Siderophores: Augmentation of Soil Health and Crop Productivity

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Rizwan Ali Ansari, Irshad Mahmood, Rose Rizvi,
Aisha Sumbul, and Safiuddin

Abstract

Microorganisms harbouring in the soil are extremely important in the sustainable agriculture. They play a very crucial role in the sustenance of ecological services/ balance. Siderophore-producing microorganisms have enormous range of application for the sustainable crop production. Application of siderophores has recently caught fire of discussion and being used in the plant disease management, maintenance of healthy soil, plant growth promotion, SAR induction, acceleration of phytohormone production, bioaugmentation of heavy metal (HM), etc. Moreover, nearly all living beings shine their cellular reactions such as electron transportation, different metabolic reactions and organic molecule formations with the help of iron. In iron-deprived environment, siderophores are the chief media by which maximum cellular reactions get completed. However, a wide range of variations among the siderophores has been noticed like bacterial siderophores that have extremely high binding affinities than fungi; however, phytosiderophores have less binding affinities than microbial siderophores. A lot of variations among the microbial siderophores such as algae, bacteria, fungi and actinomycetes have been noticed in significant manner. Additionally, beneficial job of siderophore in other sector of agriculture and allied branch of science may not be ignored. However, there are some hurdles such as lack of infrastructure and communication gap among the concerned researcher which has put such important research on hold. Research on siderophore-producing organisms will provide an arena to formulate bioprocess technology which is indeed needed to maximize the production of microbial siderophores because of its wide range of applicability. Overall, siderophores and siderophore-producing organisms are conducive to

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R.A. Ansari (✉) • I. Mahmood • R. Rizvi • A. Sumbul • Safiuddin
Section of Plant Pathology and Nematology, Department of Botany,
Aligarh Muslim University, Aligarh, India
e-mail: rizwans.ansari@gmail.com

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human kind as well as in the sustenance of ecological balance. Thus, this article discusses about the present scenario of research pertaining to siderophore applications in agriculture.

15.1 Introduction

Plants and microbes play an important role in our daily routine. Iron is ranked among the most abundant element in the Earth's crust (Kurth et al. 2016). Besides, many autotrophs face turmoil in acquiring iron due to its insoluble form, which inhibits the bioavailability of iron (Kurth et al. 2016). Generally, living organisms survive by the performance of certain cellular processes during that iron plays a significant role. Iron is the chief constituent for a variety of vital functions such as photosynthesis, enzyme cofactor, redox reagent, respiration, nucleosides and amino acid synthesis. Moreover, microbes and plants flourish themselves under iron-limited conditions by releasing iron chelator called siderophore. Siderophores are low-molecular-weight (<10 kDa) iron-chelating organic molecules, released by microbial communities thriving in the rhizosphere under iron-limited conditions. These iron chelators play a crucial role in the solubilization of iron from inorganic as well as organic molecules. Siderophores help to enhance the plant growth by scavenging iron from the nearby area and make them available to root (Hider and Kong 2010; Maheshwari 2011; Ahmed and Holmstrom 2014; Zhou et al. 2016). Siderophores play a valuable role in plant growth promotion (Yadav et al. 2011; Verma et al. 2011; Trapet et al. 2016), biocontrol agents (Verma et al. 2011; Di Francesco et al. 2016), bioremediation agents (Wang et al. 2011; Ishimaru et al. 2012; Ma et al. 2016) and mineral weathering (Reichard et al. 2005; Buss et al. 2007; Shirvani and Nourbakhsh 2010; Ahmed and Holmstrom 2015). In addition, various plants have been reported to release phytosiderophore that sequester the iron by the roots which assist the Fe complex uptake under iron-deprived state (Kannahi and Senbagam 2014). It has been ascertained that competition for iron in the rhizosphere is governed by the empathy of the siderophores for iron (Bernd and Rehm 2008; Munees and Mulugeta 2014). It has been well known fact that alkaline soils are strong inducers of iron deficiency in plants. Besides, if soil pH exceeds 6.5–7.0, the availability of iron in the soil is considerably reduced; however, calcareous soils, having high pH, diminish the affinity of plants for Fe and hence hinder Fe uptake.

Iron is a vital nutrient necessary for almost all living organism for carrying out various cellular processes (Neilands 1995). Generally, bacteria obtain iron molecule after producing iron chelators, siderophores having high affinity for iron complexing. In cellular context, there are two types of siderophores, and they can be divided into extracellular and intracellular siderophores. Also, there is a large variation in rhizobacteria pertaining to siderophore utilization ability. It has been seen that there were restrictions of siderophore utilization while no such bar were detected in other genus of rhizobacteria (Khan et al. 2009). It is well known that during Fe^{3+} complex, Fe^{3+} is reduced into Fe^{2+} on bacterial membrane which is later on delivered into the cell through a gating mechanism; however, this process leads to sometime loss of siderophores (Rajkumar et al. 2010; Neilands 1995). In this way, siderophores have the capability to solubilize iron from organic compounds or minerals under iron-deprived conditions (Indiragandhi et al. 2008). Besides, siderophores also bind with other HMs which are actively involved in some environmental concerns (Kiss and Farkas 1998; Neubauer et al. 2000). Formation of stable complex with siderophore to HMs enhances the soluble metal concentration (Rajkumar et al. 2010). Therefore, in such way, iron chelators assist in the alleviation of abiotic stress such as HMs imposed on plants. As far as assimilation of iron is concerned, in plants, various possible pathways such as chelation and production of iron, direct accumulation of siderophore–Fe complex and through ligand exchange process have been put forward (Schmidt 1999). Recent studies have generated the information pertaining to enhanced plant growth promotion after inoculation of siderophore-producing PGPR (plant growth-promoting rhizobacteria) (Rajkumar et al. 2010). In addition to PGPR uptake, machinery of the plants also determines the level of significance like application of siderophore-producing bacteria in oat plants under iron-deprived conditions leads to significant plant growth promotion which may be due to plants having the mechanisms for using Fe–siderophore complexes under iron-limited conditions (Crowley and Kraemer 2007). Similar results were also seen in *Arabidopsis thaliana* plants by *Pseudomonas fluorescens* C7 which leads to large accumulation of iron and thereby enhancement in plant growth (Vansuyt et al. 2007).

Siderophore and its derivative have a broad range of significance in sustainable agriculture in the form of enhancement of soil fertility and as potent biocontrol agent for fungal pathogen. Therefore, the present article accounts for the role of siderophores in sustainable agriculture with special emphasis on maintenance of soil health, management of fungal pathogens and crop growth promotion.

15.2 Iron Bioavailability in Iron-Deprived Environment

Generally, iron is found as Fe(III), insoluble under physiological conditions (Powell et al. 1980; Matzanke et al. 1989). Many enzymes and cofactors are responsible for carrying out various cellular processes like respiration, oxygen activation, hydrogen peroxide and hydroxyl radicals' degradation, etc. (Andrews 1998).

Ferrous is more soluble state at neutral pH which is available for living cells for further process. In addition, most of bacterial communities accumulate Fe(II) through divalent metal transporters (Miethke and Marahiel 2007). Moreover, iron is the key element for the life to be processed; however, there are some exceptions such as lactic acid bacteria, and they do not have heme enzymes (Neilands 1995). Additionally, iron may be toxic because high intracellular concentration of ferrous ion starts producing hydroxyl radicals (Crichton and Charloteaux-Wauters 1987). However, such problem no longer exists and can be alleviated with the help of certain antioxidants. The toxicity of the iron may be nullified by the presence of glutathione and endonucleases which repair DNA (Andrews 1998). It has been a well-established fact that iron imports toxicity towards rice plants being grown in lowland. This may be advocated that rice plants accumulate large values of ferrous after reduction of iron oxides and hydroxides which leads to disruption of metabolic process and plants become damaged (Becker and Asch 2005).

Chief iron pool in soil and water ecosystems is comprised by oxides of iron (Kraemer 2004). Production of siderophores is a specialized iron acquisition system which reveals competitive benefit to many microorganisms in biotic and abiotic environments. Plenty of research on biological iron acquisition have stated about significant increase in iron solubility (Kraemer 2004). Availability of iron depends on its properties such as particle size, pH, ionic strength and amount of organic ligands in solution (Kraemer 2004). For instance, Fe(II) quickly oxidizes to Fe(III) at neutral pH and oxic conditions (Stumm and Morgan 1995). In the weak organic ligand, Fe(III) precipitates quickly as a hydrous ferric oxide, and citrate is too weak to bind iron which inhibits Fe(III) precipitation in the culture medium (Konigsberger et al. 2000).

In soil at neutral pH concentrations, the ferric oxide hydrate is around 10^{-17} M (Budzikiewicz 2010). However, living systems require 10^{-6} M, as soon as cells that detect the necessities of iron siderophore production begin (Miethke and Marahiel 2007). Siderophores have a manifold impact on the solubility of iron oxides with a varying range of pH because of extraordinary thermodynamic stability of soluble siderophore–iron complexes.

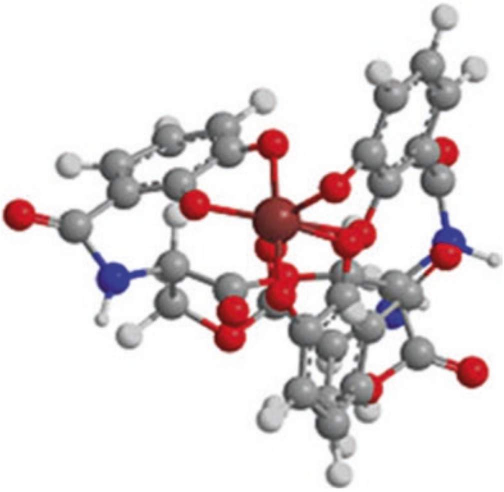
15.3 Types of Siderophores

A lot of variation have been detected in the structure of siderophores produced by the microbes especially bacteria. They are categorized on co-ordinating atom basis on which they chelate the Fe(III) ion. Hydroxamate, catecholate and carboxylate are important groups of siderophores.

15.3.1 Catecholate

These types of siderophores are produced by not all but only some bacteria. Each catecholate composed of two oxygen atoms with iron forming a hexadentate octahedral complex, a cyclic trimer composed of 2,3-dihydroxy-*N*-benzoylserine is the best example of the catecholate.

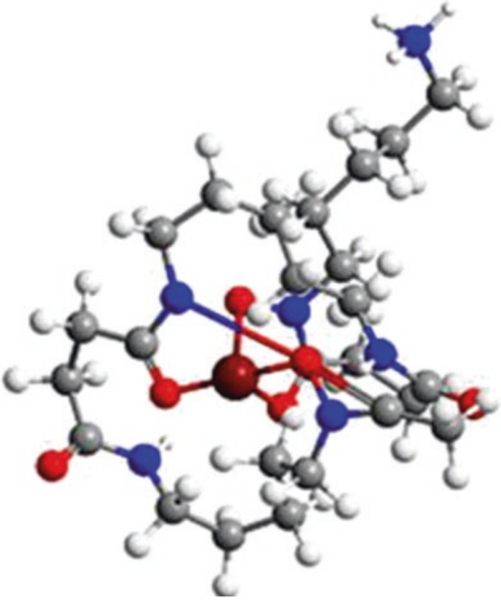
For the first time, a tricatechol siderophore, enterobactin, was isolated from *Escherichia coli*, *Aerobacter aerogenes* and *Salmonella typhimurium* (Ward et al. 1999). A bacterium of the family Enterobacteriaceae produces enterobactin; possibly, all strain have the capability to bind with iron. In addition, *S. typhimurium*, *Klebsiella pneumoniae* and *Erwinia herbicola* are well-studied models to produce enterobactin. Enterobactin is blessed with the capacity to trap the iron even from the environment where iron content is far away from its reach (Raymond et al. 2003).



Enterobactin

15.3.2 Hydroxamate

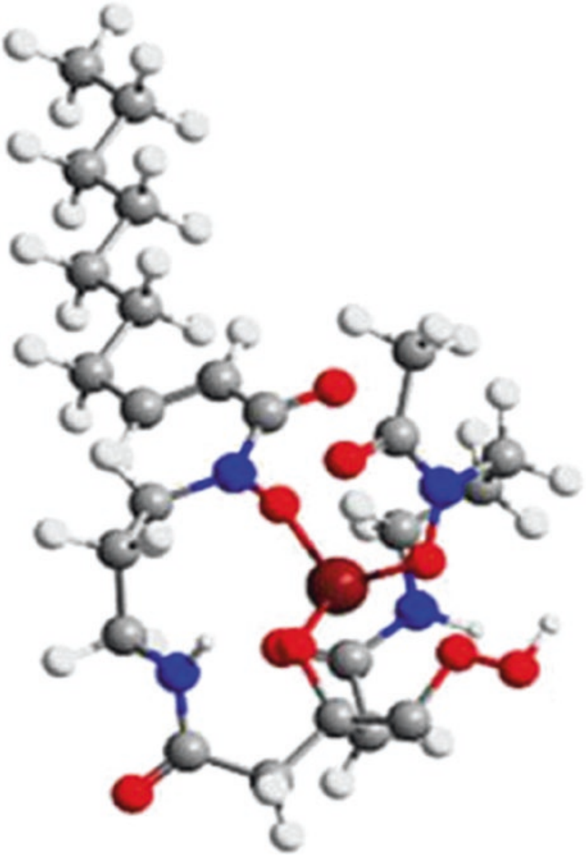
Ferrichrome-type hydroxamate is produced by many soil fungi including some mycorrhiza (Schalk et al. 2011) A plenty of research have provided extensive support that hydroxamate siderophores may provide iron to only certain plant species. Mostly, they are produced by fungi not by bacteria belonging to class Zygomycotina (*Mucorales*), Ascomycotina (*Aspergilli*, *Penicillia*, *Neurospora crassa*) and Deuteromycotina (*Fusarium dimerum*).



Ferrioxamine B

15.3.3 Carboxylate

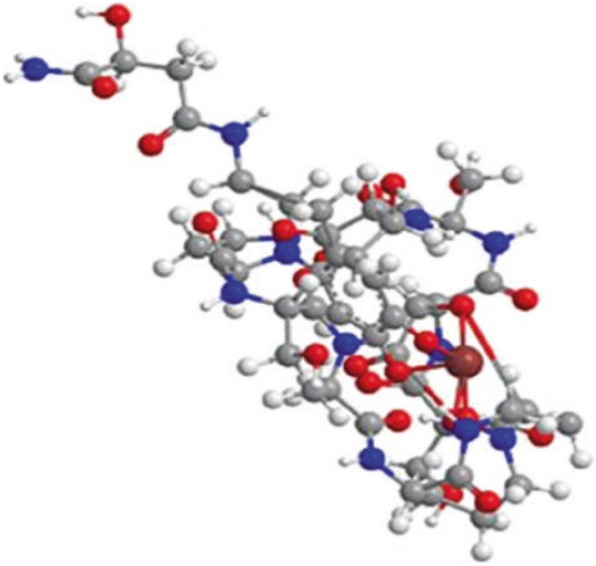
This is a special type of siderophore where iron binding is accomplished by hydroxyl carboxylate and carboxylates (Schwyn and Neiland 1987). These siderophores have shown their presence in the group of bacteria as well as fungi. Carboxylates produced by *Rhizobium* and *Staphylococcus* species and members of *Mucorales* are commonly found where iron with carboxyl and hydroxyl groups is coordinated.



Rhizobactin

15.3.4 Miscellaneous

In addition to the above different siderophores, some have derivatives of mixed ligands of lysine, ornithine and histamine. An array of fluorescent chromopeptide siderophore called as pseudobactin and pyoverdines that contain a dihydroxyquinoline derivative are currently in vogue of research. There are two types of significant siderophore-mediated iron uptake scheme in these bacteria; first it involves the fluorescent siderophore pseudobactin and second it contains the siderophore pyochelin (Meyer 2000; Meneely and Lamb 2007).



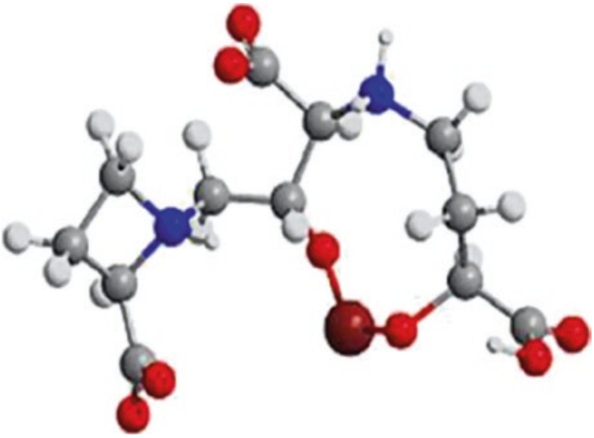
Pyoverdine

15.4 Siderophores from Different Organisms

15.4.1 Plants

Certain plants have acquired-specialized mechanism for iron uptake in plants belonging to the family Poaceae through roots by releasing iron chelators known as phytosiderophores. Plants begin acquisition of iron by different strategies

(Römheld and Marschner 1986). According to one theory, strategy I is used by most non-Poaceae plants having inducible plasma membrane-bound reductase with the significant increase in H^+ release, while in strategy II, a significant increase in phytosiderophores characterized by an enhanced release with highly specific uptake system is reported. Strategy II has several ecological benefits over strategy I such as solubilization of inorganic Fe(III) compounds in the rhizosphere and lowering down of pH. There are lower affinities in phytosiderophores as compared to microbial siderophores which is replenished by high exudation rates by Poaceae plant roots.



Mugineic acid

15.4.2 Fungi

Fungi are the important source of siderophore-producing microorganisms and ranked after bacteria (Scavino and Pedraza 2013). Common genera of important siderophore-producing fungi are *Aspergillus nidulans*, *A. versicolor*, *Penicillium chrysogenum*, *P. citrinum*, *Mucor*, *Rhizopus* and *Trametes versicolor. Ustilago sphaerogina*, *Saccharomyces cerevisiae*, *Rhodotorula minuta* and *Debaryomyces* species. Majority of the fungi produce a wide range of siderophores covering a large range of physico-chemical properties. These particular characters of siderophores make it capable to overcome the adverse conditions (Winkelmann 2007). A large number of structurally different fungal siderophores are reported having a peptidic ring in common. Generally, all aerobic bacteria and fungi generate siderophores (Neilands and Leong 1986). However, this property reveals a clear picture of benefit for microbes occupying in aerobic environments. For example, many facultative bacteria from paddy field soils are found on siderophore producers (Loaces et al. 2011). However, there are some other microbes having no mechanism to synthesize and produce siderophores such as *Saccharomyces* *cerevisiae*; however, they utilize the siderophore produced by other species (Eissendle et al. 2003).

15.4.3 Bacteria

Bacteria occupying the metal-contaminated environment are able to accumulate and transport the HMs (Rajkumar and Freitas 2008; Weyens et al. 2009;). Bacterial cell produces polysaccharide sheath that determines metal-binding affinities (Sheng et al. 2008). Normally, four types of siderophores are produced by bacteria, and they are hydroxamate, catecholate, salicylate and carboxylate (Rajkumar et al. 2010). These siderophores play a pivotal role in the accumulation of iron from various organic materials. Certain common siderophore-producing bacteria are *Escherichia coli*, *Salmonella*, *Klebsiella pneumoniae*, *Vibrio cholerae*, *Vibrio anguillarum*, *Aeromonas*, *Aerobacter aerogenes*, *Enterobacter*, *Yersinia* and *Mycobacterium* species (Balagurunathan and Radhakrishnan 2007).

15.4.4 Actinomycetes

Actinomycetes are filamentous bacteria having high quantity of guanine + cytosine (G+C) content which form asexual spores. Generally, they are saprophytic in nature which rely on complex substrate for their development and have the capability to nullify the impact of HMs even their concentration is extremely high. *Actinomadura madurae*, *Nocardia asteroides and Streptomyces griseus* are important genera suitable for such stressed environment (Khamna et al. 2009; Taj and Rajkumar 2016).

15.4.5 Algae

The production of siderophore has been reported also from some algae. *Anabaena* sp. produces an important siderophore, schizokinen, a dihydroxamate which helps in the facilitation of iron acquisition. In addition, certain siderophores produced by *Anabaena flos-aquae* and *Anabaena cylindrica* have been reported to accumulate copper instead of iron (Balagurunathan and Radhakrishnan 2007).

15.5 Role of Siderophores

The significance of microbial siderophores extends beyond our imagination (Kurth et al. 2016). Applications of iron chelators in sustainable agriculture are enormous especially in certain branches. Siderophores are produced by different bacteria having a wide range of application in different branches of agriculture such as soil science, plant pathology, environmental sciences, etc.

15.5.1 Maintenance of Soil Health

Soil is a dynamic place where trillions of microorganisms such as algae, bacteria, fungi, protozoans, insects, mites and worms complete their life cycle. It has been well studied that 1 gm of soil may carry about 10 billion microorganism (Torsvik and Øvreås 2002; Crecchio et al. 2004).

Soil bioremediation process has been well studied by the use of different types of siderophores just to maintain a healthy environment in soil ecosystem. There are some siderophores which have the ability to bind with metals other than iron. In this context, a wide range of bioreactors have been developed for the solubilization of the HMs (Diels et al. 2009). It has been found that the quantity of some HMs was reduced by 16-folds from its original state in the soil treated with *Cupriavidus metallidurans* which produces citrate siderophores staphyloferrin B (Munzinger et al. 1999; Diels et al. 2009). Similarly, *Pseudomonas azotoformans* have the potential to purify catecholate–hydroxamate siderophore (Nair et al. 2008). A major problem in the selection of the microorganisms is the persistence and metal tolerance limit in the new environment (Thompson et al. 2005; Braud et al. 2015). Conjoint implementation of bioaugmentation with phytoextraction has recently caught a fire of discussion among the researchers. Siderophore-producing microorganisms are well adopted for bioaugmentation because they help in the promotion of biomass as well as accumulation of HMs in various ways. Plant siderophores like mugineic acid and avenic acid are not always be able to fulfil the demand of iron, particularly in HM-polluted soil (Ma et al. 2011). However, some plants have been found to be able to access iron from bacterial siderophores by different mechanisms such as direct accumulation, chelate degradation or ligand exchange process (Schmidt 1999). Many siderophores have been reported to bind with other than iron and help in the accumulation of HMs. The bioaugmenting process of contaminated soil with *Ralstonia metallidurans* and *Pseudomonas aeruginosa* enhanced the capability of accumulation of Cr in *Zea mays* L. by 5.4 times (Takemoto et al. 1978). Similarly, application of *Streptomyces tendae* F4 enhanced the uptake of Cd and Fe in sunflowers and assisted well in plant growth promotions (Dimpka et al. 2009). In this way, it can be apprehended that siderophores may be enough to solubilize the HMs transporting them to the plants which ultimately lower down the HM concentration from the environment. In this way, siderophore helps in normalizing the soil ecosystem which is necessary in the present scenario.

15.5.2 Management of Plant Diseases

Biological control of plant disease has been fascinating and eco-friendly (Lugtenberg and Kamilova 2009). This way illustrates the indirect pathways of plant growth promotion by managing the disease significantly (Glick 2012). The main activity of biocontrols is food competition, colonization, ISR induction and antifungal compound production (Lugtenberg and Kamilova 2009). A large number of rhizobacteria have been found to produce antifungal compounds such as HCN, phenazines, pyrrolnitrin, 2, 4-diacetylphloroglucinol, pyoluteorin, viscosinamide and tensin (Bhattacharyya and Jha 2012). Resistance against some pathogenic bacteria, fungi and viruses is induced due to the interaction between rhizobacteria and plant root, called as induced systemic resistance (ISR). In addition, ISR activates the jasmonate and ethylene signalling pathway (Lugtenberg and Kamilova 2009). ISR involves in the activation of host plant's defence system against a wide range of plant pathogens. There are several other which induce bacterial components, ISR, lipopolysaccharides, flagella, iron-chelating compounds, cyclic lipopeptides, 2,4-diacetylphloroglucinol, homoserine lactones and volatiles like acetoin and 2,3-butanediol (Lugtenberg and Kamilova 2009).

Frequent and haphazard use of pesticides has escorted to the development of pest-resistant strains which facilitate in the transformation of fungicides ineffective. However, microbial metabolites can improve the management strategies of plant pathogens either by augmenting the action of antagonistics or by paving the ways to develop healthier alternatives as compared to synthetic pesticides (Rizvi et al. 2015). Additionally, there is a lot of variation in the production of siderophores. Production of siderophores is correlated with the types of strain and how that specific strain is familiar with target pathogens. The use of mutants that were effective once in siderophore secretion was less effective than the wild-type strains in crop protection (Buysens et al. 1996). Pseudomonads form a line of siderophores pertaining to enhance plant yield through the management of harmful pathogens. It has been found that many rhizobacteria suppress the growth of harmful microorganism by releasing siderophore and other related organic molecules (Husen 2003). In addition, siderophores inhibit the growth of various plant pathogenic fungi, like *Phytophthora parasitica* (Seuk et al. 1988), *Pythium ultimum* (Hamdan et al. 1991), *Fusarium oxysporum* var. *dianthi* (Buysens et al. 1996) and *Sclerotinia sclerotiorum* (Kraemer et al. 2006).

15.5.3 Promotion of Crop Yield

Although most of the soil is blessed with sufficient iron for plant growth, plant iron deficiency is a common problem in some range of soil especially calcareous soil which may be due to low solubility of Fe(III) hydroxide. Calcareous soil harbours around 30% of the world's agricultural land. In such case, some plants (grasses, cereals and rice) secrete phytosiderophores into the soil. Some plant species such as barley and wheat are well efficient to sequester iron by releasing phytosiderophores via their root into the surrounding soil rhizosphere (Hershko et al. 2002). Many studies have advocated that plants are able to incorporate and use Fe^{3+} of siderophores into their biomass. In addition to this, some plants are efficient to assimilate iron through siderophores produced by microorganism harbouring rhizospheric soil. The use of microbial siderophore has been extensively studied and found that this organic molecule has rescued groundnut from iron chlorosis. A significant improvement in some growth attributes and plants health has been extensively observed after the treatment of seeds with siderophorogenic bioinoculants.

A considerable increase in the percentage of germination, and some plant growth attributes including chlorophyll content, has been achieved when seeds were bacterized with siderophore of *Pseudomonas* (Manwar et al. 2001). The effect of bacterial siderophores on plant growth has been seen in various studies. For instance, the use of radiolabelled ferric siderophore as a sole source of iron explained that plants are able to take up the labelled iron; mung bean plants treated with *Pseudomonas* strain GRP3 grown under iron-deprived conditions showed less chlorotic symptoms and a significant chlorophyll level (Sharma et al. 2003). Similarly, considerable enhancements in iron content were recorded in *Arabidopsis thaliana* plant tissues leading to improved plant growth (Vansuyt et al. 2007). Siderophores play a crucial role in the dissolution of iron, making it available for microbial and plant growth.

15.5.3.1 Role of *Pseudomonads*

Siderophores, pseudobactin (pyoverdine), produced from *Pseudomonas* (B10) isolated from suppressive soils when inoculated to soils conducive to Fusarium wilt or take all disease caused by *Gaeumannomyces graminis* transformed them to disease-suppressive soils (Desai and Archana 2011). Moreover, addition of exogenous iron(III) to disease-suppressive soils leads to conversion of them into conductive soils. A large number of bacteria are found effective in biocontrol of plant diseases due to their antagonistic ability to phytopathogenic bacteria or fungi having a higher binding affinity for iron (Raaijmakers et al. 1995; Loper and Henkel 1999). Production of siderophore by *Pseudomonas* spp. has been reported to involve in the control of *G. graminis* var. *tritici* (Kloepper et al. 1980), *F. oxysporum* (Elad and Baker 1985) and *Pythium* spp. (Becker and Cook 1988; Loper 1988). It has been well documented that the antagonistic activity of pseudomonads against phytopathogens leads to a significant enhancement in plant growth and yield (Loper and Henkel 1999) also against detrimental phytopathogens (Becker and Cook 1988; Schippers et al. 1987), thereby increasing plant growth. Siderophores have been also found to be the inducers of defence mechanisms in a wide range of plants. For example, *P. fluorescens* CHA0 was reported to induce systemic acquired resistance (SAR) of tobacco; however, at varying extent, its pvd mutant registered minimum improvement than the wild one (Maurhofer et al. 1994). Some microbial siderophores including pyoverdines have played a pivotal role in the direct improvement of the iron nutrition in many plant species (Crowley et al. 1988; Hordt et al. 2000). A significant enhancement in iron content and uptake has been reported in various horticultural crops (Bar-Ness et al. 1991). Vansuyt et al. (2007) reported that iron chelated to pyoverdine was transported to *A. thaliana* plants in an independent pathway which leads to enhanced plant growth.

15.5.3.2 Role of *Rhizobia*

Rhizobium spp. has impacted a large in cash crop especially on pulses. The information on the advantageous effect of siderophore conferred by a free-living *Rhizobium* strain in the siderophore production and uptake are still meagre. However, available literature have suggested that rhizobial siderophores play a pivotal role in rhizosphere competition possibly in the same manner as pseudomonads do (Joshi et al. 2008). Some rhizobia are efficient enough to produce siderophores leading to plant growth promotion and nodulation (Bai et al. 2002; Dahsti et al. 1998; Rao and Pal 2003). In addition to this, some phytopathogenic bacteria harbouring in the soil have the capability to colonize the rhizosphere, leaving negative effects on plant growth. Besides rhizobial nitrogen fixation, they are also effective as biocontrol agents for the management of certain soilborne phytopathogen enhancements of plant growth by IAA production and accumulation of some minerals and phosphorous (Chakraborty and Purkayastha 1984). A large number of rhizobial strains promote plant growth in one hand, while, on the other hand, inhibit the growth of pathogenic fungi/bacteria. *Rhizobium meliloti* and *B. japonicum* are examples which reduced the detrimental effect of *Macrophomina* disease severity considerably. Reduction of disease severity caused by *Macrophomina phaseolina* was significant over control because of starvation of iron (Arora et al. 2001; Deshwal et al. 2003; Desai and Archana 2011).

15.6 Microbial Interaction

The role of siderophores among organisms' interaction has been well researched and found to be greatly influenced. Production of siderophores modifies the niche area of an organism through various mechanisms such as cooperation, competition, etc. (Scavino and Pedraza 2013). A large number of microbes have the machinery to utilize the Fe(III) siderophore complex synthesized by the siderophore-producing organisms. Several enterobacteria have the receptors for uptaking such siderophores leading to modification of the current environment (Winkelmann 2007). The siderophores produced by bacteria have been reported to get utilized by fungi (Hass 2003; Heymann et al. 2000). Similarly, enterobactin produced by enterobacteria can be used by *Saccharomyces* sp. (Winkelmann 2007).

Microbial interaction is a natural process and necessary for maintaining the ecological balance (Kurth et al. 2016) which may be positive, negative or neutral. There are wide ranges of alteration in interacted microorganism-producing siderophores. For example, bacterial siderophore has higher affinity to bind Fe than the fungi which explain the reason of biocontrol of plant pathogenic fungi (Loper and Henkels 1999). Besides, some siderophore producers are invaded by non-siderophore-producing chelators either from same or different species. Generally, siderophore production is very expensive to a single producer but that enables other cell of the same species present in the vicinity to capture iron siderophore complexes (Harrison et al. 2008). Interestingly, some siderophore-producing microorganisms synthesize some different siderophores just to bypass the cheaters' tactic. *Streptomyces* spp. have distinct type of siderophore production system. They are generally categorized into two types of independent uptake system. For example, ferrioxamine can be used by different organisms, while ferric coelichelin can only be absorbed by *Streptomyces coelicolor* (Challis and Hopwood 2003). Moreover, some microorganisms have the capability to destruct the siderophore leading towards the modification of interaction process. For instance, *Azospirillum* sp. in pure keeps the capability to vandalize the ferrioxamine during iron-free state. In addition to this, it was seen that unculturable bacteria were stimulated and transformed into culturable form in the presence of some siderophore-producing bacteria. Acyl-desferrioxamine, a prominent siderophore, enables the uncultured microorganisms to get flourished themselves and helps in the plant growth promotion (D'Onofrio et al. 2010).

15.7 Environmental Research

Siderophores have the potential ability to settle down a range of ecological issues such as HM accumulation, rust removal, biofouling, dye degradation, sewage treatment and bioleaching, etc. Soil biota promotes mineral weathering by the production of enormous type of siderophores which offer competent Fe acquisition organization due to its high binding affinity for Fe(III) (McGrath et al. 1995; Kraemer 2004). HMs such as Cd, Cr, Cu, Hg, Pb and Ni are commonly found in the soil, but geological and anthropogenic activities have increased the concentration of these HMs to the extents which are beyond the permissible limits. Excessive uptake of HMs is found toxic to living organisms posing significant environmental problem which leads to bad heath of human kinds. Some activities such as mining, smelting of metals, burning of fossil fuels, application of fertilizers and chemicals in agriculture, manufacturing of batteries and other goods produced in industries, sewage sludge and municipal waste disposal are the chief producers of HMs. HMs are deteriorated during phytoremediation; however, it is transformed from one organic molecule composite to another. Thus, changing in their oxidation state, HMs are converted to low carcinogens, easily volatilized and more water soluble (Wang et al. 1989). A large number of microorganisms especially rhizobacteria such as *Bacillus subtilis*, *P. putida* and *Enterobacter cloacae* are being used for the reduction of Cr(VI) to Cr(III) which is less toxic (van der Lelie et al. 1999; Haja et al. 2010). *B. subtilis* has been involved in the reduction of nonmetallic elements such as toxic selenite to less toxic Se (Garbisu et al. 1995). Another instance, *B. cereus* and *B. thuringiensis* enhance the ability of extraction of Cd and Zn from Cd-rich soil and soil polluted with garbage and effluent from metal industry (Ruggiero et al. 2000). It is, therefore, surmised that siderophore production by rhizobacteria has provided the avenues for the extraction of these HMs from the soil ecosystem. This is what siderophore productions are found to play a pivotal role in the accumulation HMs (Von Gunten and Benes 1995). In addition, siderophore production by *A. vinelandii* was markedly enhanced in the presence of Zn(II). Plant growth-promoting rhizobacteria are able to play a significant role in providing the assistance for the phytoremediation of HMs from contaminated soils. Therefore, HMs influence the role of bacteria-producing siderophore which in turn help in the mobilization and extraction of HMs from soil. Siderophores have the ability to resolve these environmental issues such as accumulation of heavy metal from various industries.

Moreover, siderophores are used in the treatment of radioactive waste before long storage (Von Gunten and Benes 1995; Bouby et al. 1998). Some fungi, like *Fusarium* sp., and bacteria, *P. aeruginosa*, are rich in production of siderophores which are able to modify the pH and maximize the chelation of some elements such as uranium (U^{6+}) and thorium (Th^{4+}) (Joshi et al. 2014).

15.8 Mechanisms for Siderophore-Mediated Iron Transport

Microorganisms catch up iron with the help of iron chelator molecules that fulfil the demands of needy plants. To send iron into the cellular machinery, bacteria trap iron-loaded siderophores at the surface of the cell and push them to enter into the cytosol. Siderophore-binding affinities for Fe(III) are extremely high in bacteria which illustrates that these organic molecules can significantly catch up the Fe(III) from a wide range of environment (Stintzi et al. 2000; Bernd and Rehm 2008). To explore the ferric–siderophore complex mechanism and how iron gets trapped by siderophore-producing microorganism, an outline has been presented. Initially, receptors present at the outer membrane specifically bind ferric siderophore and transport them into the periplasm. Thereafter, a system which is basically composed of protein Ton B transduces the energy from proton force into transport-proficient structural changes of the receptor. Lastly, one specific protein present in the periplasm helps in transferring the iron into transporter molecules associated with the cytoplasmic membrane (Fig. 15.1; Sah and Singh 2015). ABC transporter is made up of a protein channel in the membrane of the cytoplasm coupled with a cytoplasmic ATPase which determines ferric siderophore internalization at the expense of cytoplasmic ATP hydrolysis. ABC transporter complex is composed of two distinct proteins, each one has its own function. For instance, the first one separates the membrane which acts as permease and the second one provides energy for transport via hydrolysis reaction. There are certain different transmembrane permeases such as Fhu B (hydroxamate), FepD4 (enterobactins) and Fec CA (ferric dicitrate).

The ferric–siderophore complex is released at the specific site of the cytoplasmic membrane from its vehicle/transport system through reduction reaction. There is then ligand exchange on the cell surface which involves the exchange of iron from ferric pyoverdine to iron-free pyoverdine which is tightly bound with the receptor of FpvA (Schalk et al. 2011).

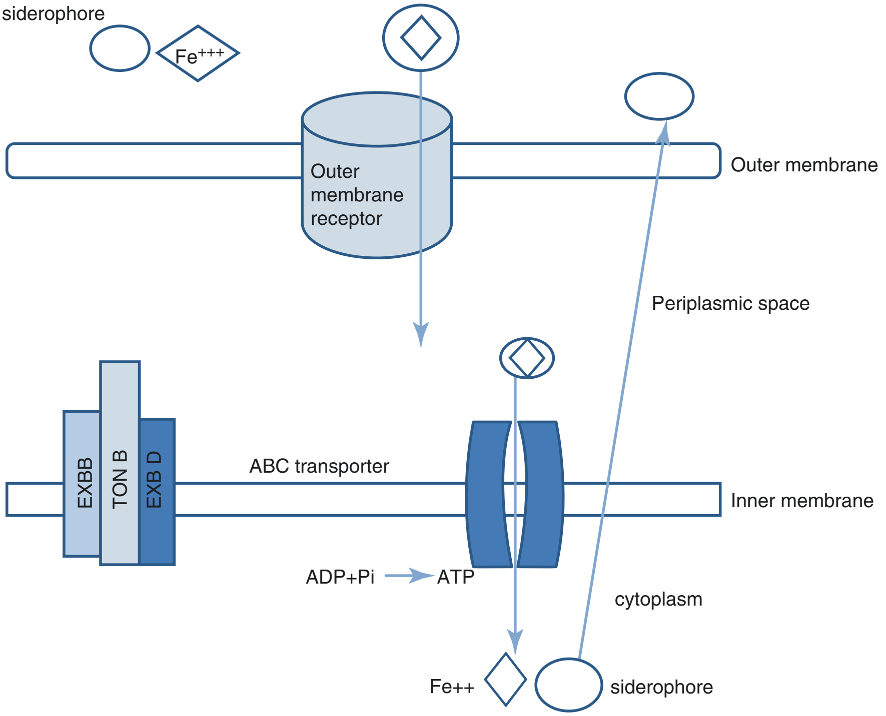


Fig. 15.1 Pathway of iron transport across the outer and inner membrane (Source: Sah and Singh 2015)

15.9 Conclusions and Future Perspective

The information pertaining to siderophore production have suggested that newer avenues related to maximization of siderophore production are needed to be explored. Application of siderophore-producing microorganism has played a pivotal role in maintaining the ecological balance. These microbes have provided a new vista of research towards the utilization of microbes for plant disease protection, plant growth promotion, SAR induction, environmental research and maintenance of soil health. Siderophores have also accelerated the production of many phytohormones such as IAA leading to induction of SAR and growth promotion. It is also summarized that there are a lot of variations in the siderophore-binding affinities which may be due to structural differentiations. However, this variation enables siderophores to quench iron from soil and mobilize them to a specific target. Siderophore-producing microorganisms containing extremely high binding affinities for iron are ecologically sound communities. Therefore, such communities may be determinant of better plant growth. Information pertaining to maintenance of soil health revealed that the contaminants are reduced and less toxic in the siderophore-producing-rich microorganisms. This organic molecule has a significant role in the purification of HM-polluted soil. Environmental research is a separate segment of thrust area of research where it has a wide range of applicability, for example, removal of HMs, purification of oceanic contaminants, elimination of algal bloom, etc. Overall, application of siderophores is conducive to the human welfare as well as in the sustenance of ecological balance. Further emphasis just to promote the siderophore production will open new door for researchers leading to resolve the "yet to be answered" questions.

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