



Review Article

Secretion of Root Exudates in Response to Biotic and Abiotic Environment

Arba Aleem, Norrizah Jaafar Sidik*, Wan Razarinah Wan, Abdul Razak and Norfatimah Mohamed Yunus

School of Biology Faculty of Applied Sciences, Universiti Teknologi MARA (UiTM), Jalan Ilmu 1/1, 40450 Shah Alam, Selangor, Malaysia.

Abstract | Complex chemical molecules called root exudates are crucial for crop yield and plant development. Root exudates are secreting into the soil via the plant roots where they shape the soil microbiology and helps to create the symbiotic interaction. It is controlled by a complex network of mechanisms impacted by symbiotic interaction which incorporates the complex network mechanism of biotic and abiotic method. In abiotic conditions, plant exudates via roots to deal with different stresses from the environment such as salinity, drought, and heat stress. In biotic conditions, plant roots secrete exudates which may attract or repel microbes. Certain microorganisms present in the soil may cause the activation of plant defense system. Root exudates secreted by plants roots can attract beneficial microbes that help plants by boosting nutrient intake and improving plant growth. Sustainable agriculture and ecosystem management potentially benefit from an understanding of the mechanisms and purposes of root exudates under biotic and abiotic conditions. Harnessing the potential of plant-microbe interactions enables the infrastructure development for more effective strategies to enhance plant growth and productivity.

Received | November 07, 2024; **Accepted** | June 08, 2024; **Published** | July 17, 2024

***Correspondence** | Norrizah Jaafar Sidik, School of Biology Faculty of Applied sciences, Universiti Teknologi MARA (UiTM), Shah Alam, Malaysia; **Email:** norri536@uitm.edu.my

Citation | Aleem, A., N.J. Sidik, W.R. Wan, A. Razak and N.M. Yunus. 2024. Secretion of root exudates in response to biotic and abiotic environment. *Sarhad Journal of Agriculture*, 40(3): 760-773.

DOI | <https://dx.doi.org/10.17582/journal.sja/2024/40.3.760.773>

Keywords | Abiotic response, Biotic response, Rhizosphere, Root exudates, PGPR, Soil microbiology



Copyright: 2024 by the authors. Licensee ResearchersLinks Ltd, England, UK.

This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

Introduction

The occurrence of sudden and drastic changes in the global climate is seen as a risk for all natural habitats. These sudden and dramatic changes in climate can result in unfavorable environmental conditions that impact the natural Earth's ecosystem through a variety of mechanisms including biotic and abiotic mechanisms (Chaudhry and Sidhu, 2021). There are several forms of stress, which include

both biotic and abiotic elements. Among the biotic factors are the pathogens that attack the plants, such as different types of microbes, insects, weeds, and various infections (Mulla, 2013; Pantazi *et al.*, 2019). However, abiotic factors include radiation, high and low temperatures, water stress such as drought, floods, submergence, and salinity stress. Plant growth and yield suffer greatly from these alterations. Nevertheless, these stresses due to climate change are being researched within regulated circumstances

in the lab to understand and overcome the stress tolerance behavior of plants (Suzuki *et al.*, 2014). Naturally, plants secrete various primary and secondary metabolites into their surrounding region via various organs such as roots, shoots, and leaves in different aggregate states, for instance, solid, liquid, and gaseous. This process is called exudation (Vives-Peris *et al.*, 2020). However, this evaluation is centered around the secretion of these root exudates under biotic and abiotic conditions that contribute to the plant's beneficial and potential growth and development. The root exudation process involves the secretion of ions, a variety of primary and secondary metabolites that include carbon, as well as various enzymes (Bertin *et al.*, 2003). The secretion of root exudates leads to various interactions in the rhizosphere. However, the most positive and productive interaction is symbiotic communication, which is caused by PGPR, mycorrhizal fungi, and other microbial components. According to Vishwakarma (2017a, b), the significant changes in the microbiology of the rhizosphere region are due to the different biotic and abiotic stress factors, which can be extremely influenced by root exudation. Several investigations have been carried out on various herbaceous plants and show that PGPR and mycorrhizal fungi may have the ability to lessen the harm that biotic and abiotic variables might cause when there is root exudation (Lumibao *et al.*, 2020; Wang *et al.*, 2021; Sharma *et al.*, 2023).

Root exudates

Root exudates are substances released by rhizodeposits by passive diffusion into the surrounding region of the rhizosphere (Canarini *et al.*, 2019). These root exudates secrete a wide variety of substances that are divided into classes called main and secondary metabolites. They contain low and high molecular weights (Vives-Peris *et al.*, 2019). Primary metabolites that are secreted include sugars, amino acids, and organic acids in a bulk, as compared to secondary metabolites such as auxin, glucosinolates, and flavonoids (Badri and Vivanco, 2009; Canarini *et al.*, 2019). Prior research conducted on *Arabidopsis*, Soybean, and Cucumber showed that primary metabolites are released in significantly greater amounts than secondary metabolites. Secreted metabolites include sugars, organic acids, and amino acids secreted by root exudation (Strehmel *et al.*, 2014; Tawaraya *et al.*, 2014).

Conversely, however, the microbial diversity of the soil

and plant development are impacted by root exudates. A recent study by Zhalnina *et al.* (2018) on *Avena barbata* plant indicates that plant growth influences root exudation secretion and the bacteria community existing inside the rhizosphere.

The release of symbiosis signaling molecules is the main purpose of the root exudates. Symbiotic signal molecules exist in a wide variety of amino acids, flavonoids, non-flavonoids. These signaling metabolites perform various symbiotic functions such as root colonization, biofilm formation for plants and beneficial microbial interaction, constrain the growth of competitive plant species, and also inhibit the growth of pathogenic microbes by secreting secondary metabolites (Bertin *et al.*, 2003; Haichar *et al.*, 2014). Additionally, plant root exudates may leak as much as 50% of photosynthetic products (Dam and Bouwmeester, 2016). Different plant species and stages can have an impact on the quantity and diversity of root exudates of plant aging the variety of microorganisms, and by different biotic and abiotic conditions (Rovira, 1969; Vives-Peris *et al.*, 2019). Different root exudate secretion was observed on *Arabidopsis* plants at different growth stages, the study was performed by using GC-MS approach. It is observed that in the early stages of plant development, the concentration of sugars and sugar alcohols is higher as compared to later stage in the study. However, at the conclusion of plant development, there is an active rise in the synthesis of amino acids and phenolic chemicals (Chaparro *et al.*, 2013).

Mechanism of root exudate secretion

Root exudates are released from various plants via root tips in the rhizosphere. The roots react differentially depending on the environment and under different stress conditions, such as biotic and abiotic conditions (Doan *et al.*, 2017; Canarin *et al.*, 2019). Generally, the secretion mechanism of primary and secondary metabolites by root is thought to be mainly passive process, which is further facilitated through three different routes that vary based on the root exudates' makeup. Diffusion, vesicle transport, and ion channels (Badri and Vivanco, 2009). Certain transporters responsible for the transport of exudates across plasma membranes are also subdivided based on what makes up root exudates, such as ATP-binding cassette (ABC), aluminium activated malate transporter (ALMT). Usually, multiple acid moves in and move out transporter (UMAMIT), multidrug and toxic

compound extrusion MATE (Canarin *et al.*, 2019).

The diffusion process typically involves the transport of polar molecules, uncharged and low-molecular-weight organic metabolites such as sugars, amino and carboxylic acid, and phenolic compounds are transported across plasma membrane. This process is a passive process that depends on the different concentration gradient between the inter cytoplasmic region of the rhizosphere's outer layer and the root cell. The permeability of the membrane determines the secretion, the cytosolic pH and the polarity of the secreted metabolites (Bertin *et al.*, 2003; Badri and Vivanco, 2009; Vives-Peris *et al.*, 2019).

The release of organic acids such as sugars, amino acids, malate involves two different mechanisms such as passive efflux transport of anions and active transport of protons, which involves the pumping of H⁺ ions by using ATPase energy (Yan *et al.*, 2002; Hedrich, 2012; Huang *et al.*, 2021). Therefore, these organic acids transport through the plasma membrane, which transports these metabolites via a specific transmembrane protein, also known as transporter, that transports them from the inner region of the plasma membrane to outer region of plasma membrane without the interaction of polar and charged molecules with hydrophobic layer of the plasma membrane (Sasee *et al.*, 2018; Yang and Hinner, 2014). Transporters that involve H⁺ ion pumping active transport using ATPase energy include ATP- dependent ABC transporters responsible for secondary metabolite's secretion and MATE transporter responsible for the secretion of organic acid (Badri and Vivanco, 2009; Radchenko *et al.*, 2015).

Passive efflux of certain compounds is transported via simple diffusion or facilitated diffusion which in turn are divided into two different mechanisms, namely membrane channels. and carrier-mediated pathway. These pathways transport various types of primary metabolites from high concentration to low concentration without using ATP energy (Chen and Lui, 2019). The transporter responsible for the amino acids is recognized as UMAMIT, cationic amino acid transporter (CAT) and glutamine Dumper (amino acid transporter) (GDU) transporter (Yang *et al.*, 2010; Dinkeloo *et al.*, 2017; Suleiman and Tran, 2018).

Sugar will eventually be exposed transporters, or SWEET transporters, are responsible for sugar

transport (Sleewinski, 2011; Breia *et al.*, 2021). ALMT transporters, on the other hand, are responsible for the transport of organic acids (Sharma *et al.*, 2016). The transportation of polysaccharides, mucilage, and other high-molecular-weight substances that are secreted via the root cap, is referred to as the vesicle transport pathway (Becard, 2017). To understand the full mechanism of membrane transport, read the review article by Inada and Ueda (2014). These-high-molecular weight compounds facilitate the defense mechanism (Preston, 2017). Studies related to Al⁺ toxicity and P deficiency have shown that transporter are involved in the root exudation process (Canarin *et al.*, 2019).

Root exudates stress mediator

As mentioned earlier, root exudates play a significant role in plant growth promotion. Badri and Vivanco (2009), on the other hand, state that the root exudation pattern may have an impact under biotic and abiotic stress. In general, the biotic factor promotes the negative and positive interaction in the rhizosphere between plants and microorganisms like fungus, bacteria, and insects, or the control of the nod gene in plant roots (Bais *et al.*, 2006; Vishwakarma *et al.*, 2020). Whereas abiotic factors are usually involved with environmental stress, such as insufficient nutrient availability, salinity stress, drought stress, pH, and temperature. These factors or conditions alter the root exudate composition, which affects the overall soil structure, including microbial communication, nutrient availability, and plant defense mechanisms. (Henry *et al.*, 2007). In this investigation, we will focus on biotic and abiotic elements influencing the composition of the root exudates.

Abiotic stress

Abiotic stress comprises various non-living factors that cause different stresses. These stresses can negatively affect a plant's ability to grow and develop and, under certain conditions may cause the plant cells to deteriorate. Abiotic stress factors include salinity stress, drought stress, also known as water deficit stress, and heat or temperature stress (Ben-Ari and Lavi, 2012; Kopecká *et al.*, 2023). In this review, we have exchanged information on the various and diverse root exudates that can support plants under various stress situations and get through the difficulties they face in the stages of development and expansion of various plants seen in Table 1.

Table 1: Root exudates and their function in various plants in abiotic stress condition.

Root exudates metabolites	Abiotic factor	Function	Plant	References
7',4-Dihydroxyflavone, Hesperetin, Isoliquiritigenin, Naringenin, Quercetin and Umbelliferone	Salinity stress	Plant growth regulation	<i>Phaseolus vulgaris</i>	Dardanelli <i>et al.</i> , 2012; Mondal <i>et al.</i> , 2023
Caffeic, Cinnamic acids, Ferulic, Gallic, Syringic, Quercetin and Vanillic	Salinity stress	Plant growth and development	<i>Triticum aestivum</i>	Tiwar <i>et al.</i> , 2011; Wang <i>et al.</i> , 2021
Absciscic acid, Acacetin, Choline, Homoorientin, Leucine, Malic acid, and Proline	Drought stress	Plant defense mechanisms, symbiotic signaling system, antioxidant properties, drought tolerance, cellular redox buffering, and plant growth regulation.	<i>Quercus ilex</i>	Gargallo-Garriga <i>et al.</i> , 2018
Fumaric acid, Malic acid and Succinic acid	Drought stress	Plant growth regulation	<i>Agropyron cristatum</i>	Bertin <i>et al.</i> , 2003; Henry <i>et al.</i> , 2007; Qu <i>et al.</i> , 2018; Meena <i>et al.</i> , 2020
abscisic acid, indole acetic acid, jasmonic acid and salicylic acid,	Heat stress	Plant growth regulation	<i>Citrus macrophylla</i>	Vives-Peris <i>et al.</i> , 2018a
ascorbate, carotene, glutathione, or various flavonoids	Heat and drought stress	Help plants by providing potential antioxidants, Plant growth and development	<i>Sorghum bicolor</i>	Yaqoob <i>et al.</i> , 2020

Salinity stress

Salinity stress is a major abiotic problem that affects agricultural land by creating limited ways of crop production. The Na⁺ causes toxicity and disrupts ion channels in plants (Kudo *et al.*, 2010; Isayenkov and Maathuis, 2019). In addition, salt stress not only impairs plant growth and nutrient distribution through plant roots, it also adversely impacts the pace at which plant roots absorb nutrients and water. It also causes an increase in salt concentration and produce high toxicity in plants (Munns and Tester, 2008; Fageria *et al.*, 2011). Therefore, many plant species, including *P. australis* and *P. vulgaris*, release a wide range of organic compounds, such as flavonoids, amino acids, sugars, and other components, in the form of root exudates throughout the salt stress to adjust plants to overcome the stress condition and up-regulate plant growth and health (Dardanelli *et al.*, 2012; Xie *et al.*, 2020).

Salt stress causes some physiological and biochemical changes in plants that make them adaptive to the stress condition. These changes include the root exudation patterns, different compounds released by plants in the rhizosphere ecosystem that affect the microbial community in the soil, and the nutrients available in the soil (Acosta-motos *et al.*, 2017; Arif *et al.*, 2020). Massive amounts of organic acid, such as malic acid and citric acid, are released in the soil by roots to improve ion absorption as well as preserve

homeostasis during salinity stress (Chakraborty *et al.*, 2018). Refer to Table 1.

Furthermore, various root exudates released from root exudates act as signaling molecules, which creates a symbiotic relationship. This relationship between roots and microbes helps plants with nutrient uptake and mobilization and reduces the harmful effects of salinity stress on plants. Increasing nutrient availability improves water absorption efficiency (Tahjib-Ul-Arif *et al.*, 2021). Gaining knowledge of and control over these root exudation processes are sustainable and friendly farming methods for salt-tolerant plants.

Drought stress

Drought or lack of water is a known stress that occurs for various reasons, for example changes in temperature, high light intensity, and low rainfall. Drought stress can regulate plant activities by affecting morphological, physiological, biochemical, and genetic changes (Salehi-Lisar and Bakhshayeshan-Agdam, 2016; Seleiman *et al.*, 2021; Takahash *et al.*, 2020). Drought stress can strongly influence different chemical cycles, like the nitrogen and carbon cycles. Root exudates are significant in the rhizosphere region, creating an excellent symbiotic environment to combat drought stress. The key role of root exudation is to provide Nitrogen when there is little nitrogen in the soil. During the drought stress stage, the plants produce primary and secondary metabolites to

support plant growth and development (Canarini *et al.*, 2016; Gargallo-Garriga *et al.*, 2018).

In times of drought, plants modify soil interactions and enhance water absorption by releasing a range of chemicals into the rhizosphere. The exudation of organic acids, such as citric and malic acids, increases the solubility of minerals and facilitates the uptake of nutrients (Xu *et al.*, 2021). As osmoprotectants, sugars and amino acids assist in preserving cellular turgor and reducing water loss (Khan *et al.*, 2020).

The significance of root exudate secretion during drought stress is to create a symbiotic relationship by releasing various chemicals in the form of root exudates, which facilitates microbial movement. This collaboration improves the soil structure, optimizes water retention, and increases nutrient availability, which creates a favorable environment in the rhizosphere that is crucial during drought stress (Bhattacharyya *et al.*, 2021).

Heat stress

Heat and temperature stress caused by climate change is an irreversible stress that can cause severe damage to crop production (Hasanuzzaman *et al.*, 2013a). High temperature can affect plant growth by denaturing their enzymes and destroying metabolism in various ways, which can affect plants both physiologically and physically (Firmansyah and Argosubekti, 2020). The physiological damage caused by heat stress is permanent and irreversible, which can cause the death of various cells, tissues, and organs, which affects the growth and overall development of plants. Long term heat stress can affect the seed sprouting stage as well as the overall health of seed formation in plants (Weaich *et al.*, 1996).

Table 1 represents the various abiotic conditions and several root exudates secreted in different conditions. Each root exudate plays an important role and functions to help plants overcome stress and provide sufficient nutrients. According to Dardanelli *et al.* (2009) and Schlaman *et al.* (1998), phenolic compounds such as flavonoids and isoflavonoids play an important role in nod gene regulation, which stimulates the nodulation process in stem and root cells, also known as DNA promoters. They perform a wide variety of functions to regulate plant growth and development, such as UV protection, defense mechanisms against various pathogens, antioxidant

components, and the symbiosis signaling pathway between the leguminous plant root and rhizobia (Dardanelli *et al.*, 2012; Hassan and Mathesius, 2012).

Root exudates are categorized as organic acids and amino acids can play a vital function in preventing plant diseases as well as helping suppress various pathogens (Wen *et al.*, 2021; Yuan *et al.*, 2018). Moreover, proline root exudation plays an essential function during abiotic stress, such as membrane protection and protection of proteins that have antagonistic properties against inorganic ions. Moreover, in *Pancreaticum maritime*, proline improves the NaCl tolerance level by upregulating the stress-protective proteins and by guarding the protein turnover machinery against stress and damage caused by abiotic factors (Khedr *et al.*, 2003). During salt stress conditions, proline plays an important role in acclimatizing the plant via adjusting the osmotic regulation and also by protecting the plant cell (Ashraf and Harris, 2004; Naliwajski and Skłodowska, 2021).

Biotic stress

Biotic stress is a factor that affects plant growth and development via living organisms. These living organisms are bacteria, fungi, nematodes, protists, insects, viruses, and viroids (Hill *et al.*, 1998; Das and Rakshit, 2016). Plant growth and development AND quality of crop yield are the factors that can be influenced by environmental differences in various regions, country to country, as well as the resistance level of plants to certain aspects that can be studied and observed under the intensity of biotic stress (Angessa and Li, 2016). Various root exudates that secrete in response to these biotic stresses can act as attractants and signaling molecules for various microbes. Signaling molecules can also have certain effects as stimulants. The root exudates can inhibit and repel various pathogens and pests (Baetz and Martinoia, 2014). Root exudates in rhizodeposits emit lower-molecular-weight compounds with antibacterial capabilities (VanEtten *et al.*, 1994; Hassan *et al.*, 2019). Other primary metabolites act as growth regulators in certain plants (Li *et al.*, 2013). Certain root exudate compounds, which are secondary metabolites, have strong antibacterial and antifungal qualities (Hasegawa *et al.*, 2010; Vukovic *et al.*, 2013; Wurst *et al.*, 2010). Overall, root exudates play an important role in plants affected by various biotic factors and help in the plant's growth and regulation both internally and externally.

Table 2: Root exudates and their function in various plants in biotic stress condition.

Root exudates metabolites	Function	Plants	References
Alanine, Benzoic acid, p-coumaric acid, p-hydroxybenzoic acid and sugars	Regulating the growth of <i>Fusarium oxysporum</i> <i>Fusarium solani</i>	Peanut Cultivars	Li <i>et al.</i> , 2013; Ho <i>et al.</i> , 2017
Daidzein and Genistein	Control the expression of nod genes, the nodYABCSUIJ operon, and the nod box-associated genes.	Soybean plant	Lang <i>et al.</i> , 2008
Succinic acid	Suppress the growth of soil-borne fungus <i>F. oxysporum</i> and <i>F. sp. niveum</i>	Watermelon	Wu <i>et al.</i> , 2011, Ragman <i>et al.</i> , 2021
2,4-di-tert-butylphenol and 3,3-dimethyloctane	Nematicidal activity against <i>M. incognita</i>	Tomato	Li <i>et al.</i> , 2019; Du <i>et al.</i> 2021
Benzoic acid and Salicylic acid	Inhibits the growth of Fungus <i>Sclerotium rolfsii</i>	Ground nut	Ankati <i>et al.</i> , 2018; Mahatma, <i>et al.</i> , 2021
α -terthienyl	Nematicidal, Insecticidal, Fungicidal, Antiviral and Cytotoxic activities	Marigold	Wang <i>et al.</i> , 2007; Hamaguchi <i>et al.</i> , 2019
Ferulic acid	Decomposition of organic matter in soil	Strawberry Taro	Asao <i>et al.</i> , 2003; Asaduzzaman and Asao, 2020; Lal and Biswas, 2023
2,4-Dihydroxy-7-methoxy-2 H -1 and 4-benzoxazin-3(4 H)-1	Allelopathic and antibiotic properties reduce the harmful trichothecene (mycotoxin) produce by fungi.	Maize plant	Neal <i>et al.</i> , 2012; Etzerodt <i>et al.</i> , 2015

In Table 2, the root exudates that it secretes in various biotic conditions may impact its growth and regulation in a positive way. The most common function of these exudates is their antimicrobial effect. Different types of exudates prevent the growth of various microbes in soil, which can have devastating effects on the plant's growth.

Conclusions and Recommendations

In a nutshell, root exudates are an essential component of plant-soil interactions and play a critical role in plant growth, nutrition, and adaptation to changing environments. The secretion of root exudates is regulated by complex signaling pathways, which respond to both biotic and abiotic factors. The functions of root exudates are diverse and include nutrient acquisition, soil conditioning, defense against herbivores and pathogens, and communication with other plants. Understanding the mechanisms and functions of root exudate secretion is of great importance for developing sustainable agricultural practices, improving soil health, and enhancing plant growth and productivity. For future recommendation more research on the regulation of root exudate secretion can be done by isolating microbes from various mangrove sites will helps to study the specific functions that contribute to the creation of cutting-edge, economically, and ecologically sustainable farming techniques.

Novelty Statement

This review paper offers a comprehensive synthesis of current knowledge on the multifaceted roles of root exudates under both biotic and abiotic stress conditions. Further, this work uniquely elucidates how root exudates contribute to plant resilience, nutrient acquisition, and symbiotic interactions, presenting novel insights into the potential applications of root exudate manipulation for enhancing crop productivity and soil health.

Author's Contribution

Arba Aleem: Wrote the paper

Norrizah Jaafar Sidik: Corrected the manuscript.

Wan Razarinah Wan, Norfatimah Mohamed

Yunus and Abdul Razak: Reviewed the study and the manuscript.

Conflict of interest

The authors have declared no conflict of interest.

References

- Acosta-Motos, J.R., M.F. Ortuño, A. Bernal-Vicente, P. Diaz-Vivancos, M.J. Sanchez-Blanco and J.A. Hernandez. 2017. Plant responses to salt stress: Adaptive mechanisms. *Agronomy*, 7(1): 18. <https://doi.org/10.3390/agronomy7010018>

- Angessa, T.T., and C. Li. 2016. Exploration and utilization of genetic diversity exotic germplasm for barley improvement. In Exploration, identification, and utilization of barley germplasm. Academic Press. pp. 223-240. <https://doi.org/10.1016/B978-0-12-802922-0.00009-1>
- Ankati, S., T.S. Rani and A.R. Podile. 2019. Changes in root exudates and root proteins in groundnut–*Pseudomonas* sp. interaction contribute to root colonization by bacteria and defense response of the host. *J. Plant Growth Regul.*, 38: 523–538. <https://doi.org/10.1007/s00344-018-9868-x>
- Argosubekti, N., 2020. A review of heat stress signaling in plants. In IOP Conference Series: Earth and Environmental Science. 012041. <https://doi.org/10.1088/1755-1315/484/1/012041>
- Arif, Y., P. Singh, H. Siddiqui, A. Bajguz and S. Hayat. 2020. Salinity induced physiological and biochemical changes in plants: An omic approach towards salt stress tolerance. *Plant Physiol. Biochem.*, 156: 64–77. <https://doi.org/10.1016/j.plaphy.2020.08.042>
- Asaduzzaman, M. and T. Asao. 2020. Autotoxicity in strawberry under recycled hydroponics and its mitigation methods. *Hortic. J.*, 89(2): 124–137. <https://doi.org/10.2503/hortj.UTD-R009>
- Asao, T., K. Hasegawa, Y. Sueda, K. Tomita, K. Taniguchi, T. Hosoki, M.H. Pramanik and Y. Matsui. 2003. Autotoxicity of root exudates from taro. *Scientia Hort.*, 97(3–4): 389–396. [https://doi.org/10.1016/S0304-4238\(02\)00197-8](https://doi.org/10.1016/S0304-4238(02)00197-8)
- Ashraf, M. and P.J.C. Harris. 2004. Potential biochemical indicators of salinity tolerance in plants. *Plant Sci.* 166: 3–16. <https://doi.org/10.1016/j.plantsci.2003.10.024>
- Badri, D. and J.M.V. Vivanco. 2009. Regulation and function of root exudates. *Plant Cell Environ.*, 32: 666–681. <https://doi.org/10.1111/j.1365-3040.2009.01926.x>
- Baetz, U. and E. Martinoia. 2014. Root exudates: The hidden part of plant defense. *Trends Plant Sci.*, 19(2): 90–98. <https://doi.org/10.1016/j.tplants.2013.11.006>
- Bais, H.P., T.L. Weir, L.G. Perry, S. Gilroy and J.M. Vivanco. 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu. Rev. Plant Biol.*, 57: 233–266. <https://doi.org/10.1146/annurev.arplant.57.032905.105159>
- Barbour, W., M.D.R. Hattermann and G. Stacey. 1991. Chemotaxis of *Bradyrhizobium japonicum* to soybean exudates. *Appl. Environ. Microbiol.*, 57(9): 2635–2639. <https://doi.org/10.1128/aem.57.9.2635-2639.1991>
- Becard, G., 2017. How plants communicate with their biotic environment. London: Elsevier/AP.
- Ben-Ari, G. and U. Lavi. 2012. Marker-assisted selection in plant breeding. *Plant Biotechnol. Agric.*, pp. 163–184. <https://doi.org/10.1016/B978-0-12-381466-1.00011-0>
- Bertin, C., X.H. Yang and L.A. Weston. 2003. The role of root exudates and allelochemicals in the rhizosphere. *Plant Soil*, 256: 67–83. <https://doi.org/10.1023/A:1026290508166>
- Bhattacharyya, A., C.H. Pablo, O.V. Mavrodi, D.M. Weller, L.S. Thomashow and D.V. Mavrodi. 2021. Rhizosphere plant-microbe interactions under water stress. In: *Advances in applied microbiology*. Academic Press. 115: 65–113. <https://doi.org/10.1016/bs.aambs.2021.03.001>
- Breia, R., A. Conde, H. Badim, A.M. Fortes, H. Gerós and A. Granell. 2021. Plant SWEETS: from sugar transport to plant–pathogen interaction and more unexpected physiological roles. *Plant Physiol.*, 186(2): 836–852. <https://doi.org/10.1093/plphys/kiab127>
- Bulgarelli, D., K. Schlaeppli, S. Spaepen, E.V. Van Themaat and P. Schulze-Lefert. 2013. Structure and functions of the bacterial microbiota of plants. *Annu. Rev. Plant Biol.*, 64: 807–838. <https://doi.org/10.1146/annurev-arplant-050312-120106>
- Canarini, A., C. Kaiser, A. Merchant, A. Richter and W. Wanek. 2019. Corrigendum: Root exudation of primary metabolites: Mechanisms and their roles in plant responses to environmental stimuli. *Front. Plant Sci.*, 10. <https://doi.org/10.3389/fpls.2019.00420>
- Canarini, A., A. Merchant and F.A. Dijkstra. 2016. Drought effects on *Helianthus annuus* and *Glycine max* metabolites: from phloem to root exudates. *Rhizosphere*, 2: 85–97. <https://doi.org/10.1016/j.rhisph.2016.06.003>
- Chakraborty, K., N. Basak, D. Bhaduri, S. Ray, J. Vijayan, K. Chattopadhyay and R.K. Sarkar. 2018. Ionic basis of salt tolerance in plants: Nutrient homeostasis and oxidative stress tolerance. *Plant nutrients and abiotic stress tolerance*, pp. 325–362. <https://doi.org/10.1016/j.rhisph.2016.06.003>

- org/10.1007/978-981-10-9044-8_14
- Chaparro, J.M., D.V. Badri, M.G. Bakker, A. Sugiyama, D.K. Manter and J.M. Vivanco. 2013. Correction: Root exudation of phytochemicals in Arabidopsis follows specific patterns that are developmentally programmed and correlate with soil microbial functions. PLoS One, 8(8). <https://doi.org/10.1371/annotation/51142aed-2d94-4195-8a8a-9cb24b3c733b>
- Chaudhry, S. and G.P.S. Sidhu. 2021. Climate change regulated abiotic stress mechanisms in plants: A comprehensive review. Plant Cell Rep., <https://doi.org/10.1007/s00299-021-02759-5>
- Chen, I. and Lui, F. 2019. Physiology, Active Transport. Treasure Island (FL): StatPearls Publishing.
- Classen, A.T., M.K. Sundqvist, J.A. Henning, G.S. Newman, J.A. Moore, M.A. Cregger, L.C. Moorhead and M.C. Patterson. 2015. Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? Ecosphere, 6(8): 1–21. <https://doi.org/10.1890/ES15-00217.1>
- Contreras-Cornejo, HA., L. Macías-Rodríguez, R. Alfaro-Cuevas and J. López-Bucio. 2014. *Trichoderma* spp. improve growth of Arabidopsis seedlings under salt stress through enhanced root development, Osmolite production, and Na elimination through root exudates. Mol. Plant Microbe Interact., 27(6): 503–514. <https://doi.org/10.1094/MPMI-09-13-0265-R>
- Dam, N.M.V. and H.J. Bouwmeester. 2016. Metabolomics in the rhizosphere: Tapping into belowground chemical communication. Trends Plant Sci., 21(3): 256–265. <https://doi.org/10.1016/j.tplants.2016.01.008>
- Dardanelli, M.S., F.J. de Córdoba, J. Estévez, R. Contreras, M.T. Cubo, M.A. Rodríguez-Carvajal and A.M. Gil-Serrano, F.J. López-Baena, R., Bellogín, H. Manyani, F.J. Ollero, and M. Megías. 2012.. 2012. Changes in flavonoids secreted by *Phaseolus vulgaris* roots in the presence of salt and the plant growth-promoting rhizobacterium *Chryseobacterium balustinum*. Appl. Soil Ecol., 57: 31–38. <https://doi.org/10.1016/j.apsoil.2012.01.005>
- Dardanelli, M.S., H. Manyani, S. González-Barroso, M.A. Rodríguez-Carvajal, A.M. Gil-Serrano, M.R. Espuny and F.J. López-Baena. 2009. Effect of the presence of the plant growth promoting rhizobacterium (PGPR) *Chryseobacterium balustinum* Aur9 and salt stress in the pattern of flavonoids exuded by soybean roots. Plant Soil, 328(1-2): 483–493. <https://doi.org/10.1007/s11104-009-0127-6>
- Das, G., S.K. Sen, Shin and J.K. Patra. 2016. Endophytes: A Treasure house of bioactive compounds of medicinal importance. Front. Microbiol., 7: 1–8. <https://doi.org/10.3389/fmicb.2016.01538>
- Das, I.K. and S. Rakshit. 2016. Millets, their importance, and production constraints. Biotic Stress Resistance in Millets, pp. 3–19. <https://doi.org/10.1016/B978-0-12-804549-7.00001-9>
- de Weert, S., H. Vermeiren, I.H. Mulders, I. Kuiper, N. Hendrickx, G.V. Bloemberg and J. Vanderleyden, R. De Mot and B.J. Lugtenberg. 2002. Flagella-driven chemotaxis towards exudate components is an important trait for tomato root colonization by *Pseudomonas fluorescens*. Mol. Plant-Microbe Interact., 15(11): 1173–1180. <https://doi.org/10.1094/MPMI.2002.15.11.1173>
- DeAngelis, K.M., E.L. Brodie, T.Z. DeSantis, G.L. Andersen, S.E. Lindow and M.K. Firestone. 2009. Selective progressive response of soil microbial community to wild oat roots. ISME J., 3: 168–178. <https://doi.org/10.1038/ismej.2008.103>
- Delauney, A.J. and D.P.S. Verma. 1993. Proline biosynthesis and osmoregulation in plants. Plant J., 4: 215–223. <https://doi.org/10.1046/j.1365-313X.1993.04020215.x>
- Dinkeloo, K., S. Boyd and G. Pilot. 2017. Update on amino acid transporter functions and on possible amino acid sensing mechanisms in plants. Semin. Cell Dev. Biol., 74: 105–113. <https://doi.org/10.3389/fpls.2017.01513>
- Doan, T.H., T.A. Doan, M.J. Kangas, A.E. Ernest, D. Tran, C.L. Wilson and A.E. Holmes, E.L. Doyle and T.L. Durham. 2017. A low-cost imaging method for the temporal and spatial colorimetric detection of free amines on maize root surfaces. Front. Plant Sci., 8: 1513. <https://doi.org/10.3389/fpls.2017.01513>
- Du, J., Q. Gao, C. Ji, X. Song, Y. Liu, H. Li and X. Liu. 2022. *Bacillus licheniformis* JF-22 to control *Meloidogyne incognita* and its effect on tomato rhizosphere microbial community. Front. Microbiol., 13: 863341. <https://doi.org/10.3389/fmicb.2022.863341>

- org/10.3389/fmicb.2022.863341
- Dutta, S., T.S. Rani and A.R. Podile. 2013. Root exudate-induced alterations in *Bacillus cereus* cell wall contribute to root colonization and plant growth promotion. PLoS One, 8(10). <https://doi.org/10.1371/journal.pone.0078369>
- Etzerodt, T., K. Maeda, Y. Nakajima, B. Laursen, I.S. Fomsgaard, and M. Kimura. 2015. 2,4-Dihydroxy-7-methoxy-2 H-1,4-benzoxazin-3(4 H)-one (DIMBOA) inhibits trichothecene production by *Fusarium graminearum* through suppression of Tri6 expression. Int. J. Food Microbiol., 214: 123–128. <https://doi.org/10.1016/j.ijfoodmicro.2015.07.014>
- Fageria, N.K., H.R. Gheyi and A. Moreira. 2011. Nutrient bioavailability in salt affected soils. J. Plant Nutr., 34(7): 945–962. <https://doi.org/10.1080/01904167.2011.555578>
- Feng, H., N. Zhang, W. Du, H. Zhang, Y. Liu, R. Fu, J. Shao, G. Zhang, Q. Shen and R. Zhang. 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(10): 995–1005. <https://doi.org/10.1094/MPMI-01-18-0003-R>
- Firmansyah and N. Argosubekti. 2020. A review of heat stress signaling in plants. IOP Conf. Ser. Earth Environ. Sci., 484(1): 012041. <https://doi.org/10.1088/1755-1315/484/1/012041>
- Gargallo-Garriga, A., C. Preece, J. Sardans, M. Oravec, O. Urban and J. Peñuelas. 2018. Root exudate metabolomes change under drought and show limited capacity for recovery. Sci. Rep., 8(1). <https://doi.org/10.1038/s41598-018-30150-0>
- Haichar, F.Z., C. Santaella, T. Heulin and W. Achouak. 2014. Root exudates mediated interactions belowground. Soil Biol. Biochem., 77: 69–80. <https://doi.org/10.1016/j.soilbio.2014.06.017>
- Hamaguchi, T., K. Sato, C.S.L. Vicente and K. Hasegawa. 2019. Nematicidal actions of the marigold exudate α -terthienyl: Oxidative stress-inducing compound penetrates nematode hypodermis. Biology Open, 8(4). <https://doi.org/10.1242/bio.038646>
- Hasanuzzaman, M., K. Nahar and M. Fujita. 2013. Extreme temperature responses, oxidative stress and antioxidant defense in plants. Abiotic stress-plant responses and applications in agriculture, 13: 169–205. <https://doi.org/10.5772/54833>
- Hasegawa, M., I. Mitsuhara, S. Seo, T. Imai, J. Koga, K. Okada and H. Yamane and Y. Ohashi. 2010. Phytoalexin accumulation in the interaction between rice and the blast fungus. Mol. Plant Microbe Interact., 23: 1000–1011 17. <https://doi.org/10.1094/MPMI-23-8-1000>
- Hassan, M.K., J.A. McInroy and J.W. Kloepper. 2019. The interactions of rhizodeposits with plant growth-promoting rhizobacteria in the rhizosphere: A review. Agriculture, 9(7): 142. <https://doi.org/10.3390/agriculture9070142>
- Hassan, S. and U. Mathesius. 2012. The role of flavonoids in root–rhizosphere signalling: Opportunities and challenges for improving plant–microbe interactions. J. Exp. Bot., 63(9): 3429–3444. <https://doi.org/10.1093/jxb/err430>
- Hedrich, R., 2012. Ion channels in plants. Physiol. Rev., 92(4): 1777–1811. <https://doi.org/10.1152/physrev.00038.2011>
- Henry, A., W. Doucette, J. Norton and B. Bugbee. 2007. Changes in crested wheatgrass root exudation caused by flood, drought, and nutrient stress. J. Environ. Qual., 36: 904–912. <https://doi.org/10.2134/jeq2006.0425sc>
- Hill, J., H.C. Becker and P.M.A. Tigerstedt. 1998. Quantitative and ecological aspects of plant breeding. Chapman and Hall, London, UK. <https://doi.org/10.1007/978-94-011-5830-5>
- Ho, Y.N., D.C. Mathew and C.C. Huang. 2017. Plant-microbe ecology: Interactions of plants and symbiotic microbial communities. Plant ecology-traditional approaches to recent trends, pp. 93–119. <https://doi.org/10.5772/intechopen.69088>
- Huang, X.Y., C.K. Wang, Y.W. Zhao, C.H. Sun and D.G. Hu. 2021. Mechanisms and regulation of organic acid accumulation in plant vacuoles. Horticulture research, pp. 8. <https://doi.org/10.1038/s41438-021-00702-z>
- Inada, N. and T. Ueda. 2014. Membrane trafficking pathways and their roles in plant–microbe interactions. Plant Cell Physiol., 55(4): 672–686. <https://doi.org/10.1093/pcp/pcu046>
- Isayenkov, S.V. and F.J. Maathuis. 2019. Plant salinity stress: Many unanswered questions remain. Front. Plant Sci., 10: 80. <https://doi.org/10.3389/fpls.2019.00080>
- Khan, N., S. Ali, P. Zandi, A. Mehmood, S. Ullah, M. Ikram and M.A. Babar. 2020. Role of sugars,

- amino acids and organic acids in improving plant abiotic stress tolerance. *Pak. J. Bot.*, 52(2): 355–363. [https://doi.org/10.30848/PJB2020-2\(24\)](https://doi.org/10.30848/PJB2020-2(24))
- Khedr, A.H., M.A. Abbas, A.A. Wahid, W.P. Quick and G.M. Abogadallah. 2003. Proline induces the expression of salt-stress-responsive proteins and may improve the adaptation of *Pancreaticum maritimum* L. to salt-stress. *J. Exp. Bot.*, 54: 2553–2562. <https://doi.org/10.1093/jxb/erg277>
- Kloepper, J.W. and C.J. Beachamp. 1992. A review of issues related to measuring colonization of plant roots by bacteria. *Can. J. Microbiol.*, 38: 1219–1232. <https://doi.org/10.1139/m92-202>
- Kopecká, R., M. Kameniarová, M. Černý, B. Brzobohatý and J. Novák. 2023. Abiotic stress in crop production. *Int. J. Mol. Sci.*, 24(7): 6603. <https://doi.org/10.3390/ijms24076603>
- Kudo, N., T. Sugino, M. Oka and H. Fujiyama. 2010. Sodium tolerance of plants in relation to ionic balance and the absorption ability of microelements. *Soil Sci. Plant Nutr.*, 56(2): 225–233. <https://doi.org/10.1111/j.1747-0765.2009.00436.x>
- Lal, N. and A.K. Biswas. 2023. Allelopathic interaction and eco-physiological mechanisms in agri-horticultural systems: A review. *Erwerbs-Obstbau*, pp. 1–12. <https://doi.org/10.1007/s10341-023-00864-1>
- Lang, K., A. Lindemann, F. Hauser and M. Göttfert. 2008. The genistein stimulon of *Bradyrhizobium japonicum*. *Mol. Genet. Genom.*, 279(3): 203–211. <https://doi.org/10.1007/s00438-007-0280-7>
- Lee, H.I., J.H. Lee, K.H. Park, D. Sangurdekar and W.S. Chang. 2012. Effect of soybean coumestrol on *Bradyrhizobium japonicum* nodulation ability, biofilm formation, and transcriptional profile. *Appl. Environ. Microbiol.*, 78(8): 2896–2903. <https://doi.org/10.1128/AEM.07336-11>
- Li, X., H.J. Hu, J.Y. Li, C. Wang, S.L. Chen and S.Z. Yan. 2019. Effects of the endophytic bacteria *Bacillus cereus* BCM2 on tomato root exudates and *Meloidogyne incognita* infection. *Plant Dis.*, 103(7): 1551–1558. <https://doi.org/10.1094/PDIS-11-18-2016-RE>
- Li, X.G., T.L. Zhang, X.X. Wang, K. Hua, L. Zhao and Z.M. Han. 2013. The composition of root exudates from two different resistant peanut cultivars and their effects on the growth of soilborne pathogen. *Int. J. Biol. Sci.*, 9: 164–173. <https://doi.org/10.7150/ijbs.5579>
- Liu, Y., L. Chen, G. Wu, H. Feng, G. Zhang, Q. Shen and R. Zhang. 2017. Identification of root-secreted compounds involved in the communication between cucumber, the beneficial *Bacillus amyloliquefaciens*, and the soil-borne pathogen *Fusarium oxysporum*. *Mol. Plant Microbe Interact.*, 30(1): 53–62. <https://doi.org/10.1094/MPMI-07-16-0131-R>
- Liu, Y., H. Feng, R. Fu, N. Zhang, W.S. Du and R. Zhang. 2020. Induced root-secreted D-galactose functions as a chemoattractant and enhances the biofilm formation of *Bacillus velezensis* SQR9 in an McpA-dependent manner. *Appl. Microbiol. Biotechnol.*, 104: 785–797. <https://doi.org/10.1007/s00253-019-10265-8>
- Lugtenberg, B. and G. Girard. 2013. Role of phenazine-1-carboxamide produced by *Pseudomonas chlororaphis* PCL1391 in the control of tomato foot and root rot. *Microb. Phenazines*, pp. 163–175. https://doi.org/10.1007/978-3-642-40573-0_8
- Lugtenberg, B. and F. Kamilova. 2009. Plant-growth-promoting rhizobacteria. *Annu. Rev. Microbiol.*, 63: 541–556. <https://doi.org/10.1146/annurev.micro.62.081307.162918>
- Lumibao, C.Y., E.R. Kimbrough, R.H. Day, W.H. Conner, K.W. Krauss and S.A. Van Bael. 2020. Divergent biotic and abiotic filtering of root endosphere and rhizosphere soil fungal communities along ecological gradients. *FEMS Microbiol. Ecol.*, 96(7). <https://doi.org/10.1093/femsec/fiaa124>
- Mahatma, M.K., L.K. Thawait, K.S. Jadon, P.P. Thirumalaisamy, S.K. Bishi, K.J. Rathod and B.A. Golakiya. 2021. Metabolic profiling for dissection of late leaf spot disease resistance mechanism in groundnut. *Physiol. Mol. Biol. Plants*, 27(5): 1027–1041. <https://doi.org/10.1007/s12298-021-00985-5>
- Mariutto, M. and M. Ongena. 2015. Molecular patterns of rhizobacteria involved in plant immunity elicitation. *Plant Microbe Interact.*, pp. 21–56. <https://doi.org/10.1016/bs.abr.2015.07.002>
- Matilla, M.A. and T. Krell. 2018. The effect of bacterial chemotaxis on host infection and pathogenicity. *FEMS Microbiol. Rev.*, 42(1).

- <https://doi.org/10.1093/femsre/fux052>
- Meena, S.K., R. Pandey, S. Sharma, G. Gayacharan, T. Kumar, M.P. Singh and H.K. Dikshit. 2020. Physiological basis of combined stress tolerance to low phosphorus and drought in mungbean core set derived from diverse germplasm. <https://doi.org/10.20944/preprints202012.0001.v1>
- Mendis, H.C., V.P. Thomas, Schwientek, R. Salamzade, J.T. Chien, P. Waidyarathne and J. Kloepper and L. De La Fuente. 2018. Strain-specific quantification of root colonization by plant growth promoting rhizobacteria *Bacillus firmus* I-1582 and *Bacillus amyloliquefaciens* QST713 in non-sterile soil and field conditions. *PLoS One*, 13(2). <https://doi.org/10.1371/journal.pone.0193119>
- Mondal, S., K. Pramanik, P. Pal, S. Mitra, S.K. Ghosh and Mondal. 2023. Multifaceted roles of root exudates in light of plant-microbe interaction. In *Unravelling Plant-Microbe Synergy*. Academic Press. pp. 49-76. <https://doi.org/10.1016/B978-0-323-99896-3.00003-5>
- Mulla, D., 2013. Twenty-five years of remote sensing in precision agriculture: Key advances and remaining knowledge gaps. *Biosyst. Eng.*, 114: 358–371. <https://doi.org/10.1016/j.biosystemseng.2012.08.009>
- Munns, R. and M. Tester. 2008. Mechanisms of salinity tolerance. *Annu. Rev. Plant Biol.*, 59: 651–681. <https://doi.org/10.1146/annurev.arplant.59.032607.092911>
- Naliwajski, M. and M. Skłodowska. 2021. The relationship between the antioxidant system and proline metabolism in the leaves of cucumber plants acclimated to salt stress. *Cells*, 10(3): 609. <https://doi.org/10.3390/cells10030609>
- Neal, A.L., S. Ahmad, R. Gordon-Weeks and J. Ton. 2012. Benzoxazinoids in root exudates of maize attract *Pseudomonas putida* to the rhizosphere. *PLoS One*, 7(4). <https://doi.org/10.1371/journal.pone.0035498>
- Nicolson, T.H., 1967. Vesicular-arbuscular mycorrhiza a universal plant symbiosis. *Sci. Progress*, 1933: 561–581.
- Pantazi, X.E., D. Moshou and D. Bochtis. 2019. Intelligent data mining and fusion systems in agriculture. Academic Press. <https://doi.org/10.1016/B978-0-12-814391-9.00001-7>
- Pistillo, G. and A.D. Heritage. 2010. Propagation and establishment of *Phragmites australis* for environmental, agricultural, and industrial use in constructed wetlands. *Wetlands Australia*, 15(2): 39. <https://doi.org/10.31646/wa.178>
- Possell, M., C. Nicholas Hewitt and D.J. Beerling. 2009. Ecosystem feedback and cascade processes: Understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Glob. Change Biol.*, 15(5): 1153–1172. <https://doi.org/10.1111/j.1365-2486.2008.01801.x>
- Preston, G.M., 2017. Profiling the extended phenotype of plant pathogens. *Mol. Plant Pathol.*, 18(3): 443–456. <https://doi.org/10.1111/mpp.12530>
- Pugnaire, F.I., J.A. Morillo, J. Peñuelas, P.B. Reich, R.D. Bardgett, A. Gaxiola and D.A. Wardle. 2019. Climate change effects on plant-soil feedback and consequences for biodiversity and functioning of terrestrial ecosystems. *Sci. Adv.*, 5(11): 1–11. <https://doi.org/10.1126/sciadv.aaz1834>
- Putten, W.H.V.D., 2012. Climate change, aboveground-belowground interactions, and species range shifts. *Ann. Rev. Ecol. Evol. Syst.*, 43(1): 365–383. <https://doi.org/10.1146/annurev-ecolsys-110411-160423>
- Qu, M., G. Chen, J.A. Bunce, X. Zhu and R.C. Sicher. 2018. Systematic biology analysis on photosynthetic carbon metabolism of maize leaf following sudden heat shock under elevated CO₂. *Sci. Rep.*, 8(1): 7849. <https://doi.org/10.1038/s41598-018-26283-x>
- Radchenko, M., J. Symersky and R. Nie and M. Lu. 2015. Structural basis for the blockade of MATE multidrug efflux pumps. *Nat. Commun.*, 6(1). <https://doi.org/10.1038/ncomms8995>
- Rahman, M.Z., K. Ahmad, A.B. Kutawa, Y. Siddiqui, N. Saad, T. Geok Hun and M.I. Hossain. 2021. Biology, diversity, detection and management of *Fusarium oxysporum* f. sp. *niveum* causing vascular wilt disease of watermelon (*Citrullus lanatus*): A review. *Agronomy*, 11: 1310. <https://doi.org/10.3390/agronomy11071310>
- Raina, J.B., V. Fernandez, B. Lambert, R. Stocker and J.R. Seymour. 2019. The role of microbial motility and chemotaxis in symbiosis. *Nat. Rev. Microbiol.*, 17(5): 284–294. <https://doi.org/10.1038/s41579-019-0182-9>
- Rovira, A.D., 1969. Plant root exudates. *Bot. Rev.*, 35(1): 35–57. <https://doi.org/10.1007/>

BF02859887

- Rudrappa, T., K.J. Czymmek, P.W., Paré. and H.P. Bais. 2008. Root-secreted malic acid recruits beneficial soil bacteria. *Plant Physiol.*, 148(3): 1547-1556. <https://doi.org/10.1104/pp.108.127613>
- Salehi-Lisar, S.Y. and H. Bakhshayeshan-Agdam. 2016. Drought stress in plants: Causes, consequences, and tolerance. *Drought Stress Tolerance in Plants*, pp. 1–16. https://doi.org/10.1007/978-3-319-28899-4_1
- Sasse, J., E. Martinoia and T. Northen. 2018. Feed your friends: Do plant exudates shape the root microbiome? *Trends Plant Sci.*, 23(1): 25–41. <https://doi.org/10.1016/j.tplants.2017.09.003>
- Scharf, B.E., M.F. Hynes and G.M. Alexandre. 2016. Chemotaxis signaling systems in model beneficial plant-bacteria associations. *Plant Mol. Biol.*, 90(6): 549–559. <https://doi.org/10.1007/s11103-016-0432-4>
- Schirawski, J. and M. Perlin. 2018. Plant–microbe interaction 2017. The good, the bad and the diverse. *Int. J. Mol. Sci.*, 19(5): 1374. <https://doi.org/10.3390/ijms19051374>
- Schlaman, H.R., D.A. Phillips and E. Kondorosi. 1998. Genetic organization and transcriptional regulation of rhizobial nodulation genes. *The rhizobiaeae: Molecular biology of model plant-associated bacteria*, pp. 361–386. https://doi.org/10.1007/978-94-011-5060-6_19
- Seleiman, M.F., N. Al-Suhaibani, N. Ali, M. Akmal, M. Alotaibi, Y. Refay and T. Dindaroglu, H.H. Abdul-Wajid and M.L. Battaglia. 2021. Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants*, 10(2): 259. <https://doi.org/10.3390/plants10020259>
- Sharma, I., S. Kashyap and N. Agarwala. 2023. Biotic stress-induced changes in root exudation confer plant stress tolerance by altering rhizospheric microbial community. *Front. Plant Sci.*, 14: 1132824. <https://doi.org/10.3389/fpls.2023.1132824>
- Sharma, T., I. Dreyer, L. Kochian and M.A. Piñeros. 2016. The ALMT family of organic acid transporters in plants and their involvement in detoxification and nutrient security. *Front. Plant Sci.*, 7. <https://doi.org/10.3389/fpls.2016.01488>
- Singh, D.P., H.B. Singh and R. Prabha. 2017. Plant-microbe interactions in agro-ecological perspectives. Singapore: Springer. <https://doi.org/10.1007/978-981-10-6593-4>
- Slewiniski, T.L., 2011. Diverse functional roles of monosaccharide transporters and their homologs in vascular plants: A physiological perspective. *Mol. Plant*, 4(4): 641–662. <https://doi.org/10.1093/mp/ssr051>
- Strehmel, N., C. Böttcher, S. Schmidt and D. Scheel. 2014. Profiling of secondary metabolites in root exudates of *Arabidopsis thaliana*. *Phytochemistry*, 108: 35–46. <https://doi.org/10.1016/j.phytochem.2014.10.003>
- Suleiman, S. and L.S.P. Tran. 2018. Legume nitrogen fixation in soils with low phosphorus availability: Adaptation and regulatory implication. Cham: Springer. <https://doi.org/10.1007/978-3-319-55729-8>
- Suzuki, N., R.M. Rivero, V. Shulaev, E. Blumwald and R. Mittler. 2014. Abiotic and biotic stress combinations. *New Phytol.*, 203: 32–43. <https://doi.org/10.1111/nph.12797>
- Tahjib-Ul-Arif, M., M.I. Zahan, M.M. Karim, S. Imran, C.T. Hunter, M.S. Islam and Y. Murata. 2021. Citric acid-mediated abiotic stress tolerance in plants. *Int. J. Mol. Sci.*, 22(13): 7235. <https://doi.org/10.3390/ijms22137235>
- Takahashi, F., T. Kuromori, K. Urano, K. Yamaguchi-Shinozaki and K. Shinozaki. 2020. Drought stress responses and resistance in plants: From cellular responses to long-distance intercellular communication. *Front. Plant Sci.*, 11. <https://doi.org/10.3389/fpls.2020.556972>
- Tambalo, D.D., C.K. Yost and M.F. Hynes. 2015. Motility and chemotaxis in the rhizobia. *Biological Nitrogen Fixation*, Wiley New York, pp. 337–348. <https://doi.org/10.1002/9781119053095.ch33>
- Tan, S., C. Yang, X. Mei, S. Shen, W. Raza, Q. Shen and Y. Xu. 2013. The effect of organic acids from tomato root exudates on rhizosphere colonization of *Bacillus amyloliquefaciens* T-5. *Appl. Soil Ecol.*, 64: 15–22. <https://doi.org/10.1016/j.apsoil.2012.10.011>
- Tawaraya, K., R. Horie, T. Shinano, T. Wagatsuma, K. Saito and A. Oikawa. 2014. Metabolite profiling of soybean root exudates under phosphorus deficiency. *Soil Sci. Plant Nutr.*, 60: 679–694. <https://doi.org/10.1080/00380768.2014.945390>
- Tiwari, S., P. Singh and R. Tiwari. 2011. Salt-tolerant rhizobacteria-mediated induced

- tolerance in wheat *Triticum aestivum* and chemical diversity in the rhizosphere enhance plant growth. *Biol. Fertil. Soils*, 47: 907. <https://doi.org/10.1007/s00374-011-0598-5>
- Trivedi, P., T. Spann and N. Wang. 2011. Isolation and characterization of beneficial bacteria associated with citrus roots in Florida. *Microb. Ecol.*, 62: 324–336. <https://doi.org/10.1007/s00248-011-9822-y>
- VanEtten, H.D., J.W. Mansfield, J.A. Bailey and E.E. Farmer. 1994. Two classes of plant antibiotics: Phytoalexins versus phytoanticipins. *Plant Cell*, 6(9): 1191. <https://doi.org/10.2307/3869817>
- Vishwakarma, K., N. Kumar, C. Shandilya, S. Mohapatra, S. Bhayana and A. Varma. 2020. Revisiting plant–microbe interactions and microbial consortia application for enhancing sustainable agriculture: A review. *Front. Microbiol.*, 11: 560406. <https://doi.org/10.3389/fmicb.2020.560406>
- Vishwakarma, K., M. Mishra, S. Jain, J. Singh, N. Upadhyay, R.K. Verma and P. Verma, D.K. Tripathi, V. Kumar, R. Mishra and S. Sharma. 2017. Exploring the role of plant-microbe interactions in improving soil structure and function through root exudation: A key to sustainable agriculture. *Plant-Microbe Interactions in Agro-Ecological Perspectives: Volume 1: Fundamental Mechanisms, Methods and Functions*, pp. 467–487. https://doi.org/10.1007/978-981-10-5813-4_23
- Vishwakarma, K., S. Sharma, V. Kumar, N. Upadhyay, N. Kumar, R. Mishra and G. Yadav, R.K. Verma and D.K. Tripathi. 2017. Current scenario of root exudate-mediated plant-microbe interaction and promotion of plant growth. *Probiot. Agroecosyst.*, pp. 349–369. https://doi.org/10.1007/978-981-10-4059-7_18
- Vives-Peris, V., C. de Ollas, A. Gómez-Cadenas and R.M. Pérez-Clemente. 2020. Root exudates from plant to rhizosphere and beyond. *Plant Cell Rep.*, 39(1): 3–17. <https://doi.org/10.1007/s00299-019-02447-5>
- Vives-Peris, V., C. de Ollas, A. Gómez-Cadenas and R.M. Pérez-Clemente. 2019. Root exudates from plant to rhizosphere and beyond. *Plant Cell Reports. Plant Cell Rep.*, 39(1): 3–17. <https://doi.org/10.1007/s00299-019-02447-5>
- Vives-Peris, V., A. Gomez-Cadenas and R.M. Pérez-Clemente. 2018. Salt stress alleviation in citrus plants by plant growth-promoting rhizobacteria *Pseudomonas putida* and *Novosphingobium* sp. *Plant Cell Rep.*, 37: 1557–1569. <https://doi.org/10.1007/s00299-018-2328-z>
- Vives-Peris, V., A. Gómez-Cadenas and R.M. Pérez-Clemente. 2017. Citrus plants exude proline and phytohormones under abiotic stress conditions. *Plant Cell Rep.*, 36(12): 1971–1984. <https://doi.org/10.1007/s00299-017-2214-0>
- Vuković, R., N. Bauer and M. Ćurković-Perica. 2013. Genetic elicitation by inducible expression of b-cryptogein stimulates secretion of phenolics from *Coleus blumei* hairy roots. *Plant Sci.*, 199–200: 18–28. <https://doi.org/10.1016/j.plantsci.2012.10.009>
- Wang, H.W., C.Y. Ma, F.J. Xu, F. Lu, W. Zhang and C.C. Dai. 2021. Root endophyte-enhanced peanut-rhizobia interaction is associated with regulation of root exudates. *Microbiol. Res.*, 250: 126765. <https://doi.org/10.1016/j.micres.2021.126765>
- Wang, K.H., C.R. Hooks and A. Ploeg. 2007. Protecting crops from nematode pests: Using marigold as an alternative to chemical nematicides. *Plant Disease Publication*.
- Wang, M., Y. Zhu, P. Wang, Z. Gu and R. Yang. 2021. Effect of γ -aminobutyric acid on phenolics metabolism in barley seedlings under low NaCl treatment. *Antioxidants*, 10(9): 1421. <https://doi.org/10.3390/antiox10091421>
- Weaich, K., K.L. Bristow and A. Cass. 1996. Modeling preemergent maize shoot growth: I. physiological temperature conditions. *Agron. J.*, 88(3): 391–397. <https://doi.org/10.2134/agronj1996.00021962008800030006x>
- Weisskopf, L., E.L. Abou-Mansour, N. Fromin, N. Tomasi, D. Santelia, I. Edelkott and G. Neumann, M. Aragno, R. Tabacchi and E. Martinoia. 2006. White lupin has developed a complex strategy to limit microbial degradation of secreted citrate required for phosphate acquisition. *Plant, Cell Environ.*, 29(5): 919–927. <https://doi.org/10.1111/j.1365-3040.2005.01473.x>
- Wen, T., M. Zhao, J. Yuan, G.A. Kowalchuk and Q. Shen. 2021. Root exudates mediate plant defense against foliar pathogens by recruiting beneficial microbes. *Soil Ecol. Lett.*, 3(1): 42–51. <https://doi.org/10.1007/s42832-020-0057-z>

- Wu, H.S., Y.D. Liu, G.M. Zhao, X.Q. Chen, X.N. Yang and X.D. Zhou. 2011. Succinic acid inhibited growth and pathogenicity of in vitro soil-borne fungus *Fusarium oxysporum* sp. niveum. *Acta Agric. Scandinav. B Plant Soil Sci.*, 61(5): 404–409. <https://doi.org/10.1080/09064710.2010.496737>
- Wurst, S., R. Wagenaar, A. Biere and W.H. Van der Putten. 2010. Microorganisms and nematodes increase levels of secondary metabolites in roots and root exudates of *Plantago lanceolata*. *Plant Soil*, 329: 117–126. <https://doi.org/10.1007/s11104-009-0139-2>
- Xie, E., X. Wei, A. Ding, L. Zheng, A. Wu and B. Anderson. 2020. Short-term effects of salt stress on the amino acids of phragmites australis root exudates in constructed wetlands. *Water*, 12(56): 1–12. <https://doi.org/10.3390/w12020569>
- Xu, Q., H. Fu, B. Zhu, H.A. Hussain, K. Zhang, X. Tian and L. Wang. 2021. Potassium improves drought stress tolerance in plants by affecting root morphology, root exudates, and microbial diversity. *Metabolites*, 11(3): 131. <https://doi.org/10.3390/metabo11030131>
- Yan, F., Y. Zhu, C. Müller, C. Zörb and S. Schubert. 2002. Adaptation of H⁺-pumping and plasma membrane H⁺ ATPase activity in proteoid roots of white lupin under phosphate deficiency. *Plant Physiol.*, 129(1): 50–63. <https://doi.org/10.1104/pp.010869>
- Yang, H., M. Bogner, Y.D. Stierhof and U. Ludewig. 2010. H⁺-independent glutamine transport in plant root tips. *PLoS One*. <https://doi.org/10.1371/journal.pone.0008917>
- Yang, N.J. and M.J. Hinner. 2014. Getting across the cell membrane: An overview for small molecules, peptides, and proteins. *Site-Spec. Protein Labeling Methods Mol. Biol.*, pp. 29–53. https://doi.org/10.1007/978-1-4939-2272-7_3
- Yao, J. and C. Allen. 2006. Chemotaxis is required for virulence and competitive fitness of the bacterial wilt pathogen *Ralstonia solanacearum*. *J. Bacteriol.*, 188(10): 3697–3708. <https://doi.org/10.1128/JB.188.10.3697-3708.2006>
- Yaqoob, S., H.N. Bhatti, B. Sultana and M. Shahid. 2020. Prognosticating the potential of sorghum bicolor root exudates in response to abiotic stress. *Pak. J. Agric. Sci.* 57: 1661–1668.
- Yuan, J., N. Zhang, Q. Huang, W. Raza, R. Li, J.M. Vivanco and Q. Shen. 2015. Organic acids from root exudates of banana help root colonization of PGPR strain *Bacillus amyloliquefaciens* NJN-6. *Sci. Rep.*, 5(1). <https://doi.org/10.1038/srep13438>
- Yuan, J., J. Zhao, T. Wen, M. Zhao, R. Li, P. Goossens and Q. Huang, Y. Bai, J.M. Vivanco, G.A. Kowalchuk, R.L. Berendsen and Q. Shen. 2018. Root exudates drive the soil-borne legacy of aboveground pathogen infection. *Microbiome*, 6(1): 1–12. <https://doi.org/10.1186/s40168-018-0537-x>
- Zhalnina, K., K.B. Louie, Z. Hao, N. Mansoori, U.N. da Rocha, S. Shi, H. Cho, U. Karaoz, D. Loqué, B.P. Bowen, M.K. Firestone, T.R. Northen and E.L. Brodie. 2018. Dynamic root exudate chemistry and microbial substrate preferences drive patterns in Rhizosphere Microbial Community Assembly. *Nature Microbiol.*, 3(4): 470–480. <https://doi.org/10.1038/s41564-018-0129-3>
- Zhang, N., D. Wang, Y. Liu, S. Li, Q. Shen and R. Zhang. 2013. Effects of different plant root exudates and their organic acid components on chemotaxis, biofilm formation and colonization by beneficial rhizosphere-associated bacterial strains. *Plant Soil*, 374(1-2): 689–700. <https://doi.org/10.1007/s11104-013-1915-6>
- Zhang, N., K. Wu, X. He, S.Q. Li, Z.H. Zhang, B. Shen and X.M. Yang, R. Zhang, Q. Huang and Q. Shen. 2011. A new bioorganic fertilizer can effectively control banana wilt by strong colonization with *Bacillus subtilis* N11. *Plant Soil*, 344(1-2): 87–97. <https://doi.org/10.1007/s11104-011-0729-7>