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Root exudates a key factor for soil and plant: An overview

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Abstract
Root exudate is one of the ways for plant communication to the neighboring plant and adjoining of microorganisms present in the rhizosphere of the root. The chemicals ingredients of the root exudates are specific to a particular plant species and also depend on the nearby biotic and abiotic environment. The chemical ingredient exuded by plant roots include amino acids, sugars, organic acids, vitamins, nucleotides, various other secondary metabolites and many other high molecular weight substances as primarily mucilage and some unidentified substances. Through the exudation of a wide variety of compounds, roots may regulate the soil microbial community in their immediate vicinity, cope with herbivores, encourage beneficial symbioses, change the chemical and physical properties of the soil and inhibit the growth of competing plant species. Root exudates mediate various positive and negative interactions like plant-plant and plant-microbe interactions. The present review has been undertaken to examine the possible role of root exudates on nourishing the neighboring microorganisms present in the rhizosphere of the root. Plants secrete both high-and low-molecular weight compounds from their roots, and these root exudates function not only as nutrients for soil microbes but as signal molecules in plant–microbe interactions. All plants establish symbiotic interactions with rhizobia and arbuscular mycorrhizal fungi to obtain several nutrients such as nitrogen and phosphate. In these interactions, flavonoids and strigolactones in root exudates serve as signal molecules to establish the symbiotic interactions. Root exudates from some plants also function to acidify surrounding soils to acquire phosphate. Here, we provide an overview of the functions of root exudates with emphasis on the interaction between plants and soil microbes and also on the acquisition of nutrients from surrounding soil.

Keywords: Root exudates, rhizosphere, phytosiderophores, organic acids etc.

Introduction
Unseen part of the plant secretes chemical compounds which acts as communication signal between the adjacent plant and microbial community present in the rhizosphere of the root. Root exudates correspond to an important source of nutrients for microorganisms in the rhizosphere and seem to participate in early colonization inducing chemotactic responses of rhizospheric bacteria (Bacilio *et al*., 2002) [1]. Rhizosphere is defined as a zone of most intense bacterial activity around the roots of plant (Shukla *et al*, 2011) [11]. However, for the sake of practical investigation, the rhizosphere is most often defined as the soil adhering to plant roots when they are rigorously shaken, throughout which the rhizosphere effect must be observed to some extent (Kang and Mills, 2004) [25]. The compounds secreted by plant roots serve important roles as chemical attractants and repellants in the rhizosphere, the narrow zone of soil immediately surrounding the root system (Estabrook and Yoder, 1998; Bais *et al.,* 2001) [14, 2]. The chemicals secreted into the soil by roots are broadly referred to as root exudates. Through the exudation of a wide variety of compounds, roots may regulate the soil microbial community in their immediate vicinity, cope with herbivores, encourage beneficial symbioses, change the chemical and physical properties of the soil, and inhibit the growth of competing plant species (Nardi *et al*., 2000) [35]. The ability to secrete a vast array of compounds into the rhizosphere is one of the most remarkable metabolic features of plant roots, with nearly 5% to 21% of all photosynthetically fixed carbon being transferred to the rhizosphere through root exudates (Marschner, 1995) [31]. Although root exudation clearly represents a significant carbon cost to the plant, the mechanisms and regulatory processes controlling root secretion are just now beginning to be examined. Root exudates have traditionally been grouped into low- and high-M_r compounds. However, a systematic study to determine the complexity and chemical composition of root exudates from diverse plant species has not been undertaken. Low-M_r compounds such as amino acids, organic acids, sugars, phenolics, and various other secondary metabolites are believed to comprise the majority of root exudates, whereas high-M_r exudates

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primarily include mucilage (high-M_r polysaccharides) and proteins. The rhizosphere is a densely populated area in which the roots must compete with the invading root systems of neighboring plant species for space, water, and mineral nutrients, and with soil-borne microorganisms, including bacteria, fungi, and insects feeding on an abundant source of organic material (Ryan *et al*, 2001) [43]. Thus, root-root, root-microbe, and root-insect communications are likely continuous occurrences in this biologically active soil zone, but due to the underground nature of roots, these intriguing interactions have largely been overlooked. Root-root and root-microbe communication can either be positive (symbiotic) to the plant, such as the association of epiphytes, mycorrhizal fungi, and nitrogen-fixing bacteria with roots; or negative to the plant, including interactions with parasitic plants, pathogenic bacteria, fungi, and insects. Thus, if plant roots are in constant communication with symbiotic and pathogenic organisms, how do roots effectively carry out this communication process within the rhizosphere?

A large body of knowledge suggests that root exudates may act as messengers that communicate and initiate biological and physical interactions between roots and soil organisms. This update will focus on recent advancements in root exudation and rhizosphere biology.

The Rhizodeposits in soil

Plant species are likely to vary in the radial extent of their rhizosphere, determined by the amount and composition of their soluble rhizodeposits, which may exhibit relative differences in mobility in soil (Jones *et al*., 2004) [23]. Generally, the mineralization of rhizodeposits is thought to be rapid (Nguyen *et al*., 1999; Kuzyakov & Cheng, 2001) [36, 23]. For example, mucilages are reported to have a half-life of approximately 3 days (Jones *et al*., 2009) [24], and Ryan *et al*. (2001) [43] reported that most amino acids, sugars, and organic acids are mineralized with a half-life of 30–120 min when added to the rhizosphere at ecologically realistic concentrations. However, these latter estimates were arrived at by adding the compounds to a root mat (a dense population of roots formed at the base of a container in which a plant is grown as a consequence of spatial constraint). While it is possible to find root mats in nature (e.g. between rock cracks), their form is not representative of most root systems. Exudate turnover rates based on root mats may be considered 'averages' for the entire rhizosphere because bacterial density is generally greater at basal when compared with apical root regions of plants grown in soil; therefore, root exudate turnover rates are likely to be greater at the base when compared with the apices.

Root rhizosphere communication

Survival of any plant species in a particular rhizosphere environment depends primarily on the ability of the plant to perceive changes in the local environment that require an adaptive response. Local changes within the rhizosphere can include the growth and development of neighboring plant species and microorganisms. Upon encountering a challenge, roots typically respond by secreting certain small molecules and proteins (Stintzi and Browse, 2000; Stotz *et al*., 2000) [46, 47]. Root secretions may play symbiotic or defensive roles as a plant ultimately engages in positive or negative communication, depending on the other elements of its rhizosphere. In contrast to the extensive progress in studying plant-plant, plant-microbe, and plant-insect interactions that

occur in aboveground plant organs such as leaves and stems, very little research has focused on root-root, root-microbe, and root-insect interactions in the rhizosphere. The following sections will examine the communication process between plant roots and other organisms in the rhizosphere.

Root-Root Communication

In natural settings, roots are in continual communication with surrounding root systems of neighboring plant species and quickly recognize and prevent the presence of invading roots through chemical messengers. Allelopathy is mediated by the release of certain secondary metabolites by plant roots and plays an important role in the establishment and maintenance of terrestrial plant communities. It also has important implications for agriculture; the effects may be beneficial, as in the case of natural weed control, or detrimental, when allelochemicals produced by weeds affect the growth of crop plants (Callaway and Aschehoug, 2000) [12]. A secondary metabolite secreted by the roots of knapweed (*Centaurea maculosa*) provides a classic example of root exudates exhibiting negative root-root communication in the rhizosphere. Interestingly, (−)-catechin was shown to account for the allelochemical activity, whereas (+)-catechin was inhibitory to soil-borne bacteria (Bais *et al*., 2002c) [4]. In addition to racemic catechin being detected in the exudates of *in vitro*-grown plants, the compound was also detected in soil extracts from knapweed-invaded fields, which strongly supported the idea that knapweed's invasive behavior is due to the exudation of (−)-catechin. Moreover, this study established the biological significance of the exudation of a racemic compound such as catechin, demonstrating that one enantiomer can be responsible for the invasive nature of the plant, whereas the other enantiomer can contribute to plant defense. Although studies have reported the biosynthesis of the common enantiomer (+)-catechin, little is known regarding the synthesis of (−)-catechin or (±)-catechin as natural products. One possibility is that (+)-catechin production is followed by racemization in the root or during the exudation process. Alternatively, there could be a deviation from the normally observed stereo- and enantio specific biosynthesis steps. The flavonols kaempferol and quercetin are generally perceived as final products, rather than intermediates, in the pathway (Winkel-Shirley, 2001) [53]. The correlation of these experiments to the root exudation process has yet to be determined, but the data should provide a starting point for further studies on the characterization of specific committed steps in the synthesis of racemic catechin in knapweed roots. The above example demonstrates how plants use root-secreted secondary metabolites to regulate the rhizosphere to the detriment of neighboring plants. However, parasitic plants often use secondary metabolites secreted from roots as chemical messengers to initiate the development of invasive organs (haustoria) required for heterotrophic growth (Keyes *et al*., 2000) [27]. Some of the most devastating parasitic plants of important food crops such as maize (*Zea mays*), sorghum (*Sorghum bicolor*), millet (*Panicum milaceum*), rice (*Oryza sativa*), and legumes belong to the Scrophulariaceae, which typically invade the roots of surrounding plants to deprive them of water, minerals, and essential nutrients (Yoder, 2001) [55]. It has been reported that certain allelochemicals such as flavonoids, *p*-hydroxy acids, quinones, and cytokinins secreted by host roots induce haustorium formation (Estabrook and Yoder, 1998✦; Yoder, 2001) [14, 55], but the exact structural requirements of the

secreted compounds for haustorium induction is not fully understood.

Root-Microbe Communication

Root-microbe communication is another important process that characterizes the underground zone. Some compounds identified in root exudates that have been shown to play an important role in root-microbe interactions include flavonoids present in the root exudates of legumes that activate *Rhizobium meliloti* genes responsible for the nodulation process (Peters *et al.*, 1986) [39]. Although the studies are not yet conclusive, these compounds may also be responsible for vesicular-arbuscular mycorrhiza colonization (Becard *et al.*, 1992, 1995; Trieu *et al.*, 1997) [6, 7, 49]. In contrast, survival of the delicate and physically unprotected root cells under continual attack by pathogenic microorganisms depends on a continuous "underground chemical warfare" mediated by secretion of phytoalexins, defense proteins, and other as yet unknown chemicals (Flores *et al.*, 1999) [11, 16]. The unexplored chemodiversity of root exudates is an obvious place to search for novel biologically active compounds, including antimicrobials. For instance, Bais *et al.* (2002b) [4] recently identified rosmarinic acid (RA) in the root exudates of hairy root cultures of sweet basil (*Ocimum basilicum*) elicited by fungal cell wall extracts from *Phytophthora cinnamoni*. Basil roots were also induced to exude RA by fungal in situ challenge with *Pythium ultimum*, and RA demonstrated potent antimicrobial activity against an array of soil-borne microorganisms including *Pseudomonas aeruginosa* (Bais *et al.*, 2002b) [4]. Similar studies by Brigham *et al.* (1999) with *Lithospermum erythrorhizon* hairy roots reported cell-specific production of pigmented naphthoquinones upon elicitation, and other biological activity against soil-borne bacteria and fungi. Given the observed antimicrobial activity of RA and naphthoquinones, these findings strongly suggest the importance of root exudates in defending the rhizosphere against pathogenic microorganisms. Moreover, the aforementioned studies complement earlier research that mainly focused on the regulation and production of these compounds by providing valuable insights into the biological importance of RA and shikonin.

Root-Insect Communication

The study of plant-insect interactions mediated by chemical signals has largely been confined to leaves and stems, whereas the study of root-insect communication has remained largely unexplored due to the complexity of the rhizosphere and a lack of suitable experimental systems. However, root herbivory by pests such as aphids can cause significant decreases in yield and quality of important crops including sugar beet (*Beta vulgaris*), potato (*Solanum tuberosum*), and legumes (Hutchison and Campbell, 1994). One attempt to study root-insect communication was developed by Wu *et al.* (1999) using an *in vitro* coculture system with hairy roots and aphids. In this study, it was observed that aphid herbivory reduced vegetative growth and increased the production of polyacetylenes, which have been reported to be part of the phytoalexin response (Flores *et al.*, 1988) [15]. In a more recent study, Bais *et al.* (2002a) [3] reported the characterization of fluorescent β-carboline alkaloids from the root exudates of *O. tuberosa* (oca). The main fluorescent compounds were identified as harmine (7-methoxy-1-methyl-β-carboline) and harmaline (3, 4-dihydroharmine; Bais *et al.*, 2002a [3]; Fig. 1,

B-E). In addition to their fluorescent nature, these alkaloids exhibit strong phototoxicity against a polyphagous feeder, *Trichoplusia ni*, suggesting their insecticidal activity may be linked to photoactivation (Larson *et al.*, 1988). The Andean highlands, where *O. tuberosa* is primarily cultivated, are subjected to a high incidence of UV radiation, and it was observed that the strongest fluorescence intensity occurred with oca varieties that showed resistance to the larvae of *Mycrotrypes* spp., the Andean tuber weevil (Flores *et al.*, 1999) [11, 16]. These data suggest that UV light penetrating soil layers could photoactivate fluorescent β-carboline alkaloids secreted by oca roots to create an insecticidal defense response.

Exudation Alters the Soil Characteristics

A large range of organic and inorganic substances are secreted by roots into the soil, which inevitably leads to changes in its biochemical and physical properties (Rougier, 1981) [13]. Various functions have been attributed to root cap exudation including the maintenance of root-soil contact, lubrication of the root tip, protection of roots from desiccation, stabilization of soil micro-aggregates, and selective adsorption and storage of ions (Griffin *et al.*, 1976; Rougier, 1981; Bengough and McKenzie, 1997; Hawes *et al.*, 2000) [13, 8]. Root mucilage is a reasonably studied root exudate that is believed to alter the surrounding soil as it is secreted from continuously growing root cap cells (Vermeer and McCully, 1982; McCully, 1995; Sims *et al.*, 2000) [34, 45]. Soil at field capacity typically possesses a matric potential of −5 to −10 kPa (Chaboud and Rougier, 1984) [42]. It has been speculated that as the soil dries and its hydraulic potential decreases, exudates will subsequently begin to lose water to soil. When this occurs, the surface tension of the exudates decreases and its viscosity increases. As the surface tension decreases, the ability of the exudates to wet the surrounding soil particles will become greater. In addition, as viscosity increases, the resistance to movement of soil particles in contact with exudates will increase, and a degree of stabilization within the rhizosphere will be achieved. For instance, McCully and Boyer (1997) [34] reported that mucilage from the aerial nodal roots of maize has a water potential of −11 Mpa, indicating a large capacity for water storage when fully hydrated, whereas the mucilage loses water to the soil as it begins to dry.

This speculation supports the idea that root exudates could play a major role in the maintenance of root-soil contact, which is especially important to the plant under drought and drying conditions, when hydraulic continuity will be lost. The largest, most coherent soil rhizosheaths are formed on the roots of grasses in dry soil (Watt *et al.*, 1994). However, sheath formation requires fully hydrated exudates to permeate the surrounding soil particles that are then bonded to the root and each other as the mucilage dries. Young (1995) found that rhizosheath soil was significantly wetter than bulk soil and suggested that exudates within the rhizosheath increase the water-holding capacity of the soil. Furthermore, it has recently been proposed that in dry soil, the source of water to hydrate and expand exudates is the root itself. Modern cryo-scanning microscopy has helped researchers determine that the rhizosheath of a plant is more hydrated in the early morning hours compared with the midday samplings (McCully and Boyer, 1997) [34]. This implies that the exudates released from the roots at night allow the expansion of the roots into the surrounding soil. When transpiration resumes, the exudates

begin to dry and adhere to the adjacent soil particles. Thus, the rhizosheath is a dynamic region, with cyclic fluctuations in hydration content controlled to some extent by roots.

Factors affecting root exudates
Microbial activity
Organic compounds in root exudates are continuously metabolized by root-associated microorganisms at the rhizoplane and in the rhizosphere. Microbial activity results in quantitative and qualitative alterations of the root exudate composition due to degradation of exudate compounds and the release of microbial metabolites.

Sorption at the soil matrix
Root exudate compounds in soils are differentially affected by adsorption processes, depending on their charge characteristics and on ion-exchange properties of the soil matrix. The lack of charges prevents interactions of sugars with metal ions both in soil solution and at the soil matrix. However, adsorption of more hydrophobic organic exudate compounds such as flavonoids and simple phenolics may be mediated by hydrophobic interactions with humic compounds, and also abiotic oxidation of phenolics and organic acids at Fe and Mn surfaces has been reported. The adsorption of charged compounds such as carboxylic acids, though largely dependent on the soil type and pH, generally tends to increase with the number of negative charges available for anionic interactions with metal surfaces at the soil matrix, resulting in rapid removal of certain carboxylate species from the rhizosphere soil solution. Since metal complexation and ligand-exchange are mechanisms involved in mobilization of mineral nutrients (P, Fe) and exclusion of toxic elements (Al), the most effective organic chelators (e.g. citrate, oxalate, malate) for these elements frequently exhibit the most intense soil adsorption. In contrast, sorption of proteinaceous amino acids and the related mobilization of mineral nutrients in soils seems to be comparably low, due to slow reaction kinetics with metal ions. However, the so called phytosiderophores as nonproteinaceous, tricarboxylic amino acids behave differently and exhibit a fast reaction with amorphous iron (ferrihydrite) in soils.

Retrieval mechanisms
Carbon flow in the rhizosphere is not a strictly uni-directional process from root to soil. Active retrieval mechanisms for sugars and amino acids have been identified in plant roots, which were capable of recovering up to 90% of the exudates passively lost into the rhizosphere. Even the preferential uptake of organic nitrogen has been reported for plant species adapted to ecosystems such as arctic tundras, where the rate of nitrogen mineralization is generally low. These findings are in good agreement with recent reports on the molecular biological characterization of root specific transporters for amino acids and small peptides in higher plants. Similarly, induction of a re-uptake system for phytosiderophores as Fe complexes has been reported in graminaceous plant species under iron deficient conditions. In contrast, no such retrieval mechanisms could be identified for carboxylic acids. The ecological significance of retrieval mechanisms for plants may be related to improved nitrogen and Fe acquisition and to limitation of carbon losses. Especially for long term studies on root exudation in closed systems (e.g sterile culture systems), the impact of selective re-absorption of exudate compounds has to be taken into account.

Root injury
Various techniques for collection of root exudates are associated with the risk of root injury by rupture of root hairs and epidermal cells or rapid change of the environmental conditions (e.g temperature, pH, oxygen availability) during transfer of root systems into trap solutions, application of absorbtion materials onto the root surface, and preparation of root systems for exudate collection. The possible impact of those stress treatments may be assessed by measuring parameters of plant growth in plants either subjected or not subjected to the collection procedure, and by comparing exudation patterns after exposure of roots to the handling procedures with different intensity.

Mechanisms of Root Exudation
Diffusion
Release of the major low molecular weight (LMW) organic constituents of root exudates such as sugars, amino acids, carboxylic acids and phenolics is a passive process along the steep concentration gradient, which usually exists between the cytoplasm of intact root cells (millimolar range) and the external (soil) solution (micromolar range). Direct diffusion through the lipid bilayer of the plasmalemma is determined by membrane permeability, which depends on the physiological state of the root cell and on the polarity of the exudate compounds, facilitating the permeation of lipophilic exudates. At the cytosolic pH of approximately 7.1-7.4, more polar intracellular LMW organic compounds such as amino acids and carboxylic acids usually exist as anions with low plasma lemma permeability. A positive charge gradient, which is directed to the outer cell surface as a consequence of a large cytosolic K^+ diffusion potential and of plasma lemma ATPase mediated proton extrusion, not only promotes uptake of cations from the external solution, but also the outward diffusion of carboxylate anions.

Ion-Channels
Root exudation of extraordinary high amounts of specific carboxylates (e.g. citrate, malate, oxalate, and phytosiderophores) in response to nutritional deficiency stress or Al toxicity in some plant species cannot simply be attributed to diffusion processes. The controlled release of these compounds, involved in mobilization of mineral nutrients and in detoxification of Al, may be mediated by more specific mechanisms. Inhibitory effects by exogenous application of various anion channel antagonists indicate the involvement of anion channels with a concomitant release of protons or K^+, probably mediated by plasma lemma ATPase or K^+ channels respectively.

Vesicle transport
Vesicle transport is involved in root secretion of high molecular weight compounds. The release of mucilage polysaccharides from hypersecretory cells of the root cap is mediated by Golgi vesicles. Subsequently the secretory cells degenerate and are sloughed off. Secretory proteins such as ecto-enzymes (e.g. acid phosphatase, phytase, peroxidase, phenoloxidase) are synthesized by membrane-bound polysomes and cotranslationally enter the endomembrane system by vectorial segregation into the ER-lumen. While passing through the Golgi apparatus they are separated from proteins destinated for the vacuolar compartment, and are transported to the plasmalemma by transfer vesicles. Processes involved in exocytosis such as formation of vesicles

and their fusion with the plasma membrane strongly depend on extracellular and intracellular calcium levels.

Vesicles have also been implicated in storage and release of low molecular weight compounds such as phenolics and phytosiderophores in plant roots but the characterization of mechanisms remains to be established.

Nutritional Factors
Phosphorus (P)
Root-induced P mobilization in soils

Phosphorus is one of the major limiting factors for plant growth in many soils. Plant availability of inorganic phosphorus (Pi) can be limited by formation of sparingly soluble Ca phosphates, particularly in alkaline and calcareous soils, by adsorption to Fe- and Al-oxide surfaces in acid soils and by formation of Fe/Al-P complexes with humic acids. Phosphorus deficiency can significantly alter the composition of root exudates in a way, which is at least in some plant species related to an increased ability for mobilization of sparingly soluble P sources. Increased root exudation of carboxylates (e.g. citrate, malate, oxalate, organic compounds) is a P deficiency response, particularly in dicotyledonous plant species. Mobilization of Pi by exogenous application of carboxylates to various soils with low P availability has been demonstrated in numerous studies and seems to be mediated by mechanisms of ligand exchange, dissolution, and occupation of P sorption sites (e.g. Fe/Al-P and Ca-P) in the soil matrix. Citrate and oxalate were found to be the most efficient carboxylates with respect to P mobilization in many of these model experiments, according to high stability constants for complex formation with Fe, Al and Ca.

Physiology of carboxylate exudation

Only limited information is available on the physiological basis of P deficiency-induced root exudation of carboxylates. Increased carboxylate release is frequently observed in later stages of P deficiency. Major exudate compounds are malate, citrate, and also oxalate, especially in plant species where oxalate replaces malate as the major internal carboxylate anion. The plant species with intense P deficiency-induced carboxylate exudation, such as oil-seed rape, chickpea and white lupin accumulated organic acids mainly in the root tissue and, moreover, in the root zones where exudation was most intense (e.g. subapical root zones, proteoid roots). In contrast, root exudation of carboxylates even decreased in response to P deficiency in plant species such as *Sysimbrium officinale*, wheat, and tomato and was associated with predominant carboxylate accumulation in the shoots. The accumulation of organic acids in the root tissue is a prerequisite for enhanced root exudation of carboxylates under P-deficient conditions and may be determined by shoot/root partitioning of carboxylates or of carbohydrates as related precursors.

Exudation of phenolic compounds

In many plants, P deficiency also enhances production and root exudation of phenolic compounds. Increased biosynthesis of phenolics under P deficient conditions was suggested as another metabolic bypass reaction involved in liberation and recycling of Pi in P-starved cells. Antibiotic properties of certain phenolic compounds (e.g. isoflavonoids) in root exudates may not only counteract infection by root pathogens, but also prevent the microbial degradation of exudate compounds involved in P mobilization. Certain root flavonoids have been identified as signal molecules for spore germination and hyphal growth of arbuscular mycorrhiza, and flavonoids are likely to be important also as signaling compounds for the establishment of ectomycorrhiza. Phenolics may further contribute to P mobilization by reduction of sparingly soluble FeIII phosphates. The specific release of piscidic acid (p-hydroxyphenyl tartaric acid) from roots of P-deficient pigeon pea (*Cajanus cajan* L.), which is a strong chelator for FeIII, has been related to enhanced mobilization of Fe phosphates in Alfisols. However, considering comparatively low exudation rates, piscidic acid may be more relevant as a signalling compound for the establishment of microbial associations (e.g. AM, rhizobia).

Root-secretory phosphohydrolsases

Enhanced secretion of acid phosphatases and phytases by plant roots and also by rhizosphere microorganisms under P-deficient conditions may contribute to Pi acquisition by hydrolysis of organic P esters in the rhizosphere, which can comprise up to 30-80% of the total soil phosphorus. In many soils, however, the availability of organic phosphorus seems to be limited mainly by the low solubility of certain P forms such as Ca and Fe/Al-phytates, which can make up a major propotion of the soil-organic P. The oxalic acid in root exudates can contribute to some extent to phytate mobilization in soils. Similarly, in a P-deficient sandy soil, more Pi was liberated by simultaneous application of acid phosphatase and organic acids identified in rhizosphere soil solutuion of *Hakea undulata*, than by separate application of organic acids or acid phosphatase, respectively. Another limiting factor for phosphatase-mediated P mobilization, is the low mobility of the hydrolytic enzymes (APase, phytase), mainly associated with the root cell wall and with mucilage in apical root zones. An alternative function of root secretory acid phosphatases may be the rapid retrieval of phosphorus by hydrolysis of organic P, which is permanently lost by diffusion or from sloughed off and damaged root cells.

Nitrogen and Potassium
Nitrate assimilation

At least in some plant species such as maize, *Lupinus angustifolius* L. and tomato, root exudation of di- and tricarboxylic acids (mainly malate and citrate) seems to be affected by the form of nitrogen supplied as nitrate or ammonium. Generally, exudation of the carboxylates increased with increasing levels of nitrate in the culture medium. This may be related to the function of carboxylates in intracellular pH stabilization. Nitrate reduction in roots and in the shoot is stimulated with increasing nitrate supply, and results in the production of an equivalent amount of OH^-, which is neutralized by increased biosynthesis of organic acids or released into the rhizosphere when produced in the root tissue. The carboxylate anions can be stored in the leaf vacuoles but are also retranslocated to the roots via phloem transport when the leaf storage capacity is limited. In the root tissue, the carboxylate anions are either metabolized by decarboxylation or can be released into the rhizosphere.

Ammonium assimilation

Excess uptake of cations over anions as a consequence of increased ammonium supply is balanced by extrusion of protons and by synthesis of carboxylic acids for pH stabilization in the root tissue. The remaining carboxylate

anions are required as acceptors for ammonium assimilation in the roots, which is associated also with the production of protons and decarboxylation of organic acids. As a consequence, tissue concentrations and root exudation of carboxylates are declining with increased ammonium supply. High nitrogen concentrations inhibit the production and release of isoflavonoids from lupin roots. Compared with nitrate supply, exudation was strongly enhanced by ammonium application. Similarly, the well-known inhibitory effect of nitrogen on nodulation during establishment of the legume-rhizobium symbiosis is mainly caused by nitrate. In short-term, intense rhizosphere acidification induced by NH_4^+ nutrition or low rates of NO_3^- supply may directly stimulate the release of phenolics and other low molecular weight root exudate compounds as a consequence of an increased electrochemical transmembrane potential gradient but also due to acid-induced impairment of membrane integrity. Since flavonoids have important functions as chemoattractants, and nod-gene inducers for rhizobia, nitrogen effects on nodulation may be explained by differential exudation of these compounds depending on N form supply and the N nutritional status of the plants. Root flavonoids are involved also in pathogen and allelopathic interactions, and these processes might be similarly affected by nutritional modifications in root exudation.

Potassium nutrition
Only limited information is available on effects of potassium (K) supply on root exudation. Increased exudation of sugars, organic acids and amino acids has been detected in maize as a response to K limitation. This may be related to a K deficiency-induced preferential accumulation of low molecular weight N and C compounds at the expense of macromolecules.

Iron
Although iron (Fe) is one of the major soil constituents (0.5 - 5%) where it is usually present in the oxidized state (Fe^{3+}), plant availability is severely limited by the low solubility of Fe⁻ (hydroxides at pH levels favourable for plant growth. Therefore, plants need special mechanisms for aquiring Fe from sparingly soluble Fe forms to fit the requirements for growth, especially in neutral and alkaline soils, where the availability of Fe is particularly low.

Other micronutrients and heavy metals
Mobilization of micronutrients such as Zn, Mn, Cu, Co and of heavy metals (Cd, Ni) in soil extraction experiments with root exudates isolated from various axenically grown plants is well documented and has been related to the presence of complexing agents.

Role of Phytosiderophores
Formation of stable chelates with phytosiderophores occurs with Fe, but also with Zn, Cu, Co and Mn, and can mediate the extraction of considerable amounts of Zn, Mn, Cu and even Cd in calcareous soils. There is increasing evidence that PS release in graminaceous plants is also stimulated in response to Zn deficiency but possibly also under Mn and Cu deficiency. Similar to Fe deficiency, the tolerance of different graminaceous plant species to Zn deficiency was found to be related to the amount of released PS but correlation within cultivars of the same species seems to be low.

Role of carboxylates
Mobilization of micronutrients (Mn, Zn, Cu), heavy metals

(Cd), and even uranium in the rhizosphere has been also related to rhizosphere acidification and to complexation with organic acids (e.g. citrate) in root exudates. This view is further supported by intense mobilization of Mn, Zn, Cu, and Cd observed in soil extraction experiments with leachates from rhizosphere soil or with organic acid mixtures according to the root exudate composition of plant species such *as Lupinus albus*, *Hakea undulata* and *Spinacia oleracea* under P-deficient conditions, where exudation of carboxylates and protons is particularly expressed. However, only limited information exists about the plant availability and uptake of the metal-carboxylate complexes. Phenolics and organic acids in root exudates (especially malate) are involved in both complexation and reduction of Mn. In cluster-rooted plant species such as *Lupinus albus* and members of the *Proteaceae*, particulary intense exudation of organic acids and phenolics in response to P deficiency is frequently associated also with enhanced Mn mobilization in the rhizosphere and accumulation of high or even toxic Mn levels in the shoot tissue. Similarly, Mn toxicity was indirectly induced by the iron deficiency response in flax grown in a calcareous soil high in extractable Mn but low in Fe. Besides mobilizing effects of plant root exudates, Mn availability in the rhizosphere is also strongly affected by the activity of microorganisms involved in Mn oxidation and Mn reduction, which in turn depend on root exudates as a carbon source. Utilization of Cu complexes with humic acids and citrate has been reported for red clover especially under P-deficient conditions. Roots of young seedlings of barnyard grass, maize, rye and wheat secret hydroxamic acids, their complexes with Fe/III/-ions are available sources of iron. It is possible that the cyclic hydroxamic acids play a role in the alternative mechanism of iron uptake. The hydroxamic acids secreted by barnayard grass roots have an allelopathic role by inhibiting the roots growth of rice. The cyclic hydroxamic acid, 2,4-dihydroxy-1,4-benzoxazin-3-one (DIBOA) and its methoxy analogue, 2-4-dihydroxy-7methoxy-1,4-benzoxazin-one (DIMBOA), occur as glycosides in the Poaceae, including maize, wheat and rye, and are implicated in the resistance of plants to pathogens and insects (Niemeyer 1988) [37]. In addition to their toxic properties, the cyclic hydroxamic acids have also been associated with detoxification of triazine herbicides, inhibition of plant growth regulators (Hasegawa *et al*. 1992) [18] and may even have allelopathic properties (Perez and Ormeno-Nunez 1991) [38].

The grasses possess a special iron uptake mechanism. They exudate mugineic type compounds (phytosiderophores) through their roots into the rhizosphere, where they form complexes with the iron. The grasses take up these mobilized chelates. There are great differences in phytosiderophore activity between the plants. So maize and sorghum exude very little amount of phytosiderophore. The cyclic hydroxamic acids also form complexes with the Fe (III)-ions, and already (Klun *et al*. 1970) [28] supposed them to play a role in the iron uptake. The tissues of barnyard grass (*Echinochloa crus-galli* (L.) P.B.)synthesize cyclic hydroxamic acids, which are secreted by its roots in free or glycosidic forms. Hydroxamic acids inhibit rice root growth. The concentration of hydroxamic acids accumulating in the rhizosphere exceeds the level that is necessary for a 50% root growth retardation of rice. Based on this, we assume that cyclic hydroxamic acids secreted by barnyard grass roots have an allelopathic role by inhibiting the growth of rice (Petho 1993) [40].

Role of phytosiderophores in zinc efficiency of wheat
In Zn-deficient nutrient solution, durum wheat showed a more

rapid development of visible Zn-deficiency symptoms than bread wheat types. Bread wheat types were Zn-efficient and produced more biomass and durum wheat types under Zn-deficiency. Under Zn-deficiency, Zn-inefficient durum wheat lines HI-8498 and PDW-233 released significantly lower amounts of phytosiderophores than the Zn-efficient bread wheat PBW-343 and HD-2329. The phytosiderophore release in bread and durum wheat types was related to efficiency of Zn uptake across genotypes. The phytosiderophore release in durum types under Zn deficiency was limited by phytosiderophore availability in the roots rather than by release of phytosiderophores. The mixed culture experiment showed that rhizospheric availability of phytosiderophores is a factor limiting the acquisition of Zn by Zn-inefficient wheat. When grown in mixed culture with bread types, Zn-inefficient durum grew better and acquired more Zn compared to growth in monoculture. Furthermore, durum types showed a low transcript level of NAA T which correlated well with the production and release of phytosiderophores in Zn-deficient plants (Singh and Kumar 2002) [2].

Role on the Nodulation of Root Nodule Bacteria
The growth of *Bradyrhizobium japonicum* as well as *Rhizobium leguminosarum bv. Phaseoli* growing in minimal medium was repressed by the addition of hydroxylysine (Hyl), although the sensitivity of the former to Hyl, seemed to be lower than that of the latter (Keiko *et al.* 1999) [26]. The nodulation efficiency of both *Glycine max* (L.) inoculated with *B. japonicum* cells and *Phaseolus vulgaris* (L.) inoculated with *R. leguminosarum bv. phaseoli* cells was reduced in the presence of Hyl, concomitantly with the decrease in the elongation of roots. Besides, the Hyl contents in the seed (seedling) exudates tended to increase when the host plants were inoculated with an unfavorable strain for their nodulation. These results suggest that the Hyl plays a role in the effective symbiotic relationship by regulating the growth of the root nodule bacteria on the root surface and / or the elongation of the host plant's roots.

Donor-receiver bioassay was designed to eliminate the effects of the competitive interference for resources from allelopathic effects (Hisashi *et al* 2007) [21]. Seeds of cress (*Lepidium sativum*), lettuce (*Lactuca sativa*), timothy (*Phleum pratense*) or ryegrass (*Lolium multiflorum*) were incubated with 4-dayold buckwheat (*Fagopyrum esculentum*) seedlings for 3 days in Petri dishes under controlled laboratory condition. The growth of cress, lettuce, timothy and ryegrass seedlings was inhibited by the presence of buckwheat seedlings, and increasing the number of buckwheat seedlings increased the growth inhibition. One inhibiting substance was found in the culture solution in which buckwheat seedlings were hydroponically grown for 10 days. These results suggest that buckwheat seedlings may inhibit the neighboring plant growth due to exudation of allelopathic substance into the neighboring environment. Thus, the inhibitory effect of buck heat was probably caused by allelopathic chemical reactions.

Rhizodeposition under combined soil physical stresses
We investigated the effects of combined soil physical stresses of compaction and drought on the production of fully hydrated mucilage (mucilage) and root border cells (RBCs) in maize Somasundaram *et al*. 2009. [48] The exudation of carbon and water were also estimated using stable isotopes of 13Cand deuterated water (D20) under same soil Conditions. As plant age progressed during seedling stage, mucilage production increased, however, RBCs release did not. Soil compaction increased the release of D_2O, RBCs, and production of mucilage which implies the function of roots to reduce mechanical impedance during root penetration. Drying stress increased only carbon release, but reduced the others. This indicates that RBCs adhere more strongly to the root cap due to drying of mucilage, and water release may be reduced to save the water loss. The highest rhizodeposition of mucilage, RBCs and D_2O were occurred under wet compact soil condition, however, that of carbon occurred under dry compact soil condition. Roots of grasses in response to iron deficiency markedly increase the release of chelating substances ('phytosiderophores') which are highly effective in solubilization of sparingly soluble inorganic Fe^{III} compounds by formation of Fe^{III} phytosiderophores (Romheld and Marschner 1986) [51]. In barley (Hordeam vulgare L.), the rate of iron uptake from Fe^{III} phytosiderophores is 100 to 1000 times faster than the rate from synthetic Fe chelates (eg. Fe ethylene Diamine Tetraacetate) or microbial Fe siderophores (e.g. ferrichrome). Reduction of Fe^{II} is not involved in the preferential iron uptake from Fe^{III} phytosiderophores by barley. This is indicated by experiments with varied pH, addition of bicarbonate or of a strong chelator for Fe^{II} (e.g. bathophenanthroline disulfonate). The results indicate the existence of a specific uptake system for Fe^{III} phytosiderophores in roots of barley and all other graminaceous species. In contrast to grasses, cucumber plants (*Cucumis sativus* L.) take up iron from Fe^{III} phytosiderophores at rates similar to those from synthetic Fe chelates. Furthermore, under Fe deficiency in cucumber, increased rates of uptake of Fe^{III} phytosiderophores are based on the same mechanism as for synthetic Fe chelates, namely enhanced Fe^{III} reduction and chelate splitting. Two strategies are evident from the experiments for the acquisition of iron by plants under iron deficiency.

Table 1: Root exudates detected in higher plants

Class of compounds	Single components
Sugars	Arabinose, glucose, fructose, galactose, maltose, raffinose, rhamnose, ribose, sucrose, xylose
Amino acids and amides	all 20 proteinogenic amino acids, aminobutyric acid, homoserine, cysrathionine, mugineic acid phytosiderophores (mugineic acid, deoxymugineic acid, hydroxymugineic acid, epi-hydroxymugineic acid, avenic acid, distichonic acid A)
Aliphatic acids	Formic, acetic, butyric, popionic, malic, citric, isocitric, oxalic, fumaric, malonic, succinic, maleic, tartaric, oxaloacetic, pyruvic, oxoglutaric, maleic, glycolic, shikimic, cis-aconitic, trans-aconitic, valeric, gluconic
Aromatic acids	p-hydroxybenzoic, caffeic, p-coumaric, ferulic, gallic, gentisic, protocatechuic, salicylic, sinapic, syringic
Miscellaneous phenolics	Flavonols, flavones, flavanones, anthocyanins, isoflavonoids
Fatty acids	Linoleic, linolenic, oleic, palmitic, stearic
Sterols	Campestrol, cholesterol, sitosterol, stigmasterol

Enzymes	Amylase, invertase, cellobiase, desoxyruibonuclease, ribonuclease, acid phosphatase, phytase, pyrophosphatase apyrase, peroxidase, protease
Micellaneous	Vitamins, plant growth regulators (auxins, cytokinins, gibberellins), alkyl sulphides, ethanol, H+,K+ Nitrate, Phosphate, HCO_3^-

Rioval and Hanson, in 1993 study on Evidence for a large and sustained glycolytic flux to lactate in anoxic roots of some members of the halophytic genus Limonium

Momilactone B., 12.5 μg, was detected in culture solution in which three 80 day-old rice plants were grown hydroponically. At this time, the stage of these rice plants was panicle initiation, and length of their shoots and roots was about 110 and 35 cm, respectively. Since the culture solutions were renewed every two days during the experiment, one rice plant considered releasing 2.1μg of momilactone B into the solution per day. Mimilactone B was detected in shoots and roots of 80-day-old rice plants and the concentration of mimilactone in the shoots was 3.5-fold greater than that in the roots. Mimilactone B had already been found in rice leaves and straw. However, it was first reported by Hisashi and Takashi (2004) [20] that rots of rice seedlings contain mimilactone B. The present result suggests that roots of development rice plants also have mimilactone B.

Plants are usually stressed and competing with neighbouring plants for resources such as light, nutrients and water in the natural ecosystems. As one of the strategies for survival, many plant species release allelochemical to inhibit the germination and growth of their neighboring plants. Rice was also found to produce and release growth inhibiting allelochemical into their neighboring environments (Hisashi and Takashi 2004) [20]. However, the chemical structures of these allelochemicals are still unknown. Mimilactone B inhibited the germination and growth of other plant species, and the inhibitory activity was comparable to that of ABA. The rice seedlings at an early developmental stage released mom lactone B into their neighboring environment and the level released was enough to inhibit the growth of their neighboring plants. Momilactone B may act as an allelochemical and play an important role in the competition with neighboring plants. Using symbiotically N_2-fixing legumes as green manures is a way to supply N from the atmosphere to cropping ecosystems. Usually whole plants of the green manure are incorporated into soil; hence, the belowground parts as well as the aboveground parts would contribute to N transfer to succeeding crops. However, little is known about the contribution of the belowground parts alone (Bongsu et al., 2008) [10]. We assessed N transfer from below ground parts compared to whole plants of two legumes, *Crotalaria spectabilis* and *Sesbania rostrata*. Each of the legumes was grown approximately for 3 months in a Ij2000a Wagner pot filled with soil media, and then the roots alone (R) or shoot and root (5 +R) were harvested and incorporated in the pots. Tender green mustard (*Brassica rapa*) as the succeeding crop was grown for 66 days in these pots without additional fertilizer. Although the amount of N in green manure in 5 +R pots was approximately 4-fold higher than that in R pots, differences in N uptake by tender green mustard between the 5+R and R pots were smaller (1.7-fold for *C. spectabilis* and 2.3-fold for *S. rostrata*). This means that N recovery rate by tender green mustard was significantly higher in R than in 5+R pots with either green manures. Differences in C/N ratio of the green manures could not likely explain the higher N recovery rate in R pots. Bioassay of the aqueous extracts from the green manure with lettuce seedlings suggested that growth inhibitory effects might be responsible for the lower recovery rate in 5+R treatment.

The influence of root exudates on colonization of arbuscular mycorrhizal (AM) fungi was evaluated. Root exudates of cucumber (*Cucumis sativus*) and carrot (D*aucus carota*) were supplied to each of the seedlings grown in soil containing AM fungi (Kubota et al 2004) [32]. AM colonizaiton was significantly suppressed in C. sativus treated with root exudates from D. carota as well as in D. carota treated with root exudates from C. sativus. Detection (%) of AM fungi belonging to Glomus and Acaulospora and/or Entrophospora was remarkably reduced in C. sativus and D. carota treated with root exudates from D. carota and C. sativus, respectively. Percent of colonization in cucmber treated with root exudates of carrot was 68% while it was 81 and 79 % in cucumber treated with root exudates from cucmber and water, respectively. Percent of colonizaiton in carrot showed similar tendency with low AM colonization (58%) by cucumber root exudates treatment and high AM colonization (74 and 82%) by carrot root exudates and water treatment, respectively. Such supression effect on AM colonization by the plant root exudates was reported in case of supplying root exudates from non-mycorrhizal plant species such as mustard and sugar beet. In this study, root exudates collected even from the mycorrhizal plant species, cucumber and carrot, showed suppression on AM colonization in ach plant.
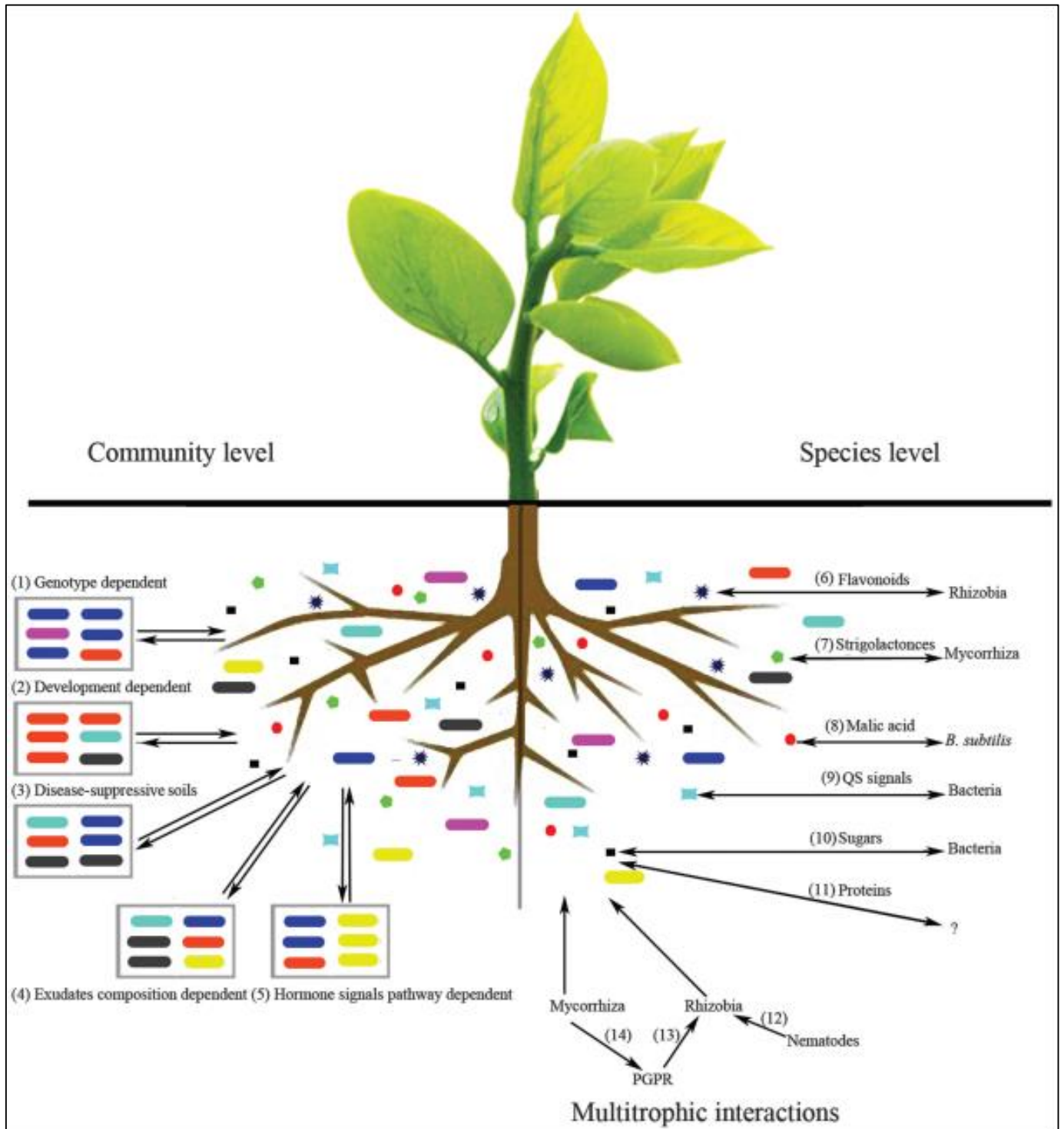
Fig 1: Plant root exudates mediate a rhizospheric interactions: At the species level (right side), Multitrophic interactions (bottom), and At the community level (left side). http://www.nrcresearchpress.com/doi/full/10.1139/cjb-2013-0225

Conclusion

Root exudates serve important role as chemical attractant and repellants in the rhizosphere. It changes the chemical and physical properties of soil and inhibit the growth of competing plant species. Nearly 5% to 21% of all photo synthetically fixed carbon being transferred to the rhizosphere through root exudates. Root exudates in their various forms may regulate plant and microbial communities in the rhizosphere. Flavonoids and other phenolic compounds released by plant roots have important functions in plant pathogenic interactions, feeding deterrence, nematode resistance, all opathic interactions and as signal molecules for the establishment of symbiotic association. Hydroxylysine plays a role in the effective symbiotic relationship by regulating the growth of the root nodule bacteria on the root surface. Rice plant produce mom lactone B and it may acts as an allelochemical and play and important role in the competition with Neighbouring plant.

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