



Root Exudates, Rhizosphere Biodiversity and Plant Defense Mechanism-An Underrated Triangle of Rhizosphere in Agroforestry Ecosystem

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Abstract

Plants in general threaten by different biotic (caused by pathogen attack) and abiotic stresses. Although different chemical compound has been discovered so far which can manage this biotic threats but the chances of growing resistance, mutation in organism, environmental hazards and impact over non target organism are always there. To Tackle this issues finding of some sustainable method is the need of hour. In this condition biological control not only depends upon predatism and parasitism but also antibiosis, induced defense mechanism, competitive suppressiveness, production of defensive enzymes, phytoalexin, toxins etc. Enhancement of the plant's innate immunity and strengthening of defense mechanism by acquired and induced way is becoming a new line of thought for researchers. In the rhizosphere specially in the complex agroforestry cultivation process the roots of many forest plant secret different complex compounds like phenols, propanoids, sugars, etc. in the root zone that harbors rhizosphere colonizer micro-organisms and turns the rhizosphere into an amazing place with the enriched microbe diversity and biomass. This microorganism are responsible for the production of plant defense modulator that enhance the innate capacity of the plant against pathogen attack. In this chapter, we will focus on the connection between these three components i.e. root exudates; rhizosphere biodiversity, and their effect on plant defense mechanisms. Their well-established interaction, mass effect, and the perspective of the trident will be discussed here in an elaborative manner.



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Introduction

Plants in nature are always threatened by different biotic and abiotic stresses among which biotic stress caused by different pathogens plays an important role and sometimes causes upto 20% yield loss in production of crops in worldwide.¹ With the passing time and advances in research, more and more active compounds have been developed which can control the pathogen attack, but still they are not fully successful as because there are different challenges like resistance against chemicals, mutation controlled pathogen supremacy, environmental hazard, health concern, effect on non target organism etc. For identifying the solution of these burning issues, the crop disease management through sustainable methods has come upon the rows. According to Cook and Baker (1983), "Biological control is the reduction of the amount of inoculum or diseaseproducing activity of a pathogen accomplished by or through one or more organisms other than man".² Basically biological control not only depends upon predatism and parasitism but also on antibiosis, induced defense mechanism, competitive suppressiveness and the production of defense related chemicals like enzymes, phytoalexin, toxin etc.³⁻⁵ Enhancement of the plant innate immunity and strengthening of defense mechanism by acquired and induced way by the activity of other organism is becoming a new line of thought for the researchers. This type of beneficial microorganisms are generally centralized in the rhizosphere of the plant.⁶ By the natural activity, plants are blessed with the secretion of different complex compounds like phenols, propanoids, sugars in the root zone which somehow harbors these kind of microorganisms and turns the rhizosphere into an amazing place with the enriched

microbes diversity and biomass. In this review article we will focus on the connection between these three components i.e. root exudates, rhizosphere biodiversity and their effect on plant defense mechanism. Their well-established interaction, mass effect and the perspective of the trident will be discussed here in elaborative manner.

Root Exudates-A Shield of Plant Base

Root exudates are the complex organic substances that are secreted by plant through its different physiological activity and freely releases root-cell material or mucilage and deposits in rhizosphere zone.⁷ It is estimated that at least 40% carbon released from photosynthetic process released as different exudates through plant roots.^{8,9} The secretion of the plant as root exudates greatly influenced by different factors like environmental stimulation,¹⁰ physiological condition of plants, plant species¹¹ and development stages.¹² The exudates from roots are generally classified into two broad categories i.e. low molecular amino acids, organic acids, sugars and other secondary metabolites (having low molecular weight) and mucilage (polysaccharides), proteins etc. (high molecular weight).¹³ It is also not a true fact that root exudates should be very unique to a plant as the same can be secreted by different plant species and even in various life stages e.g. benzoxazinoids (BXs) found to be produced by different species of poaceae family including maize, wheat, and rye.¹⁴ The chemicals found in rhizosphere zone are not always secreted by plant itself but sometimes they can be produce by cell lysis which is mediated by cell rupturing due to different biotic and abiotic damage.⁷

Table 1: Root exudates profiles of different crops

Sl. No.	Associated Plant	Root exudates	Chemical Nature of root exudates	Growth Media / Substrate	Reference
1	Tomato	Citric Acid, Piruvic Acid, Malic Acid, Succinic Acid, Fumaric, Pyroglutamic Glucose, Fructose, Maltose, Ribose, Xylose Tryptophane	Organic Acid Sugars Growth hormone	Stone wool and Glass beads	¹⁵

2	Cucumber	Citric Acid, Piruvic Acid, Malic Acid, Succinic Acid, Fumaric, Pyroglutamic Glucose, Fructose, Maltose, Ribose, Xylose, Melibiose Tryptophane	Organic Acid Sugars Growth hormone	Stone wool and Glass beads	16
3	Lettuce	Alanine,Aspertate, Glutamine,Glycine, Leucine,Isoleucine, Proline,Serine, Threonine,Valine, Prutresine Fructose,Maltose, Trehalose,Sucrose, Glycerol Malate,Fumarate, Succinate, Lauric Acid,Benzoic Acid	Amino acids and amines Sugars and Sugar alcohols Organic Acid	Loess Loam, Alluvial Loam	17
4.	Banana	Oxalic, Malic and Fumaric acid	Organic Acid	Vermiculite	18
5.	Water melon	Gallic acid, Coumaric acid, β -hydroxybenzoic acid, Chlorogenic acid, Vanillic acid, Caffeic acid, Syringic acid, Ferulic acid, Benzoic acid, Salicylic acid and Cinnamic acid	Phenolic Compund	Mixture of surface soil	19
6.	Cotton	Glucose, Xylose Lysin,Threonine, Arginine Oxalic acid, Succinic Acid, Maleic Acid	Sugars Amino acids Organic Acid	Mixture of soil	20
7.	Wheat	Glucose, Fructose, Sucrose, Xylose Arginine,Threonine, Methionine Succinic, Oxalic, Malonic	Sugars Amino Acids Organic Acid	Soil mixture	20

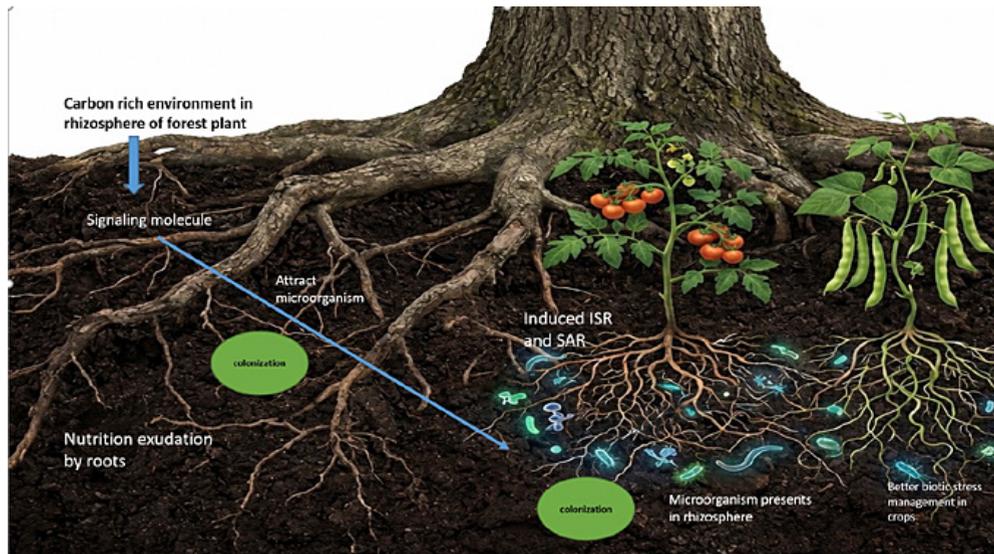


Fig 1: Cross talk between plant rhizosphere, their root exudates and effect on microorganism present in the soil environment in agroforestry.

Relationship of Root Exudates and Soil Microbiomes

The plants are well known for engaging different beneficial microbiomes that actively do their assigned activity and this incidence have ample evidences that cannot be denied.²¹ The chemical cross talk between the microbiomes and host plant make the primary basis and foundation bridge among themselves (Fig. 1). Additionally, it demonstrated how the host plant actually prepares and blueprints its shape, bulk and affinity of their microbiomes in root zones by the presence, composition and quantity of the exudation which directly or indirectly but actively impact on soil invading or soil inhibiting micro-organisms.²² Before illustrating the mode of action in between the primary metabolite of root exudation and microbiomes' reaction towards them, we have to concentrate on the most sensitive part of plants root i.e. root tip which is the first to react or expose into the environmental stimulation.²³ Rhizosphere is also well known as microbial hot spot of the rhizosphere²⁴ where bacterial population scored highest followed by other microorganism like fungi, algae and actinomycetes²⁵ The thumb rule for the successful communication between the host plant and microbes solely depends on the two main factors; the production and circulation of specified signals and the responses produce by this signals taking as stimuli²⁶ In the process of symbiosis, the *Nod-factors* or lipo-chitoooligosaccharides that act

as the signaling molecule of nodulation generally get activated by the secondary metabolite like flavonoids.²⁷ These Nod-factors actually plays an important role by triggering plant growth leading to formation of root nodule through the changes in root hair structure. On the other hand, it was also proven that presence of micro-organism in plant growth solution actually enhance the root exudation. e.g. secretion from the cell wall of *Phytophthora cinnamoni* mediate secretion of rosmarinic acid as root exudate in the rhizosphere of sweet basil.¹³ In case of the antagonistic relationship between the beneficial microbiomes and soil borne pathogen, colonization in the rhizosphere is the first and foremost step between them. According to the popular "rhizosphere effect" described by Hiltner (1904) nutrients exuded by plants roots are the key attraction for the vicinity of the microorganism in the root zone. In this condition a cross talk generally ignited where carbon-rich environment produced by plant root through exudation produce signals for microbiome and in reply responses for colonization produce by microbiome. The most crucial characteristic of the microbiomes is motility, which determines the kind of relationship between the pathogenic and beneficial bacteria and which of them will be successful in colonizing the environment through this chemotaxis process.⁶ This chemotaxis process regulates the maximum

colonization process in rhizosphere whereas some of the portion, also involved electrogenic process. As an illustration, consider the application of electrophysical potential in plant roots, which convey at the root surface and draw swimming oomycete plant disease zoospores to plant rhizosphere.¹³ From one of the compelling theory for root exudation describe pressure-driven mechanism of Munch's phloem flow, responsible for the transport of carbon in source organs to sinks through differences in concentration gradients that vary in turgor pressure based on source-sink activities, controls the driving carbon transport to roots and then extraction from roots to soil.^{28,29} In this regard, the statement of Ross-Elliott *et al.* (2017) described that in the root tip portion, phloem/batch unloading occurs through plasmodesmata by the combination of mass flow and diffusion.³⁰

Transportation of Primary Metabolites in Extra Cellular Zone of Root Tip

As mentioned previously, plasma membrane considered as the permeable to gas and molecules while impermeable to charged molecules like ions. As a result, these molecules can only pass through particular transmembrane proteins that create tiny holes in the bilayer lipid zone, enabling charged molecules to go through the membrane excluding the chances of being in contact with the fatty acid chains of the phospholipids which is hydrophobic in nature.²³ Many researchers mentioned about the efflux carriers readily channels present to mediate the exudation flux regulation controlled by gene expression.

A list of metabolites has been enlisted below with their efflux transporters

Table 2: Primary metabolites and corresponding transporters

Sl. No.	Primary metabolites	Transporters	Reference
1	Amino acids	UMAMIT transporters	31
		CAT transporters	32
		GDU transporters	33
2	Sugars	SWEET transporter	34
3	Organic acids	ALMT/malate and	35
		MATE/citrate transporters	

In some of cases, nutrient imbalances, environmental factors or some edaphic factors are also seemed to be responsible to regulate the gene transcription related to specific efflux transporter. For an instance, expression of SWEET, activated by the pathogen-driven molecule increase glucose efflux into the root apoplast³⁶ whereas, some metallic ion like Al³⁺ toxicity or scarcity of P triggers the secretion of the malate by the process of ALMT up-regulation mechanism in rhizosphere.³⁵ After removal of metabolites from cell plasma membrane of phloem used by the microbes of the rhizosphere. After attaining the apoplastic pathway, the secondary work is the well-defined diffusion process in the mentioned zone lacking of no barrier produced by the plasma membranes through root tip. Diffusion rate also differs from each other according to the zone of root tip. As an instance, in the immature elongation zone it is found to be higher rate of diffusion up to 10 times than the mature zone of root tip in the roots of Arabidopsis.³⁷

Networking System in rhizosphere

The microorganism residing in the rhizosphere zone generally act as fostering community that community that participate in plant development and plant health.³⁷ This rich microorganism biodiversity and its composition vary with the two main factors, i.e. plant species and soil properties.³⁸ Among the same species the assembly of rhizobacterial communities shows the differences even with the differences of genotypes and on the other hand can be same even in different environment and in different region.^{39,40} Plants are generally select the microbiome network in their rhizosphere according to their needs for fitness like particular need of nutrient of plants, biotic stress control procedure and symbiotic relationship etc.⁴¹ As an example, root inhibiting bacteria were generally found to be well established in the grassland of C3 grasses than the grassland of C4 grasses on the other hand, *Burkholderia* and *Variovorax* were found enriched in

the rhizosphere of *Leguminosae*, while the root zone of *Gramineae* predominated by *Pedobacter* and *Aeromicrobium*.⁴² Here some of the examples have

been cited which indicates the special microbiome present in the special agroforestry cropping model.

Table 3: Microbiome profiles of forest plants and their associated agricultural crops.

Forest plant	Agricultural crop	Presence of micro-organism	reference
Poplar	Barley and Maize	Bradyrhizobium and Mesorhizobium	43,44
Olive tree	Durum wheat, Barley, Chickpea and Faba bean	Actinobacteria, Proteobacteria, Crenarchaeota, Acidobacteria, Bacteroidetes, Planctomycetes, Firmicutes, Chloroflexi and Verrucomicrobia	45
Poplar, willow	Wheat, Maize, and Rapeseed	Acidobacteria, Actinobacteria, Alpha- and Gammaproteobacteria, Firmicutes, and Verrucomicrobia	46
Atractylodes lancea	Pea nut	Gram-negative (G-) bacteria	47

Plant Defense Modulators

Root exudates secreted in the rhizosphere zone not only helpful for modifying the soil's own physiochemical property but also modulate the proportion of microbial communities which is directly or indirectly helpful for the bioremediation of soil contaminants and as well as plant defense against the pathogen (Fig.1). This defense mechanism centered in creating the endophytic mutualism, development of antimicrobial activity and mimicry of quorum sensing etc.⁴⁸ Although Viché *et al.* (2005) has described a different defense mechanism called border cell organization in *Arabidopsis*, where specialized root cells with the capability of active secretion of metabolites, would be arranged not only to attract the beneficial microorganisms but to engulf harmful disease causing prokaryotes and nematode by producing mucilage covering.⁴⁹ The mechanism and the specificity of targeting pathogen differ from microbes to microbe and depends on even root exudates variation. On the other hand *Pseudomonas* spp. Specific traits for colonization in a particular rhizosphere zone depends on the flagella motility which mediated by the amount of secretion in root zone.⁵⁰ Here the interesting fact is that sometimes the presence of some specific microflora resulted in the changes of composition in rhizosphere zone. As an example use of biocontrol strain *Pseudomonas fluorescens* WCS365 (WCS365) on tomato roots increase the quantity of the total organic acids.¹⁵ The

augmentation of antagonistic bacteria of fluorescent *Pseudomonas* spp strain showed a certain decline *Gaeumannomyces graminis* var. *tritici* (Ggt) causing take all disease in wheat monoculture field where the pathogen accumulation was very severe due to repetitive cultivation. This take-all decline (TAD) wheat rhizosphere was due secretion of antibiotic 2,4-diacetylphloroglucinol (DAPG) by antagonist 51 (Kwak *et al.*, 2009). Long chain fatty acids and amino acids secretion in rhizosphere zone proliferate the presence of *Sphingomonas*, *Pseudomonas*, *Roseiflexus*, and *Flavitalea* helpful for suppressing the foliar pathogen.⁵² *Pseudomonas syringae* pv. *tomato* DC3000 (*Pst*) causing the leaf infection in *Arabidopsis* encouraged the secretion of large amounts of malic acid acted receptor of chemical sensitivity for the quorum sensing of *Bacillus subtilis* FB17 in the rhizosphere.⁵³ *Ocimum basilicum* infected with the *Pythium ultimum* encouraged to produce caffeic acid derivative-rosmarinic acid, which can inhibit the multiple soilborne and soil inhibiting microorganisms.¹³ Use of fluorescent *Pseudomonas* spp. has also been identified to suppress Fusarium wilt in radish⁵⁴ by its tremendous root-colonizing capability and enormous production of antimicrobial compounds.⁵⁵ On the other hand as a part of creating competition for food and space the chemo attractant bioagents employes a good role. As an example, WCS358 strain of fluorescent *Pseudomonas* spp produce the siderophore

pseudobactin-358 which makes the iron status unavailable by chelating Fe in the rhizosphere and as they have the highly specific receptor for the Fe absorption. This monopoly condition forced the pathogen to show back off as competition for iron defeat them by compromising with their growth suppression and reduced colonization.⁵⁶ *Pseudomonas cepacia* is well known for its capability of the production of lytic enzymes are such as cellulases, glucanases, proteases, and chitinases which suppress the *Rhizoctonia solani*, *Sclerotium rolfsii*, and *P. ultimum* by degrading the fungus cell structure.⁵⁷

SAR and ISR in rhizosphere Mediated by Microbiome

Induced systemic Resistance (ISR) has been reported to be modulated by the rhizosphere bacteria although it depends on the successful interaction of the rhizosphere inhibiting strain and with the host plant species. This complex compatibility between these two depends on some environmental conditions also. Some example hence been provided for better understanding

- 1) *P. fluorescens* WCS417r has been reported to be evoked the ISR in radish where the unsuccessful WCS358r strain in case of radish was found to be effective to elicit the ISR in Arabidopsis accession Columbia (Col-0).⁶
- 2) But the same WCS417r-elicited ISR reaction was failed to show ISR in case of the accessions RLD1 and Wassilewskija (WS-0) of Arabidopsis.⁵⁸

The most important and first line of defense against any pathogen is the recognition where plant phyllo plane possess the Pattern Recognition Receptors (PRRs) which act as the recognizer of the potential harmful pathogen by working on pathogen-associated molecular patterns (PAMPs). As like as potential pathogen, the non-pathogenic microorganism produce the elicitor named Microbe-Associated Molecular Patterns (MAMPs).⁵⁹ Plant immunity can be enhanced through the activation of a defensive signaling cascade triggered by the recognition of any of these PAMPs/MAMPs.⁶ *Chinchilla et al.* (2006) mentioned such an example where in Arabidopsis, the transmembrane leucine-rich-repeat receptor kinase FLS2 is directly bound by flg22, a conserved 22-amino-acid peptide of

bacterial flagellin was found to activate mitogen-activated protein kinase (MAPK) signaling cascade that causes the stimulation of plant defenses by forming the antimicrobial compounds.⁶⁰ Not only the microbial compounds, Plant defense are also mediated by the plant hormone secretion like Salicylic acid (SA), Jasmonic acid (JA), Abscisic acid, auxins, gibberellins, cytokinins etc. Typically, JA/ET-dependent reactions are effective against microorganism that possess necrotrophic lifestyle, while SA-dependent resistance that effective against bio trophic pathogens. SAR is related to localized deposition SA and the regulation of pathogenesis-related (PR) genes whereas, ISR regulate the JA and ET.

Conclusion

In this chapter we tried to enlighten the interconnection between plant rhizosphere and its dynamic microflora which are deviated or controlled by the root exudates. On the other hand, we discussed about the counteraction of the plant host against the harmful pathogen attacking them which is the contribution of the microflora that inhibited in rhizosphere. In this vast world of microbiomes, the identification followed by harbor the growth of beneficial microorganism and using them against the harmful one is the new tactics which can be proved as the time of need.

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Author Contributions

- **Debanjana Debnath:** Conceptualization, Methodology, Writing – Original Draft.

- **Rini Labanya:** Supervision, Writing – Review & Editing.
- **Chinmayee mohapatra:** Visualization, Supervision
- **Suraj Goldar:** Funding Acquisition, Resources.

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