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Root-exudates in Relation to Microbial Activity

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ABSTRACT

Plant root exudate is a naturally occurring resource, constituting various chemical compounds which alter the micro-environment around the root and plays a significant role in plant-microbe interaction. The interaction may be positive or nagetive. Root exudates are often divided into two classes of compounds. Low-molecular weight compounds such as amino acids, organic acids, sugars, phenolics, and other secondary metabolites account for much of the diversity of root exudates, whereas high molecular weight exudates, such as mucilage (polysaccharides) and proteins, are less diverse but often compose a larger proportion of the root exudates by mass. The present paper tries to understand the nature of chemical composition of root exudate and type of interaction with microbe.

Keywords: Root exudate, compostition, microbe, interaction

The 'hidden half' of a plant, the roots, is an underground growth system with complex architectures and varies with cultivars, age and environmental conditions (Bohm, 1979; Feldman, 1984). All plants have the ability to produce root exudates, however, the quantity and the chemical composition vary. Root exudates mainly include release of carbon containing compounds along with ions and water. All living root hairs, as well as primary and secondary roots produce large quantities of exudates. The production and nature of chemical components in root exudates depend on the amount of photosynthates devoted for roots. In general, seedling root exudate represents 30-40% of potosynthate, where as a young plant root exudate represents up to 30% of total dry matter production (Sauerbeck *et al.*, 1981; Whipps, 1990). In recent years, investigators have tried to discover the secrate of root exudate, a resource which plays very significant role in rhizosphere.

Composition of root exudate

The production and nature of root exudate varies type of plant cultivar, age and environmental factors. Root exudation includes the secretion of ions, free oxygen and water, enzymes, mucilage, and a diverse array of carbon-containing primary and secondary metabolites (Table 1). Root exudates are often divided into two classes of compounds. Low-molecular weight compounds such as amino acids, organic acids, sugars, phenolics, and other secondary metabolites account for much of the diversity of root exudates, whereas high molecular weight exudates, such as mucilage (polysaccharides) and proteins, are less diverse but often compose a larger proportion of the root exudates by mass. Bertin *et al.* (2003) determined root exudate composition of plants.

Knee *et al.* (2001) studied the exudate composition (sugars, glycosidic linkages and amino acids) of different crops (Table 2-4). The arabinose and galactose accounted for over 60% of the sugars. They found a different composition of amino acid in the exudate of different crops.

Root exudates also contain a large amount of secondary metabolites (Fig. 1). Narasimhan *et al.* (2003) analyzed the proportions of phenolic compounds in the root exudates of Arabidopsis to focus on the secondary metabolites. They identified 149 hydrophobic compounds consisting of 125 secondary metabolites in the root exudates. Phenylpropanoid compounds including lignins,

Table 1: Organic compound released in plat root exudates

Class of Compounds	Single components	Functions
Carbohydrates	Arabinose, glucose, fructose, galactose, maltose, raffinose, rhamnose, ribose, sucrose, and xylose	Provide favourable environment for the growth of microorganisms
Amino acids and amides	All 20 proteinogenic amino acids, aminobutyric acid, homoserine, cystathionine, mugineic acid.	Inhibit nematodes and root growth of different plant species.
Aliphatic acids	Formic, acetic, butyric, propionic, maleic, citric isocitric, oxalic, fumaric, malonic, succinic, maleic, tartaric, oxaloacetic, pyruvic, oxaloglutaric, glycolic, shikimic, acetonic, valeric, gluconic	Plant growth regulation and inhibition
Aromatic acids	p-hydroxybenzoic, caffeic, p-coumeric, ferulic, gallic, gentisic, protocatechuic, salicylic, sinapic, syringic	Stimulation depending on concentration
Miscellaneous phenolics	Favanol, flavones, falvanones, anthocyanins, isoflavonoids	Plant growth inhibition on stimulation depending on concentration
Fatty acids	Linoleic, linolenic, oleic, palmitic, stearic	Plant growth regulation
Sterols	Campestrol, cholesterol, sitosterol, stigmasterol	Plant growth regulation
Enzymes and Miscellaneous		Unknown

Table 2: Sugar compositions of root exudates

Sugar	Recovered carbohydrate %				
	Pea	Cowpea	Wheat	Maize	Rice
Arabinose	33.5	31.0	31.0	16.0	13.7
Fucose	0.5	9.0	3.0	21.0	502
Galactose	30.5	28.0	16.5	33.5	20.3
Galacturonic acid	5.5	11.5	3.0	Trace	Not determined
Glucose	6.0	18.5	15.0	13.0	37.9
Glucuronic acid	7.5	0.0	1.0	3.0	Not determined
Mannose	7.0	6.0	1.5	2.0	4.6
Rhamnose	5.0	2.0	Trace	0.0	0.0
Xylose	4.0	7.0	33.0	14.0	18.3

coumarins, flavonoids, aurones, sinapates, and anthocyanins were identified as the most abundant class.

Exudate as a source of carbon

Knee *et al.* (2001) showed that *R. leguminosarum* 8401 grew on 0.1% purified pea root mucilage to about 16% of the cell numbers seen on 0.1% glucose. This growth was about 25 times higher than the control. Broeckling *et al.* (2008) showed *Arabidopsis thaliana* and *Medicago truncatula* root exudate was able to maintain resident soil fungal populations.

Chemical interaction between exudate and microbes

The chemical nature of root exudate determines the interaction type between the plant and microbe (Fig 2). According to Bais *et al.* (2006) root exudate-microbe interactions may be classified as either positive or negative. Positive interactions include symbiotic associations with epiphytes and mycorrhizal fungi, and root colonization by bacterial biocontrol agents and plant growth–promoting bacteria (PGPB).

Winans *et al.* (2005) studied root exudate-released molecules which are recognized as signals for induction of specific responses in various plant-associated bacteria. Luteolin (A) and genistein (B) are flavonoids that induce the transcription of nodulation genes in various rhizobia (Fig 3.). Stachydrine (C) and trigonelline (D) are nonflavonoids that induce nod genes in *S. meliloti*. Tetronic acid (E) and erytronic acid (F) activate nod expression in *S. meliloti, M. loti, and R. lupini*. Acetosyringone (G) and ferulate (H) are phenolic

Table 3: Glycosidic linkage compositions of purified root exudate

Monosaccharide	Deduced glycosidic linkage	Recovered carbohydrate (mole %)			
		Pea	Cowpea	Wheat	Maize
Arabinose(f)	Terminal	17	10	22	4
	2-linked	—	0.5	1	6
	3-linked	1	4	1	—
	5-linked	11	9	1.5	Trace
	3,5-linked	1	1	—	—
	2,3,5-linked	2	5	2	—
Arabinose(P)	Terminal	—	Trace		1
Galactose(P)	Terminal	4	3	3	4
	2-linked	—	Trace	—	8
	3-linked	11	10	3	3
	4-linked	—	2	—	—
	6-linked	5	6	2	Trace
	2,3-linked	—	—	—	6
	2,6-linked	—	—	—	Trace
	3,4-linked	8	0.5	—	—
	3,6-linked	10	14	11	7
	3,4,6-linked	—	1	—	—
Fucose(p)	Terminal	—	3	0.5	14.5
	2-linked	—	—	—	1.5
	3-linked	—	—	—	8
Rhamnose(P)	Terminal	1	0.5	—	—
	2-linked	—	0.5	—	—
Glucose(P)	Terminal	8	6	3	Trace
	3-linked	?	—	1	3
	4-linked	?	7	6	5
	6-linked	—	—	1	—
	4,6-linked	2	2.5	3	7
	2,4,6-linked	?	—	—	2
Mannose(P)	Terminal	—	0.5	—	—
	2-linked	?	1	—	—
	2,3-linked	6	0.5	—	3
Xylose (P)	Terminal	—	6	4.5	8
	2-and4-Linked	2	3	17	3
	2,4-linked	—	0.5	1	—
	3,4-linked	—	—	7	3
	2,3,4-linked	—	3	9	Trace

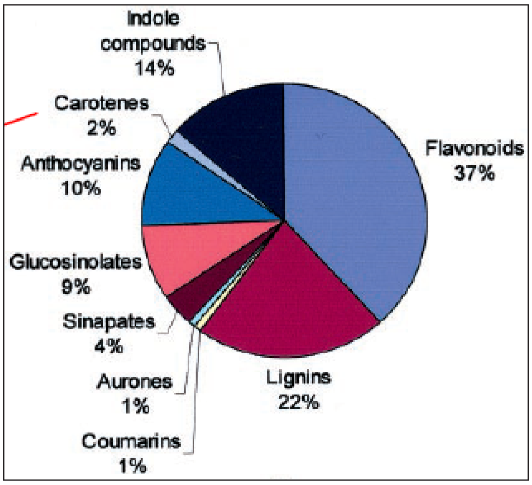

Fig. 1: Secondary metabolite composition of root exudate

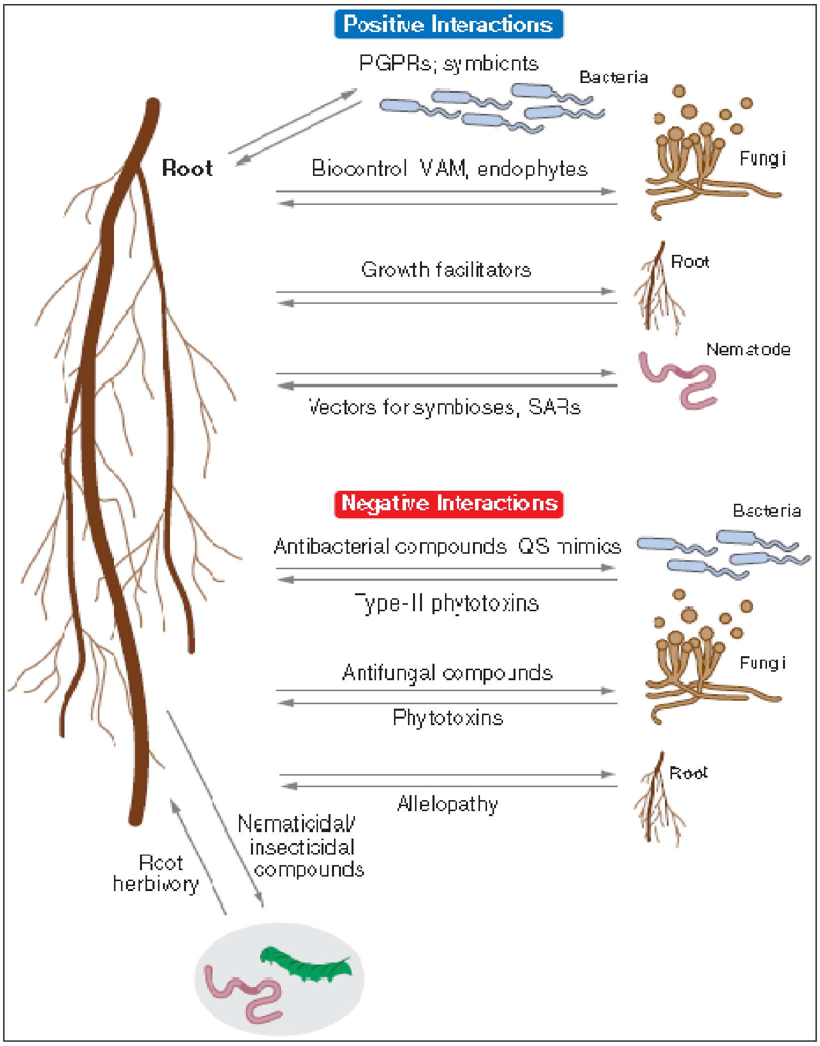

Fig. 2: Interaction type between the plant root exudate and microbe (Bais *et al.,* 2006).

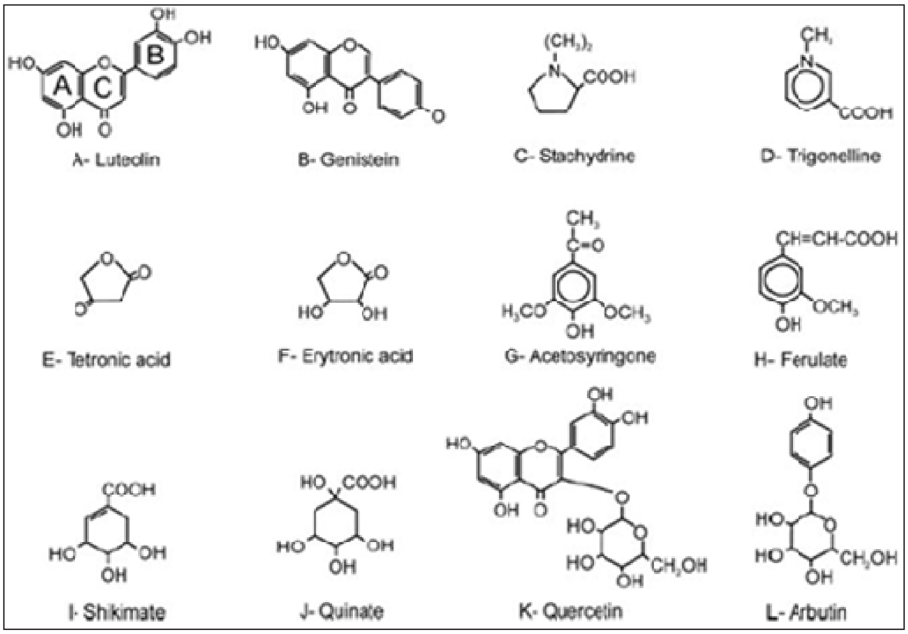

Fig. 3: Root exudate-released chemicals responsible for nodulation

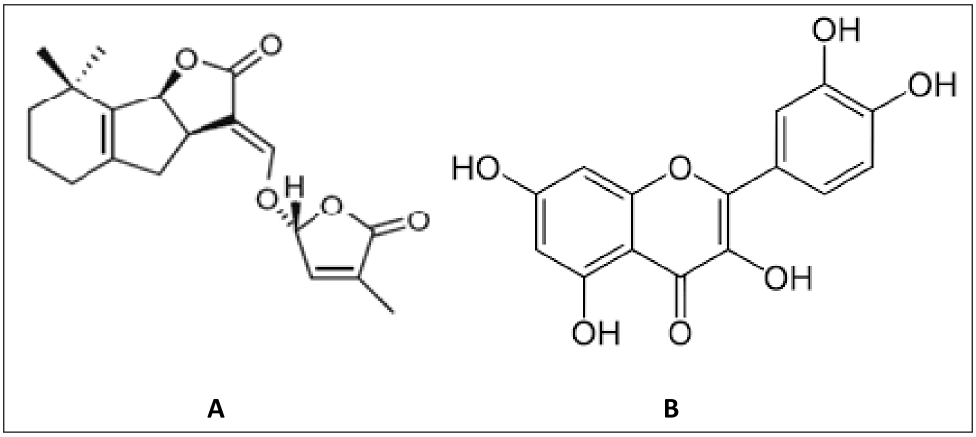

Fig. 4: (a) 5-deoxystrigol in sorghum root exudate **(b)** quercetin in adabidopsis root exudate

compounds that induce virulence genes in *A. tumefaciens*. Shikimate (I) and quinate (J) induce coronatine biosynthetic genes in *P. syringae* pv. tomato DC3000. Quercetin (K) and arbutin (L) are phenolic glycosides that activate the production of syringomycin in P. syringae pv. syringae.

Table 4: Amino acid compositions of root exudate

Amino acid	Mole %			
	Pea	Cowpea	Wheat	Maize
Hyp	12.9	Trace	0.7	0.7
Ser	14.9	7.4	8.6	6.1
Thr	9.5	5.1	7.3	5.6
Pro	6.4	5.9	6.2	8.2
Gly	12.8	13.1	10.1	13.8
Ala	8.1	7.2	9.3	8.1
His	0	0.9	1.9	1.5
Cys	0	0.4	1.1	ND
Glx	15.8	15.1	6.9	14.1
Asx	ND	14.7	9.4	10.1
Tyr	4.7	1.6	3.0	1.4
Val	4.0	5.2	7.0	4.6
Met	0	0.8	1.8	1.0
Ile	2.6	3.4	4.4	2.7
Leu	2.3	5.1	7.7	4.4
Phe	2.4	2.9	3.9	2.3
Lys	1.9	2.0	5.6	1.8
Arg	1.2	2.0	3.6	2.6

Yoneyama *et al.* (2007) found that during nitrogen defciency and as well as phosphorus defciency, sorghum promotes the production and exudation of 5-deoxystrigol from root (Fig. 4 a). 5-deoxystrigol acts as the host recognition signal for arbuscular mycorrhizal fungi.

Narasimhan *et al.* (2003) studied better colonization of the phenylpropanoid-utilizing strain like *Pseudomonas putida* PML2 in a genotobiotic system on the roots of Arabidopsis, where Quercetin (Fig 5b) is the major flavonoid leads to almost 90% removal of PCBs like Aroclor, 4Cl-PCB, and 2Cl-PCB in a 28-d period.

Burns and Shaw (2004) studied rhizosphere-enhanced biodegradation of 2,4-D. The initial step in 2,4-D breakdown, as described for R. eutropha JMP134 (pJP4), is mediated by an α-ketoglutarate-dependent dioxygenanse, encoded by the tfdA gene, which cleaves the acetate side chain to produce 2,4-D. An analog of 2,4-dichloromuconate produced in the *Trifolium pratense* rhizosphere which activates the 2,4-D degraders.

Bais *et al.* (2002) identified rosmarinic acid (RA), a caffeic acid ester, in the root exudates of hairy root cultures of sweet basil (*Ocimum bassilicum*) antimicrobial activity against an array of soil-borne microorganisms, including an opportunistic plant pathogen *Pseudomonas aeruginosa*.

Also microbial products influence the root exudation. Phillips *et al.* (2004) found 2,4-diacetylphloroglucinol (DAPG) from *Pseudomonas* bacteria and zearalenone (Z) from *Fusarium* fungi increase the net amino acid exudation from maize, wheat and medic.

Thus, various interactions between root exudate and soil microbes make the plant-microbe relation more dynamic.

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