



Does a rhizospheric microorganism enhance K⁺ availability in agricultural soils?



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ABSTRACT

The potassium solubilizing microorganisms (KSMs) are a rhizospheric microorganism which solubilizes the insoluble potassium (K) to soluble forms of K for plant growth and yield. K-solubilization is carried out by a large number of saprophytic bacteria (*Bacillus mucilaginosus*, *Bacillus edaphicus*, *Bacillus circulans*, *Acidithiobacillus ferrooxidans*, *Paenibacillus* spp.) and fungal strains (*Aspergillus* spp. and *Aspergillus terreus*). Major amounts of K containing minerals (muscovite, orthoclase, biotite, feldspar, illite, mica) are present in the soil as a fixed form which is not directly taken up by the plant. Nowadays most of the farmers use injudicious application of chemical fertilizers for achieving maximum productivity. However, the KSMs are most important microorganisms for solubilizing of fixed form of K in soil system. The KSMs are an indigenous rhizospheric microorganism which shows effective interaction between soil and plant systems. The main mechanism of KSMs is acidolysis, chelation, exchange reactions, complexolysis and production of organic acid. According to literature, currently negligible use of potassium fertilizer as a chemical form has been recorded in agriculture for enhancing crop yield. Most of the farmers use only nitrogen and phosphorus and not use the K fertilizer due to unawareness so that the problem of K deficiency occurs in rhizospheric soils. The K fertilizer is also costly as compared to other chemical fertilizers. Therefore, the efficient KSMs should be applied for solubilization of a fixed form of K to an available form of K in the soils. This available K can be easily taken up by the plant for growth and development. Our aim of this review is to elaborate on the studies of indigenous K-solubilizing microbes to develop efficient microbial consortia for solubilization of K in soil which enhances the plant growth and yield of crops. This review highlights the future need for research on potassium (K) in agriculture.

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Contents

1. Introduction	338
1.1. Potassium in soil	339
1.2. K-solubilizing microorganism (KSMs)	339
2. Mechanisms of K-solubilization	341
3. Molecular biology and transporter of potassium solubilizing microorganisms	342
3.1. Molecular genetics of potassium uptake in bacteria	342
3.2. Molecular genetics of potassium uptake in fungi	342
4. Effect of KSMs on plant growth and yield	343
5. Future prospects	344
6. Conclusion	344
Acknowledgement	345
References	345

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1. Introduction

According to United Nations estimates, the global human population is projected to reach 8.9 billion by 2050, with developing country of the Asia and Africa to absorb the vast majority of the increase (Wood 2001). The populations of most of the developing countries in the world continue to increase at an alarming rate; the demands placed upon agriculture to supply future food will be one of the greatest challenges facing the human population. In order to meet this challenge, a great deal of effort focusing on the soil biological system and the agro-ecosystem as a whole is needed, enabling better understanding of the complex processes and interactions between soil and plant-microorganisms governing the stability of agricultural lands. Soil is a dynamic natural body on the earth's crust. There are several minerals containing essential elements in the soil, but most important minerals are nitrogen (N), phosphorus (P), and potassium (K). K is the third important plant nutrient. It plays a key role in the growth, metabolism, and development of plants. Without adequate supply of potassium, the plants will have poorly developed roots, grow slowly, produce small seeds and have lower yields (McAfee 2008; White and Karley 2010) and the increased susceptibility to diseases (Amtmann et al. 2008; Armengaud et al. 2010) and pest (Amtmann et al. 2006; Troufflard et al. 2010). Sometime K requirement increases in the plant where agricultural soils lack sufficient phyto-available K for crop production (Rengel and Damon 2008). It is generally supplied as K-fertilizers in both intensive and extensive agricultural systems (Pettigrew 2008; Dasan 2012; Phua et al. 2012; Yadegari et al. 2012; Zhang et al. 2013). Large areas of the agricultural land of the world are deficient in potassium which includes three-fourth of the paddy soils of China and two-third of the wheat belt of Southern Australia. According to Hasan (2002), potassium fertility status of Indian agricultural soils is categorized as low (21%), medium (51%) and high (28%). Thus, 72% of India's agricultural area, representing 266 districts, which needs immediate K fertilization, for healthy crop production because such imbalances of K are widespread in agricultural soils and particularly show in sandy and lateritic soils due to leaching (Rengel and Damon 2008; Mengel and Kirkby 2001). Moreover, K is also an important macronutrient for plant growth, but potassium fertilizer, as potassium chloride, has been imported in large quantities every year because Vietnam has not had any potassium enriched mineral resource to produce potassium fertilizer. The world production of potash had been increased up to 37 million tons as well as the price of potash \$470 per ton since 2011 (Infomine.com, 2013). However, K fertilizer cost has increased every year. This has led to an increase in the cost of rice production and thus farmer's income should decrease. Microorganisms play a central role in the natural P and K cycles and P or K-solubilizing bacteria in soil and in plant rhizosphere (Diep and Hieu, 2013). Balanced K fertilization and avoidance of K mining (K applied by fertilizers less than that K removed by crop harvest) will prevent farmers from falling into the poverty trap and will help them leave the vicious circle of declining soil fertility. K content of the crop residue is always much higher as compared to N and P (Krauss 2003).

Soil-plant-microbe interaction has got much important in recent decades. Many types of microorganisms are known to inhabit soil, especially rhizosphere and play an important role in plant growth and development. There are abundant microorganisms thriving in soil, especially in the rhizosphere. It is well known that a considerable number of microorganisms (bacterial and fungal) species possess a functional relationship and constitute a holistic system with plants. They are able to easily multiply in a rhizosphere to promote plant growth and yield (Vessey 2003). Farmers where not applied chemical fertilizers in manage and

balance way for crop production, because they are not aware about how much fertilizer is necessary for plant and it varies from crop to crop (Fig. 1). There is a very big gap between researchers and farmers. Most of the farmers only use urea as nitrogen some di-ammonium phosphate as phosphorous but only few of them use K-fertilizer as murate of potash for crop production. Therefore, available forms of potassium decrease in soil due to removal by the crop in higher amounts. However crop residue has more potassium content than other elements. Nowadays farmers are not adding crop residue in the soil and that is one considerable reason for the depilation of potassium in the soil system, which ultimately shows the poor crop performance. To mitigate this and to maintain fertility status of the soil, the balanced used of chemical fertilizers is needed, though it is found to be a costly affair and also environmentally undesirable (Mohammadi and Sohrabi 2012).

K-solubilizing bacteria are able to release potassium from insoluble minerals (Sugumaran and Janarthanan 2007; Basak and Biswas 2009, 2012; Kalaiselvi and Anthoniraj 2009; Parmar and Sindhu 2013; Zarjani et al. 2013; Prajapati et al. 2013; Zhang et al. 2013; Gundala et al. 2013; Archana et al. 2012, 2013; Sindhu et al. 2012) (Fig. 1). In addition, researchers have discovered that K-solubilizing bacteria can provide beneficial effects on plant growth through suppressing pathogens and improving soil nutrients and structure. For example, certain bacteria can weather silicate minerals to release potassium, silicon and aluminum, and secrete bio-active materials to enhance plant growth. These bacteria are widely used in biological K-fertilizers and biological leaching (Lian et al. 2002; Bosecker 1997) (Fig. 1).

The considerable populations of KSMs are present in rhizospheric soils which promote the plant growth (Sperberg 1958). It is generally accepted that the major mechanism of mineral K-solubilization is the action of organic acids synthesized by rhizospheric microorganism. Productions of organic acids results in acidification of the microbial cell and its surroundings environment which promote the solubilization of mineral K. Silicate bacteria were found to resolve potassium, silicon and aluminum from insoluble minerals (Aleksandrov et al. 1967). Silicate bacteria exert beneficial effects upon plant growth and yield. The KSMs can promote K-solubilization from silicate mineral is very important to enhance the fertility status of soils. Rhizospheric microorganisms contribute directly and indirectly to the physical, chemical and biological parameters of soil through their beneficial or detrimental activities. Rhizospheric bacteria helps in soil processes such as exudation of soluble compounds, storage and release of nutrients, mobilization and mineralization of nutrients, soil organic matter decomposition and solubilization of K (Rajawat et al., 2012; Parmar and Sindhu 2013; Archana et al. 2013; Zeng et al. 2012; Verma et al. 2012a,b; Abhilash et al., 2013), and phosphate solubilization, nitrogen fixation, nitrification, denitrification, and sulfur reduction (Khan et al. 2007; Diep and Hieu, 2013). Those bacteria possessing potassium solubilizing ability are called potassium solubilizing bacteria (KSB) and they can convert the insoluble or mineral structural potassium compounds into soluble forms in soil as a soil solution and make them available to the plants (Zeng et al. 2012). Imbalanced or over dose use of chemical fertilizers have the negative environmental impacts and also increasing costs of crop production, therefore, there is an urgent need to imply eco-friendly and cost effective agro-technologies to increase crop production. Therefore, the utilization of KSMs is considered to be a sound strategy in improving the productivity of agricultural lands. This new technique is also claimed to show the ability to restore the productivity of degraded, marginally productive and unproductive agricultural soils (Rajawat et al. 2012; Prajapati et al. 2012; Basak and Biswas 2012). However, utilization of KSMs are found to be limited, because lack of knowledge among farmers and practitioners (World Bank 2007).

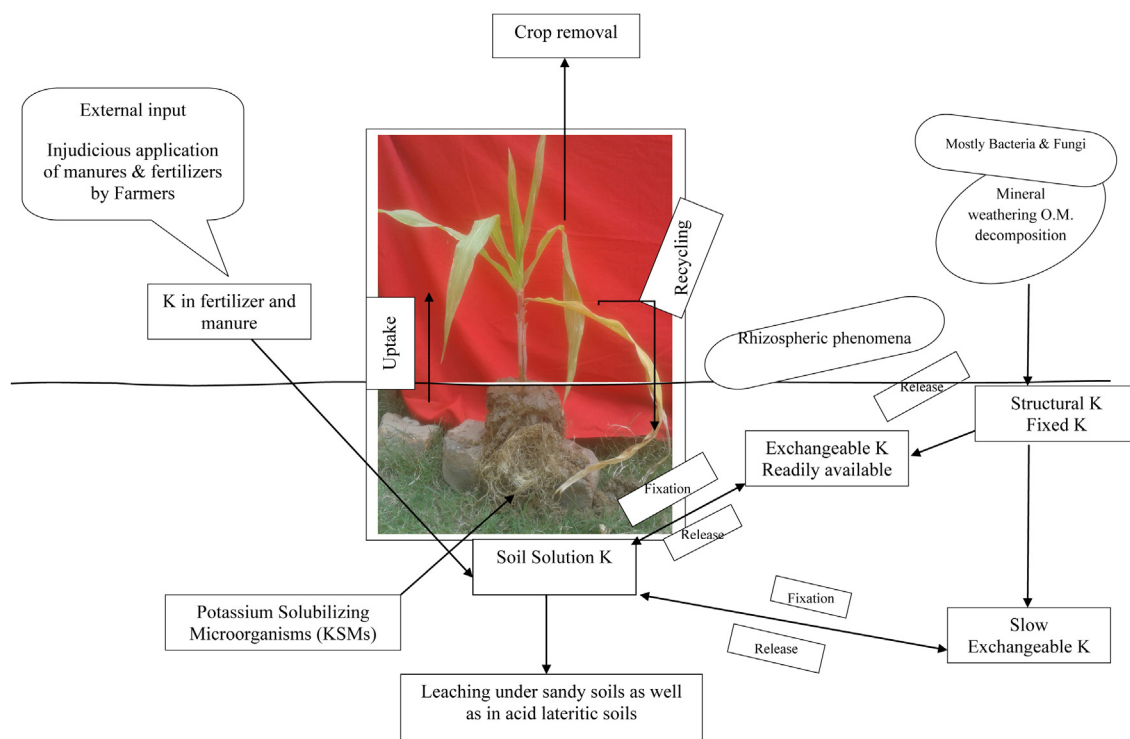


Fig. 1. Rhizospheric phenomena between Soil-Microorganism-Plant (SMP) as affected by potassium solubilizing microorganism (KSMs).

1.1. Potassium in soil

Potassium content of Indian soils has traditionally been considered as adequate, but in the recent years, the importance of K and the need for its continuous optimal availability for the better crop production has been observed as deficient due to the hidden hunger of K (Leaungvutiviroj et al. 2010; Khawilkar and Ramteke 1993). Among the major plant nutrients, potassium is one of the most abundant elements in soil. It is also one of the seven most common elements in the earth crust. On average, the surface layer (lithosphere) contains 2.6% potassium. The present conceptual understanding of soil potassium availability is the existence of four distinct K pools differing in accessibility to plant roots with reversible transfer of K between the pools (Syers 2003). The K content of Indian soils varies from less than 0.5–3.00%. The average total potassium content of those soils is 1.52% (Mengel and Kirkby 1987). However, total K is rather poorly correlated with available K and is rarely used to describe K fertility status of soil. The immediate source of K for plants is the small amount that present in the soil solution its average concentration is of the range from 1% to 2%. As this is removed, the equilibrium is distributed and K in the non-exchangeable and soil mineral fraction will be drawn upon. The availability of K to the plants depends directly on the concentration of K in soil solution and indirectly on soil (Sparks and Huang 1985; Goldstein 1994). Soil solution K plays a vital role in providing the pathway for K uptake from the soil by plant roots (Oborn et al. 2005). According to Mclean and Watson (1985), this pool is very low in K content, representing only 0.1–0.2% of the total soil K (5% of total crop demand), it is immediately available and replenished by both the exchangeable K (EK, readily plant available K) and the slowly or non-exchangeable K (SEK, slowly plant available K) pools. These two pools, EK and SEK make up about 1–2% and 1–10% of the total K respectively and are the main contributors to K uptake by plants. The exchangeable fraction i.e. the K held on negatively charged sites of clay minerals and soil organic matter is in rapid equilibrium with soil solution K and is considered to be readily available to plants (Figs. 2 and 3).

Potassium is released from the slowly or non-exchangeable K pool from the lattice wedge sites of weathered micaceous clay minerals which are selective for K ions (Mengel and Kirkby 2001). The remaining pool or major pool of K which holds the bulk 90–98% of the total soil K, is held in structure of the primary K bearing minerals soils, K occurs in the form of silicate minerals viz., muscovite, orthoclase, biotite, feldspar, illite, mica (ruby mica, mica powder, mica scrap, mica stone, mica flakes), vermiculite, smectite, etc. Total pool of soil K is extremely complex and this can be solubilized by the KSMs through production of acids and it will be available for plant (Ullman et al. 1996; Basak and Biswas 2012; Singh et al. 2010), most of the total soil K available to plants is usually located in the topsoil.

These different K pools are not only of relevance to K acquisition by plants but also to K leaching through the soil profile under sandy soils as well as in acid lateritic soils containing kaolinitic clay minerals low in cation exchange capacity, rates of K leaching can be very high so that considerable amounts of K can be lost (Wulff et al. 1998). According to Prasad (2009) in Indian condition, the EK values are inadequate for fertilizer recommendations because of the contributions of non-exchangeable and subsoil K to plant uptake.

1.2. K-solubilizing microorganism (KSMs)

A diverse group of soil micro-flora was reported to be involved in the solubilization of insoluble and fixed forms of K into available forms of K which is easily absorbed by plants (Li et al. 2006; Zarjani et al. 2013; Gundala et al. 2013). Microbial inoculants that are able to dissolve K from mineral and rocks, that enhanced plant growth and yield, and also economically viable and eco-friendly. The first evidence of microbial involvement in solubilization of rock potassium had shown by Muentz (1890). A wide range of KSMs namely *Bacillus mucilaginosus*, *Bacillus edaphicus*, *Bacillus circulans*, *Paenibacillus* spp., *Acidithiobacillus ferrooxidans*, *Pseudomonas*, *Burkholderia* (Sheng et al. 2008; Lian et al. 2002; Rajawat et al. 2012; Liu et al. 2012; Basak and Biswas 2012; Singh et al. 2010) have been reported to release potassium in accessible form from K-bearing

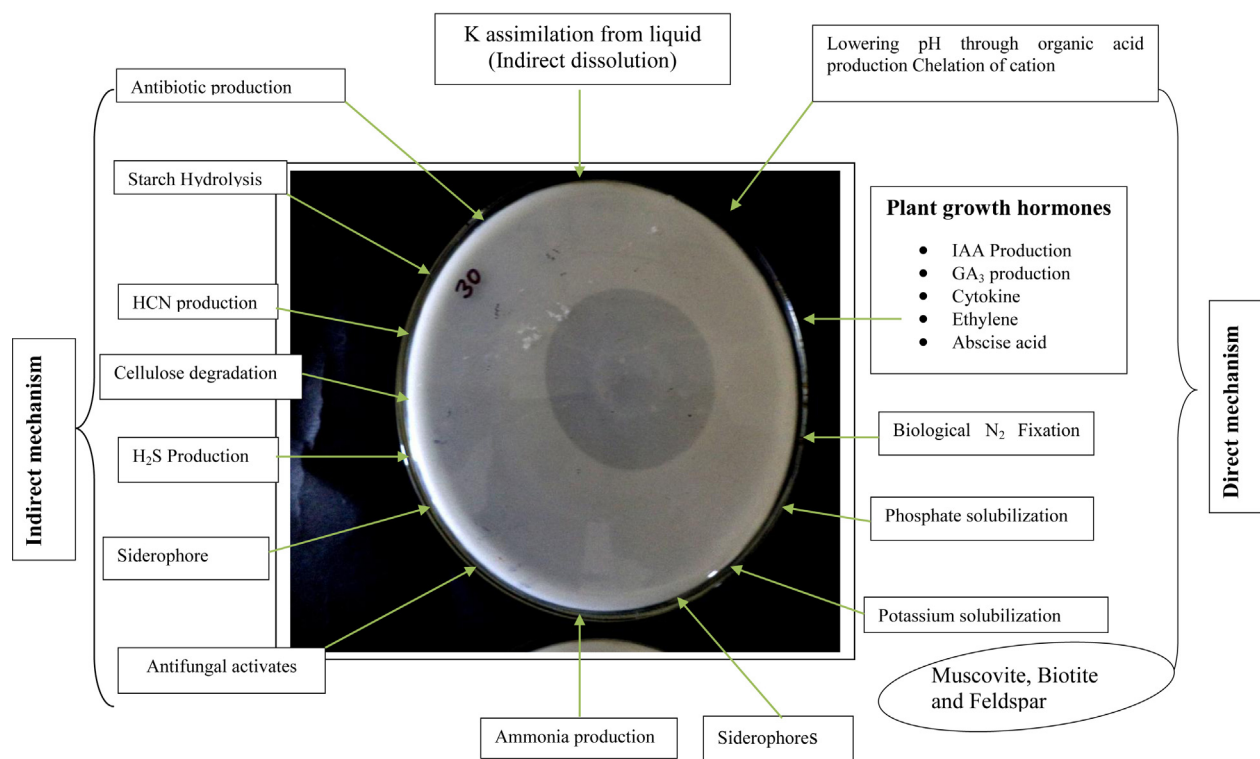


Fig. 2. Direct and indirect mechanisms of plant growth promoting properties of potassium solubilizing microorganism (KSMs) and their K-Solubilizing ability of mica (K-bearing mineral) on Aleksandrov medium.

minerals in soils. Several fungal and bacterial species, popularly called as KSMs that assist plants growth by mobilization of insoluble forms of K. The KSMs are ubiquitous whose numbers vary from soil to soil. Rhizospheric microorganisms contribute significantly in the solubilization of bound form of soil minerals in the soil (Supanjani et al. 2006; Lian et al. 2002; Sindhu et al. 2009). A variety of soil microorganisms have been found to solubilizers silicate minerals (Sheng et al. 2002). Many microorganisms like bacteria, fungi and actinomycetes were colonized even on the surface of mountain rocks (Groudev 1987; Gundala et al. 2013) have been reported that the silicate solubilizing bacteria *B. mucilaginosus* sub spp. *Siliceus* liberates K from feldspar and aluminosilicates. According to Aleksandrov et al. (1967) that were isolated from agricultural land

at different location and found that different bacterial species like silicate bacteria were found to dissolve K, silicates and aluminum from insoluble minerals, it also help in decomposition of organic matter, crop residues etc. and suggested that they play a major role in nutrients cycling in soil-plant system. *B. mucilaginosus* strain CS1 is a silicates bacterium which exhibited inhibitory activity on the growth of gram negative bacteria. It has also been reported as silicate solubilizing bacteria present in rhizosphere as well as non-rhizosphere soil (Lian et al. 2002; Liu 2001). The K-solubilizing rhizobacteria were isolated from the roots of cereal crops which grown in potassium and silicate amended soil (Mikhailouskaya and Tcherhysh 2005). Hutchens et al. (2003) reported that 27 strains of heterotrophic bacteria were isolated and grown in liquid and solid minimal media as well as mica containing media under aerobic condition.

A wide range of the rhizospheric microorganisms are reported as the K-solubilizers include *B. mucilaginosus* (Zhao et al. 2008; Basak and Biswas 2009; Raj 2004; Sugumaran and Janarthanam 2007; Zarjani et al. 2013), *B. edaphicus* (Sheng 2005), *B. circulans* (Lian et al. 2002), *Burkholderia*, *A. ferrooxidans* (Sheng and Huang 2002; Sheng and He 2006) *Arthrobacter* sp. (Zarjani et al. 2013), *Enterobacter hormaechei* (KSB-8) (Prapapati et al. 2013); *Paenibacillus mucilaginosus* (Liu et al. 2012; Hu et al. 2006), *P. frequentans*, *Cladosporium* (Argelis et al. 1993); *Aminobacter*, *Sphingomonas*, *Burkholderia* (Uroz et al. 2007); *Paenibacillus glucanolyticus* (Sangeeth et al. 2012). These microbial strains have the ability to solubilize of K from K-bearing minerals, but only a few bacteria, such as *B. mucilaginosus* and *B. edaphicus*, have high activity in mobilizing and solubilizing of K from minerals (Zhao et al. 2008; Sheng 2005; Lian et al. 2002; Li et al. 2006; Li 2003; Rajawat et al. 2012). Bacteria have wide applications in mining, metallurgy, microbial fertilizer, and feed (Zhao et al. 2008; Sheng 2005; Lian et al. 2002; Li et al. 2006; Li 2003).

Arbuscular mycorrhizal can increase the solubility of mineral form of potassium by releasing protons, H^+ or CO_2 and organic acid

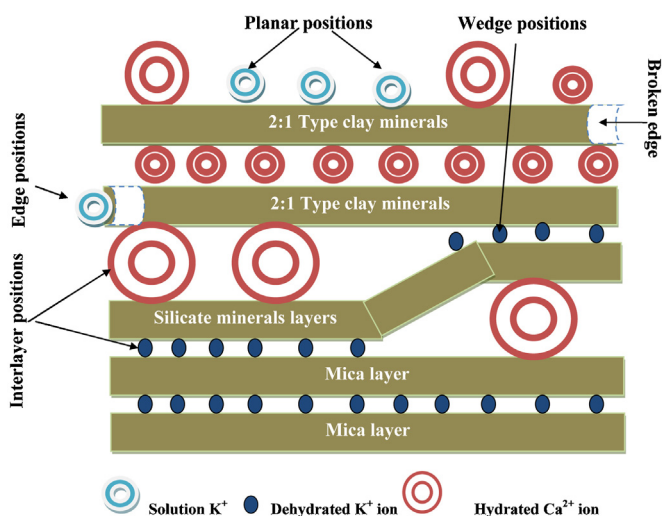


Fig. 3. Different potassium adsorption positions for K^+ in a mica-silicate minerals in soil system (this is modified figure of Rich, C.I. 1968).

anions such as citrate, malate and oxalate. This also increased the nitrogen, potassium, calcium and iron in the plant leaves and fruits (Jones et al., 2009; Veresoglou et al., 2011; Yousefi et al., 2011). The inocula of the two arbuscular mycorrhizal fungi (AMF) species, *G. mosseae* and *G. intraradices*, were applied in soil on weight basis, recorded that the increasing the potassium uptake by maize crop (Wu et al., 2005). Information on acquisition of the macronutrient cations by AM plants has been relatively inconsistent in that increases, no effects, and decreases have been reported (Clark and Zeto, 1996) in case of potassium its depend on the soil condition as well as nature of plant growth and other condition (Clark and Zeto 2000). Alves et al. (2010) reported that after 90 days, the plant height, shoot dry weight, root length, phosphorus and potassium contents, and mycorrhizal colonization were increased as compared to the control. Potassium acquisition compared to calcium and magnesium was especially enhanced in AM switch grass grown in acid soil (Clark et al., 1999). Ectomycorrhizal fungi, particularly isolates UFSC-Pt22 and UFSC-Pt186, contributed to the increase of the efficiency of alkaline breccia as a source of P and K to the plants growth of *Eucalyptus dunnii* seedlings, respectively (Alves et al., 2010).

Prajapati et al. (2012) reported that the potassium solubilizing fungi (KSF) strains such as *Aspergillus terreus* and *Aspergillus niger* were isolated from various K rich soil samples and observed. *A. terreus* and *A. niger*, which could solubilize insoluble potassium and showed the highest available potassium in liquid medium by using two various insoluble sources of potassium i.e., feldspar and potassium aluminum silicate, based on their colonies and morphology characters. *A. terreus* shows the highest solubilization as well as acid production on both of the insoluble potassium sources. The concentration of trace elements is another relevant factor in the context of rock solubilization by fungi (*A. niger*), also reported by the production of acids (Vandenbergh et al., 1999; Mirminachi et al., 2002).

Furthermore, symbiotic nitrogen fixing rhizobia and *Pseudomonas*, which fix atmospheric nitrogen into ammonia and export the fixed nitrogen to the host plants, have also shown K and P-solubilizing activity (Fig. 2). For instance, *Aspergillus* spp., *A. terreus* (Prajapati et al. 2013), *A. niger* (Lian et al. 2002; Prajapati et al. 2012), *Penicillium* sp. (Sangeeth et al. 2012) enhanced the K-solubilization by mobilizing inorganic and organic K and release of structural K from rocks and minerals.

2. Mechanisms of K-solubilization

Currently, little information is available on the K-solubilization by the rhizospheric microorganism, which has mechanisms of the K-solubilization by production of organic acid to provide potassium nutrients as well as others nutrients for enhancing of crop growth. Sheng and Huang (2002) found that K release from the minerals was affected by pH, oxygen, and the bacterial strains used. The efficiency of the K-solubilization by different microorganisms was found to vary with the nature of potassium bearing minerals and aerobic conditions (Uroz et al. 2009). The extent of potassium solubilization by *B. edaphicus* in the liquid media was greater and better growth was observed on illite than feldspar (Sheng and He 2006). Indigenous rhizospheric microorganisms have the potential to absorb and mobilize the fixed form of nutrients (potassium) from trace mineral sources. Silicate bacteria were found to dissolve potassium, silica, and aluminum from insoluble minerals. Hydrogen ion of soil or soil solution is directly related to releases of K from minerals. Sheng and Huang (2002) reported that K release from minerals was influenced by pH, dissolved oxygen, and strains used. The content of potassium solubilization was enhanced 84.8–127.9% in microbial inoculated as compared to un-inoculated treatment. The extent of potassium

solubilization was higher in illite by *B. edaphicus* in the broth culture was as compared to feldspar (Sheng and He 2006). Badr (2006) reported that the extent of potassium solubilization by silicate solubilizing bacteria were recorded 4.90 mg L⁻¹ at pH 6.5–8.0. *B. mucilaginosus* solubilized the 4.29 mg L⁻¹ K-solubilization in media supplemented with muscovite mica (Sugumaran and Janarthanam 2007). The K-releasing affected pH aerobic conditions and soil mineral properties (Lian 1998; Lian et al. 2008; Chen et al. 2008; Bin et al. 2010).

The mechanism of potassium solubilization means by which insoluble potassium and structural unavailable forms of potassium compounds are mobilized and solubilized due to the production of various type organic acids. These acids are accompanied by acidolysis, complexolysis exchange reactions and these are key processes attributed to their conversion in soluble form (Uroz et al. 2009). The organic and inorganic acids convert insoluble K (mica, muscovite, biotite feldspar) to the soluble form of K (soil solution form) with the net result increasing the availability of the nutrients to the plants. The various types of organic acid produced by KSMs differed with different organisms. Organic acids were detected in the microbial suspension (Sheng et al. 2008). KSMs have the ability to weather phlogopite via aluminum chelation and acidic dissolution of the crystal network (Leyval and Berthelin 1989; Abou-el-Seoud and Abdel-Megeed 2012).

The release of various types of organic acids were reflected by microorganisms to solubilize the insoluble K to an available form of K which is easily taken up by the plant. Researchers suggested that the plant growth promotion was related to K solubilization as well as the release of organic acids by the K-solubilizing strains. Sheng and He (2006) reported that solubilization of illite and feldspar by microorganisms is due to the production of organic acids like oxalic acid and tartaric acids, gluconic acid and 2-ketogluconic acid, oxalic acid, citric acid, malic acid, and succinic acid. Tartaric acid seems to be the most frequent agent of mineral K-solubilization (Zarjani et al. 2013; Prajapati et al. 2012; Prajapati and Modi 2012). Other organic acids, such as acetic, citric, lactic, propionic, glycolic, oxalic, malonic, succinic acid, fumaric, tartaric, etc. have also been identified among K-solubilizers (Wu et al. 2005).

The solubilization of structural K compounds by naturally-abundant KSMs are common under *in vitro* conditions (Raj 2004; Sugumaran and Janarthanam 2007; Zarjani et al. 2013; Sheng and He 2006; Prajapati et al. 2012), field and greenhouse condition (Basak and Biswas 2009, 2012; Singh et al. 2010; Prajapati et al. 2013; Parmar and Sindhu 2013). The indigenous rhizospheric microorganisms are effective in releasing K from structural K through solubilization and from exchangeable pools of total soil K by acidolysis, chelation, and solubilization by KSMs (Uroz et al. 2009). Biomass of the rhizospheric microorganism in soil also contains a significant quantity of fixed K that is potentially available to plants (Girgis 2006; Jones et al. 2003).

The mechanisms for KSMs to solubilization of K are by: (i) lowering the pH, or (ii) by enhancing chelation of the cations bound to K, and (iii) acidolysis of the surrounding area of microorganism. The lowering in pH of the medium suggests the release of organic acids and protons by the K-solubilizing microorganisms (Zarjani et al. 2013; Parmar and Sindhu 2013; Uroz et al. 2009). Such acidolysis by organic acids produced by the rhizospheric microorganisms can either directly dissolve the mineral K as a result of slow releases of exchangeable K, readily available exchangeable K or can chelate both Si and Al ions associated with K minerals (Romheld and Kirkby 2010). Thus, the synthesis and discharge of organic acids by the microorganisms into the surrounding environment acidify the microbe's cells and their surrounding environment that ultimately lead to the release of K ions from the mineral K by protonation and acidification (Goldstein 1994). Of the different organic acids involved in the solubilization of insoluble K, succinic, citric,

Table 1
Potassium solubilizing microorganisms (KSMs) produce various organic acids in different strains, which help in solubilization of insoluble potassium to soluble potassium.

Organism	Predominant acid produced	References
<i>Penicillium frequentans</i> , <i>Cladosporium</i>	Oxalic, Citric, Gluconic Acids	Argelis et al. (1993)
<i>Paenibacillus mucilaginosus</i>	Tartaric, Citric, Oxalic	Liu et al. (2012) and Hu et al. (2006)
<i>Aspergillus niger</i> , <i>Penicillium</i> sp.	Citric, Glycolic, Succinic	Sperberg (1958)
<i>B. megaterium</i> , <i>Pseudomonas</i> sp., <i>B. subtilis</i>	Lactic, Malic, Oxalic, Lactic	Taha et al. (1969)
<i>B. megaterium</i> , <i>E. freundii</i>	Citric, Gluconic	Taha et al. (1969)
<i>Arthrobacter</i> sp., <i>Bacillus</i> sp., <i>B. firmus</i>	Lactic, Citric	Bajpai and Sundara (1971)
<i>Aspergillus fumigatus</i> , <i>Aspergillus candidus</i>	Oxalic, Tartaric, Citric, Oxalic	Banik and Dey (1982)
<i>Pseudomonas aeruginosa</i>	Acetate, Citrate, Oxalate	Sheng et al. (2003) and Badar et al. (2006)
<i>B. mucilaginosus</i>	Oxalate, Citrate	Sheng and He (2006)
<i>Pseudomonas</i> spp.	Tartaric, Citric	Krishnamurthy (1989)

gluconic, α -ketogluconic and oxalic acids are the most prominent acids released by microbial strains (Table 1).

Organic acids produced by the KSMs can be detected by high performance liquid chromatography and enzymatic methods (Archana et al. 2012, 2013; Zhang et al. 2013). However, the acidification does not seem to be the only mechanism of solubilization, as the ability to reduce the pH in some cases did not correlate with the ability to solubilize mineral K (Zarjani et al. 2013; Rosa-Magri et al. 2012). Furthermore, the chelating ability of the organic acids is also important, as it has been shown that the addition of 0.05 M EDTA to the medium has the same solubilizing effect as inoculation with *Penicillium bilaii* (Kucey 1988; Sheng and He 2006; Liu et al. 2006).

3. Molecular biology and transporter of potassium solubilizing microorganisms

For maintaining turgid pressure of microbial and plant cells, potassium (K^+) is one of the important elements. Stimulation of potassium uptake is the most rapid response to an osmotic up shock in bacteria. K is the most abundant intracellular cation, which has major role in maintaining the turgor pressure of the cells and also play an important role in bacterial osmoadaptation, pH regulation, gene expression, and activation of cellular enzymes (Epstein, 2003).

3.1. Molecular genetics of potassium uptake in bacteria

In prokaryotes, K^+ uptake is essential for the homeostatic processes of turgor pressure regulation and maintenance of cytoplasmic pH (Csonka and Epstein 1996; Stumpe et al. 1996). Three different types of K transporters (Trk, Kdp, and Kup) have been involved for the uptake of K. *Escherichia coli* K-12 contains two major types of K^+ uptake systems (Trk and Kdp) and one minor K^+ uptake system (Kup) (Schleyer and Bakker 1993). The inducible Kdp system belongs to the family of P-type ATPases. It transports K^+ with high affinity (Siebers and Altendorf 1993; Silver 1996). TrkH and TrkG are two constitutive, rapid K^+ -uptake systems with a relatively low affinity for K^+ (Dosch et al. 1991). Trk is a multi-component complex widespread in bacteria and archaea and it has a moderate affinity for the K uptake. Trk consist of a trans-membrane protein named TrkH or TrkG, which is the actual K-trans-locating subunit, and a cytoplasmic membrane surface protein, TrkA, which is a NAD-binding protein required for the system's activity (Sleator and Hill, 2002). Kdp is an inducible system with high affinity and specificity for K, found in *Escherichia coli* and many other bacteria. Kdp is the only bacterial K uptake system whose expression is strongly regulated at the transcriptional level, which is mediated by the KdpD sensor kinase and the KdpE response regulator (Epstein, 2003; Domínguez-Ferreras et al., 2009). *Bacillus subtilis* has the Ktr gene which involves K uptake. KT/KUP/HAK family: The genes of this family are homologous to bacterial KUP (TrkD) potassium transporters. The KUP transporter from *E. coli* is characterized by a midrange (0.37 mM) KM for K^+ and a similar affinity for Rb^+ and

Cs^+ (Bossemeyer et al., 1989). Complementation of TK2463 cells by *AtKUP1*. The *E. coli* TK2463 mutant is defective in three K^+ uptake transporters (Trk, Kup, and Kdp) (Epstein and Kim, 1971) and was transformed with plasmids containing the *AtKUP1* gene or with an empty vector. *Vibrio alginolyticus* contained two adjacent genes, *ktrA* and *ktrB*, which encode a new type of bacterial K^+ -uptake system. KtrA and KtrB are peripheral and integral membrane proteins, respectively, and they help in potassium transportation (Nakamura et al. 1998). The production of organic acids is considered to be the principal mechanism for solubilization of mineral phosphate and potassium by a microorganism. This assumption has been corroborated by the cloning of two genes involved in gluconic acid production viz., pqq and gab Y. Gluconic acid is the principal organic acid produced by *Pseudomonas* spp., *Bacillus* spp., *Arthrobacter* spp. (Table 1). Other organic acids such as lactic, isovaleric, isobutyric, acitic, glycolic, oxalic, malonic and succinic, citric, acetic, tartaric, and succinic acids are also secreted by the phosphate solubilizing microorganisms. Chelating substances and inorganic acids such as sulphidic, nitric, and carbonic acid are considered to be like other mechanisms for potassium and phosphate solubilization. Xiufang et al. (2006) identified and characterized the potassium solubilizing bacteria by 16S rDNA gene sequence analysis using universal primers. The recombinant plasmids were developed from the cloned products and the relatedness between the strains was estimated from phylogenetic analysis (Xiufang et al., 2006). For molecular characterization, we first isolated the genomic DNA of the microbial strains, and then we amplified the conserved gene of 16S ribosomal gene by using universal primers with specific PCR protocol and chemicals. After this, amplified 16S rDNA gene has been purified and sequenced by an automatic sequencer. The conformation of the microbial strains by using BLAST (basic local alignment tool) and then submitted it to NCBI Genbank to get an accession number of particular strains. The phylogenetic tree was constructed by using online software ClustalW2 and MEGA 4.0 (Figs. 4 and 5).

3.2. Molecular genetics of potassium uptake in fungi

The high-affinity Na^+ -uptake occur in fungi and is mediated by transporters of P-type ATPases that is close to that of animal Na^+ , K^+ and H^+ , K-ATPases. These ATPases mediate high affinity K^+ uptake primarily and Na^+ uptake secondarily, when K^+ is at very low concentrations. Fungi have an absolute requirement for K^+ , but K^+ may be partially replaced by Na^+ . Na^+ uptake in *Ustilago maydis* and *Pichia sorbitophila* was found to exhibit a fast rate, low K_m , and apparent independence of the membrane potential (Benito et al. 2004). The fungal strains e.g. *U. maydis* and *P. sorbitophila* have been found three genes *Umacu1*, *Umacu2* and *PsACU1*, respectively, that could encode P-type ATPases of a novel type Na^+ and K^+ transporter. The fungal high-affinity Na^+ -uptake mediated by ACU ATPases is functionally identical to the uptake that is mediated by some plant HKT transporters. ACU ATPases possibly exist in many fungi. In the

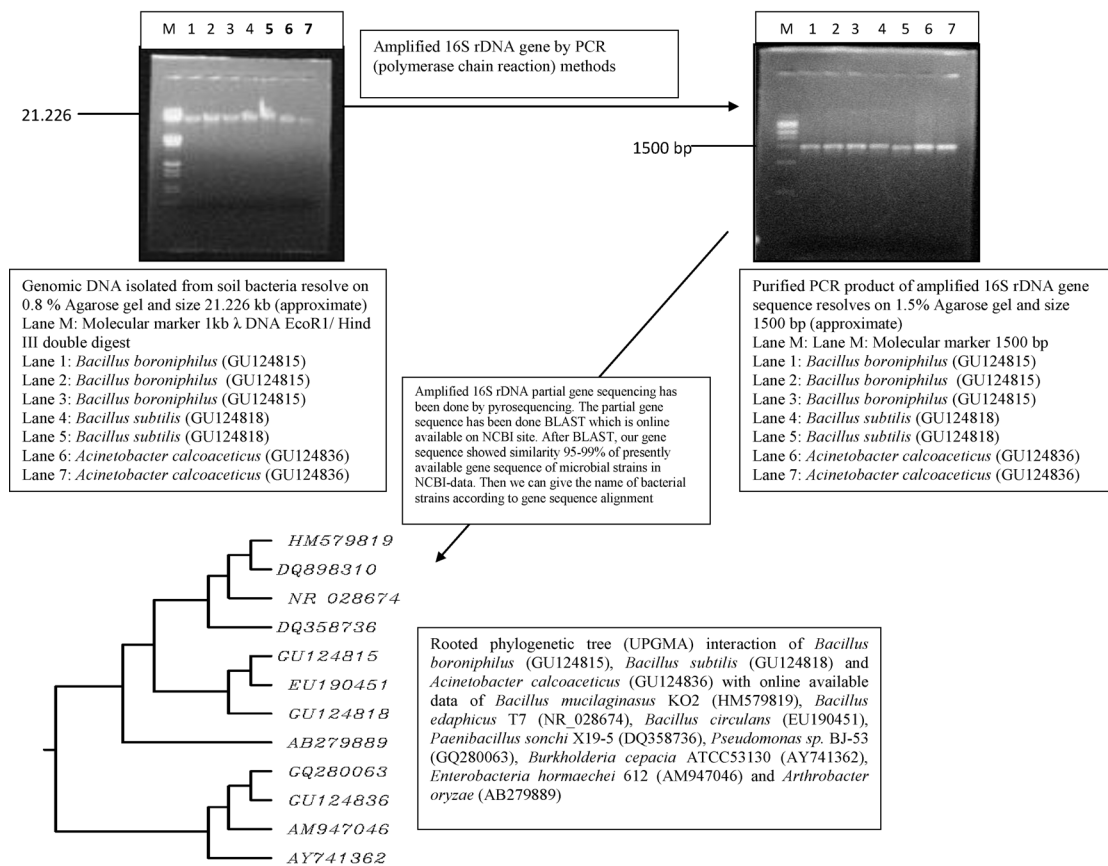


Fig. 4. Rooted phylogenetic tree (UPGMA) interaction of *Bacillus boroniphilus* (GU124815), *Bacillus subtilis* (GU124818) and *Acinetobacter calcoaceticus* (GU124836) with online available data of *Bacillus mucilaginosus* KO2 (HM579819), *Bacillus edaphicus* T7 (NR_028674), *Bacillus circulans* (EU190451), *Paenibacillus sonchi* X19-5 (DQ358736), *Pseudomonas* sp. BJ-53 (GQ280063), *Burkholderia cepacia* ATCC53130 (AY741362), *Enterobacteria hormaechei* 612 (AM947046) and *Arthrobacter oryzae* (AB279889).

genome of *Saccharomyces cerevisiae* there are no genes encoding ATPases that are similar to the ACU ATPases of *P. sorbitophila* and *U. maydis* (Catty et al. 1997), and we also found that they are absent in the genomes of *Neurospora crassa* and *Schizosaccharomyces pombe*. A phylogenetic study of the ACU ATPases along with other P-type ATPases revealed that ACU ATPases were more related to animal Na^+ , K^+ - or H^+ , K^+ -ATPases (type IIC [Axelsen and Palmgren 1998]) than to Ca^{2+} - or ENA-ATPases (types IIA, IIB, and IID). The update the models of K^+ uptake in fungi, investigated that the presence of TRK and HAK transporters and ACU ATPases in those fungal species for which the complete genomic sequences are available, i.e., *S.*

cerevisiae, *S. pombe*, *Candida albicans*, *U. maydis*, and *Magnaporthe grisea*. The models of K^+ uptake in fungi are very diverse. The only type of K^+ transporters that seems to be present in all fungi is TRK, probably because these transporters have a role in controlling the membrane potential (Banelos et al. 2000; Madrid et al. 1998). The HAK transporters or ACU ATPases may be present or not, either together or independently present in fungi. For molecular characterization of fungi, we first isolated the genomic DNA of the strains, and then amplified the conserved gene of 18S ribosomal gene of ITS region in eukaryote by using universal primers with specific PCR protocol and chemicals. After this, an amplified 18S rDNA gene was purified and sequenced by an automatic sequencer. The conformation of the microbial strains was accomplished by the use of BLAST (basic local alignment tool) and then submitted in NCBI Genbank for the accession number of particular strains. The phylogenetic tree was constructed by using online software ClustalW2 and MEGA 4.0 (Fig. 5).

4. Effect of KSMs on plant growth and yield

Inoculation of seeds and seedling treatments of plants with the KSMs generally showed significant enhancement of germination percentage, seedling vigor, plant growth, and yield and K uptake by plants under glasshouse and field conditions (Basak and Biswas 2009, 2010, 2012; Youssef et al. 2010; Singh et al. 2010; Awasthi et al. 2011; Zhang et al. 2013). The application of organo minerals with combination of siliate bacteria for enhancing plant growth and yield of maize and wheat was first reported by Aleksandrov (1985). More importantly, research investigation conducted under field level test crops such as wheat, forage crop, maize, and sudan

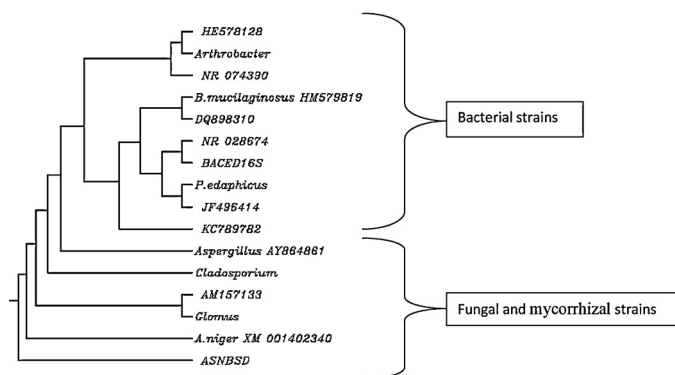


Fig. 5. Rooted phylogenetic tree (UPGMA) relation between potassium solubilizing bacteria, fungi and mycorrhizal strains. The gene sequence of microbial strains collected from the NCBI-GenBank. this phylogenetic tree shows the grouping between bacteria and fungi.

grass crops have revealed that KSMs could drastically reduce the usage of chemical or organic fertilizers (Xie 1998). As reported by previous researchers (Singh et al., 2010; Sindhu et al., 2012; Zeng et al., 2012), the enhancement of plant K nutrition might be due to the stimulation of root growth or the elongation of root hairs by specific microorganisms. Thus, no direct increase in the availability of soil solution K is expected. The KSMs have been isolated from rhizospheric soil of various plants and from K-bearing minerals such as wheat (Parmar and Sindhu 2013; Zhang et al. 2013), feldspar (Sheng et al. 2008), potato–soybean cropping sequence (Biswas 2011), Iranian soils (Zarjani et al. 2013), Ceramic industry soil (Prajapati and Modi 2012), mica core of Andhra Pradesh (Gundala et al. 2013), common bean (Kumar et al. 2012), biofertilizers (Zakaria 2009), sorghum, maize, bajra, chilli (Archana et al. 2013), cotton, tomato, soybean, groundnut and banana (Archana et al. 2012), soil of Tianmu Mountain, Zhejiang Province (China) (Hu et al. 2006), rice (Muralikannan and Anthomiraj, 1998), tea (Bakyalakshmi et al. 2012), valencia orange (Shaaban et al. 2012), black pepper (Sangeeth et al. 2012), potato (Abdel-Salam and Shams 2012), growth by improving by N-fixer, P, and K-solubilizers are another beneficial effect of microorganisms with K-solubilizing potential (Verma et al. 2009, 2010; Basak and Biswas 2012). A hydroponics study was carried out by Singh et al. (2010) to evaluate the effect of *B. mucilaginosus*, *Azotobacter chroococcum*, and *Rhizobium* spp. on their ability to mobilize K from waste mica using maize and wheat as the test crops under a phytotron growth chamber. The significant K assimilation was recorded in maize and wheat, where waste mica was the sole source of K, this was translated into higher biomass accumulation, K content and uptake by plants as well as chlorophyll and crude protein content in plant tissue. Among the rhizobacteria, *B. mucilaginosus* resulted in significantly higher mobilization of potassium than *A. chroococcum* and *Rhizobium* inoculation. According to Sheng and He (2006), investigation of K mobilization by the wild-type strain NBT of *B. edaphicus*, in a pot experiment, wheat was grown in a yellow-brown soil that had a low amount of available K. After inoculation with bacterial strains, the root growth and shoot growth of wheat were significantly increased and they had higher NPK contents of plant components as compared to those un-inoculated.

Inoculation with the KSMs have been reported to exert beneficial effects on growth of cotton and rape (Sheng 2005), pepper and cucumber (Han et al. 2006), khella (Hassan et al. 2010), sorghum (Badr 2006), wheat (Sheng and He 2006), tomato (Lin et al. 2002), chilli (Ramarethinam and Chandra 2005) and Sudan grass (Basak and Biswas 2009, 2010). Similarly, Zahra et al. (1984) reported that the effect of soil inoculation of the silicate bacteria *B. cirulans* for solubilization of K and (silicate) Si from different minerals and soil showed significant increase of organic matter and 17% yield of rice (Muralikannan and Anthomiraj, 1998). Increased wheat yield up to 1.04 t ha⁻¹ reported by Mikhailouskaya and Tcherhysh (2005) with inoculation of KSMs on several eroded soils which are comparable with yields on moderately eroded soil without bacterial inoculation and dry matter production also increased. According to Badar et al. (2006), the co-inoculation of KSMs with K and P bearing minerals on sorghum were recorded to enhanced dry matter yield (48%, 65% and 58%), P (71%, 110%, and 116%), and K (41%, 93% and 79%) uptake in three different soils, clay, sandy, and calcareous soils, respectively. Archana et al. (2008) reported that the KSMs was isolated from rock and rhizosphere soils of greengram (*Vigna radiata*) and reported that these KSMs enhanced the solubilization of K in acid leached soil as well as increased seedling growth and yield of greengram. Sugumaran and Janarthanam (2007) reported that an increase in the dry matter by 25% and oil content 35.4% groundnut crop and available P and K increased from 6.24 to 9.28 mg/kg and 86.57 to 99.60 mg/kg respectively in soil due to inoculation of *B.*

mucilaginosus as compared to the un-inoculated control. According to Archana et al. (2012) the efficient K solubilizing bacteria *Bacillus* spp. showed increase in growth and yield of maize. It indicates that the KSMs significantly increased plant growth, nutrient uptake, and yield component over absolute fertilizer control. Supanjani et al. (2006) reported that integration of P and K rocks with inoculation of P and K-solubilizing bacteria increased P availability from 12% to 21% and K availability from 13% to 15%, respectively. Soil application of KSMs plant has 16% photosynthesis and 35% higher leaf area to control. Overall results of this finding is the treatment of P and K rocks with P and K solubilizing bacterial strain were sustainable alternative of chemical fertilizer for crop production. Bagyalakshmi et al. (2012) reported that the K-solubilizing strains were isolated from rhizosphere of tea and used as biofertilizers of K in tea that have solubilizing capacity of murate of potass (MOP) was increased as comparison to mineral K sources. Supplementation of ammonium nitrate and glucose were found to be more effective in solubilization of MOP than other sources which should be considered prior to the use of these strains in tea soils as bio-inoculants.

Therefore, the K-solubilizing bacteria are extensively used as biofertilizers in Korea and China as significant areas of cultivated soils in these countries are deficiency in plant-available K is considered to be a major limiting factor to food production in many agricultural soils (Xie 1998). Thus, the application of K-solubilizing bacteria as biofertilizers for agriculture improvement can reduce the use of agrochemicals and support ecofriendly crop production (Archana et al. 2012, 2013; Kloepper et al. 1989; Requena et al. 1997; Sheng et al. 2003; Sindhu et al. 2010; Prajapati et al. 2012, 2013). Therefore, it is imperative to isolate more species of mineral-solubilizing bacteria to enrich the pool of microbial species and genes as microbial fertilizers, which will be of great benefit to the ecological development of agriculture (Liu et al. 2012).

5. Future prospects

KSMs are an integral component of soil microbial community and play an important role in the K cycle in soil rendering the unavailable K form to plants. These KSMs have enormous potential for making use of fixed K and very slowly release K under soil systems with low K availability in tropical and subtropical developing countries. The mechanism of K-solubilization by microorganisms have been studied in detail but the K solubilization is a complex phenomenon affected by many factors, such as KSMs used, nutritional status of soil, soil, mineral type, amount of mineral, size of mineral, and environmental factors. Moreover, the stability of the KSMs after inoculation in soil is also important for K solubilization to benefit crop growth and development. Therefore, further study is needed to understand the problem of development of efficient and indigenous potassium solubilizing microbial consortium for growth and yield of crops. Another big problem is the commercial propagation of potassium solubilizing consortium and their preservation and transportation at farmer's fields for crop production.

6. Conclusion

Rhizosphere microorganisms contribute significantly in solubilization of fixed forms of soil minerals K in the soil solution K. Inoculation of KSMs in soil has been shown to improve solubilization of insoluble mineral K resulting in higher crop performances. Apart from the K-solubilizing abilities, the KSMs have the ability of production of plant growth hormones, ammonia, siderophore, and solubilization of phosphorus etc. Although the KSMs are abundant

in many of the soils, presently it has not been successfully commercialized and thus its application is still found to be limited. This communication highlighted contributions of K-solubilizing microorganisms from rhizospheric soil to develop efficient indigenous microbial consortia which are required for enhancing plant growth and yield of various crops as well as improving the soil fertility. This type of microbial consortium is cost effective and environmentally friendly for enhancing the sustainable agriculture.

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References

- Abdel-Salam MA, Shams AS. Feldspar-K fertilization of potato (*Solanum tuberosum* L.) augmented by biofertilizer. *J Agric Environ Sci* 2012;12(6):694–9.
- Abhilash PC, Dubey RK, Tripathi V, Srivastava P, Verma JP, Singh HB. Remediation and management of POPs-contaminated soils in a warming climate: challenges and perspectives. *Environ Sci Pollut Res* 2013., <http://dx.doi.org/10.1007/s11356-013-1808-5>.
- Abou-el-Seoud, Abdel-Megeed A. Impact of rock materials and biofertilizations on P and K availability for maize (*Zea mays*) under calcareous soil conditions. *Saudi J Biol Sci* 2012;19:55–63.
- Aleksandrov VG. Organo-mineral fertilizers and silicate bacteria. *Dokl Akad Nauk* 1985;7:43–8.
- Aleksandrov VG, Blagodyr RN, Ilev IP. Liberation of phosphoric acid from apatite by silicate bacteria. *Microchem J* 1967;29:111–4.
- Alves L, Oliveira VL, Filho GNS. Utilization of rocks and ectomycorrhizal fungi to promote growth of eucalypt. *Braz J Microbio* 2010;41:676–84.
- Amtmann A, Hammond JP, Armengaud P, White PJ. Nutrient sensing and signaling in plants: potassium and phosphorus. *Adv Bot Res* 2006;43:209–57.
- Amtmann A, Troufflard S, Armengaud P. The effect of potassium nutrition on pest and disease resistance in plants. *Physiol Plant* 2008;133:682–91.
- Archana DS, Savalgi VP, Alagawadi AR. Effect of potassium solubilizing bacteria on growth and yield of maize. *Soil Biol Ecol* 2008;28(1–2):9–18.
- Archana DS, Nandish MS, Savalgi VP, Alagawadi AR. Screening of potassium solubilizing bacteria (KSB) for plant growth promotional activity. *Bioinfolet* 2012;9(4):627–30.
- Archana DS, Nandish MS, Savalgi VP, Alagawadi AR. Characterization of potassium solubilizing bacteria (KSB) from rhizosphere soil. *Bioinfolet* 2013;10:248–57.
- Argelis DT, Gonzala DA, Vizcaino C, Gartia MT. Biochemical mechanism of stone alteration carried out by filamentous fungi living in monuments. *Biogeochemistry* 1993;19:129–47.
- Armengaud P, Breitling R, Amtmann A. Coronatine-intensive 1 (COI1) mediates transcriptional responses of *Arabidopsis thaliana* to external potassium supply. *Mol Plant* 2010;3(2):390–405.
- Awasthi R, Tewari R, Nayyar H. Synergy between plants and P-solubilizing microbes in soils: effects on growth and physiology of crops. *Int Res J Microbiol* 2011;2:484–503.
- Axelsen KB, Palmgren MG. Evolution of substrate specificities in the P-type ATPase superfamily. *J Mol Evol* 1998;46:84–101.
- Badar MA, Shafei AM, Sharaf El-Deen SH. The dissolution of K and phosphorus bearing minerals by silicate dissolving bacteria and their effect on sorghum growth. *Res J Agric Biol Sci* 2006;2:5–11.
- Badr MA. Efficiency of K-feldspar combined with organic materials and silicate dissolving bacteria on tomato yield. *J Appl Sci Res* 2006;2:1191–8.
- Bagyalakshmi B, Ponmurugan P, Balamurugan A. Impact of different temperature, carbon and nitrogen sources on solubilization efficiency of native potassium solubilizing bacteria from tea (*Camellia sinensis*). *J Biol Res* 2012;3(2):36–42.
- Bajpai PD, Sundara R. Phosphate solubilizing bacteria, solubilization of phosphate in liquid culture by selected bacteria as affected by different pH values. *Soil Sci Plant Nutr* 1971;17:41–3.
- Banik S, Dey BK. Available phosphate content of an alluvial soil as influenced by inoculation of some isolated phosphate solubilizing microorganisms. *Plant Soil* 1982;69:353–64.
- Banuelos MA, Madrid R, Rodríguez-Navarro A. Individual functions of the HAK and TRK potassium transporters of *Schwanniomyces occidentalis*. *Mol Microbiol* 2000;37:671–9.
- Basak BB, Biswas DR. Influence of potassium solubilizing microorganism (*Bacillus mucilaginosus*) and waste mica on potassium uptake dynamics by sudan grass (*Sorghum vulgare* Pers.) grown under two Alfisols. *Plant Soil* 2009;317: 235–55.
- Basak BB, Biswas DR. Co-inoculation of potassium solubilizing and nitrogen fixing bacteria on solubilization of waste mica and their effect on growth promotion and nutrient acquisition by a forage crop. *Biol Fertil Soils* 2010;46:641–8.
- Basak BB, Biswas DR. Modification of waste mica for alternative source of potassium: evaluation of potassium release in soil from waste mica treated with potassium solubilizing bacteria (KSB). Germany: Lambert Academic Publishing; 2012, ISBN 978-3-659-29842-4.
- Benito M, Parker J, Du Q, Wu J, Xiang D, Perou CM, Marron JS. Adjustment of systematic microarray data biases. *Bioinformatics* 2004;20:105–14.
- Bin L, Bin W, Mu P, Liu C, Teng HH. Microbial release of potassium from K-bearing minerals by thermophilic fungus *Aspergillus fumigatus*. *Geochim Cosmochim Acta* 2010;72:87–98.
- Biswas DR. Nutrient recycling potential of rock phosphate and waste mica enriched compost on crop productivity and changes in soil fertility under potato–soybean cropping sequence in an Inceptisol of Indo-Gangetic Plains of India. *Nutr Cycl Agroecosyst* 2011;89:15–30.
- Bosecker K. Bioleaching: metal solubilization by microorganisms. *FEMS Microbiol Rev* 1997;20:591–604.
- Bossemeyer D, Schlosser A, Bakker EP. Specific cesium transport via the *Escherichia coli* kup (Trkd) K⁺ uptake system. *J Bacteriol* 1989;171:2219–21.
- Catty P, Kerchove AD, d'Exaerde, Goffeau A. The complete inventory of the yeast *Saccharomyces cerevisiae* P-type transport ATPases. *FEBS Lett* 1997;409: 325–32.
- Chen S, Lian B, Liu CQ. *Bacillus mucilaginosus* on weathering of phosphorite and primary analysis of bacterial proteins during weathering. *Chin J Geochem* 2008;27(2):209–16.
- Clark RB, Zeto SK. Growth and root colonization of mycorrhizal maize grown on acid and alkaline soil. *Soil Biol Biochem* 1996;28:1505–11.
- Clark RB, Zeto SK. Mineral acquisition by arbuscular mycorrhizal plants. *J Plant Nutr* 2000;23:867–902.
- Clark RB, Zobel RW, Zeto SK. Effects of mycorrhizal fungus isolate on mineral acquisition by *Panicum virgatum* in acidic soil. *Mycorrhiza* 1999;9:167–76.
- Csonka LN, Epstein W. Osmoregulation. In: Neidhardt FC, Curtiss R III, Ingraham JL, Lin ECC, Low KB, Magasanik B, Reznikoff WS, Riley M, Schaechter M, Umberger HE, editors. *Escherichia coli* and *Salmonella*. 2nd edn Washington, DC: ASM Press; 1996. p. 1210–23.
- Dasan AS. Compatibility of agrochemicals on the growth of phosphorous mobilizing bacteria *Bacillus megaterium* var. phosphaticum potassium mobilizing bacteria *Frateriura aurantia*. *Appl Res Dev Inst J* 2012;6(13):118–34.
- Diep CN, Hieu TN. Phosphate and potassium solubilizing bacteria from weathered materials of denatured rock mountain, Ha Tien, Kiên Giang province Vietnam. *Am J Life Sci* 2013;1(3):88–92.
- Dominguez-Ferreras A, Munoz S, Olivares J, Soto MJ, Sanjuan J. Role of potassium uptake systems in *Sinorhizobium meliloti* osmoadaptation and symbiotic performance. *J Bacteriol* 2009;213:43–43.
- Dosch DC, Helmer GL, Sutton SH, Salvacion FF, Epstein W. Genetic analysis of potassium transports loci in *Escherichia coli*: evidence for three constitutive systems mediating uptake of potassium. *J Bacteriol* 1991;173:687–96.
- Epstein W. The roles and regulation of potassium in bacteria. *Prog Nucleic Acid Res Mol Biol* 2003;75:293–320.
- Epstein W, Kim BS. Potassium transport loci in *Escherichia coli* K-12. *J Bacteriol* 1971;108:639–44.
- Girgis MGZ. Response of wheat to inoculation with phosphate and potassium mobilizers and organic amendment. *Ann Agric Sci Ain Shams Univ Cairo* 2006;51(1):85–100.
- Goldstein AH. Involvement of the quinoprotein glucose dehydrogenase in the solubilization of exogenous mineral phosphates by gram-negative bacteria. In: Torriani-Gorni A, Yagil E, Silver S, editors. *Phosphate in microorganisms: cellular and molecular biology*. Washington: ASM Press; 1994, ISBN 1555810802 p. 197–203.
- Groudev SN. Use of heterotrophic microorganisms in mineral biotechnology. *Acta Biotechnol* 1987;7:299–306.
- Gundala PB, Chinthala P, Sreenivasulu B. A new facultative alkaliphilic, potassium solubilizing, *Bacillus* Sp. SVUNM9 isolated from mica cores of Nellore District, Andhra Pradesh, India. Research and Reviews. *J Microbiol Biotechnol* 2013;2(1):1–7.
- Han HS, Lee KD. Phosphate and potassium solubilizing bacteria effect on mineral uptake, soil availability and growth of eggplant. *Res J Agric Biol Sci* 2005;1(2):176–80.
- Han HS, Supanjani, Lee KD. Effect of co-inoculation with phosphate and potassium solubilizing bacteria on mineral uptake and growth of pepper and cucumber. *Plant Soil Environ* 2006;52:130–6.
- Hasan R. Potassium status of soils in India. *Better Crops Int* 2002;16:3–5.
- Hassan EA, Hassan EA, Hamad EH. Microbial solubilization of phosphate–potassium rocks and their effect on khella (*Ammi visnaga*) growth. *Ann Agric Sci* 2010;55(1):37–53.
- Hu X, Chen J, Guo J. Two phosphate- and potassium-solubilizing bacteria isolated from Tianmu Mountain, Zhejiang, China. *World J Microbiol Biotechnol* 2006;22:983–90.
- Hutchens E, Valsami-Jones E, McElDowney S, Gaze W, McLean J. The role of heterotrophic bacteria in feldspar dissolution – an experimental approach. *Mineral Mag* 2003;67(6):1157–70.
- Jones DL, Dennis PG, Owen AG, Van-Hees PAW. Organic acid behavior in soils misconceptions and knowledge gaps. *Plant Soil* 2003;248:31–41.
- Jones DL, Nguyen C, Finlay RD. Carbon flow in the rhizosphere: carbon trading at the soil-root interface. *Plant Soil* 2009;321:5–33.

- Kalaiselvi P, Anthoniraj S. In vitro solubilization of silica and potassium from silicate minerals by silicate solubilizing bacteria. *J Ecobiol* 2009;24(2):159–68.
- Khan MS, Zaidi A, Wani PA. Role of phosphate-solubilizing microorganisms in sustainable agriculture – a review. *Agron Sustain Dev* 2007;27:29–43.
- Khawilkar SA, Ramteke JR. Response of applied K in cereals in Maharashtra. *Agriculture* 1993;84–96.
- Kloepper JW, Lifshitz R, Zablutowicz RM. Free-living bacterial inocula for enhancing crop productivity. *Trends Biotechnol* 1989;7:39–43.
- Krauss A. The International Potash Institute in retrospect and prospect. In: Johnston AE, editor. Proceedings of the IPI Golden Jubilee Congress 1952–2002, 8–10 October 2002, volume 1: Invited papers “Feed the soil to feed the people. The role of potash in sustainable agriculture”. Basel Switzerland: International Potash Institute; 2003. p. 11–22.
- Krishnamurthy HA. Effect of pesticides on phosphate solubilizing microorganisms. M.Sc. (Agri.) thesis. Dharwad: University of Agricultural Sciences; 1989.
- Kucey RMN. Effect of *Penicillium biloji* on the solubility and uptake of P and micronutrients from soil by wheat. *Can J Soil* 1988;68:261–7.
- Kumar P, Dubey RC, Maheshwari DK. *Bacillus* strains isolated from rhizosphere showed plant growth promoting and antagonistic activity against phytopathogens. *Microbiol Res* 2012;67:493–9.
- Leaungvutiviroj C, Ruangphisarn P, Hansanimitkul P, Shinkawa H, Sasaki K. Development of a new biofertilizer with a high capacity for N₂ fixation, phosphate and potassium solubilization and auxin production. *Biosci Biotechnol Biochem* 2010;74(5):1098–101.
- Leyval C, Berthelin J. Interaction between *Laccaria laccata*, *Agrobacterium radiobacter* and beech roots: influence on P, K, Mg and Fe mobilization from minerals and plant growth. *Plant Soil* 1989;117:103–10.
- Li DX. Study on the effects of silicate bacteria on the growth and fruit quality of apples. *J Fruit Sci* 2003;20:64–6.
- Li FC, Li S, Yang YZ, Cheng LJ. Advances in the study of weathering products of primary silicate minerals, exemplified by mica and feldspar. *Acta Petrol Mineral* 2006;25:440–8.
- Lian BA. A study on how silicate bacteria GY92 dissolves potassium from illite. *Acta Mineral Sinica* 1998;18(2):234–8.
- Lian B, Fu PQ, Mo DM, Liu CQ. A comprehensive review of the mechanism of potassium release by silicate bacteria. *Acta Mineral Sinica* 2002;22:179.
- Lian B, Wang B, Pan M, Liu C, Teng HH. Microbial release of potassium from K-bearing minerals by thermophilic fungus *Aspergillus fumigatus*. *Geochim Cosmochim Acta* 2008;72(1):87–98.
- Liu GY. Screening of silicate bacteria with potassium releasing and antagonistic activity. *Chin J Appl Environ Biol* 2001;7:66–8.
- Liu W, Xu X, Wu S, Yang Q, Luo Y, Christie P. Decomposition of silicate minerals by *Bacillus mucilaginosus* in liquid culture. *Environ Geochem Health* 2006;28:133–40.
- Liu D, Lian B, Dong H. Isolation of *Paenibacillus* sp. and assessment of its potential for enhancing mineral weathering. *Geomicrobiol J* 2012;29(5):413–21.
- Madrid R, Gomez MJ, Ramos J, Rodríguez-Navarro A. Ectopic potassium uptake in *trk1 trk2* mutants of *Saccharomyces cerevisiae* correlates with a highly hyperpolarized membrane potential. *J Biol Chem* 1998;273:14838–44.
- McAfee J. Potassium, a key nutrient for plant growth. Department of Soil and Crop Sciences; 2008. <http://jimmcafee.tamu.edu/files/potassium>
- Mclean EO, Watson ME. Soil measurement of plant-available potassium. In: Mundson RDE, editor. Potassium in agriculture. Madison, WI: ASA CSSA and SSSA; 1985. p. 277–8.
- Mengel K, Kirkby EA. Principles of plant nutrition. 4th ed. Bern: International Potash Institute; 1987.
- Mengel K, Kirkby EA. Principles of plant nutrition. 5th ed. Dordrecht: Kluwer Acad. Publishers; 2001. p. 849.
- Mikhailouskaya N, Tcherhys A. K-mobilizing bacteria and their effect on wheat yield. *Latvian J Agron* 2005;8:154–7.
- Mirmirachi F, Zhang A, Roehr M. Citric acid fermentation and heavy metal ions. *Acta Biotechnol* 2002;22:363–73.
- Mohammadi K, Sohrabi Y. Bacterial biofertilizers for sustainable crop production: a review. *ARPN J Agric Biol Sci* 2012;7:307–16.
- Muentz A. Surla decomposition des roches et la formation de la terre arable. *C R Acad Sci* 1890;110:1370–2.
- Muralikannan N, Anthoniraj S. Occurrence of silicate solubilizing bacteria in rice ecosystem. *Madras Agric J* 1998;85:47–50.
- Nakamura T, Yuda R, Unemoto T, Bakker EP. KtrAB, a new type of bacterial K⁺-uptake system from *Vibrio alginolyticus*. *J Bacteriol* 1998;180(13):3491–4.
- Oborn I, Andrist-Rangel Y, Askegaard M, Grant CA, Watson CA, Edwards AC. Critical aspects of potassium management in agricultural systems. *Soil Use Manage* 2005;21:102–12.
- Parmar P, Sindhu SS. Potassium solubilization by rhizosphere bacteria: influence of nutritional and environmental conditions. *J Microbiol Res* 2013;3(1):25–31.
- Pettigrew WT. Potassium influences on yield and quality production for maize, wheat, soybean and cotton. *Physiol Plant* 2008;133:670–81.
- Phua CKH, Abdul Wahid AN, Abdul Rahim K. Development of multifunctional biofertilizer formulation from indigenous microorganisms and evaluation of their N₂-fixing capabilities on Chinese cabbage using 15 N tracer technique. *Pak J Trop Agric Sci* 2012;35(3):673–9.
- Prajapati KB, Modi HA. Isolation and characterization of potassium solubilizing bacteria from ceramic industry soil. *CIBTech J Microbiol* 2012;1:8–14.
- Prajapati K, Sharma MC, Modi HA. Isolation of two potassium solubilizing fungi from ceramic industry soils. *Life Sci Leaflets* 2012;5:71–5.
- Prajapati K, Sharma MC, Modi HA. Growth promoting effect of potassium solubilizing microorganisms on *Abelmoschus esculantus*. *Int J Agric Sci* 2013;3(1):181–8.
- Prasad R. Potassium fertilization recommendations for crops need rethinking. *Indian J Fert* 2009;5:31–3.
- Raj SA. Solubilization of silicate and concurrent release of phosphorus and potassium in rice ecosystem. In: Book chapter – Conference Paper Biofertilizers Technology; 2004. p. 372–8, Coimbatore, India.
- Rajawat MVS, Singh S, Saxena AK. Isolation and characterization of K-solubilizing bacteria isolated from different rhizospheric soil. In: Proceeding of 53rd Annual Conference of Association of Microbiologists of India; 2012. p. 124.
- Ramarethnam S, Chandra K. Studies on the effect of potash solubilizing/mobilizing bacteria *Frateruria aurantia* on brinjal growth and yield. *Pestol* 2005;11:35–9.
- Rengel Z, Damon PM. Crops and genotypes differ in efficiency of potassium uptake and use. *Physiol Plant* 2008;133:624–36.
- Requena BN, Jimenez I, Toro M, Barea JM. Interactions between plant growth promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi and *Rhizobium* spp. in the rhizosphere of *Anthyllus cytisioides*, a model legume for revegetation in Mediterranean semi-arid ecosystem. *New Phytologist* 1997;136:667–77.
- Rich CI. Mineralogy of soil potassium. In: Kilmer VJ, et al., editors. The role of potassium in agriculture. Madison, WI: ASA, CSSA, SSSA; 1968. p. 79–108.
- Romheld V, Kirkby EA. Research on potassium in agriculture: needs and prospects. *Plant Soil* 2010;335:155–80.
- Rosa-Magri MM, Avansini SH, Lopes-Assad ML, Tauk-Tornisiello SM, Ceccato-Antonini SR. Release of potassium from rock powder by the yeast *Torulaspora glabiosa*. *Braz Arch Biol Technol* 2012;55:577–82.
- Sangeetha KP, Bhai RS, Srinivasan V. *Paenibacillus glucanolyticus*, a promising potassium solubilizing bacterium isolated from black pepper (*Piper nigrum* L.) rhizosphere. *J Spic Aromat Crops* 2012;21(2):118–24.
- Schleyer M, Bakker EP. Nucleotide sequence and 39-end deletion studies indicate that the K⁺-uptake protein Kup from *Escherichia coli* is composed of a hydrophobic core linked to a large and partially essential hydrophilic C terminus. *J Bacteriol* 1993;175:6925–31.
- Shaaban EA, El-Shamma IMS, El-Shazly S, El-Gazzar A, Abdel-Hak RE. Efficiency of rock-feldspar combined with silicate dissolving bacteria on yield and fruit quality of Valencia orange fruits in reclaimed soils. *J Appl Sci Res* 2012;8:4504–10.
- Sheng XF. Growth promotion and increased potassium uptake of cotton and rape by a potassium releasing strain of *Bacillus edaphicus*. *Soil Biol Biochem* 2005;37:1918–22.
- Sheng XF, He LY. Solubilization of potassium-bearing minerals by a wild type strain of *Bacillus edaphicus* and its mutants and increased potassium uptake by wheat. *Can J Microbiol* 2006;52:66–72.
- Sheng XF, Huang WY. Mechanism of potassium release from feldspar affected by the strain NBT of silicate bacterium. *Acta Pedologica Sinica* 2002;39(6):863–71.
- Sheng XF, He LY, Huang WY. The conditions of releasing potassium by a silicate-dissolving bacterial strain NBT. *Agric Sci China* 2002;1:662–6.
- Sheng XF, Xia JJ, Chen J. Mutagenesis of the *Bacillus edaphicus* strain NBT and its effect on growth of chili and cotton. *Agric Sci China* 2003;2:40–1.
- Sheng XF, Zhao F, He H, Qiu G, Chen L. Isolation, characterization of silicate mineral solubilizing *Bacillus globisporus* Q12 from the surface of weathered feldspar. *Can J Microbiol* 2008;54:1064–8.
- Siebers A, Altendorf K. K⁺-translocating Kdp-ATPases and other bacterial P-type ATPases. In: Bakker EP, editor. Alkali cation transport systems in prokaryotes. Boca Raton, FL: CRC Press; 1993. p. 225–52.
- Silver S. Transport of inorganic cations. In: Neidhardt FC, Curtiss R III, Ingraham JL, Lin ECC, Low KB, Magasanik B, Reznikoff WS, Riley M, Schaechter M, Umberger HE, editors. *Escherichia coli* and *Salmonella*. 2nd ed. Washington, DC: ASM Press; 1996. p. 1091–102.
- Sindhu SS, Verma MK, Suman M. Molecular genetics of phosphate solubilization in rhizosphere bacteria and its role in plant growth promotion. In: Khan MS, Zaidi A, editors. Phosphate solubilizing microbes and crop productivity. USA: Nova Science Publishers; 2009. p. 199–228.
- Sindhu SS, Dua S, Verma MK, Khandelwal A. Growth promotion of legumes by inoculation of rhizosphere bacteria. In: Khan MS, Zaidi A, Musarrat J, editors. Microbes for legume improvement. New York, Germany: Springer-Wien; 2010. p. 95–235.
- Sindhu SS, Parmar P, Phour M. Nutrient cycling: potassium solubilization by microorganisms and improvement of crop growth. In: Parmar N, Singh A, editors. Geomicrobiology and biogeochemistry: soil biology. New York, Germany: Springer-Wien; 2012.
- Singh G, Biswas DR, Marwah TS. Mobilization of potassium from waste mica by plant growth promoting rhizobacteria and its assimilation by maize (*Zea mays*) and wheat (*Triticum aestivum* L.). *J Plant Nutr* 2010;33:1236–51.
- Sleator RD, Hill C. Bacterial osmoadaptation: the role of osmolytes in bacterial stress and virulence. *FEMS Microbiol Rev* 2002;26:49–71.
- Sparks DL, Huang PM. Physical chemistry of soil potassium. In: Munson RD, et al., editors. Potassium in agriculture. Madison, WI: ASA; 1985. p. 201–76.
- Sperberg JJ. The incidence of apatite-solubilizing organisms in the rhizosphere and soil. *Aust J Agric Res Econ* 1958;9:778.
- Stumpe SA, Schlosser M, Schleyer, Bakker EP. K⁺ circulation across the prokaryotic cell membrane: K⁺-uptake systems. In: Konings WN, Kaback HR, Lolkema JS, editors. Handbook of biological physics, vol. 2. Amsterdam, The Netherlands: Elsevier Science B.V.; 1996. p. 474–99.
- Sugumaran P, Janarthanam B. Solubilization of potassium containing minerals by bacteria and their effect on plant growth. *World J Agric Sci* 2007;3:350–5.
- Supanjani, Han HS, Jung SJ, Lee KD. Rock phosphate potassium and rock solubilizing bacteria as alternative sustainable fertilizers. *Agro Sust Dev* 2006;26:233–40.

- Syers JK. Potassium in soils: current concepts. In: Johnston AE, editor. Proceedings of the IPI Golden Jubilee Congress 1952–2002 held at Basel Switzerland 8–10 October 2002. Feed the soil to feed the people. The role of potash in sustainable agriculture. Basel: International Potash Institute; 2003. p. 301–10.
- Taha SM, Mahmood SAZ, Halim El-Damaty A, Hafez AM. Activity of phosphate dissolving bacteria in Egyptian soils. *Plant Soil* 1969;31:149–60.
- Troufflard S, Mullen W, Larson TR, Graham IA, Crozier A, Amtmann A, Armengaud P. Potassium deficiency induced the biosynthesis of oxylipins and glucosinolates in *Arabidopsis thaliana*. *Plant Biol* 2010;10(1):172.
- Ullman WJ, Kirchman DL, Welch SA, Vandevivere P. Laboratory evidence for microbially mediated silicate mineral dissolution in nature. *Chem Geol* 1996;132:11–7.
- Uroz S, Calvaruso C, Turpault MP, Pierrat JC, Mustin C, Frey-Klett P. Effect of the mycorrhizosphere on the genotypic and metabolic diversity of the bacterial communities involved in mineral weathering in a forest soil. *Appl Environ Microbiol* 2007;73:3019–27.
- Uroz S, Calvaruso C, Turpault M-P, Frey-Klett P. Mineral weathering by bacteria: ecology, actors and mechanisms. *Trends Microbiol* 2009;17:378–87.
- Verma JP, Yadav J, Tiwari KN. Effect of *Mesorhizobium* and plant growth promoting rhizobacteria on nodulation and yields of chickpea. *Biol Forum – An Int J* 2009;1(2):11–4.
- Vandenbergh LPS, Soccol CR, Pandey A, Lebeault JM. Microbial production of citric acid *Braz Arch Biol Technol* 1999;42:263–76.
- Veresoglou SD, Mamolos AP, Thornton B, Voulgari OK, Sen R, Veresoglou S. Medium-term fertilization of grassland plant communities masks plant species-linked effects on soil microbial community structure *Plant Soil* 2011;344:187–96.
- Verma JP, Yadav J, Tiwari KN, Lavakush, Singh V. Impact of plant growth promoting rhizobacteria on crop production. *Int J Agric Res* 2010;5:954–83.
- Verma JP, Yadav J, Tiwari KN. Enhancement of nodulation and yield of chickpea by co-inoculation of indigenous *Mesorhizobium* spp. and plant growth-promoting rhizobacteria in eastern Uttar Pradesh. *Commun Soil Sci Plant Anal* 2012a;43:605–21.
- Verma JP, Yadav J, Tiwari KN, Kumar A. Effect of indigenous *Mesorhizobium* spp. and plant growth promoting rhizobacteria on yields and nutrients uptake of chickpea (*Cicer arietinum* L.) under sustainable agriculture. *Ecol Eng* 2012b;51:282–6.
- Vessey KJ. Plant growth promotion rhizobacteria as biofertilizer. *Plant Soil* 2003;25:557–86.
- White PJ, Karley AJ. Potassium. In: Hell R, Mendel RR, editors. Cell biology of metals and nutrients, plant cell monographs, vol. 17. Berlin: Springer; 2010. p. 199–224.
- Wood N. Nodulation by numbers: the role of ethylene in symbiotic nitrogen fixation. *Trends Plant Sci* 2001;6:501–2.
- World Bank. World development report 2008: agriculture for development. Washington, DC: The World Bank; 2007.
- Wu SC, Cao ZH, Li ZG, Cheung KC, Wong MH. Effects of biofertilizer containing N-fixers, P and K solubilizers and AM fungi on maize growth: a greenhouse trial. *Geoderma* 2005;125:155–66.
- Wulff F, Schulz V, Jungk A, Claassen N. Potassium fertilization on sandy soils in relation to soil test, crop yield and K-leaching. *Z Pflanzenernaehr Bodenkd* 1998;161:591–9.
- Xie JC. Present situation and prospects for the world's fertilizer use. *Plant Nutri Fertil Sci* 1998;4:321–30.
- Xiufang H, Jishuang C, Guo J. Two phosphate and potassium solubilizing bacteria isolated from Tianmu Mountain, Zhejiang. *China World J Microbio Biotech* 2006;22:983–90.
- Yadegari M, Farahani GHN, Mosadeghzad Z. Biofertilizers effects on quantitative and qualitative yield of Thyme (*Thymus vulgaris*). *Afr J Agric Res* 2012;7(34):4716–23.
- Youssef GH, Seddik WMA, Osman MA. Efficiency of natural minerals in presence of different nitrogen forms and potassium dissolving bacteria on peanut and sesame yields. *J Am Sci* 2010;6(11):647–60.
- Yousefi AA, Khavazi K, Moezi AA, Rejali F, Nadian NH. Phosphate solubilizing bacteria and arbuscular mycorrhizal fungi impacts on inorganic phosphorus fractions and wheat growth *World Appl Sci J* 2011;15(9):1310–8.
- Zahra MK, Monib MS, Abdel-Al, Heggo A. Significance of soil inoculation with silicate bacteria. *Zentralblatt fur Mikrobiologi* 1984;139:349–57.
- Zakaria AAB. Growth optimization of potassium solubilizing bacteria isolated from biofertilizer. Malaysia Pahang: Bachelor of Chem. Eng. (Biotech.), Fac. of Chem., Natural Resources Eng. Univ; 2009. p. 40.
- Zarjani JK, Aliasgharzad N, Oustan S, Emadi M, Ahmadi A. Isolation and characterization of potassium solubilizing bacteria in some Iranian soils. *Arch Agro Soil Sci* 2013;77:7569, <http://dx.doi.org/10.1080/03650340.2012>.
- Zeng X, Liu X, Tang J, Hu S, Jiang P, Li W, et al. Characterization and potassium-solubilizing ability of *Bacillus circulans* Z1-3. *Adv Sci Lett* 2012;10:173–6.
- Zhang A, Zhao G, Gao T, Wang W, Li J, Zhang S, et al. Solubilization of insoluble potassium and phosphate by *Paenibacillus kribensis* CX-7: a soil microorganism with biological control potential. *Afr J Microbiol Res* 2013;7(1):41–7.
- Zhao F, Sheng X, Huang Z, He L. Isolation of mineral potassium-solubilizing bacterial strains from agricultural soils in Shandong Province. *Biodiv Sci* 2008;16:593–600.