

MICROBIAL SOLUBILISATION OF PHOSPHATE: *PSEUDOMONAS* VERSUS *TRICHODERMA*

M.H. JOSEPH, T.S. DHARGAVE*, C.P. DESHPANDE** AND A.K. SRIVASTAVA***

Department of Microbiology, Lakshminarayan Institute of Technology, Nagpur – 440 033 (Maharashtra)

Received: May, 2015; Revised accepted: July 2015

ABSTRACT

Phosphorus is one of the important primary plant nutrients required by the plant for sustaining long term performance. *Trichoderma* and *Pseudomonas* are premier microbes having known for their dynamism in phosphate solubilisation. An incisive analysis of the work done on mechanistic differences in phosphate solubilization by these two microbes showed almost the same mechanisms, though; one is fungus, while another is bacteria. Both besides being good colonizers, are capable of competing under nutrient deficient medium. The solubilization of phosphate is accomplished through number of processes viz., producing chelating compounds like siderophores as chelating agent, secondary metabolites (antibiotics formation), organic acids production and secretion of growth regulators predominantly indole acetic acid.

Key words: *Pseudomonas*, *Trichoderma*, phosphorus solubilization, chelating compounds, antibiotics.

INTRODUCTION

Plant rhizosphere is highly competitive ecosystem for its space, food and protection from various biotic and abiotic stresses (Srivastava, 2012; Ngunllie *et al.*, 2015). Plant growth and nutrition largely depend upon the combination and concentration of mineral nutrients available in the soil (Srivastava *et al.*, 2008). Plants often face significant challenges in obtaining an adequate supply of nutrients to meet the demands of basic cellular processes due to their relative immobility, phosphorus being of them (Srivastava, 2013). The organisms possessing phosphate solubilizing ability are called phosphate solubilizing microorganisms (PSM). They can convert the insoluble compounds into soluble forms in soil and make them available for plants to absorb (Pradhan and Sukla, 2005; Srivastava and Malhotra, 2014). Strains from bacterial genera viz., *Pseudomonas*, *Bacillus*, *Rhizobium*, and *Enterobacter* and *Aspergillus* and *Penicillium* from fungal genera (Xiao *et al.*, 2011; Kreditsu and Srivastava, 2014) are the most powerful phosphate solubilizers (Whitelaw, 2000). In this, background, mechanistic efficacy of two most researched PSMs viz., *Pseudomonas* and *Trichoderma* have been compared at cellular level (via biochemical and antibiotic production) and organ/whole plant level (through growth-associated responses). Compared with other major nutrients, phosphorus is by far the least mobile and available to plants in most soil conditions. Although, P is abundant in soils in both organic and inorganic forms, it is frequently a major or even the prime limiting factor for plant growth (Goldstein, 1986; Srivastava and Singh, 2008).

SOLUBILISATION PROCESS

The major microbiological means by which insoluble phosphorus compounds are mobilized is the production of organic acids, accompanied by the acidification of the medium (Srivastava and Ngunllie, 2009). The type of organic acid produced and their amounts differ with different organisms. Among them, gluconic acid and 2-ketogluconic acid seem to be the most frequent agent of mineral phosphate solubilization (Song *et al.*, 2008; Srivastava *et al.*, 2015a). Other organic acids, such as acetic, citric, lactic, propionic, glycolic, oxalic, malonic, succinic, fumaric, tartaric etc. have also been identified among phosphate solubilizers (Ahmed and Shahab, 2011). Phosphorous acquisition behavior microorganisms enhance the capacity of plants to acquire phosphorus from soil through various mechanisms that are summarized as:

- i. Alteration of sorption equilibria that may result in increased net transfer of orthophosphate ions into soil solution or facilitate the mobility of organic phosphorus either directly or indirectly through microbial turnover (Seeling and Zasoski, 1993; Wu *et al.*, 2013).
- ii. Induction of metabolic processes that are effective in directly solubilizing and mineralizing phosphorus from sparingly available forms of soil inorganic and organic phosphorus (Richardson *et al.*, 2009). These include the efflux of protons and organic anions, production of siderophores and release of and cellulolytic enzymes required for the hydrolysis of organic P or mineralization of organic residues and organic matter. Organic anions and protons are particularly effective in solubilizing precipitated forms of P (Eg. Ca phosphates under alkaline conditions), chelating metal ions that are

Email:-mariajosephmj143@gmail.com *Shivaji Science College, Nagpur, trisha.dhargave@gmail.com,

G.H.Raisoni Institute of Interdisciplinary Science, Nagpur-,chaitanyaunique@gmail.com, *ICAR-Central Citrus Research Institute, Nagpur-aksrivastava2007@gmail.com

- iii. Commonly associated with complex form of soil P (as is for the role of siderophores in mediating Fe availability), or by facilitating the release of absorbed orthophosphate or organic P through ligand-exchange reactions (Ryan *et al.*, 2001; Wu and Srivastava, 2012).
- iv. Increased root growth through either an extension of existing root systems (Eg. mycorrhizal associations) or by hormonal stimulation of root growth branching, or root hair development (phytostimulation Eg; production of indole-3-acetic acid, GA's or other enzymes that alter plant ethylene precursors such as 1-aminocyclopropane-1-carboxylate deaminase (Richardson *et al.*, 2009; Hayat *et al.*, 2010; Wu *et al.*, 2013).

PHOSPHATE SOLUBILIZATION BY PSEUDOMONAS

Pseudomonas are particularly good colonizers of space in the rhizosphere, especially where there is low nutrient availability. The synthesis of lipopolysaccharides by rhizobacteria is important

for spatial colonization in their rhizosphere and in case of *Pseudomonas*, it is equally a crucial factor (Lugtenberg and Dekkers, 1999). *Pseudomonas* is capable of rapid growth and therefore shows good colonization in the rhizosphere. One reason for this is that, it can use various substrates as nutrients and survive in different conditions that would be stressful for other bacteria. Its ability to produce various compounds such as antibiotics, polysaccharides and siderophore add further dynamisms.

The principle mechanism for mineral phosphate solubilization by *Pseudomonas* is through production of organic acid and acid phosphatase which play a major role in the mineralization of organic phosphorus. Production of organic acids results in acidification of microbial cell and its surroundings consequently; Pi is released from mineral phosphate by proton substitution for Ca (Goldstein, 1999). Various roles of *Pseudomonas* in phosphate solubilization has been further summarized (Table 1).

Table 1: Mechanisms involved with phosphate solubilization by *Pseudomonas*

| Functions of <i>Pseudomonas</i> | Source |
|---|--|
| Physiological responses | |
| -Good colonizer of space in rhizosphere | Harman <i>et al.</i> (2004) |
| - Imparts antagonism through antioxidants | Pant and Mukhopadhyay (2001) |
| -Solubilization of insoluble form of P into soluble form | Mahdi <i>et al.</i> (2011) |
| -Chelating molecules (Siderophores) | Budzikiewicz (1993) |
| -Indirectly by reduction of manganese | Altomare <i>et al.</i> (1999) |
| Antibiotic production | |
| -Secondary metabolites in form antibiotics such as phenazine-1-carboxylic acid; 2,4 diacetyl-phloroglucinol; <i>Pseudomonas fluorescens</i> HV37a, Afu Ia, Afu Ib; phenazine-1-carboxylic acid; 2,4-diacetylphloroglucinol; pyoverdine or pseudobactin; ferripyoverdine | Howell and Stipanovic (1980), Weller (1988), Myxolla (1999), Douglas <i>et al.</i> (1986), Raaijmakers <i>et al.</i> (1997), Meyer and Abdallah, (1978), Francesco <i>et al.</i> (2009), Dieter Haas and Genevieve Defago, (2005), Phoebe <i>et al.</i> (2001) |
| pyrrolnitrin, pyochelin, phenazines, phloroglucinols, pyoluteorin, pyrrolnitrin, cyclic lipopeptides | |
| Biochemical response | |
| -Polysaccharide secretion | Santoyo <i>et al.</i> (2012) |
| -Organic acids production | Dennis and Webster (1971) |
| -Production of indole acetic acid | Bernard <i>et al.</i> (2002) |

Some antagonistic root-colonizing *Pseudomonas* react to limiting iron conditions by using a high-affinity iron uptake system based on the release of Fe³⁺ chelating molecules in form of siderophores (Weller, 2007; Cornelis, 2010). This chelated iron is not available to plant pathogens, whose activity is thereby reduced (Baker *et al.*, 1986), while plant roots can take up chelated iron either directly or after reduction of Fe³⁺ (Welch *et al.*, 1993) and Mn³⁺ (Graham *et al.*, 1991) by plasma membrane reductases. *Pseudomonas* can synthesis siderophores in iron-limiting conditions, being a factor that induces

gene expression in operons involved in siderophore synthesis. It is known that compounds such as siderophores are synthesized mainly during the exponential growth phase, which is the stage in which the population requires more nutrients for cell division (Loper and Schroth, 1986). Likewise, the pseudofactor-Fe complex has a high stability constant (Chen *et al.*, 1994), suggested that virtually all excreted pseudobactin molecules bind to Fe present in the medium. This complex acts as a Fe (III) delivery system for its introduction through bacterial cells (Koster *et al.*, 1995; Loper and Henkels., 1999).

Phosphate solubilization by *TRICHODERMA*

Trichoderma species are one of the most effective groups of fungi and known to fix nitrogen and solubilize nutrients (Altomare *et al.*, 1999). The mechanism of phosphate solubilization by *Trichoderma* involves; acidification of the medium by

production of organic acids including acetic, butyric, citric, fumaric (Scervino *et al.*, 2010). The other processes include chelation, reduction and enzymatic degradation of complex organic P compounds (e.g., acid and alkaline phosphatases) (Khan *et al.*, 2014).

Table 2: Mechanisms involved with phosphate solubilization by *Trichoderma*

| Functions of <i>Trichoderma</i> | References |
|---|--|
| Physiological response | |
| - Good colonizer of space in rhizosphere | Lugtenberg and Dekkers (1999) |
| - Antagonism expression | Harman <i>et al.</i> (2004) |
| - Solubilization of insoluble form of P into soluble form | Altomare <i>et al.</i> (1999) |
| - Production of chelating molecules | Baker <i>et al.</i> (1986) |
| - Oxidization or reduction of manganese | Altomare <i>et al.</i> (1999) |
| Antibiotic production | |
| - Production of secondary metabolites in form of antibiotics such as gliotoxin, N-desmethyl, phytolaccoside β , gliovirin, pyrones, viridin, peptaibols | Sivasithamparam and Ghisalberti (1998), Kobayashi <i>et al.</i> (1995), Howell (1980), Harman <i>et al.</i> (2004) |
| Biochemical response | |
| - Production of polysaccharides | Gomes <i>et al.</i> (1992) |
| - Production of organic acids | Akintokun <i>et al.</i> (2007) |
| - Production of indole acetic acid vis-à-vis root growth | Vessey (2003) |

Trichoderma species react to iron limiting conditions by using a high-affinity iron uptake system based on the release of iron chelating molecules as Siderophores (Baker *et al.*, 1986), while plant roots can take up chelated irons either directly or after reduction of Fe^{3+} by plasma membrane reductases (Welch *et al.*, 1993; Srivastava *et al.*, 2015b). *Trichoderma* has been found to evolve mechanisms that are involved in solubilization of Mn by either oxidizing or reducing manganese and thus influence its availability (Huber and McCay-Buis, 1993). If some strains of *Trichoderma* possess the ability to solubilize many different nutrients, it would not be surprising to find that multiple mechanisms are involved, even for a single element. For example, solubilization of iron may involve reduction of Fe^{3+} to Fe^{2+} as well as chelation of Fe^{3+} by siderophores or chelating agents. Various processes involved in phosphate solubilization by *Trichoderma* (Table 2) further revealed the similarity in mechanisms of phosphate solubilisation, although physiological and biochemical responses differed greatly. *Pseudomonas* and *Trichoderma*, thus, function in solubilization of phosphorus. While doing so, they help in solubilization process of other important nutrients essential for plant growth and control of plant growth. These two microbes showed same mechanisms in solubilizing essential nutrients such as iron and manganese as well.

Conclusion

Pseudomonas and *Trichoderma*, though belonging to different classes of microbes, still both the microbes play same important role in plant growth promotion. Both show more or less same mechanisms in solubilizing essential nutrients such as phosphorus, iron, manganese etc. in addition to promoting plant growth.

Future Research

Many studies on the interaction of PSMs have been conducted in different crop plants. However, the information on the capability of these organisms in localized soil conditions, in promoting plant growth and the biochemical characterization of phosphate solubilizing bacteria and fungi isolated from different soil types of different zones, is very much limited. It is suggested to isolate, identify and characterize rhizo-competent of species of these two predominant microbes which can be used as best bioinoculants in promoting plant growth. However, the information on the capability of these organisms in localized soil conditions in promoting plant growth alongwith their biochemical characterization isolated from different soil types of different agro-climatic zones will be the future lines of research. It is further suggested to study the type of synergisms at different levels of their taxa between *Pseudomonas* and *Trichoderma* in order to promote plant growth. It will be equally interesting to know the complementarity of these two microbes with other microbes in consortium mode in order to harness the value added benefits for plant growth.

REFERENCES

- Ahmed N. and Shahab, S. (2011) Phosphate solubilization: Their mechanism genetics and application. *International Journal of Microbiology* **9**: 4408-4412.
- Akintokun, A.K., Akande, G.A., Akintokun, P. O., Popoola, T.O.S. and Babalola, A.O. (2007) Solubilization on insoluble phosphate by organic acid-producing fungi isolated from Nigerian soil. *International Journal of Soil Science* **2**(4): 301-307.
- Altomare, C., Norvell, W. A., Björkman, T. and Harman, G.E. (1999) Solubilization of phosphates and micronutrients by the plant growth promoting and biocontrol fungus *Trichoderma harzianum* Rifai 1295-22. *Applied and Environmental Microbiology* **65**: 2926-2933.
- Baker, R., Elad, Y. and Sneh, B. (1986) Physical, biological and host factors in iron competition in soils. In: Swinburne TR (ed). Iron siderophores and plant diseases. New York, N.Y: Plenum Publishing Corp. pp. 77-84.
- Bernard, P., Chosidow, O. and Vaillant, L. (2002) Oral prestinamycin versus standard penicillin regimen to treat erysipelas in adults: Randomised, non-inferiority, open trial. *British Medical Journal* **325**: 364.
- Budzikiewicz, H. (1993) Secondary metabolites from Fluorescent *pseudomonads*. FEMS by plant growth-promoting rhizobacteria on potato plant development and yield', by siderophores produced by plant growth-promoting rhizobacteria'. *Natur.* **286**: 885.
- Chen, Y., Jurkevitch, E., Bar-Ness, E., and Hadar, Y. (1994) Stability Constants of Pseudobactin Complexes With Transition Metals'. *Soil Science Society of America Journal* **58**: 390-396.
- Cheryl L. Patten and Bernard R. Glick (2002) Role of *Pseudomonas putida* indole acetic acid in development of the host plant root system. *Applied and Environmental Microbiology*. **68**(8) PMC124051.
- Compant, S., Duffy, B., Nowak, J., Clément, C., and Barka, E.A. (2005) Use of plant competence? *Environmental Microbiology* **1**: 9-13.
- Cornelis, P. (2010) Iron uptake and metabolism in *Pseudomonads*'. *Applied Microbiology and Biotechnology* **86** (6): 1637-1645.
- Dieter, H. and Genevieve D. (2005) Biological control of soil-borne pathogens by fluorescent *Pseudomonas*. *Nature Reviews (Soil Sci.)* **3**: 307-319.
- Douglas, W. J. Jr. and Gutterson, N.I. (1986) Multiple antibiotics produced by *Pseudomonas fluorescens* HV37a and their differential regulation by glucose. *Applied and Environmental Microbiology* **52**: 1183-1189.
- Dennis, C. and Webster, J. (1971) Antagonistic properties of species groups of *Trichoderma*. I. Production of non-volatile antibiotics. *Transactions of the British Mycological Society* **57**: 25-29.
- Francesco I., Fedrica T. and Paolo V. (2009) Molecular basis of pyoverdine siderophore recycling in *Pseudomonas aeruginosa*. *Proceedings of the National Academy of Sciences* **106**(48): 20440-20445.
- Goldstein, A.H. (1986) Bacterial solubilization of mineral phosphate: historical perspectives and future prospects. *American Journal of Alternative Agriculture* **1**: 57-65.
- Goldstein, A.H. (1999) Involvement of the quinoprotein glucose dehydrogenase in the solubilization of exogenous phosphates by gram-negative bacteria. In: Torriani-Gorini A., Yagil E. and Silver, S. (eds.). Phosphate in Microorganisms: Cellular and Molecular Biology. Washington, DC: ASM Press, 1994. pp. 197-203.
- Gomes, I., Gomes, J., Steiner, W. and Esterbauer, H. (1992) Production of cellular and xylanase by a wild strain of *Trichoderma viride*. *Applied Microbiology Biotechnology* **36**: 701-707.
- Graham R. D. and Webb, M. J. (1991) Micronutrients and disease resistance and tolerance in plants. In: Mortvedt, J.J., Cox, F.R., Schuman, L.M. and Welch R. M. (eds.). Micronutrients in Agriculture. 2nd Edition Soil Science Society of America Madison, Wisconsin, USA, pp. 329-370.
- Harman, G.E., Howell, C.R., Viterbo, A., Chet, I. and Lorito, M. (2004) *Trichoderma* species-opportunistic, avirulent plant symbionts. *Nature Reviews* **2**: 43-56
- Hayat, R., Ali, S., Amara, U., Khalid, R. and Ahmed, I. (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. *Annals of Microbiology* **60**: 579-598.
- Howell, C.R. and Stipanovic, R.D. (1980) Suppression of *Pythium ultimum*-Induced damping-off of cotton seedlings by and its antibiotic pyoluteorin. *Phytopathology* **70**: 712-715.

- Huber, D. M. and McCay-Buis T.S. (1993) A multiple component analysis of the take-all disease of cereals. *Plant Disease Journal* **77**:437-447.
- Keditsu R. and Srivastava, A.K. (2014). Substrate dynamics: Developments and issues. *Annals of Plant and Soil Research* **16**(1):1-8.
- Khan, M.S., Zaidi, A., Ahemad, M., Oves, M. and Wani, P.A. (2010) Plant growth promotion by phosphate solubilizing fungi-current perspective. *Archives of Agronomy and Soil Science* **56**:73-98.
- Kobayashi, T., Vieira, W.D., Potterf, S.B., Sakai, C., Imokawa, G. and Hearing, V.J. (1995) Modulation to melanogenic protein expression during the switch from euto pheomelanogenesis. *Journal of Cell Science* **108**: 2301-2309.
- Koster, M., Ovaas, W., Bitter, W. and Weisbeek, P. (1995) Multiple outer membrane receptors for uptake of ferric pseudobactins in *Pseudomonas putida* WCS358. *Molecular Genetics and Geneomics* **248**(6): 735-743.
- Loper, J.E., and Henkels, M.D. (1999) Utilization of heterologous siderophores enhance levels of iron available to *Pseudomonas putida* in the rhizosphere. *Applied and Environmental Microbiology* **65**(12):5357.
- Loper, J.E. and Schroth, M.N. (1986) Importance of siderophores in microbial interactions in the rhizosphere. In: Swinburne, T.R. (ed.). Iron, Siderophores and Plant Diseases. New York, USA, Plenum Press, pp. 85-98.
- Lugtenberg, B.J. and Dekkers, L.C. (1999) What makes pseudomonas bacteria rhizosphere competent? *Environmental Microbiology* **1**(1): 9-13.
- Mahdi S. S., Hassan G. I., Hussain A., Faisal-ur-Rasool (2011) Phosphorus availability issue-its fixation and role of phosphate solubilizing bacteria in phosphate solubilization. *Agricultural Science Research Journal* **2**(1):174-179.
- Meyer, J.M. and Abdallah, M.A. (1978) The fluorescent pigment of *Pseudomonas fluorescens*: biosynthesis, purification and physicochemical properties. *Journal of General Microbiology* **107**: 319-328.
- Myxolla M. (1999) Transformation of soil microbiology community structure and Rhizoctonia suppressive potential in response to apple roots. *Phytopathology* **89**: 920-927.
- Ngullie, Ethel, Singh, A.K., Sema Akali and Srivastava A.K. (2015) Citrus growth and rhizosphere properties. *Communications in Soil Science and Plant Analysis*.
- Pant, R. and Mukhopadhyay, A.N. (2001) Integrated management of seed and seedling rot complex of soy bean. *Indian Phytopathology* **54**(3): 346-350.
- Phoebe, C.H. Jr., Combie, J., Albert, F.G., Van Tran, K., Cabrera, J., Correia, H.J., Guo, Y., Linderemuth, J., Rauert, N., Galbraith, W. and Selitrennikoff C.P. (2001) Extremophilic organisms as an unexplored source for antifungal compounds. *Journal of Antibiotics* **54**:56-65
- Pradhan, N. and Sukla, L.B. (2005) Solubilization of inorganic phosphate by fungi isolated from agriculture soil. *African Journal of Biotechnology* **5**: 850-854.
- Raaijmakers, J.M., Weller, D.M. and Thomashow, L.S. (1997) Frequency of antibiotic producing *Pseudomonas spp.* in natural environments. *Applied and Environmental Microbiology* **63**: 881-887.
- Richardson, A.E., Barea, J.M., McNeill, A.M. and Prigent-Combaret, C. (2009) Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. *Plant and Soil* **321**:305-339.
- Ryan, P.R., Delhaize, E. and Jones, D.L. (2001) Function and mechanism of organic anion exudation from plant roots. *Annual Review Plant Physiology and Plant Molecular Biology* **52**: 527-560.
- Santoyo, G., Orozco-Mosqueda, M.C. and Govindappa M. (2012) Mechanisms of biocontrol and plant growth promoting activity in soil bacterial species of *Bacillus* and *Pseudomonas*: A review. *Biocontrol Science and Technology* **22**:855-872.
- Scervino, J.M., Mesa, M.P., Monica, I.D., Recchi, M. Moreno, N.S. and Godeas, A. (2010) Soil fungal isolates produce different organic acid patterns involved in phosphate salt solubilization. *Biology and Fertility of Soils* **46**:755-763.
- Seeling, B. and Zasoski, R.J. (1993) Microbial effects in maintaining organic and inorganic solution phosphorus concentrations in grassland topsoil. *Plant and Soil* **148**:277-284.
- Sivasithamparam, K. and Ghisalberti, E.L. (1998) Secondary metabolism in *Trichoderma* and *Gliocladium*. In: Kubicek, C.P. and

- Harman, G.E. (eds.). *Trichoderma* and *Gliocladium*, London: Taylor and Francis, Vol. 1. pp. 139–191.
- Song, O.R., Lee, S.J., Lee, Y.S., Lee, S.C., Kim, K.K. and Choi, Y.L. (2008) Solubilization of insoluble inorganic phosphate by *Burkholderia cepacia* DA 23 isolated from cultivated soil. *Brazil Journal of Microbiology* **39**:151-156.
- Srivastava, A. K. (2012) Integrated nutrient management in citrus. In: Srivastava A K. (ed). *Advances in Citrus Nutrition*. Springer Verlag, Netherlands. pp. 369-390.
- Srivastava, A.K. (2013). Recent developments in diagnosis and management of nutrient constraints in acid lime. *Scientific Journal of Agricultural* **2**(3):86-96.
- Srivastava, A.K. and Ngullie Ethel (2009) Integrated nutrient management : Theory and practice. *Dynamic Soil, Dynamic Plant*. 3(1) : 1-30.
- Srivastava, A.K. and Malhotra, S.K. (2014) Nutrient management in fruit crops: Issues and strategies. *Indian Journal of Fertilizer* **10**(12):72-88.
- Srivastava, A. K., Malhotra S.K., and Krishna Kumar N. K. (2015a) Exploiting nutrient-microbe synergy in unlocking productivity potential of perennial fruits: A review. *Indian Journal of Agricultural Sciences* **85**(4):459-481
- Srivastava, A.K. and Shyam Singh (2008) Citrus nutrition research in India: Problems and prospects. *Indian Journal of Agricultural Sciences* **78**:3-16.
- Srivastava, A.K., Shyam Singh and Albrigo L.G. (2008) Diagnosis and remediation of nutrient constraints in Citrus. *Horticulture Reviews* **34**: 277-63.
- Srivastava, A.K., Shyam Singh and Huchche, A.D. (2015b) Evaluation of INM in citrus on Vertic Ustochrept: Biometric response and soil health. *Journal of Plant Nutrition* **38**(5):1-15.
- Vessey, J.K. (2003) Plant growth promoting rhizobacteria as biofertilizers. *Plant and Soil* **255**: 571–586.
- Welch, R. M., Norvell, W. A., Schaefer, S.C., Shaff, J.E. and Kochian, L.V. (1993) Induction of iron (III) and copper (II) reduction in pea (*Pisum Sativum* L.) roots by Fe and Cu status: does the root-cell plasmalemma Fe(III)-chelate reductase perform a general role in regulating cation uptake. *Planta* **190**:555-561.
- Weller, D.M. (1988) Biological control of soil borne plant pathogens in the rhizosphere with bacteria. *Annual Review of Phytopathology* **26**:379-407.
- Weller, D.M. (2007) *Pseudomonas* biocontrol agents of soil borne pathogens: Looking back over 30 years. *Phytopathology* **97**:250-256.
- Whitelaw, M.A. (2000) Growth promotion of plants inoculated with phosphate solubilizing fungi. *Advances in Agronomy* **69**:99-151.
- Wu, Qiang-Sheng and Srivastava, A. K. (2012) Rhizosphere microbial communities: Isolation, characterization and value addition for substrate development. In: Srivastava A K. (ed). *Advances in Citrus Nutrition*. Springer Verlag, Netherlands. pp.169-194.
- Wu, Qiang-Sheng, Srivastava, A.K. and Ying-Ning Zou (2013) AMF-induced tolerance to drought stress in citrus. A review. *Scientia Horticulturae* **164**:77-87.
- Xiao, C.Q., Chi, R.A., Li, X.H., Xia, M. and Xia, Z.W. (2011) Biosolubilization of rock phosphate by three stress-tolerant fungal strains. *Applied Biochemistry and Biotechnology* **165**:719-727.