventura-Zapata E, Pérez-Campos E, Bouquelet S, Zenteno E. 2003. Chemical characterization of root exudates from rice (*Oryza sativa*) and their effects on the chemotactic response of endophytic bacteria. *Plant Soil*. **249**: 271–277.

Badri D V, Chaparro J M, Zhang R F, Shen Q R, Vivanco J M. 2013. Application of natural blends of phytochemicals derived from the root exudates of *Arabidopsis* to the soil reveal that phenolic-related compounds predominantly modulate the soil microbiome. *J Biol Chem*. **288**: 4502–4512.

Badri D V, Vivanco J M. 2009. Regulation and function of root exudates. *Plant Cell Environ*. **32**: 666–681.

Baetz U, Martinoia E. 2014. Root exudates: The hidden part of plant defense. *Trends Plant Sci*. **19**: 90–98.

Bais H P, Weir T L, Perry L G, Gilroy S, Vivanco J M. 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu Rev Plant Biol*. **57**: 233–266.

Balyan G, Pandey A K. 2024. Root exudates, the warrior of plant life: Revolution below the ground. *S Afr J Bot*. **164**: 280–287.

Barra Caracciolo A, Terenzi V. 2021. Rhizosphere microbial communities and heavy metals. *Microorganisms*. **9**: 1462.

Bednarek P, Piślewska-Bednarek M, Svatoš A, Schneider B, Doubský J, Mansurova M, Humphry M, Consonni C, Panstruga R, Sanchez-Vallet A, Molina A, Schulze-Lefert P. 2009. A glucosinolate metabolism pathway in living plant cells mediates broad-spectrum antifungal defense. *Science*. **323**: 101–106.

Begum A A, Leibovitch S, Migner P, Zhang F. 2001. Specific flavonoids induced *nod* gene expression and pre-activated *nod* genes of *Rhizobium leguminosarum* increased pea (*Pisum sativum* L.) and lentil (*Lens culinaris* L.) nodulation in controlled growth chamber environments. *J Exp Bot*. **52**: 1537–1543.

Bekbölet M, Lindner M, Weichgrebe D, Bahnemann D W. 1996. Photocatalytic detoxification with the thin-film fixed-bed reactor (TFFBR): Clean-up of highly polluted landfill effluents using a novel TiO_2-photocatalyst. *Solar Energy*. **56**: 455–469.

Bergman M E, Dudareva N. 2024. Plant specialized metabolism: Diversity of terpene synthases and their products. *Curr Opin Plant Biol*. **81**: 102607.

Bowsher A W, Ali R, Harding S A, Tsai C J, Donovan L A. 2015. Analysis of wild sunflower (*Helianthus annuus* L.) root exudates using gas chromatography-mass spectrometry. *J Plant Nutr Soil Sci*. **178**: 776–786.

Breland T A, Bakken L R. 1991. Microbial growth and nitrogen immobilization in the root zone of barley (*Hordeum vulgare* L.), Italian ryegrass (*Lolium multiflorum* Lam.), and white clover (*Trifolium repens* L.). *Biol Fertil Soils*. **12**: 154–160.

Cai Z Z, Kastell A, Knorr D, Smetanska I. 2012. Exudation: An expanding technique for continuous production and release of secondary metabolites from plant cell suspension and hairy root cultures. *Plant Cell Rep*. **31**: 461–477.

Camli-Saunders D, Villouta C. 2025. Root exudates in controlled environment agriculture: Composition, function, and future directions. *Front Plant Sci*. **28**: 1567707.

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.

Canarini A, Merchant A, Dijkstra F A. 2016. Drought effects on *Helianthus annuus* and *Glycine max* metabolites: From phloem to root exudates. *Rhizosphere*. **2**: 85–97.

Cardoza Y J, Lait C G, Schmelz E A, Huang J, Tumlinson J H. 2003. Fungus-induced biochemical changes in peanut plants and their effect on development of beet armyworm, *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae), larvae. *Environ Entomol*. **32**: 220–228.

Cawthray G R. 2003. An improved reversed-phase liquid chromatographic method for the analysis of low-molecular mass organic acids in plant root exudates. *J Chromatogr A*. **1011**: 233–240.

Chai Y N, Schachtman D P. 2022. Root exudates impact plant performance under abiotic stress. *Trends Plant Sci*. **27**: 80–91.

Chen D D, Chai S C, McIntyre C L, Xue G P. 2018. Overexpression of a predominantly root-expressed NAC transcription factor in wheat roots enhances root length, biomass and drought tolerance. *Plant Cell Rep*. **37**: 225–237.

Chen L, Liu Y P. 2024. The function of root exudates in the root colonization by beneficial soil rhizobacteria. *Biology*. **13**: 95.

Chen Z L, Kim K R, Owens G, Naidu R. 2008. Determination of carboxylic acids from plant root exudates by ion exclusion chromatography with ESI-MS. *Chromatographia*. **67**: 113–117.

Cook C E, Whichard L P, Turner B, Wall M E, Egley G H. 1966. Germination of witchweed (*Striga lutea* Lour.): Isolation and properties of a potent stimulant. *Science*. **154**: 1189–1190.

Couvillion S P, Yang I H, Hermosillo D, Leach D, Eder J, Bell S, Hofmockel K S. 2025. Root exudate lipids: Uncovering chemodiversity and carbon stability potential. *Soil Biol Biochem*. **206**: 109799.

Curl E A, Truelove B. 1986. Root exudates. *In* Curl E A, Truelove B (eds.) The Rhizosphere. Springer, Berlin, Heidelberg. pp. 55–92.

da Silva Lima L, Olivares F L, de Oliveira R R, Vega M R G, Aguiar N O, Canellas L P. 2014. Root exudate profiling of maize seedlings inoculated with *Herbaspirillum seropedicae* and humic acids. *Chem Biol Technol Agric*. **1**: 23.

Daels N, Radoicic M, Radetic M, De Clerck K, Van Hulle S W H. 2015. Electrospun nanofibre membranes functionalised with TiO_2 nanoparticles: Evaluation of humic acid and bacterial removal from polluted water. *Sep Purif Technol*. **149**: 488–494.

Dakora F D, Phillips D A. 2002. Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant Soil*. **245**: 35–47.

Darwent M J, Paterson E, McDonald A J S, Tomos A D. 2003. Biosensor reporting of root exudation from *Hordeum vulgare* in relation to shoot nitrate concentration. *J Exp Bot*. **54**: 325–334.

de Haas B, Dhooghe E, Geelen D. 2025. Root exudates in soilless culture conditions. *Plants*. **14**: 479.

de Vries F T, Williams A, Stringer F, Willcocks R, McEwing R, Langridge H, Straathof A L. 2019. Changes in root-exudate-induced respiration reveal a novel mechanism through which drought affects ecosystem carbon cycling. *New Phytol*. **224**: 132–145.

De-la-Peña C, Badri D V, Lei Z T, Watson B S, Brandão M M, Silva-Filho M C, Sumner L W, Vivanco J M. 2010. Root secretion of defense-related proteins is development-dependent and correlated with flowering time. *J Biol Chem*. **285**: 30654–30665.

Der C, Courty P E, Recorbet G, Wipf D, Simon-Plas F, Gerbeau-Pissot P. 2024. Sterols, pleiotropic players in plant-microbe interactions. *Trends Plant Sci*. **29**: 524–534.

Deshpande A, Pontaroli A C, Chaluvadi S R, Lu F, Bennetzen J L. 2011. Plant genetics for study of the roles of root exudates and microbes in the soil. *In* de Oliveira A C, Varshney R K (eds.) Root Genomics. Springer, Berlin, Heidelberg. pp. 99–111.

Dhungana I, Kantar M B, Nguyen N H. 2023. Root exudate composition from different plant species influences the growth of rhizosphere bacteria. *Rhizosphere*. **25**: 100645.

Doornbos R F, van Loon L C, Bakker P A H M. 2012. Impact of root exudates and plant defense signaling on bacterial communities in the rhizosphere. A review. *Agron Sustain Dev*. **32**: 227–243.

Dreyer I, Gomez-Porras J L, Riaño-Pachón D M, Hedrich R, Geiger D. 2012. Molecular evolution of slow and quick anion channels (SLACs and QUACs/ALMTs). *Front Plant Sci*. **3**: 263.

Elbasiouny H, El-Ramady H, Elbehiry F, Rajput V D, Minkina T, Mandzhieva S. 2022. Plant nutrition under climate change and soil carbon sequestration. *Sustainability*. **14**: 914.

Escolà Casas M, Matamoros V. 2021. Analytical challenges and solutions for performing metabolomic analysis of root exudates. *Trends Environ Anal Chem*. **31**: e00130.

Eshel A, Beeckman T. 2013. Plant Roots: The Hidden Half. 4th Edn. CRC Press, Boca Raton.

Eze M O, Amuji C F. 2024. Elucidating the significant roles of root exudates in organic pollutant biotransformation within the rhizosphere. *Sci Rep*. **14**: 2359.

Falcon W P, Naylor R L, Shankar N D. 2022. Rethinking global food demand for 2050. *Popul Dev Rev*. **48**: 921–957.

Fan T W M, Lane A N, Pedler J, Crowley D, Higashi R M. 1997. Comprehensive analysis of organic ligands in whole root exudates using nuclear magnetic resonance and gas chromatography-mass spectrometry. *Anal Biochem*. **251**: 57–68.

Fan T W M, Lane A N, Shenker M, Bartley J P, Crowley D, Higashi R M. 2001. Comprehensive chemical profiling of gramineous plant root exudates using high-resolution NMR and MS. *Phytochemistry*. **57**: 209–221.

Feng H C, Zhang N, Du W B, Zhang H H, Liu Y P, Fu R X, Shao J H, Zhang G S, Shen Q R, Zhang R F. 2018. Identification of chemotaxis compounds in root exudates and their sensing chemoreceptors in plant-growth-promoting rhizobacteria *Bacillus Amyloliquefaciens* SQR9. *Mol Plant-Microbe Interact*. **31**: 995–1005.

Fiorilli V, Wang J Y, Bonfante P, Lanfranco L, Al-Babili S. 2019. Apocarotenoids: Old and new mediators of the arbuscular mycorrhizal symbiosis. *Front Plant Sci*. **10**: 1186.

Gomez-Zepeda D, Frausto M, Nájera-González H R, Herrera-Estrella L, Ordaz-Ortiz J J. 2021. Mass spectrometry-based quantification and spatial localization of small organic acid exudates in plant roots under phosphorus deficiency and aluminum toxicity. *Plant J*. **106**: 1791–1806.

Guerrieri A, Dong L M, Bouwmeester H J. 2019. Role and exploitation of underground chemical signaling in plants. *Pest Manag Sci*. **75**: 2455–2463.

Haase S, Neumann G, Kania A, Kuzyakov Y, Römheld V, Kandeler E. 2007. Elevation of atmospheric CO_2 and N-nutritional status modify nodulation, nodule-carbon supply, and root exudation of *Phaseolus vulgaris* L. *Soil Biol Biochem*. **39**: 2208–2221.

Haichar F E Z, Santaella C, Heulin T, Achouak W. 2014. Root exudates mediated interactions belowground. *Soil Biol Biochem*. **77**: 69–80.

Haldar S, Sengupta S. 2015. Plant-microbe cross-talk in the rhizosphere: Insight and biotechnological potential. *Open Microbiol J*. **9**: 1–7.

Harmsen G W, Jager G. 1962. Determination of the quantity of carbon and nitrogen in the rhizosphere of young plants. *Nature*. **195**: 1119–1120.

Harris J M. 2015. Abscisic acid: Hidden architect of root system structure. *Plants*. **4**: 548–572.

Hayat S, Faraz A, Faizan M. 2017. Root exudates: Composition and impact on plant-microbe interaction. *In* Ahmad I, Husain F M (eds.) Biofilms in Plant and Soil Health. John Wiley & Sons Ltd., Hoboken. pp. 179–193.

Henry A, Doucette W, Norton J, Bugbee B. 2007. Changes in crested wheatgrass root exudation caused by flood, drought, and nutrient stress. *J Environ Qual*. **36**: 904–912.

Hosseinzadeh S, Verheust Y, Bonarrigo G, Van Hulle S. 2017. Closed hydroponic systems: Operational parameters, root exudates occurrence and related water treatment. *Rev Environ Sci Bio/Technol*. **16**: 59–79.

Hou F B, Hinojosa L, Enderle E, Jansen B, Morriën E, de Vries F T. 2025. Root exudates from drought-affected plants increase soil respiration across a range of grassland species. *Soil Biol Biochem*. **203**: 109731.

Huang A C, Osbourn A. 2019. Plant terpenes that mediate below-ground interactions: Prospects for bioengineering terpenoids for plant protection. *Pest Manag Sci*. **75**: 2368–2377.

Huang Y X, Zhao L J, Keller A A. 2017. Interactions, transformations, and bioavailability of nano-copper exposed to root exudates. *Environ Sci Technol*. **51**: 9774–9783.

Hunter M C, Smith R G, Schipanski M E, Atwood L W, Mortensen D A. 2017. Agriculture in 2050: Recalibrating targets for sustainable intensification. *BioScience*. **67**: 386–391.

Intergovernmental Panel on Climate Change (IPCC). 2022. Climate change 2022: Impacts, adaptation and vulnerability. Available online at https://www.ipcc.ch/report/ar6/wg2/ (verified on March 25, 2025).

Iqbal A, Hamayun M, Shah F, Hussain A. 2020. Role of plant bioactives in sustainable agriculture. *In* Fahad S, Hasanuzzaman M, Alam M, Ullah H, Saeed M, Khan I A, Adnan M (eds.) Environment, Climate, Plant and Vegetation Growth. Springer, Cham. pp. 591–605.

Jones D L, Hodge A, Kuzyakov Y. 2004. Plant and mycorrhizal regulation of rhizodeposition. *New Phytol*. **163**: 459–480.

Jones P M, George A M. 2002. Mechanism of ABC transporters: A molecular dynamics simulation of a well characterized nucleotide-binding subunit. *P Natl Acad Sci USA*. **99**: 12639–12644.

Kang J, Park J, Choi H, Burla B, Kretzschmar T, Lee Y, Martinoia E. 2011. Plant ABC transporters. *Arabidopsis Book*. **9**: e0153.

Kawasaki A, Okada S, Zhang C Y, Delhaize E, Mathesius U, Richardson A E, Watt M, Gilliham M, Ryan P R. 2018. A sterile hydroponic system for characterising root exudates from specific root types and whole-root systems of large crop plants. *Plant Methods*. **14**: 114.

Keller V, Bernhardt P, Garin F. 2003. Photocatalytic oxidation of butyl acetate in vapor phase on TiO_2, Pt/TiO_2 and WO_3/TiO_2 catalysts. *J Catal*. **215**: 129–138.

Kobayashi Y, Lakshmanan V, Kobayashi Y, Asai M, Iuchi S, Kobayashi M, Bais H P, Koyama H. 2013. Overexpression of *AtALMT1* in the *Arabidopsis thaliana* ecotype Columbia results in enhanced Al-activated malate excretion and beneficial bacterium recruitment. *Plant Signal Behav*. **8**: e25565.

Koda T, Ogiwara S, Hiroyasu T. 1977. Effects of addition of activated charcoal into the nutrient solution on the growth of mitsuba (*Cryptotaenia japonica* Hassk.) in hydroponics. *J Jpn Soc Hortic Sci*. **46**: 270–271.

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.

Kuzyakov Y. 2002. Review: Factors affecting rhizosphere priming effects. *J Plant Nutr Soil Sci*. **165**: 382–396.

Lacal J, Alfonso C, Liu X X, Parales R E, Morel B, Conejero-Lara F, Rivas G, Duque E, Ramos J L, Krell T. 2010. Identification of a chemoreceptor for tricarboxylic acid cycle intermediates: Differential chemotactic response towards receptor ligands. *J Biol Chem*. **285**: 23126–23136.

Lacal J, García-Fontana C, Callejo-García C, Ramos J L, Krell T. 2011. Physiologically relevant divalent cations modulate citrate recognition by the McpS chemoreceptor. *J Mol Recognit*. **24**: 378–385.

Lamichhane J R, Barbetti M J, Chilvers M I, Pandey A K, Steinberg C. 2024. Exploiting root exudates to manage soil-borne disease complexes in a changing climate. *Trends Microbiol*. **32**: 27–37.

Lee J E, Jayakody J T M, Kim J I, Jeong J W, Choi K M, Kim T S, Seo C, Azimi I, Hyun J, Ryu B M. 2024. The influence of solvent choice on the extraction of bioactive compounds from Asteraceae: A comparative review. *Foods*. **13**: 3151.

Leoni F, Hazrati H, Fomsgaard I S, Moonen A C, Kudsk P. 2021. Determination of the effect of co-cultivation on the production and root exudation of flavonoids in four legume species using LC-MS/MS analysis. *J Agric Food Chem*. **69**: 9208–9219.

Li C Y, Bai T H, Ma F W, Han M Y. 2010. Hypoxia tolerance and adaptation of anaerobic respiration to hypoxia stress in two *Malus* species. *Sci Hortic*. **124**: 274–279.

Li Z, Ahammed G J. 2023. Plant stress response and adaptation *via* anthocyanins: A review. *Plant Stress*. **10**: 100230.

Licá I C L, Soares A M D S, de Mesquita L S S, Malik S. 2018. Biological properties and pharmacological potential of plant exudates. *Food Res Int*. **105**: 1039–1053.

Licá I C L, Soares A M S, Ferreira A T S, Perales J, Cunha I A L, Souza P F N, Costa-Júnior L M. 2021. *In vitro* assessment of the efficacy of protein exudates from seeds against *Haemonchus contortus*. *Vet Parasitol*. **292**: 109399.

Liu J P, Magalhaes J V, Shaff J, Kochian L V. 2009. Aluminum-activated citrate and malate transporters from the MATE and ALMT families function independently to confer *Arabidopsis* aluminum tolerance. *Plant J*. **57**: 389–399.

Liu W X, Hou J Y, Wang Q L, Yang H J, Luo Y M, 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**: 109–119.

Lopez-Guerrero M G, Wang P, Phares F, Schachtman D P, Alvarez S, van Dijk K. 2022. A glass bead semi-hydroponic system for intact maize root exudate analysis and phenotyping. *Plant Methods*. **18**: 25.

López-Moral A, Sánchez-Rodríguez A R, Trapero A, Agustí-Brisach C. 2023. Establishment of a method to collect root exudates from olive plants and its validation by determining the effect of root exudates against *Verticillium dahliae*. *Plant Soil*. **483**: 625–642.

Lucas García J A, Barbas C, Probanza A, Barrientos M L, Gutierrez Mañero F J. 2001. Low molecular weight organic acids and fatty acids in root exudates of two *Lupinus* cultivars at flowering and fruiting stages. *Phytochem Anal*. **12**: 305–311.

Luo Q, Wang S Y, Sun L N, Wang H, Bao T, Adeel M. 2017. Identification of root exudates from the Pb-accumulator *Sedum alfredii* under Pb stresses and assessment of their roles. *J Plant Interact*. **12**: 272–278.

Ma J F, Zheng S J, Matsumoto H, Hiradate S. 1997. Detoxifying aluminium with buckwheat. *Nature*. **390**: 569–570.

Ma W M, Tang S H, Dengzeng Z, Zhang D, Zhang T, Ma X L. 2022. Root exudates contribute to belowground ecosystem hotspots: A review. *Front Microbiol*. **13**: 937940.

Ma Y, Oliveira R S, Freitas H, Zhang C. 2016. Biochemical and molecular mechanisms of plant-microbe-metal interactions: Relevance for phytoremediation. *Front Plant Sci*. **7**: 918.

Ma Y Y, Yang N, Wang S Y, Huo C F, Yu L Z, Gu J C. 2024. Climatic and edaphic controls of root-tip production and mortality in five temperate tree species. *J For Res*. **35**: 145.

Malik S, Kumaraguru G, Bruat M, Chefdor F, Depierreux C, Héricourt F, Carpin S, Shanmugam G, Lamblin F. 2024. Organic extracts from sustainable hybrid poplar hairy root cultures as potential natural antimicrobial and antibiofilm agents. *Protoplasma*. **261**: 1311–1326.

Maruyama H, Sasaki T, Yamamoto Y, Wasaki J. 2019. AtALMT3 is involved in malate efflux induced by phosphorus deficiency in *Arabidopsis thaliana* root hairs. *Plant Cell Physiol*. **60**: 107–115.

Micallef S A, Channer S, Shiaris M P, Colón-Carmona A. 2009. Plant age and genotype impact the progression of bacterial community succession in the *Arabidopsis* rhizosphere. *Plant Signal Behav*. **4**: 777–780.

Michalet S, Rohr J, Warshan D, Bardon C, Roggy J C, Domenach A M, Czarnes S, Pommier T, Combourieu B, Guillaumaud N, Bellvert F, Comte G, Poly F. 2013. Phytochemical analysis of mature tree root exudates *in situ* and their role in shaping soil microbial communities in relation to tree N-acquisition strategy. *Plant Physiol Biochem*. **72**: 169–177.

Miller A, Adhikari R, Nemali K. 2020. Recycling nutrient solution can reduce growth due to nutrient deficiencies in hydroponic production. *Front Plant Sci*. **11**: 607643.

Mills A, Le Hunte S. 1997. An overview of semiconductor photocatalysis. *J Photochem Photobiol A Chem*. **108**: 1–35.

Miyama Y, Hara Y, Hashimoto K, Sunada K. 2012. Closed soilless cultivation system of roses planted in rice hull substrate with TiO_2 photocatalytic treatment of waste nutrient solution. *J Sci High Technol Agric*. **24**: 31–37.

Mönchgesang S, Strehmel N, Schmidt S, Westphal L, Taruttis F, Müller E, Herklotz S, Neumann S, Scheel D. 2016. Natural variation of root exudates in *Arabidopsis thaliana*-linking metabolomic and genomic data. *Sci Rep*. **6**: 29033.

Mondal T, Nag P K. 2023. Usability assessment of pedal threshing operation in rice farming. *In* Chigullapalli S, Susha Lekshmi S U, Deshpande A P (eds.) Rural Technology Development and Delivery. Springer, Singapore. pp. 49–63.

Montiel-Rozas M M, Madejón E, Madejón P. 2016. Effect of heavy metals and organic matter on root exudates (low molecular weight organic acids) of herbaceous species: An assessment in sand and soil conditions under different levels of contamination. *Environ Pollut*. **216**: 273–281.

Narasimhan K, Basheer C, Bajic V B, Swarup S. 2003. Enhancement of plant-microbe interactions using a rhizosphere metabolomics-driven approach and its application in the removal of polychlorinated biphenyls. *Plant Physiol*. **132**: 146–153.

Nederhoff E, Stanghellini C. 2010. Water use efficiency of tomatoes. *Pract Hydroponics Greenhouses*. **115**: 52–59.

Neumann G. 2007. Root exudates and nutrient cycling. *In* Marschner P, Rengel Z (eds.) Nutrient Cycling in Terrestrial Ecosystems. Springer, Berlin, Heidelberg. pp. 123–157.

Nguyen Q T, Kozai T. 2001. Photoautotrophic micropropagation of tropical and subtropical woody plants. *Prog Biotechnol*. **18**: 335–344.

Ninković S, Motyka V, Stanišić M, Smailagić D, Živanović B, Dobrev P I, Banjac N. 2024. Phytohormone profiling of *Malus domestica* and *Chenopodium murale* hairy root exudate: Association with allelopathic effects. *J Plant Growth Regul*. **43**: 3580–3593.

Oburger E, Jones D L. 2018. Sampling root exudates—Mission impossible? *Rhizosphere*. **6**: 116–133.

Orelle C, Durmort C, Mathieu K, Duchêne B, Aros S, Fenaille F, André F, Junot C, Vernet T, Jault J M. 2018. A multidrug ABC transporter with a taste for GTP. *Sci Rep*. **8**: 2309.

Palmer A G, Ali M, Yang S K, Parchami N, Bento T, Mazzella A, Oni M, Riley M C, Schneider K, Massa N. 2016. Kin recognition is a nutrient-dependent inducible phenomenon. *Plant Signal Behav*. **11**: e1224045.

Pang Z Q, Chen J, Wang T H, Gao C S, Li Z M, Guo L T, Xu J P, Cheng Y. 2021. Linking plant secondary metabolites and plant microbiomes: A review. *Front Plant Sci*. **12**: 621276.

Pantigoso H A, Newberger D, Vivanco J M. 2022. The rhizosphere microbiome: Plant-microbial interactions for resource acquisition. *J Appl Microbiol*. **133**: 2864–2876.

Philippot L, Raaijmakers J M, Lemanceau P, van der Putten W H. 2013. Going back to the roots: The microbial ecology of the rhizosphere. *Nat Rev Microbiol*. **11**: 789–799.

Pinto A P, Simões I, Mota A M. 2008. Cadmium impact on root exudates of sorghum and maize plants: A speciation study. *J Plant Nutr*. **31**: 1746–1755.

Pratyusha S. 2022. Phenolic compounds in the plant development and defense: An overview. *In* Hasanuzzaman M, Nahar K (eds.) Plant Stress Physiology—Perspectives in Agriculture. IntechOpen, London. pp. 1–17.

Preece C, Gargallo-Garriga A, Sardans J, Oravec M, Klem K, Urban Q, Peñuelas J. 2022. Measuring root exudate metabolites in holm oak (*Quercus ilex*) under drought and recovery. *In* Beale D J, Hillyer K E, Warden A C, Jones Q A H (eds.) Applied Environmental Metabolomics: Community Insights and Guidance from the Field. Academic Press, Amsterdam. pp. 17–28.

Preece C, Peñuelas J. 2020. A return to the wild: Root exudates and food security. *Tre Plant Sci*. **25**: 14–21.

Qiu Z P, Yang Q C, Liu W K. 2013. Photocatalytic degradation of phytotoxic substances in waste nutrient solution by various immobilized levels of nano-TiO_2. *Water Air Soil Pollut*. **224**: 1461.

Rasmann S, Köllner T G, Degenhardt J, Hiltpold I, Toepfer S, Kuhlmann U, Gershenzon J, Turlings T C J. 2005. Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature*. **434**: 737.

Rathod B U, Channarayappa. 2020. Standardization of a novel method of root exudates collection and analysis of cotton root exudates by thin layer chromatography. *Int J Chem Stud*. **8**: 1261–1271.

Ray S, Mishra S, Bisen K, Singh S, Sarma B K, Singh H B. 2018. Modulation in phenolic root exudate profile of *Abelmoschus esculentus* expressing activation of defense pathway. *Microbiol Res*. **207**: 100–107.

Rial C, Varela R M, Molinillo J M G, Durán A G, Macías F A. 2020. Quantification of strigolactones. *Methods Mol Biol*. **2083**: 199–208.

Rial C, Varela R M, Molinillo J M G, López-Ráez J A, Macías F A. 2019. A new UHPLC-MS/MS method for the direct determination of strigolactones in root exudates and extracts. *Phytochem Anal*. **30**: 110–116.

Robards K, Haddad P R, Jackson P E. 2004. High-performance liquid chromatography—Separations. *In* Robards K, Haddad P R, Jackson P E (eds.) Principles and Practice of Modern Chromatographic Methods. Academic Press, London. pp. 305–380.

Rolfe S A, Griffiths J, Ton J. 2019. Crying out for help with root exudates: Adaptive mechanisms by which stressed plants assemble health-promoting soil microbiomes. *Curr Opin Microbiol*. **49**: 73–82.

Roy A, Moradkhani H, Mekonnen M, Moftakhari H, Magliocca N. 2024. Towards strategic interventions for global food security in 2050. *Sci Total Environ*. **954**: 176811.

Ruijs M N A. 1992. Economic evaluation of closed production systems in glasshouse horticulture. *Acta Hortic*. **340**: 87–94.

Salt D E, Kato N, Krämer U, Smith R D, Raskin I. 2000. The role of root exudates in nickel hyperaccumulation and tolerance in accumulator and nonaccumulator species of *Thlaspi*. *In* Terry N, Banuelos G S (eds.) Phytoremediation of Contaminated Soil and Water. CRC Press, Boca Raton. pp. 189–200.

Santana S R A, Voltolini T V, dos Reis Antunes G, da Silva V M, Simões W L, Morgante C V, de Freitas A D S, de Melo Chaves A R, de Tarso Aidar S, Fernandes-Júnior P I. 2020. Inoculation of plant growth-promoting bacteria attenuates the negative effects of drought on sorghum. *Arch Microbiol*. **202**: 1015–1024.

Sato N. 2004. Effect of the substances accumulated in the nutrients solution by the rock wool circulated hydro culture to the rose seedlings growth. *J Jpn Soc Hortic Sci*. **73**: 497.

Schenk H, Driessen R A J, de Gelder R, Goubitz K, Nieboer H, Brüggemann-Rotgans I E M, Diepenhorst P. 1999. Elucidation of the structure of solanoeclepin A, a natural hatching factor of potato and tomato cyst nematodes, by single-crystal X-ray diffraction. *Croat Chem Acta*. **72**: 593–606.

Sgherri C, Cecconami S, Pinzino C, Navari-Izzo F, Izzo R. 2010. Levels of antioxidants and nutraceuticals in basil grown in hydroponics and soil. *Food Chem*. **123**: 416–422.

Sharma G, Rana D, Sundriyal S, Sharma A, Panwar P, Mahindroo N. 2023. Plants from Annonaceae family as antimalarials: An ethnopharmacology and phytochemistry review to identify potential lead molecules. *S Afr J Bot*. **155**: 154–170.

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.

Sharma T, Dreyer I, Kochian L, Piñeros M A. 2016. The ALMT family of organic acid transporters in plants and their involvement in detoxification and nutrient security. *Front Plant Sci*. **7**: 1488.

Shi Y H, Zhang X, Zhao M, Zheng X Y, Gu J Y, Wang Z Q, Fan C Z, Gu W W. 2024. The status of research on the root exudates of submerged plants and their effects on aquatic organisms. *Water*. **16**: 1920.

Simón Solá M Z, Lovaisa N, Dávila Costa J S, Benimeli C S, Polti M A, Alvarez A. 2019. Multi-resistant plant growth-promoting actinobacteria and plant root exudates influence Cr(VI) and lindane dissipation. *Chemosphere*. **222**: 679–687.

Singh S S, Singh N S, Lamare E, Devi N R, Devi S A, Kaguijenliu R, Takum B, Upadhyay K K, Tripathi S K. 2025. Drought mitigation in plants through root exudate-mediated rhizosphere interactions: Opportunities for future research. *Current Plant Biol*. **43**: 100504.

Souza R M, Oliveira D F, Gomes V M, Viana A J S, Silva G H, Machado A R T. 2023. *Meloidogyne enterolobii*-induced changes in guava root exudates are associated with root rotting caused by *Neocosmospora falciformis*. *J Nematol*. **55**: 20230055.

Starkey R L. 1983. Some influences of the development of higher plants upon the microorganisms in the soil: VI. Microscopic examination of the rhizosphere. *Soil Sci*. **45**: 207.

Strehmel N, Böttcher C, Schmidt S, Scheel D. 2014. Profiling of secondary metabolites in root exudates of *Arabidopsis thaliana*. *Phytochemistry*. **108**: 35–46.

Sun L, Lu Y F, Kronzucker H J, Shi W M. 2016. Quantification and enzyme targets of fatty acid amides from duckweed root exudates involved in the stimulation of denitrification. *J Plant Physiol*. **198**: 81–88.

Sunada K, Ding X G, Utami M S, Kawashima Y, Miyama Y, Hashimoto K. 2008. Detoxification of phytotoxic compounds by TiO_2 photocatalysis in a recycling hydroponic cultivation system of asparagus. *J Agric Food Chem*. **56**: 4819–4824.

Suzuki K, Okazaki K, Tawaraya K, Osaki M, Shinano T. 2009. Gas chromatography-mass spectrometry associated global analysis of rice root exudates under aseptical conditions. *Soil Sci Plant Nutr*. **55**: 505–513.

Taddei P, Tugnoli V, Bottura G, Dallavalle E, Zechini D'Aulerio A. 2002. Vibrational, ^{1}H-NMR spectroscopic, and thermal characterization of gladiolus root exudates in relation to *Fusarium oxysporum* f. sp. *gladioli* resistance. *Biopolymers*. **67**: 428–439.

Tiziani R, Miras-Moreno B, Malacrinò A, Vescio R, Lucini L, Mimmo T, Cesco S, Sorgonà A. 2022. Drought, heat, and their combination impact the root exudation patterns and rhizosphere microbiome in maize roots. *Environ Exp Bot*. **203**: 105071.

Trivedi P, Leach J E, Tringe S G, Sa T, Singh B K. 2020. Plant-microbiome interactions: From community assembly to plant health. *Nat Rev Microbiol*. **18**: 607–621.

Tsai H H, Schmidt W. 2017. Mobilization of iron by plant-borne coumarins. *Tre Plant Sci*. **22**: 538–548.

Ulrich D E M, Clendinen C S, Alongi F, Mueller R C, Chu R K, Toyoda J, Gallegos-Graves L V, Goemann H M, Peyton B, Sevanto S, Dunbar J. 2022. Root exudate composition reflects drought severity gradient in blue grama (*Bouteloua gracilis*). *Sci Rep*. **12**: 12581.

United Nations. 2024. World Population Prospects 2024: Methodology of the United Nations Population Estimates and Projections. United Nations, New York.

Upadhyay S K, Srivastava A K, Rajput V D, Chauhan P K, Bhojiya A A, Jain D, Chaubey G, Dwivedi P, Sharma B, Minkina T. 2022. Root exudates: Mechanistic insight of plant growth promoting rhizobacteria for sustainable crop production. *Front Microbiol*. **13**: 916488.

Vaidya B P, Hagmann D F, Haramuniz J, Krumins J A, Goodey N M. 2022. Artificial root exudates restore microbial functioning in a metal contaminated, barren, inactive soil. *Environ Pollut*. **312**: 120007.

van Os E A. 1994. Engineering and environmental aspects of soilless growing systems. *Acta Hortic*. **396**: 25–32.

van Os E A. 1999. Closed soilless growing systems: A sustainable solution for Dutch greenhouse horticulture. *Water Sci Technol*. **39**: 105–112.

Vaughan M M, Wang Q, Webster F X, Kiemle D, Hong Y J, Tantillo D J, Coates R M, Wray A T, Askew W, O'donnell C, Tokuhisa J G, Tholl D. 2013. Formation of the unusual semivolatile diterpene rhizathalene by the *Arabidopsis* class I terpene synthase TPS08 in the root stele is involved in defense against belowground herbivory. *Plant Cell*. **25**: 1108–1125.

Vives-Peris V, Molina L, Segura A, Gómez-Cadenas A, Pérez-Clemente R M. 2018. Root exudates from citrus plants subjected to abiotic stress conditions have a positive effect on rhizobacteria. *J Plant Physiol*. **228**: 208–217.

Vranova V, Rejsek K, Formanek P. 2013. Aliphatic, cyclic, and aromatic organic acids, vitamins, and carbohydrates in soil: A review. *Sci World J*. **2013**: 524239.

Walker T S, Bais H P, Déziel E, Schweizer H P, Rahme L G, Fall R, Vivanco J M. 2004. *Pseudomonas aeruginosa*-plant root interactions. Pathogenicity, biofilm formation, and root exudation. *Plant Physiol*. **134**: 320–331.

Walker T S, Bais H P, Grotewold E, Vivanco J M. 2003. Root exudation and rhizosphere biology. *Plant Physiol*. **132**: 44–51.

Wang B L, Shen J B, Zhang W H, Zhang F S, Neumann G. 2007. Citrate exudation from white lupin induced by phosphorus deficiency differs from that induced by aluminum. *New Phytol*. **176**: 581–589.

Wang H, Zhang M Q, Xu Y J, Zong R J, Xu N, Guo M L. 2021. *Agrobacterium fabrum atu0526*-encoding protein is the only chemoreceptor that regulates chemoattraction toward the broad antibacterial agent formic acid. *Biology*. **10**: 1345.

Williams A, Langridge H, Straathof A L, Fox G, Muhammadali H, Hollywood K A, Xu Y, Goodacre R, de Vries F T. 2021. Comparing root exudate collection techniques: An improved hybrid method. *Soil Biol Biochem*. **161**: 108391.

Williams A, Langridge H, Straathof A L, Muhamadali H, Hollywood K A, Goodacre R, de Vries F T. 2022. Root functional traits explain root exudation rate and composition across a range of grassland species. *J Ecol*. **110**: 21–33.

Wu C C, Liu J, Zhang X H. 2018. Determination of organic acids in the root exudates of Cr-hyperaccumulator *Leersia hexandra* Swartz using high performance liquid chromatography. *Chin J Chromatogr* (in Chinese). **36**: 167–172.

Wu J, Ke C D, Zu Y Q, Din Y, Li T T. 2021. Root morphological, Cd accumulation and tolerance characteristics of 2 *Dianthus caryophyllus* cultivars under Cd stress. *E3S Web Conf*. **271**: 04012.

Xie X N, Yoneyama K, Nomura T, Yoneyama K. 2021. Evaluation and quantification of natural strigolactones from root exudates. *Methods Mol Biol*. **2309**: 3–12.

Xu K, Zhao J, Hou D D, Ge J, Lu L L, Qiao Y B, Ling C Y, Tian S K. 2024. Exploring lead uptake, transport mechanisms in roots of different *Sedum alfredii* ecotypes as a way of enhancing its hyperaccumulative capacity. *Chemosphere*. **367**: 143566.

Yang H, Zhang P P, Wang Q T, Deng S J, Wang G R, Zhang X J, Wang R H, Yin H J. 2025. Shifts in root exudate composition coordinate with root resource conservation along an elevation gradient. *J Ecol*. **113**: 1970–1984.

Yang M, Zhang X D, Xu Y G, Mei X Y, Jiang B B, Liao J J, Yin Z B, Zheng J F, Zhao Z, Fan L M, He X H, Zhu Y Y, Zhu S S. 2015. Autotoxic ginsenosides in the rhizosphere contribute to the replant failure of *Panax notoginseng*. *PLOS ONE*. **10**: e0118555.

Yang X F, Li L L, Xu Y, Kong C H. 2018. Kin recognition in rice (*Oryza sativa*) lines. *New Phytol*. **220**: 567–578.

Yang X Y, Lu M Q, Wang Y F, Wang Y R, Liu Z J, Chen S. 2021. Response mechanism of plants to drought stress. *Horticulturae*. **7**: 50.

Yang Y X, Li Y, Mei X Y, Yang M, Huang H C, Du F, Wu J Q, He Y Y, Sun J W, Wang H N, He X H, Zhu S S, Li Y B, Liu Y X. 2022. Antimicrobial terpenes suppressed the infection process of *Phytophthora* in fennel-pepper intercropping system. *Front Plant Sci*. **13**: 890534.

Yee M O, Kim P, Li Y F, Singh A K, Northen T R, Chakraborty R. 2021. Specialized plant growth chamber designs to study complex rhizosphere interactions. *Front Microbiol*. **12**: 625752.

Ying W C, Weber Jr W J. 1979. Bio-physicochemical adsorption model systems for wastewater treatment. *J (Water Pollut Control Fed)*. **50**: 2661–2677.

Yu J Q, Lee K S, Matsui Y. 1993. Effect of the addition of activated charcoal to the nutrient solution on the growth of tomato in hydroponic culture. *Soil Sci Plant Nutr*. **39**: 13–22.

Yu J Q, Matsui Y. 1993. Extraction and identification of phytotoxic substances accumulated in nutrient solution for the hydroponic culture of tomato. *Soil Sci Plant Nutr*. **39**: 691–700.

Zhang C S, Feng C, Zheng Y F, Wang J, Wang F L. 2020. Root exudates metabolic profiling suggests distinct defense mechanisms between resistant and susceptible tobacco cultivars against black shank disease. *Front Plant Sci*. **11**: 559775.

Zhang F G, Meng X H, Yang X M, Ran W, Shen Q R. 2014. Quantification and role of organic acids in cucumber root exudates in *Trichoderma harzianum* T-E5 colonization. *Plant Physiol Biochem*. **83**: 250–257.

Zhang J H, Mao Z Q, Wang L Q, Shu H R. 2007. Bioassay and identification of root exudates of three fruit tree species. *J Integr Plant Biol*. **49**: 257–261.

Zhang T Z, Meng F J, Yin D C. 2024. Promotion of biomass, photosynthesis, and root growth of seedling biomass, photosynthesis, and root growth of *Populus davidiana* × *P. bolleana* by two species of ectomycorrhizal fungi. *J For Res*. **35**: 101.

Zhang X, Yan J F, Khashi U Rahman M, Wu F Z. 2022. The impact of root exudates, volatile organic compounds, and common mycorrhizal networks on root system architecture in root-root interactions. *J Plant Interact*. **17**: 685–694.

Zhang Y Z, Li P M, Cheng L L. 2010. Developmental changes of carbohydrates, organic acids, amino acids, and phenolic compounds in 'Honeycrisp' apple flesh. *Food Chem*. **123**: 1013–1018.

Zhao M L, Zhao J, Yuan J, Hale L, Wen T, Huang Q W, Vivanco J M, Zhou J Z, Kowalchuk G A, Shen Q R. 2021. Root exudates drive soil-microbe-nutrient feedbacks in response to plant growth. *Plant Cell Environ*. **44**: 613–628.

Zhou X G, Zhang J Y, Khashi U Rahman M, Gao D M, Wei Z, Wu F Z, Dini-Andreote F. 2023. Interspecific plant interaction *via* root exudates structures the disease suppressiveness of rhizosphere microbiomes. *Mol Plant*. **16**: 849–864.

Zhu S S, Vivanco J M, Manter D K. 2016. Nitrogen fertilizer rate affects root exudation, the rhizosphere microbiome and nitrogen-use-efficiency of maize. *Appl Soil Ecol*. **107**: 324–333.