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Review

Influence of phytosiderophore on iron and zinc uptake and rhizospheric microbial activity

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Micronutrients play a vital role in crop production and sustainable crop yield. High crop yield varieties make soil micronutrients deficient, without incorporating external inputs. Due to deficiency of micronutrients such as iron (Fe) and zinc (Zn), yield decline drastically. It limits more than macronutrients, but requirements of these plant nutrients are very less, but plants have self regulated mechanism, which secrete the phytosiderophore (PS) and mobilize the lower concentration of these metals to soil solution for easy uptake by plants. Phytosiderophore production is a general response of plants to Fe and Zn deficiency in particular. The uptake rate of PS-chelated Fe and Zn is 100 and 5 to 10 times higher than that of free Fe and Zn, respectively. Higher amount of carbon containing organic compounds enhanced the microbial activities in rhizosphere and alter the plant nutrient chemistry in soil. This article discussed the importance of PS in microbial activity in soil and nutrient uptake mechanism in plants.

Key words: Iron, phytosiderophores, rhizospheric microbial activity, zinc.

INTRODUCTION

One of the widest ranging abiotic stresses in world agriculture arises from low iron (Fe) and zinc (Zn) availability in calcareous soils, particularly in cereals (Berg et al., 1993; Palmiter and Findley, 1995). A higher Zn acquisition efficiency, further, may be due to either or all of the following: an efficient ionic Zn uptake system, better root architecture that is long and fine roots with architecture favoring exploitation of Zn from larger soil volume (Richardson et al., 1989), higher synthesis and release of Zn-mobilizing phytosiderophore (PS) by the roots and uptake of Zn-PS complex (Dotaniya et al., 2013a). Zinc and Fe are the two most important micronutrients in crop production. More than 50% of the Indian soils are suffering from zinc and iron deficiency. It is also a big problem in well aerated calcareous soil. The release of PS is one of the most important mechanisms which enhances the mobilization of Fe and Zn in soil and their uptake by crops (Ackland and McArdle, 1990;

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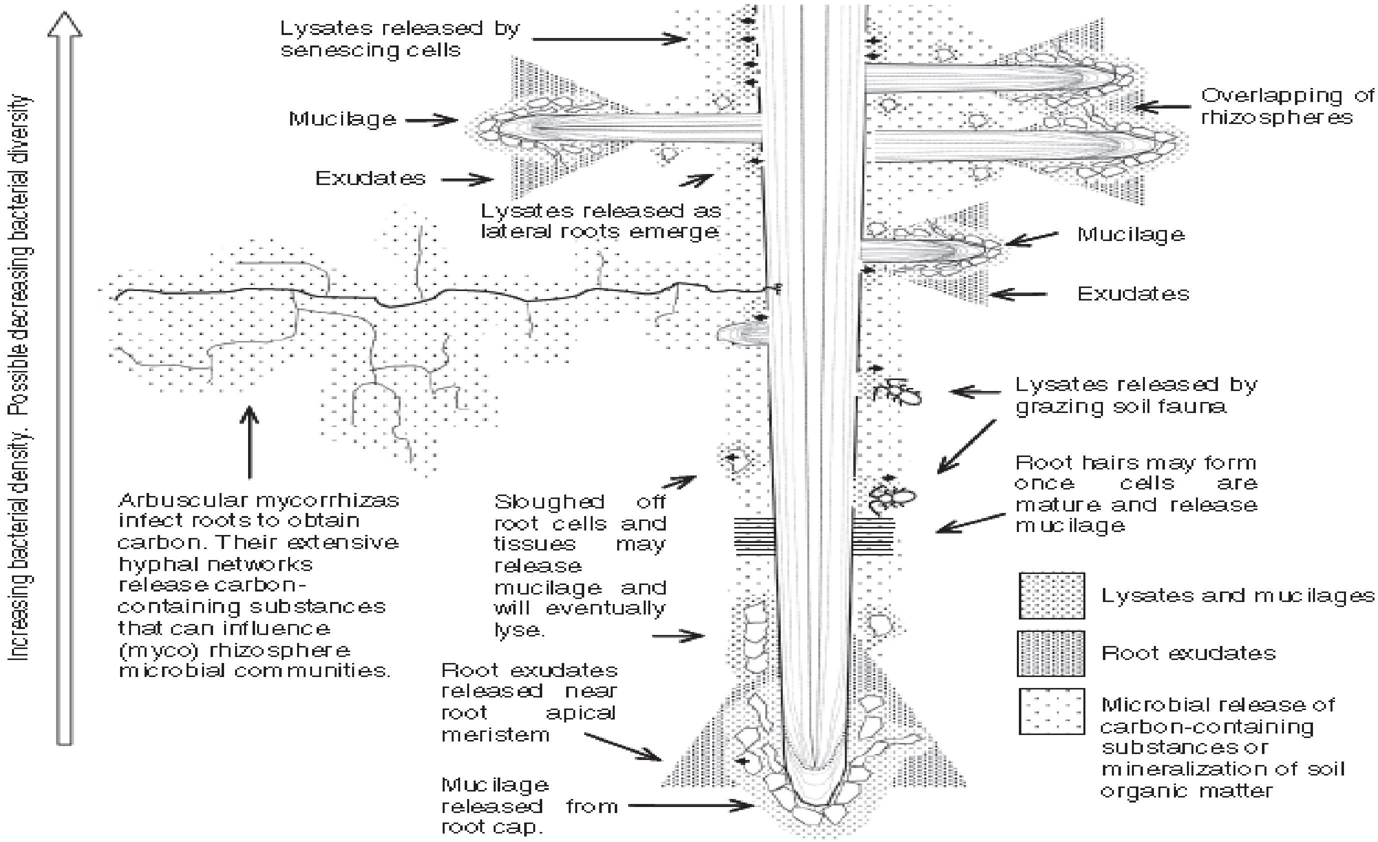

Figure 1. Origin of various pools of rhizodeposition (Dennis et al., 2010).

Bar-Ness et al., 1992). Peanut/maize intercropping was a sustainable and effective agroecosystem that evidently enhances the Fe nutrition of peanuts in calcareous soils by the influence of PS (Xiong et al., 2013).

PHYTOSIDEROPHORES

Phytosiderophores are organic substances (such as nicotinamine, mugineic acids (MAs) and avenic acid etc) produced by plants (Figure 1) (Mori and Nishizawa, 1987) under Fe-deficient conditions, which can form organic complexes or chelates with Fe^{3+}, and increase the movement of iron in soil (Ueno et al., 2007). It is non proteineous, low molecular weight acids released by the graminaceous species under the iron (Wallace, 1991) and Zn deficiency stress. The PS mobilize micronutrients Fe, Zn, Mn and Cu from the soils to plant in deficient condition (Takagi et al., 1984).

Characteristics of phytosiderophores

1) These are molecules with high affinity for Fe^{3+}, and remove the Fe^{3+} from minerals and contribute towards their dissolution.
2) These Fe-chelates are highly soluble and stable over a wide pH range.
3) They are of crucial importance for the zinc and iron transport in soils and its supply to plants.
4) Zn-PS have similar structural confirmations as Fe-PS and a similar regulatory mechanism for the biosynthesis and/or release of PS under both Zn and Fe deficiencies.
5) A plant releases PS at higher amounts about a few hours to the onset of the light period. Under continuous darkness or continuous light, the rate of release of PS is lower.
6) There has been observed a sharp rise in PS production three hours after onset of the light period, which gradually declines thereafter.

IRON DEFICIENCY: A GLOBAL CONCERN

Fe deficiency chlorosis in crop plants is a widespread nutrient problem particularly in calcareous soils in arid and semiarid regions, which often results in significant yield losses (Mortvedt, 1991). Such yield reductions have been reported in many crops, such as upland rice, maize and sorghum (Jolley et al., 1996; Dotaniya et al., 2013b).

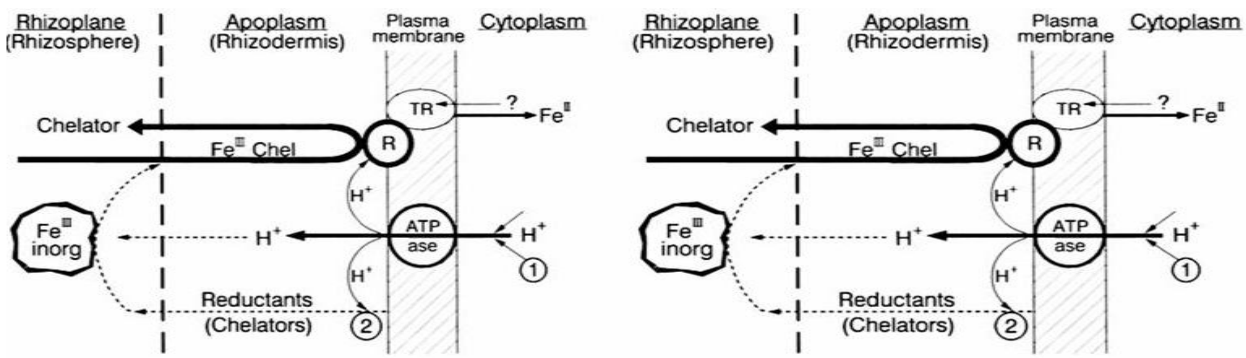

Figure 2. Strategy of Fe Acquisition by plants (Tagliavini and Rombola, 2001).

Grazing induced Fe-deficiency chlorosis in wheat was also reported (Berg et al., 1993). Soil amendments and foliar sprays of Fe are common methods to correct Fe deficiency (Bashir et al., 2010). However, these methods are expensive, time-consuming and may not be effective for more than one cropping season. Alternatively, breeding of plant genotypes with higher efficiency in the acquisition of Fe from the soil is a realistic approach (Kobayashi and Nishizawa, 2012). Selection for resistance, however, is difficult because of heterogeneous soil and highly variable environmental conditions that affect expression of Fe-deficiency chlorosis in the field (Nozoye et al., 2011). Yellow stripe 1 (ys1) and ys3 are recessive mutants of maize (*Zea mays* L.) that show typical symptoms of Fe deficiency, that is interveinal chlorosis of the leaves (Tomoko et al., 2013).

A lack of understanding of the factors influencing chlorosis expression has also impeded the development of reliable screening methods in the laboratory, controlled greenhouse, or environmental-chamber environment (Jolley et al., 1996). So the development of reliable Fe-deficiency chlorosis screening criterion is a necessary prerequisite for significant improvement of Fe-deficiency chlorosis resistance. Recently, many studies suggested that non-proteinogenic amino acids (PS) release has been linked to the ability of species and genotypes to resist Fe- deficiency chlorosis (Hansen et al., 1996; Romheld and Marschner, 1986). Therefore, PS release has been suggested as a selection criterion for Fe efficient graminaceous monocots.

ZINC DEFICIENCY: A GLOBAL CONCERN

Low availability of Zn in calcareous soils is one of the widest ranging abiotic stresses in world agriculture particularly in Turkey, Australia, China and India. Global studies initiated by the Food and Agriculture Organization (FAO) reported Zn deficiency in 50% of the soil samples collected from 25 countries (Hansen et al., 1996). It is one of the most widespread nutritional constraints in crop plants, especially in cereals. Among cereals, wheat and rice in particular, suffer from its deficiency. The yield reduction up to 80% along with reduced grain Zn level has been observed under Zn deficiency (Fageria et al., 2002). This deficiency is a serious implication for human health in countries where consumption of cereal-based diets predominates. Further, plants grown on zinc-deficient soils tend to accumulate heavy metals, which again is a potential human health hazard.

STRATEGY OF FE AND ZN ACQUISITION BY PLANTS

Iron and Zn deficiency induced chlorosis represents the main nutritional disorder in plants grown on calcareous and/or alkaline soils because of an extremely low solubility of soil Fe. Mechanisms of Fe acquisition in higher plants have been grouped into Strategy I and II (Figure 2). Strategy I plants (Tagliavini and Rombola, 2001), which include dicotyledons and non-graminaceous monocotyledons, respond to Fe deficiency by extruding both protons and reducing substances (phenols) from the roots, and by enhancing the ferric reduction activity at the root plasma membrane. This strategy is similar to the Zn acquisition by plants. The solubilized Fe must be reduced from Fe^{+3} to Fe^{+2} on the plasma membrane before Fe^{+2} is transported into the root cell through a specific Fe^{+2} transporter. Strategy II plants (graminaceous species) synthesize and secrete Fe-chelating substances, mugineic acids (MAs) from their roots to dissolve sparingly soluble Fe compounds in the rhizosphere (Figure 3) (Marschner et al., 1986) and affected by soil bacteria (Chattopadhyay, 2006; Dipanwita and Chattopadhyay, 2013). Iron is transported across the plasma membrane as a complex of PS- Fe^{+3} through a specific transport system without prior reduction.

The synthesis of mugineic acid is induced by Fe-deficiency. The chemical constituents, number and amount of mugineic acid synthesized and secreted into the rhizosphere may differ among species and even cultivars (Xiong et al., 2013). In general, the amount of

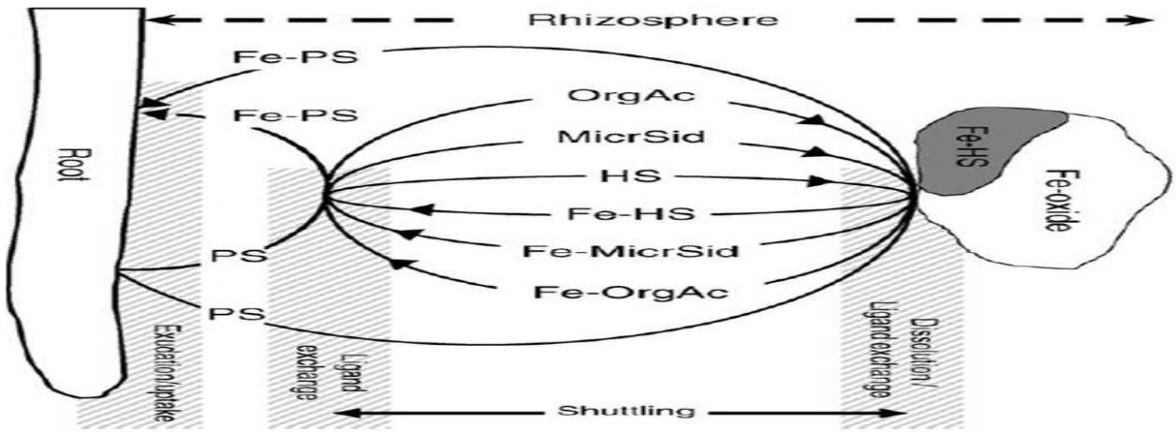

Figure 3. Schematic representations of important processes in strategy II iron acquisition (Dotaniya et al., 2013a).

MAs secreted correlates positively with the ability of the plants to tolerate Fe deficiency. But siderophore produced by microbes also enhanced the Fe uptake. If siderophores and PS are present at similar concentrations, Fe is preferentially bound to the siderophores, which may even remove Fe from the Fe-PS complex. In contrast to many bacterial siderophores, rhizoferrin from the fungus *Rhizopus arrhizus* has only a slightly higher affinity towards Fe compared to PS (Crowley and Gries, 1994; Zelenev et al., 2005). Rhizoferrin is a good Fe source for barley, probably because of exchange of Fe from rhizoferrin to the PS (Yehuda et al., 1996). It can be amply surmised from the available literature that Zn and Fe efficiency of cereals under deficiency is regulated by several factors, most importantly, the presence of an efficient Zn^{2+}, Fe^{+2} and PS complex uptake system.

Manipulation of phytosideriophore biosynthesis and release is a promising strategy to improve Fe and Zn efficiency in cereal crops (Wallace, 1991). In Alice maize cultivar, Zn uptake decreased with increasing stability constant of the chelate in the order: $ZnSO_4$ (greater than or equal to) Zn-desferrioxamine > Zn-PS > Zn-EDTA. Adding a 500-fold excess of free PS over Zn to the uptake solution depressed Zn uptake in maize mutant ys1 almost completely (von Wiren et al., 1996). It may be quite plausible that iron and zinc deficiency tolerance of graminaceous species can also be achieved through manipulation of key enzymes of PS biosynthesis that is Nicotianamine synthase (NAS) and Nicotianamine amino-transferase (NAAT). This will help in reducing and may be even totally eliminating the application of zinc and iron fertilizers to the soil.

EFFECT ON MICROBIAL ACTIVITIES IN RHIZOSPHERE

The rhizosphere is the narrow region of soil that is directly influenced by root secretions and associated soil microorganisms (Giri et al., 2005). Soil which is not part of the rhizosphere is known as bulk soil. The rhizosphere contains many bacteria that feed on sloughed-off plant cells, termed rhizodeposition and the proteins and sugars released by roots (Curl and Truelove, 1986). It is a densely microbial populated area of soil 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 and Delhaize, 2001).

In 1904, the German agronomist and plant physiologist Lorenz Hiltner first coined the term "rhizosphere" to describe the plant-root interface (Figure 4), a word originating in part from the Greek word "rhiza", meaning root (Hiltner, 1904; Hartmann et al., 2008). Microbial population is more affected by the amount and type of C in soil (Akiyama et al., 2005). Under long term study, it was found that microbial population is greater in organic soil as compared to inorganic farming plots (Tu et al., 2005). In general 10-20% more biomass was measured in organic soils (Gelsomino et al., 2004). High secretion of PS in soil, improved the soil fertility and nutrient mobility in soil (Colmer and Bloom, 1998). Microbial biomass is an indicator of soil microbial activities. Generally, in crop production, more biomass means more fertile soil, which is a good indicator of plant nutrient (Becard et al., 1992, 1995; Trieu et al., 1997). Root secretions may play symbiotic or defensive roles as a plant ultimately engages in positive or negative communication (Stintzi and Browse, 2000; Stotz et al., 2000), depending on the other elements of its rhizo-sphere such as available nutrients, water, space CO_2 concentration and C. In contrast to the extensive progress in studying plant-plant, plant-microbe (Keyes et al., 2000) and plant-insect interactions that occur in above ground plant organs such as leaves and stems, very little research has focused on root-root, root-microbe, and root-insect interactions in the rhizosphere

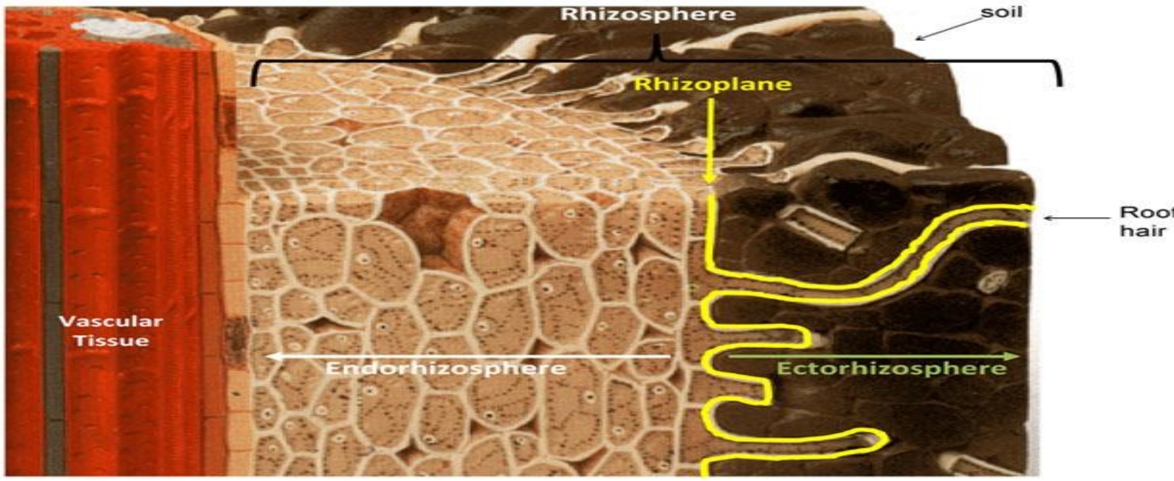

Figure 4. Structure of the rhizosphere in soil (McNear, 2013).

(Shannon et al., 2002). Bacterial siderophores are usually poor Fe sources for both monocot and dicot plants (Bar-Ness et al., 1992; Crowley et al., 1992; Walter et al., 1994). However, in some cases, microbial siderophores have alleviated Fe deficiency-induced chlorosis in dicots (Jurkevitch et al., 1988; Sharma et al., 2003; Wang et al., 1993; Yehuda et al., 2000). On the other hand, plant-derived Fe-PS complexes appear to be a good Fe source for bacteria (Jurkevitch et al., 1993; Marschner and Crowley, 1998).

The organic compounds released through these processes can be further divided into high and low molecular weight (HMW and LMW, respectively). By weight, the HMW compounds which are those complex molecules that are not easily used by microorganisms (mucilage, cellulose) make up the majority of C released from the root (Chin-A-Woeng et al., 1997); however, the LMW compounds are more diverse and thus have a wider array of known or potential functions (Bauer and Mathesius, 2004). Rooting density has a large effect on uptake per unit PS secretion as a result of overlap of the zones of influence of neighboring roots (Von Wiren et al., 1996). The list of specific LMW compounds released from roots is very long, but can generally be categorized into organic acids, amino acids, proteins, sugar, phenolics and other secondary metabolites which are generally more easily used by microorganisms. It provides the C source of energy and food, because of plenty of organic compounds released from roots enhanced the microbial activity and population. Further increase in microbial population accelerates the competition for water, C and space also (Baudoin et al., 2003).

EFFECT OF FERTILITY AND ATMOSPHERIC CO_2 CONCENTRATION ON PHYTOSIDEROPHORE

Root exudates is secreted from root in two way: (1) actively released from the root and (2) by diffuseness which are passively released due to osmotic differences between soil solution and the cell (Dakora and Phillips 2002), or lysates from autolysis of epidermal and cortical cells. These organic compounds may be sugar, non-protein amino acids mugineic acid (of barley) and avenic acid (of oats) (Darrah, 1991). Das and Dkhar (2011) conducted a research with various organic and inorganic fertilizers and their effect on physico-chemical properties of rhizosphere (Table 1). They observed that the application of vermicompost resulted in most pronounced growth of microbial population compared to inorganic treatment. Also, application of organic treatments showed increased rhizosphere soil physicoche-mical properties which in return lead to the increased microbial population which is of great importance in nutrient availability of the studied soil (Kundu et al., 2013). The soil microbial population also secrets a significant amount of sidero-phores in soil, however it promotes the root exudates from plants (Bais et al., 2001). The root exudates play an important role in root microbe interactions. Flavonoids are present in the root exudates of legumes that activate *Rhizobium meliloti* genes responsible for the nodulation process (Peters et al., 1986). Fertilizer and lime applications typically result in increased bacterial numbers and decreased fungal biomass (Lovell et al., 1995).

Bacterial communities in the rhizosphere are not static, but will fluctuate over time in different root zones, and bacterial composition will differ between different soil types, plant species, plant growth seasons and local communities (Semenov and Brooks, 1999). Changes induced in the soil by the growing root provide additional niches for soil microbes. Soil types and growth stages are important factors in shaping rhizobacterial community structure (Latour et al., 1996; Seldin et al., 1998; Herschkovitz et al., 2005) and may be the strongest factor affecting bacterial communities in potato rhizo-

Table 1. Physico-chemical properties of rhizosphere soil influenced by organic and inorganic fertilizers (Das and Dkhar, 2011).

Treatment	pH	Moisture content	SOC (%)	Total N (%)	Av- P (µ/g)	K (mg/g)	Soil Respiration (mg/g)	MBC (µ/g)
Plant compost	5.6	24.90	1.80	0.32	1.18	0.04	65.1	1015.0
Vermicompost	5.4	24.24	1.50	0.31	2.66	0.05	66.11	2145.7
Integrated plant compost	5.6	24.68	1.75	0.35	2.01	0.04	64.56	1385.1
FYM	4.6	23.82	1.27	0.31	2.24	0.08	56.5	940.9
Control	4.9	23.39	1.60	0.28	2.01	0.05	56.56	656.5
NPK	4.9	23.39	1.60	0.35	2.68	0.04	62.89	798.9

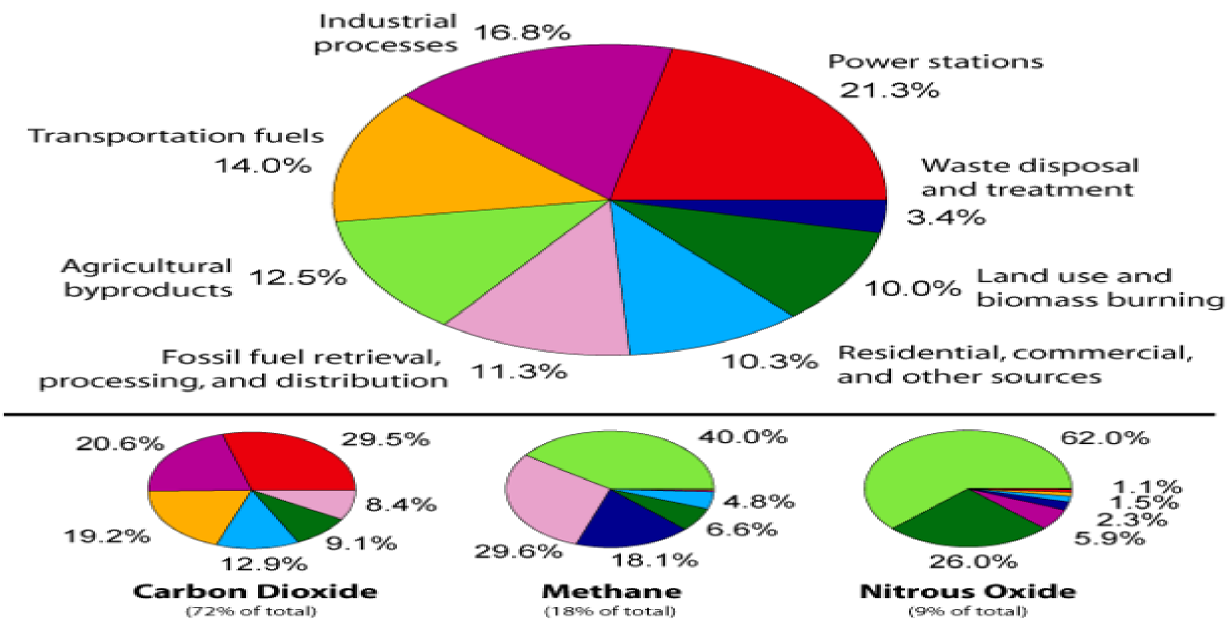

Figure 5. Annual greenhouse gas emissions by sector (www.e-education.psu.edu).

sphere (Van Overbeck and Van Elsas, 2008); plant species (Grayston et al., 1998; Smalla et al., 2001) and even 'cultivar (genotype) within the same species (Andreote et al., 2009). The rhizosphere is a highly dynamic environment for bacterial communities and even small topographical landform changes can alter environmental conditions that may accelerate or retard the activity of organisms (Ramette et al., 2005).

Soil microbial activities affected the physical, chemical and biological activities and ultimately crop production. Increasing environmental factors like CO_2 concentration and atmospheric temperature affected the root exudates and rhizospheric microbial population. Impacts of elevated CO_2 on soil ecosystems, focuse primarily on plants and a variety of microbial processes. The processes considered include changes in microbial biomass of C and N, soil enzyme activity, microbial community composition, organic matter decomposition, and functional groups of bacteria mediating trace gas emission in terrestrial and wetland ecosystems. Except from CO_2, other gases that is CH_4, N_2O and other gases play a significant role in global climate phenomena (Figure 5).

The cocktail of chemicals released is influenced by plant species, edaphic and climactic conditions which together shape and are shaped by the microbial community within the rhizosphere. There is still very little known about the role that a majority of the LMW compounds play in influencing rhizosphere processes (Cheng et al., 1996). A growing body of literature is beginning to lift the veil on the many functions of root exudates as a means of acquiring nutrients (acquisition of Fe and P), agents of invasiveness (that is allelopathy) or as chemical signals to attract symbiotic partners (chemotaxis) (rhizobia and legumes) or the promotion of beneficial microbial colonization on root surfaces (*Bacillus subtilis*, *Pseudomonas florescence*) (Bais et al., 2004, Park et al., 2003).

FUTURE NEED OF RESEARCH

1) More research should be on the biotechnological side, separation and insertion of high phytosiderophor responsible gene in crop plant, which is crucial for crop production in low fertility areas.
2) Also, research should be done on the use of alternative combat methods, against elevated CO_2 concentration without compromising positive effect on PS release.

CONCLUSIONS

A healthy crop production requires a good status of plant nutrient. It play crucial role in plant metabolism and ultimately in edible part. In nutrient deficient condition, plant growth is limited and poor yield is obtained. Phytosiderophors are secreted from plant root, and it is a life saving mechanism in plants. It enhances the plant nutrient uptake and improves the soil health. Iron availability is low in most aerobic soil, and microorganisms and plants release low molecular-weight compounds (chelators) which increase Fe availability. It specially enhances the uptake of Fe and Zn in lower concentration. Increasing root exudates in soil enhances the soil fertility level as well as microbial biomass. These soil microbes play vital role in nutrient transformation reactions in soil and nutrient uptake by crop plants.

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