Review Article

Secretion of Root Exudates in Response to Biotic and Abiotic Environment

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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, 2023; **Accepted** | June 08, 2024; **Published** | July 13, 2024
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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

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

Links Researchers

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 rhizo-deposits 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-molecule-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 (Slewinski, 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	*Phaseolus vulgaris*	Dardanelli *et al.*, 2012; Mondal *et al.*, 2023
Caffeic, Cinnamic acids, Ferulic, Gallic, Syringic, Quercetin and Vanillic	Salinity stress	Plant growth and development	*Triticum aestivum*	Tiwar *et al.*, 2011; Wang *et al.*, 2021
Abscisic 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.	*Quercus ilex*	Gargallo-Garriga *et al.*, 2018
Fumaric acid, Malic acid and Succinic acid	Drought stress	Plant growth regulation	*Agropyron cristatum*	Bertin *et al.*, 2003; Henry *et al.*, 2007; Qu *et al.*, 2018; Meena *et al.*, 2020
abscisic acid, indole acetic acid, jasmonic acid and salicylic acid,	Heat stress	Plant growth regulation	*Citrus macrophylla*	Vives-Peris *et al.*, 2018a
ascorbate, carotene, glutathione, or various flavonoids	Heat and drought stress	Help plants by providing potential antioxidants, Plant growth and development	*Sorghum bicolor*	Yaqoob *et al.*, 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 *Pancratium 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 *Fusarium oxysporum Fusarium solani*	Peanut Cultivars	Li *et al.*, 2013; Ho *et al.*, 2017
Daidzein and Genistein	Control the expression of nod genes, the nodYABCSUIJ operon, and the nod box-associated genes.	Soybean plant	Lang *et al.*, 2008
Succinic acid	Suppress the growth of soil-borne *fungus F. oxysporum* and *F. sp. niveum*	Watermelon	Wu *et al.*, 2011, Ragman *et al.*, 2021
2,4-di-tert-butylphenol and 3,3-dimethyloctane	Nematocidal activity against *M. incognita*	Tomato	Li *et al.*, 2019; Du *et al* 2021
Benzoic acid and Salicylic acid	Inhibits the growth of Fungus *Sclerotium rolfsii*	Ground nut	Ankati *et al.*, 2018; Mahatma, *et al.*, 2021
α-terthienyl	Nematicidal, Insecticidal, Fungicidal, Antiviral and Cytotoxic activities	Marigold	Wang *et al.*, 2007; Hamaguchi *et al.*, 2019
Ferulic acid	Decomposition of organic matter in soil	Strawberry Taro	Asao *et al.*, 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 *et al.*, 2012; Etzerodt *et al.*, 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.

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