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Review

Arbuscular mycorrhizal fungi and plant root exudates bio-communications in the rhizosphere

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The pre-symbiosis of arbuscular mycorrhizal fungi (AMF) is induced by the production of specific plant root exudates. Mycorrhizal fungi symbiotic relationships have many benefits to the plants. These benefits include, improved plant growth and developments, and enhanced plant tolerance to several diseases. Over the pre-symbiotic phase, the root releases essential metabolites necessary for fungal growth and root colonization. Root exudates compounds were reported and identified by several researchers. Root exudates have sugar, amino acids, proteins, carbon, some lipophilic compounds, flavonoids, and other bio-molecules. These compounds were presented as a critical and fundamental signal in plant, fungal and microbe bio-communications in the soil. Root-microbe interactions are continuous occurrences in the biological active soil zone. Mycorrhizal fungi bio-interaction can be classified as positive (symbiotic) to the host or could be negative to the plant. Root exudates may act as messengers that communicate and initiate biological and physical interactions between soil organisms and roots. The current review will illustrate the role of root exudates in mycorrhizal fungi association, the major components of root exudates and more focus on the disease control by root exudates derived from plants mycorrhizosphere.

Key words: Mycorrhizal fungi, exudates, bio-communications, root, volatiles, non-volatiles.

INTRODUCTION

Arbuscular mycorrhizal fungi (AMF) are the major component of soil and land plant (Smith and Read, 2008). Arbuscular mycorrhizal symbiosis is the most widespread type of mycorrhizal association. It is estimated in about 250,000 of plants species, including many crops, vegetables, herbs and trees (Smith and Read., 1997; Koide and Dickie, 2002). More than 80% of the world’s plant species are myorrhizas, ranging from flowering to non flowering plants, while only a few plant families do not form this association (Schenck, 1981; Schreiner and Bethlenfalvay, 1995; Harrier, 2001). Arbuscular mycorrhizal fungi are the key of soil microorganism components, which affect plant development and minerals uptake strongly (Tahat et al., 2008b). Plant roots influence the physical, chemical, and biological conditions of the soil in the rhizosphere (Gregory, 2006; Smith and Read, 2008).

Plant root exude a lot of valuable small molecular compounds into the mycorrhizosphere (Bais et al., 2005). Root derived chemicals are the major signal between plant root and other soil microbes (Bais et al., 2005). Root exudates produce chemical compounds which may deter some organisms while attracting another. The typical example for that are the flavonoes chemical signals produced by soybean which attract mutualist *Bradyribizobium japonicum* and *Phytophthora sojae* pathogen (Morris et al., 1998). Plant fungal bio-communications and interactions are critical and essential tools for understanding the abundance and distribution of plant species (Bongard, 2012). The rhizosphere is the area for highly dynamic interactions and communications between plant roots system and the pathogens and other beneficial microbes (Hirsch et al., 2003).

The term, rhizosphere was induced initially by nutrients produced from host roots. The concept was expanded to mycorrhizosphere to describe the combination between micro-flora and mycorrhizae (Linderman, 1988). The combination of AMF and soil micro-flora in natural undisturbed agro-ecosystem would contribute to the

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effective growth and health of plants (Linderman, 2008). Chemicals secreted into the soil by roots are referred to as root exudates (Walker et al., 2003). Mycorrhizosphere composition included two sources, firstly; rhizosphere soil which is influenced by root exudates and secondly; mycorrhizosphere soil which is relative to mycorrhizae and impacted by exudates from the root tissues and hyphal fungi (Olsson et al., 1996; Andrade et al., 1997; Johansson et al., 2004).

Root exudates play a significant role in the mobilization of moderately soluble nutrients in the rhizosphere (Carvalhais et al., 2001). The microbial populations are an essential part of the rhizosphere and they affect soil rhizosphere by their several activities such as nutrient uptake, biological transformations and exudation (Filion et al., 1999). The presence of root exudates may influence chemical reaction mobility within the soil environment and subsequently affect biological activities, such as biogeochemical processes within the soil, which is fundamental for developing bioremediation technologies of inorganic and organic contaminants (Marschner, 1998). Therefore, the aims of current review were to focus on the mycorrhzial fungi and root exudates relationship in the mycorrhizosphere and to understand the ability of root exudates to control soil borne diseases.

ARBUSCULAR MYCORRHIZAL FUNGI AND ROOT EXUDATES

There are a number of researches on AMF and root exudates (Naghashi and Doudes, 2003; Vierheilig and Bago, 2005; Basi, 2003, 2005; Yu et al., 2003; Harrison, 2005). Root exudates play an important role in AMF establishment symbiosis (Vierheilig et al., 2003). The establishment of AMF symbiosis and infection structure can occur only in the presence of signals released by host roots (Smith and Read, 1997; Czarnota et al., 2003). AMF can find the presence of plant host through root exudates that is perceived as a signal from the plant (Naghashi and Douds, 2003). Plants colonized by AMF differ from non-mycorrhizal plant in rhizosphere microbial community and result in alterations in root respiration rate quality and quantity of the exudates (Marschner et al., 2001). AM colonization has been shown to change the amount and quality of host root exudates (Azaizeh et al., 1995) and the chemo tactic response of soil bacteria (Sood, 2003; Buee et al., 2000). Exudates from *in vitro* grown tomato roots colonized with *Glomus intraradices* were shown to modify the chemo tactic response of *P. nicotianae* zoospores (Lioussanne et al., 2008). Mycorrhizal fungi can alter root exudation quantitatively and qualitatively (Leyval and Berthelin, 1993). Specific relationships occur between mycorrhizosphere microbiota and mycorrhizal fungi, and there are several literatures attesting that mycorrhizal symbiosis is largely influenced by soil microbes (Bowen, 1980; Kosuta et al., 2003; Garcia and Ocampon, 2002; De Oliveira and Garbaye, 1989).

Exudates and mycorrhizae bio-action against soil-borne diseases

Symbiotic interaction between plant root and microbes depends on secondary metabolites in the root exudates for beneficial association initiation and development (Vigo et al., 2000). The pathogenic interaction depends on understanding the chemical warfare mediated by plant secretion of phytoalexins, defense protein and other unknown chemical compounds (Flores et al., 1999; Bais et al., 2004, 2003). The protective effect of mycorrhizal symbioses against root pathogenic fungi has been tested by many researchers (Caron, 1989; St-Arnaud and Vujanovic, 2007; Oger et al., 2004). Disease decrease within plants colonized by mycorrhizal species is the result of the complex interactions between pathogens, AMF and plant (Harrier and Watson, 2004). Mycorrhizal symbiosis has been shown to lessen the damage caused by soil-borne pathogens (Azcon-Aguilar and Barea, 1996). *Phytophthora parasitica* proliferation was greatly minimized when tomato root were colonized by *Glomus mosseae* and *P. parasitica* compared with non-mycorrhizal tomato roots (Cordier et al., 1996).

Several biotic and a biotic factors are very important for the determination of efficiency of AMF as a disease control agent such as soil moisture, soil contents, host genotype, mycorrhizal level inoculums, inoculation time of mycorrhiza, mycorrhizal fungi species virulence, inoculums potential of pathogen and soil microflora (Singh et al., 2000). The increasing nutrient uptake resulted in more vigorous plants; thus, the plant itself may be more resistant or tolerant to pathogen attack (Linderman, 1994). Improvements in plant growth followed by root colonization by AMF occurs as a result of enhancement of the mineral nutrient status of plants (Akhtar and Siddiqui, 2008). Phosphorus tolerant AMF reduced nematode effect under high-P conditions; therefore, non-P-mediated mechanisms are involved, probably physiological changes in the roots (Sharma et al., 2007).

Root exudates from mycorrhizal strawberry plants suppressed the sporulation of *P. fragariae* in *in vitro* study (Norman and Hooker, 2000). Differential growth of *Fusarium oxysporum f.* sp *chrysanthemi*, *Trichoderma harzianum, Clavibactor michiganesis* and *Pseudomonas chlororaphis* was explained by substances released from *G. intraradices* under *in vitro* culture conditions (Filion et al., 1999). Grandmaison et al. (1993) suggested that phenolic compounds bound to cell wall could be indirectly responsible for the resistance of AMF roots to pathogenic fungi since they increased the resistance of cell wall to the action of digestive enzymes.

Phytoalexins toxic components are not detected during the first stages of AMF formation but can be detected in the later stages of symbiosis (Morandi, 1996). *P. parasitica* development decreased in *G. mosseae* and non *G. mosseae* parts of tomato mycorrhizal root systems in association with plant cell defense responses and accumulation of phenolics. Cortical cells containing *G. mosseae* are immune to the pathogen and exhibit a localized resistance response (Cordier et al., 1998). Exudates from fungal mycelium were also shown to impact germination of other pathogens and soil microbes (Steinkellner et al., 2008). Extracts from *G. intraradices* mycelium stimulated the growth of *Ps. chlororaphis* and *T. harzianum*, had no effect on *C. michiganens* and reduced conidial germination of *F. oxysporum* f. sp. *chrysanthemi* (Filion et al., 1999). The use of natural products for the control of fungal diseases in plants is considered an interesting alternative to synthetic fungicide due to their less negative impact on the environment (Brunelli, 1995).

Root exudates are considered as one of the mechanisms that explain the ability of AMF to suppress or increase the soil-borne diseases (Mukerji et al., 2002). Root exudates vary between different hosts, and the composition of the exudates changes in the same plant at different conditions (Marschner, 1995; Tahat et al., 2011). The current knowledge about the importance of exudates in AM fungus-host interactions was recently developed in *in vitro* culture technique and *in situ* compartmental systems. Although it is believed that root exudates play a major role in the infection and colonization of hosts by AMF, the actual role or mode of action of exudates was elucidated only recently (Nagahashi, 2000; Smith and Read, 2008).

The germination of *F. oxysporum f.* sp *Lycopersici* was inhibited in the presence of root exudates from the tomato plant (Scheffknecht et al., 2006). Root exudates can have direct defensive qualities. Pathogen-activated plant defenses can result in root secretion of antimicrobial compounds. It was shown that root-derived anti-microbial metabolites from Arabidopsis confer resistance to a variety of *P. syringae* pathovars (Bais et al., 2005). In another study, it was also predicted that transgenic plants that produce antimicrobial proteins can influence rhizosphere microbial communities (Glandorf et al., 1997). Sugars and amino acids in the root exudates stimulate the germination of chlamydospores and other fungi resting spores. The hyphal length of *G. mosseae* was greatly affected by the exudates of mycorrhizal tomato root exudates and mycorrhizal corn root exudates. The growth of *Ralstonia solanacearum* was suppressed due to *G. mosseae* spores germination (Tahat et al., 2010b).

The effect of parasitic nematode in the rhizosphere root exudates was studied (Foster, 1986; Griffiths, 1989; Horiuch et al., 2005). Root feeding nematode could participate in the interaction with root and soil 'S' microorganisms (Bais et al., 2006). Most information of microbe-nematode interaction in mycorrhizosphere and rhizosphere has been derived from rhizobi, mycorrhyza and plant pathogen researches (Khan, 1993). Horiuch et al. (2005) found that *Caenorbabditis elegans* may arrange interaction between plant roots and rhizobia in a positive way luminary to nodulation. In the same study, Horiuch et al. (2005) reported that *C. elegan* can transfer the *Sinorbizobium meliloti* (rhizobium species) to the root of *Medicago truncatula* in response to volatiles that released from plant root that attract nematode.

The hairy root exudates of sweet basil (*Ocimum basilicum*) cultures of elicited by fungal cell wall were extracted from *P. cinnamoni*. Basil roots were induced to exude rosmarinic acid (RA) by fungal *in situ* challenge by *Pythium ultimum*, and RA demonstrated strong antimicrobial activity against soil-borne microorganisms such as *P. aeruginosa* (Bais et al., 2002b). Hairy roots of *Lithospermum erythrorhizon* cell specifically produced naphthoquinones pigment upon elicitation, and other biological activity against soil-borne bacteria and fungi. The observed antimicrobial activity of RA and naphthoquinones suggest the importance of root exudates in defending the rhizosphere against pathogenic microorganisms (Brigham et al., 1999).

Root exudates components

Root exudates are divided into two compound classes; firstly, low-molecular weight (amino acids, sugar, phenolic and organic acid), and secondly, high-molecular weight exudates (protein and polysaccharides) (Marschner, 1995). The composition of root exudates can be complex and ranges from mucilage, root border cells, extracellular enzymes and sugars (complex and simple) (Shi et al., 2011; Jones et al., 2004), phenolics (Marschner, 1995; Tsai et al., 1991), amino acids and organic acids (OAs) (acetic, butyric, citric, fumaric, lactic, malic, propionic, succini) (Shi et al., 2011), carbon (Bodelier et al., 1997), phenylpropanoids, flavonoids and isoflavonoids Tsai and Phillips 1991; Winkel-Shirley, 2001; Buee et al., 2000; Peters et al.,1986, proteins (Glandorf et al., 1997), vitamins, (thiamine, nicotinic acid, biotin), nitrogenous macro-molecules such as nucleosides and purines to inorganic or gaseous molecules such as HCO_3^-, OH^-, H^+, CO_2 and H_2 (Marschner, 1995; Uren and Reisennuer, 1988; Nagahashi and Jr-Douds 2003).

Enzymes (amylase, invertase, protease, phosphatase), organic substrates excreted into the rhizosphere, particularly amino acids, organic acids, proteins, carbohydrates and vitamins, promote microbial biosynthesis of ethylene (Arshad and Frankernberger, 1990; Dakora and Phillips, 2002). Root exudates are the highest source of allelochemical input into the soil environment and it is a source of many growth factors phytohormones (choline, biotin, inositol, and pyridoxine) (Su and Cheng, 2008). Root exudates are an important source of organic carbon to soil mycorrhizosphere (Foster, 1986). Different phytotoxins in root exudates were defined (Einhellig, 1995). The plant phytotoxins affect different plant aspects like photosynthesis, respiration, germination, root development shoot growth and cell mortality in target plant (Weir et al., 2004).

Factors affecting exudates

The nature and amount of chemical substances thus exuded are dependent on several factors such as soil type, soil microorganisms, nutrients availability, soil pH level, plant host species, plant age, temperature, organic, inorganic, light intercity and O_2/CO_2 level, but the most important factors are:

Microorganisms

Root exudates were found to increase microbial activities in the rhizosphere (Oger et al., 2004). In the rhizosphere, the roots must compete with the invading root systems of neighboring plant for water, space, nutrients and with soil-borne microorganisms, including fungi, bacteria, and insects feeding on an abundant source of organic material (Ryan and Delhaize, 2001; Burke et., 2002). Root exudates may act as messengers that initiate physical and biological interactions between roots and soil micro-organisms (Walker et al., 2003). Roots exudates regulate the soil microbial community in their immediate vicinity, through the exudation of a wide variety of compounds, encourage beneficial symbioses, change the chemical and physical properties of the soil, and inhibit the growth of competing plant species (Nardi et al., 2000; Sylvia et al., 2005). The exudates compounds can cause some nutrient elements to be relatively more available for uptake by plants. The exudation rate is increased by the presence of microbes in the rhizosphere (Gardner et al., 1983; Koo et al., 2005).

Soil pH and fertilizers

Root exudates compound solutions stimulated soil dehydrogenase activity, and the addition of OAs increased soil pH (Shi et al., 2011). Acidification of the rhizosphere is an important nutritional effect that organic acids have in root exudates (Dinkelaker et al., 1989). High concentrations of anions organic acid in root exudation will lade to P deficiency (Hoffland et al., 1989) and this lowers rhizosphere pH, making P and Mn, Fe and Zn to be more available in calcareous soils (Haynes, 1990; Jones and Darrah, 1994). The relationship between organic acid exudation and rhizosphere acidification is not that simple as the extrusion of H^+. Acidification below pH 5.5 can cause some major macronutrients to become limiting because micronutrients such as Mn, Fe and Al occur in high concentrations below pH (5.5) (Brady, 1990). Ammonium nutrition acidification does not result in increased phosphorus mobilization (Gahoonia et al., 1992). H^+ extrusion occurs during N fixation by symbiotic legumes (Raven et al., 1990). This can lead to rhizosphere acidification and increased availability of limiting elements nutrient like P, Mo and Fe (Gahoonia, 1993; Gillespie and Pope, 1990). There are many documents of enhanced H_2^+ extrusion under P deficiency and Fe deficiency, leading to acidification of localized areas around the root tips (Bienfait, 1988; Hoffland et al., 1989; Romheld and Marschner, 1986; Kania et al., 2003). Organic acids from root exudates can solubilize unavailable soil Ca, Fe and Al phosphates. Rooibos tea (*Aspalathus linearis* L.) can actively modify their mycorhizosphere pH by extruding OH^- and HCO_3^- to facilitate growth in low pH soils (pH 3 to 5) (Dakora and Phillips, 2002). Extracellular enzymes release P from organic compounds, and some types of molecules increase iron availability through chelation (Berg et al., 2002).

Plant characteristics (species, age, nutrients, light)

Different plant species inhabit variable microflora in the mycorrhizosphere region (Dakora and Phillips, 1996). The quantitative and qualitative differences are attributed to variations in the excretion products, rooting habits, and tissue composition (Mukerji et al., 2002). Plant age alters the rhizosphere microorganism and the stage of plant maturity controls the magnitude of rhizosphere effect and degree of response to specific microorganisms (Buée et al., 2009). Flowering is the most active period of plant metabolism and growth. The mycorrhizosphere microorganism increase in the highest number during this stage lead to increase exudates content (Walker et al., 2003; Tahat et al., 2008a). Some microbes were found to be more effective at the time of flowering than in the seedling or full maturity stage (Bais et al., 2006). The effect of light on the production of pectin and polygalacturonase (PG) in the root exudates of *Trifolium alexandrinum* inoculated with an efficient strain of *Rhizobium trifolii* was investigated. The pectin methyl esterase PME and PG increased with an increase in the duration of light to which plants were exposed (Chhonkar, 1978).

CONCLUSION

Mycorrhizal fungi associated with plant roots have existed for hundreds of millions of years. The role of mycorrhizal fungi in improving plant nutrition and their interactions with other soil biota have been investigated with reference to the host plant growth, but little is known about how these interactions affect soil structure. The combination of these organisms in natural, undisturbed ecosystems would seem to contribute to the successful growth and health of plants. Several factors influenced the production of root exudates such as plant type, age, light, soil microflora, soil fertilizer and soil pH. This view has attempted to characterize qualitative changes in populations of rhizobacteria associated with plants with mycorrhizae in what is called the “mycorrhizosphere”. Microbial populations in the mycorrhizosphere can change dynamically over time and are influenced by what microbes are present in the background soil or growth medium. The process of selective enrichment of specific functional groups of microbes from that medium is due to root and arbuscular mycorrhizal fungus, hyphal exudates.

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