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Review

Perspectives of potassium solubilizing microbes in sustainable food production system: A review

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ABSTRACT

Potassium is a major essential plant nutrient that plays a pivotal role in plant physiological and metabolic processes, and provides resistance against biotic and abiotic stresses. In order to feed an ever increasing world population, cultivation of high yielding varieties in an intensive production system during the last few decades caused depletion soil fertility status, especially potassium (K). As 90–98% K reserves in soil system are non-exchangeable mineral sources, efficient rhizospheric microbes (ERMs) are needed to effectively dissolve this mineral and make it available to plants. A diverse group of ERMs such as rhizobacteria (*Bacillus edaphicus*, *B. mucilaginosus*, *Acidothiobacillus ferrooxidans*, *B. circulans*, *Paenibacillus* sp.), fungal strains (*Aspergillus terreus* and *Aspergillus* sp.) and nitrogen fixing rhizobacteria (NFR) is involved in K mineral (orthoclase, muscovite, feldspar, biotite, mica, illite) solubilization. Mechanisms utilized by microbes for K dissolution are organic acid production, lowering soil pH, acidolysis, chelation, exchange reactions and complexation. These ERMs also contribute to other beneficial effects such as production of growth hormones, nitrogen (N) fixation, phosphorus (P) dissolution, enlargement of root system and antibiotic production. More specifically, potassium solubilizing microbes (KSMs) are being commercialized in the form of biofertilizer and inoculum to alleviate constraints of chemical fertilizers. This is an ecofriendly approach towards sustainable food production systems in many countries of the world. This report updates our current knowledge and potential for developing microbial based products.

1. Introduction

As a dynamic natural system, soil contains several mineral elements. Among soil elements, K is the third essential macronutrient, which is most abundantly absorbed by plants as cation (Sedaghathoor et al., 2009; Zia-ul-hassan and Arshad, 2010). This element plays a vital role in several physiological and metabolic processes in the plant (Zhao et al., 2001) including photosynthesis (Wang et al., 2012), plant growth, metabolism, rate of assimilation, accumulation of sugars (Khuhro et al., 2014) and overall plant growth and development (Sparks and Huang, 1985). An appropriate amount of K is required by plants (Mengel et al., 2001; White, 2003) to facilitate adequate root growth (Zia-ul-hassan and Arshad, 2010), proper seed development, higher yield (McAfee, 2008; White and Karley, 2010) and quality of fiber (Akhtar et al., 2003). Next to its role in water use efficiency (WUE), K is also involved with metabolism of carbohydrates, organic acids, fats, nitrogenous compounds, protein synthesis, photosynthesis, improving resistance to drought and cold tolerance and WUE (Rehm and Schmitt, 2002). Regulation of stomata, and thereby transpiration and water uptake, is directly linked with plant growth and development (Rajawat et al., 2016). Potassium mediated resistance against biotic stresses such as those caused by microbes (Amtmann et al., 2008; Armengaud et al., 2010) and insect pests are also well documented in the literature (Amtmann et al., 2006; Troufflard et al., 2010).

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Although K is one of the most important macronutrients and the eighth most abundant element on earth comprising about 2.1% of the earth's crust, plant uptake of K is limited due to lesser availability in the soluble form (Bhattacharya et al., 2016). There are appreciable numbers of K mineral ores in soil system (Meena et al., 2016a), which constitutes ~2.5% of lithosphere (concentration varies from 0.04 to 3.0% in soil) (Sparks and Huang, 1985). However, 80–90% of that K is in insoluble mineral form (Sparks, 1987). The other 1–10% is predominantly interlayer K of non-expanded clay minerals such as illite and lattice K in K feldspars that can be taken up by the plant (Sharpley, 1989). A third form of K is released in soil solution from a non-exchangeable pool in response to K removal through crops, erosion, leaching and runoff (Sparks, 1987; Sheng and Huang, 2002). Introduction of high yielding cultivars and intensive cropping consumes K in the amount exceeding ~10 Mt in global crop lands each year (Qi et al., 2012). This includes two-thirds of the wheat belt of Southern Australia, three-fourths of the paddy soils of China and ~51% of India (Hasan, 2002). Consistent with preceding observations, Bajwa and Rehman (1996) reported that only a small quantity of exchangeable K (~150 mg kg^{-1}) is present in Pakistani soils. Despite removal of significant amounts of K from agricultural soils, K management has been ignored for decades. In many areas of the world, common fertilization practices include application of N (urea) and P (diammonium phosphate) (Supanjani et al., 2006; Simonsson et al., 2007; Mohamed et al., 2017) without K, which results in the reduction of K in soils. Only a low percentage of farmers worldwide use muriate/sulfate of potash as K fertilizer for crop production in part because K deficiency symptoms are not as conspicuous as other macronutrients, and there is an inaccurate perception about the availability of K through canal and irrigation water (Dotaniya et al., 2016; Jaiswal et al., 2016; Jha and Subramanian, 2016).

Rapid nutrient depletion by high yielding cultivars in intensive crop cultivation systems (Regmi et al., 2002; Merbach and Deubel, 2008) coupled with lack of effective K replenishment protocols has caused increasing K deficiency in soils. According to the estimate of FAO, overall K demand worldwide would increase an approximate 3,400,000 tons from 2014 to 2018. A breakdown of this demand by continent would be 27% in America, 56% in Asia, 6% in Africa and 11% in Europe (Basak et al., 2016).

Potassium is largely absorbed by plants as cations similar to N (NH_4^+) in many crops that are most important for growth and development (Marschner et al., 1996). In some soils, phyto-available K is below the range of plant requirements (Rengel and Damon, 2008) making K fertilizers an absolute need in both intensive and extensive agricultural systems for sustainable crop production (Dasan, 2012; Phua et al., 2012; Yadegari et al., 2012; Zhang et al., 2013). Although crop residues are potential sources of K, only a few farmers are adding it in the soil worsening the K depletion in most soils (Kumar et al., 2015; Kumar et al., 2016; Meena et al., 2016b). These conditions demand augmentation of K level in soil through application of synthetic fertilizers (muriate of potash and sulphate of potash). Increased K requirement as an essential nutrient has influenced more world production of K fertilizer with concurrent increase in price. Higher fertilizer cost in turn has led to an increase in the crop production cost affecting profitability of farmers (Panday et al., 2018).

To overcome these constraints and maintain available K status in soils for sustaining crop production, an alternative indigenous source of K is needed for optimum plant uptake (Sindhu et al., 2014; Mohamed et al., 2017). In this regard, efficient soil microbes have been found playing a key role in the natural K-cycle and quick solubilization of insoluble K bearing minerals (Diep and Hieu, 2013). These observations indicate that it might be more beneficial and economical to use soil microbes through augmentative process to solubilize indigenous K minerals into plant available form of K should become sustainable and ecofriendly compared with the use of synthetic fertilizer (Zhang and Kong, 2014). From the results obtained from a large number of relevant studies, it can be inferred that utilizing these microbes that are present in soil, we may achieve enhanced plant growth (Vessey, 2003) by releasing K from insoluble K bearing minerals (Zarjani et al., 2013; Zhang et al., 2013; Gundala et al., 2013). These microbes may use diverse mechanisms such as production of siderophore, phenolic compounds, organic acids, and other metabolites, which influence pH and redox reactions (Gehan et al., 2010). Furthermore, direct contact of minerals and rhizobacteria might be significant in mineral solubilization as microbes widely known as K solubilizing microbes (KSMs) form complexes with metal ions on mineral surfaces and make them available (Badr, 2006). These KSMs can decompose alumino silicate minerals and provide an attractive mechanism to release a portion of the K contained therein (Rogers et al., 1998). Moreover, KSMs can suppress pathogen attack, change nutrient status and structure of soil. These KSMs are also involved in the weathering of silicate minerals to release K, aluminum (Al) and silicon (Si), in addition to the secretion of bioactive materials and hormones to boost plant growth. Many of these microbes are widely used in K biofertilizers as a K source for plants (Lian et al., 2002). Although solubility of these K bearing minerals is not sufficient to fulfill the total K requirement of plants compared to commercial K fertilizers, these novel approaches may significantly enhance K release from K bearing minerals. Furthermore, this review reveals the importance of substitutive K sources for optimum plant growth especially in countries having large amount of endogenous K reserves. This review is specifically focused on the soil K dynamics, presence and availability of K bearing minerals, modern approaches of K solubility from K minerals as mica and muscovite, use of K minerals as K fertilizers, and the effect of modification on K availability through microbial inoculation. This review also explains whether bio-augmentation of K bearing minerals can be a better and alternative source of synthetic K fertilizers for sustainable agriculture.

2. Potassium dynamics in soils

Potassium is the third most important common nutrient in soil, most abundant cation in plant cells and most abundant nutrient after N in the leaves (Mengel et al., 2001; White, 2003). It is more abundant than P (Sardans et al., 2012) less abundant than N and represents 2.6% of earth crusts by weight (Rittenhouse, 1979). In soil, igneous and sedimentary rocks are rich sources of K. The igneous rocks like syenites (~54 g K kg^{-1}), granites (~46 g K kg^{-1}) basalts (~7 g K kg^{-1}) and peridotites (~2 g K kg^{-1}) have higher K contents than sedimentary rocks such as clayey shales and lime stones, which contain ~30 g kg^{-1} and ~6 g kg^{-1}, respectively (Malavolta, 1985). In lithosphere, mineral soil K concentration ranges from 0.04 and 3% (Syers, 2003) and in surface soils 3000 and 100,000 kg K ha^{-1} is present. From these total K contents, ~98% K is present in non-exchangeable form (silicate minerals such as mica and feldspar (Sheng and Huang, 2002; Mohamed et al., 2017) and the remaining ~2% is available in solution for plant uptake (Bertsch and Thomas, 1985; Meena et al., 2016a).

Another form of K in soil is non-exchangeable K which is different from mineral K. The non-exchangeable K is held between adjacent tetrahedral layers of trioctahedral and dioctahedral micas, vermiculites, and intergrade clay minerals (Sparks and Huang, 1985). Non-exchangeable K^+ ions held in these interlayers and bound coulombically to the negatively charged interlayer surface sites (Kittrick, 1966). These binding forces exceed the hydration forces between individual K^+; subsequently crystal structure partially collapses, and K^+ is physically trapped within structures (Martin and Sparks, 1983). These non-exchangeable K-pools are moderately to sparsely available to plants, depending on various soil parameters (Goulding and Talibudeen, 1979; Sparks and Huang, 1985). Release of K^+ from this complex structure is possible when levels of solution K are decreased (Doll and Lucas, 1973) through plant removal or leaching (Sparks, 1980) and perhaps by large increases in microbial activity resulted the equilibrium K from non-exchangeable pool is released (Fig. 1).

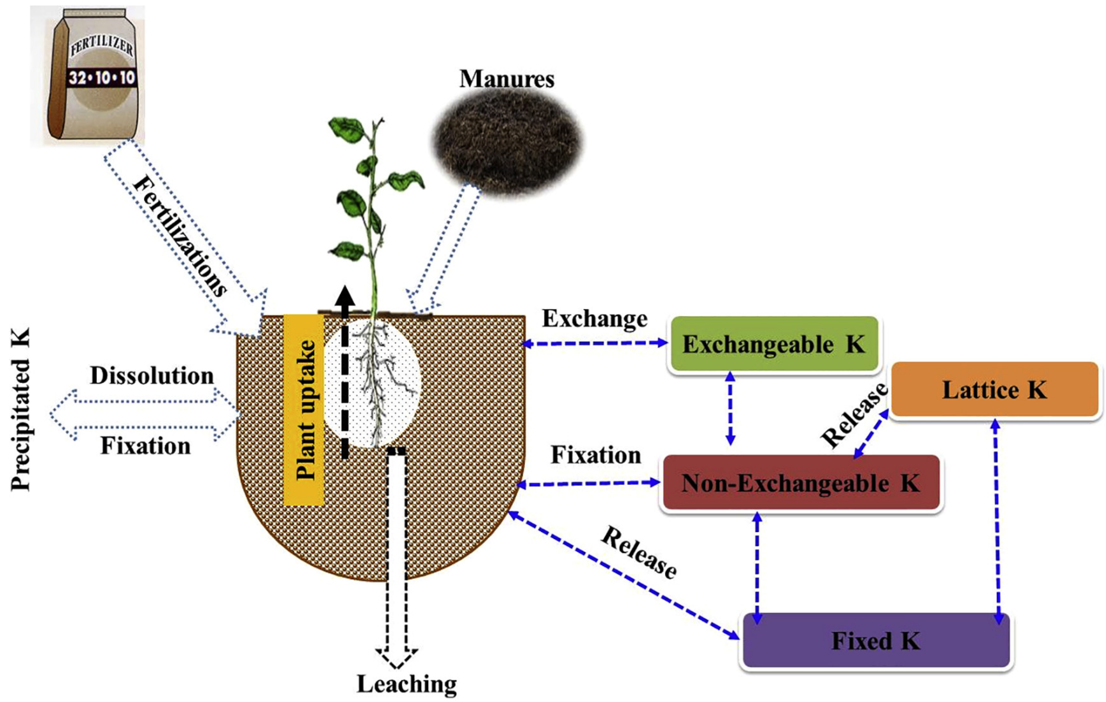

Fig. 1. Potassium dynamics in soil system.

The major K pools (90–98% of total K) in most of the soils are primary K mineral or structural K such as silicate minerals viz., biotite, orthoclase, muscovite, feldspar, mica (mica powder, ruby mica, mica stone, mica scrap and mica flakes), vermiculite, illite and smectite, etc. (Sparks and Huang, 1985). Generally, exchangeable and non-exchangeable K constitutes a very small percentage of mineral K in soils, and this pool is assumed to be slowly available for plant uptake (Jackson, 1964; Sparks and Huang, 1985) although availability is dependent on a number of factors such as (i) weathering of the K mineral fractions (feldspars and micas), (ii) level of K in the other pools such as solution, exchangeable, non-exchangeable K, (iii) nature and particle size of K bearing minerals, and (iv) soil environments such as Eh and pH condition, the nature and activity of various ions in soil solution, wetting, and drying, temperature (Huang et al., 1968; Meena et al., 2016a).

Potassium availability to plants is highly dependent upon type of minerals with respect to bio-availability, and the most important K minerals are muscovite (white mica) KAl_2 $(AlSi_3O_{10})$ $(F,OH)_2$, or $(KF)_2(Al_2O_3)_3(SiO_2)_6(H_2O)$, which is a phyllosilicate mineral of aluminium and potassium; biotite (black mica) $K(Mg,Fe)_3Al_2Si_3O_{10}(OH,F)_2$ and orthoclase ($KAlSi_3O_8$), potassium-taranakite, zeolite, vermiculite, chlorite, glauconite, illite (Huang et al., 1968; Parker et al., 1989). Among these, mica group biotite and muscovite are of special interest because these are a major source of many essential nutrients such as Mg, K, Mn and Zn and more readily soluble than other minerals (Sugumaran and Janarthanam, 2007). So, in soils with mixed minerals, such as in Pakistan where approximately 57% of applied K is fixed, K transformations are very complex (Pal et al., 1999) due to high pH, presence of interlayer K of non-expanded clay minerals such as vermiculite $(Mg, Fe^{++}, Al)_3$ $(Al, Si)_4$ O_{10} $(OH)_2$ $(4H_2O)$ and illite (K, H_3O) $(Al, Mg, Fe)_2$ $(Si, Al)_4$ O_{10} $[(OH)_2, (H_2O)]$ (Backett and Nafady, 1967; Goulding, 1987). However, bio-availability of K in different pools follows the order solution > exchangeable > fixed > mineral (Sparks, 2000).

Plants and microbes can only uptake K from solution (Oborn et al., 2005), which is normally very low in concentration (1–2%), and readily subjected to leaching/fixation. After K removal by plant and microbes, K from mineral and non-exchangeable pools is released to maintain equilibrium between intensity and quantity phases (Sparks and Huang, 1985; Goldstein, 1994). Due to intensive agriculture driven continuous plant uptake (Fig. 1), solution K is depleted with time, and its low concentration (0.1–0.2%) is not sufficient to meet plant growth (showing ~5% of total crop demand) (Sindhu et al., 2014; Meena et al., 2014a). This situation is worse in countries in the Southeast Asia, Africa, and Oceania due to a limited reserve of natural K containing minerals. For maintaining equilibrium (Fig. 1), K-released from two other K pools that are electrostatically bonded to the humic substances and clay minerals namely exchangeable K (EK) and slowly exchangeable K (SEK) make up to 1–2% and 1–10% of the total soil K, respectively (Mclean and Watson, 1985). In soil, this EK is held by negatively charged clay minerals and organic matters, which is slowly released by mineral weathering and easily exchanged by other cations from both sites (EK and SEK) in the form of K^+ ions to become bio-available (Mengel and Kirkby, 2001).

3. Potassium solubilizing microbes (KSMs)

In-depth understanding and exploitation of plant-soil-microbe interactions are very important in the current challenging global food security situation. An appreciable number of microbial groups (bacteria/rhizobacteria, fungi, actinomycetes etc.) are present and thriving in rhizosphere through one of the functional relationship such as associative, symbiotic, naturalistic/parasitic colonization of roots depending upon type of microbe, plant defense system, soil nutrient status, and micro environmental condition (Maurya et al., 2014; Verma et al., 2014). Among them, one dominant group known as plant growth-promoting rhizobacteria (PGPRs) helps in many soil processes such as weathering of soil, retention of nutrients, exudation of soluble compounds, decomposition of organic materials, mineralization of nutrients, production of siderophores, phytohormone synthesis, nutrient cycling (Fig. 2), plant nutrition and solubilization of K minerals (Abhilash et al., 2013), solubilization of phosphate, nitrification, fixation, denitrification and sulfur reduction (Khan et al., 2007; Diep and Hieu, 2013). The above-mentioned interactions indicate that some of these microbes in soil can reduce the use of synthetic fertilizers, which has been considered an ecofriendly approach (Glick, 1995; Requena et al., 1997) as it was found that sole application of minerals as

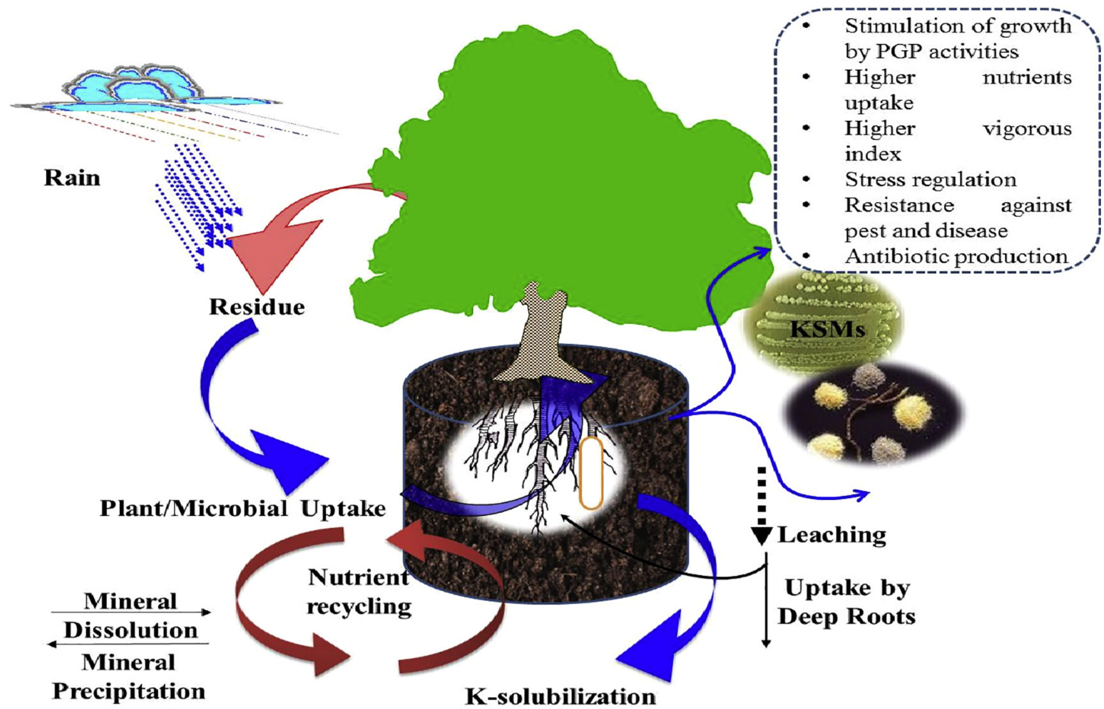

Fig. 2. Plant growth promoting (PGP) activities of potassium solubilizing microbes (KSMs) for sustainable development of agroecosystem.

synthetic fertilizers is not effective for plant growth (Basak et al., 2016).

A diverse group of microbes such as rhizobacterial species, fungal species, arbuscular mycorrhizae, yeast and many nitrogen fixing bacteria is known to possess K mineral solubilization capacity. These microbes have the ability to solubilize K minerals such as micas, illite and orthoclase (Bennett et al., 1998; Meena et al., 2016c) and convert them into soluble forms through release of organic acid (Zeng et al., 2012). Use of KSMs should be considered a pragmatic and attractive strategy for improving agricultural productivity. This technique was found to restore productivity of degraded agriculture soils by a number of investigators (Rajawat et al., 2012; Basak and Biswas, 2012). However, this technology is not popular yet because of the lack of awareness in the farming community (World Bank, 2007) but holds the potential to be accepted if appropriate outreach activities are conducted.

4. Diversity of potassium solubilizing microbes (KSMs)

Several groups of rhizobacteria and fungi are involved with solubilization of K minerals in the soil system (Sindhu et al., 2009; Singh et al., 2010). A large group of rhizobacteria (*Bacillus edaphicus*, *B. mucilaginosus*, *B. circulans*, *Acidothiobacillus ferrooxidans*, *Paenibacillus* sp., *Pseudomonas*, *Burkholderia* etc.) (Sheng et al., 2008; Lian et al., 2002; Rajawat et al., 2012; Basak and Biswas, 2012; Rajawat et al., 2016), *B. megaterium* (Hu and Boyer, 1996), *Agrobacterium tumefaciens, Rhizobium pusense* (Meena et al., 2015a) and fungi (*Aspergillus terreus*, *Glomas mosseae, G. intraradices*, *A. niger* and *Penicillium* sp.) (Lian et al., 2002; Mirminachi et al., 2002; Wu et al., 2005) have proven ability of solubilizing K minerals into plant available form. These microbes are ubiquitous, and their availability depends upon structure, texture, organic matter and other related soil properties. These microbes play a vital role in the release of nutrients from soil bound form of minerals (Lian et al., 2002; Supanjani et al., 2006; Sindhu et al., 2009). Most of the microbes such as fungi, bacteria and actinomycetes have ability to colonize surface of rocks (Gundala et al., 2013). Among these microbes, silicate solubilizing bacteria (*B. mucilaginosus* sub sp. *siliceus*) can release K from feldspar and aluminosilicate minerals as well as decomposition of organic matter and crop residues (Aleksandrov et al., 1967). The K solubilizing rhizobacteria (KSR) (for example *B. mucilaginosus* stain CS1) were isolated from the roots of several crops, which were grown in K and silicate amended soil (Mikhailouskaya and Tcherhysh, 2005). These microbes (silicate solubilizing) are present in both rhizosphere as well as non-rhizosphere soil (Lian et al., 2002; Meena et al., 2014b; Meena et al., 2015b; Zahedi, 2016).

During the last decade, a wide variety of bacterial species were found involved with K solubilization including *B. edaphicus* (Sheng, 2005), *B. mucilaginosus* (Basak and Biswas, 2009; Zarjani et al., 2013), *B. circulanscan* (Lian et al., 2002), *Burkholderia* sp., *A. ferrooxidans* (Hu et al., 2006) *Arthrobacter* sp. (Zarjani et al., 2013), *Paenibacillus mucilaginosus* (Hu et al., 2006; Liu et al., 2012), *Paenibacillus glucanolyticus* (Sangeeth et al., 2012). These bacteria can solubilize K into plant available form to some extent, but only few bacterial strains such as *B. mucilaginosus* and *B. edaphicus* are highly efficient in solubilizing K minerals (Sheng, 2005; Rajawat et al., 2012). Some strains of fungi like *A. niger* and *A. terreus,* which were isolated from K rich soil samples, can also solubilize insoluble K (Mirminachi et al., 2002). In addition to above mentioned microbes, some others including *Paenibacillus mucilaginosus* (Liu et al., 2012), *Arthrobacter* sp. (Zarjani et al., 2013), *Cladosporium* (Argelis et al., 1993), *Paenibacillus glucanolyticus* (Sangeeth et al., 2012), *Aminobacter*, *Penicillium frequentans, Burkholderia, Sphingomonas* (Uroz et al., 2009), *Pseudomonas* have the ability to solubilize both K and P.

5. Mechanisms utilized by potassium solubilizing microbes (KSMs)

There is a mutual relationship between soil microflora (bacteria, fungi, algae, protozoa, nematode etc.) and solubilization of minerals present in soil environment, and these interactions have been extensively studied by many investigators to improve the nutrient (K) status of soil for optimum crop growth. Microflorae adopt several mechanisms to solubilize complex soil minerals thereby enhancing plant growth and development for higher crop production, which are discussed below (Fig. 3).

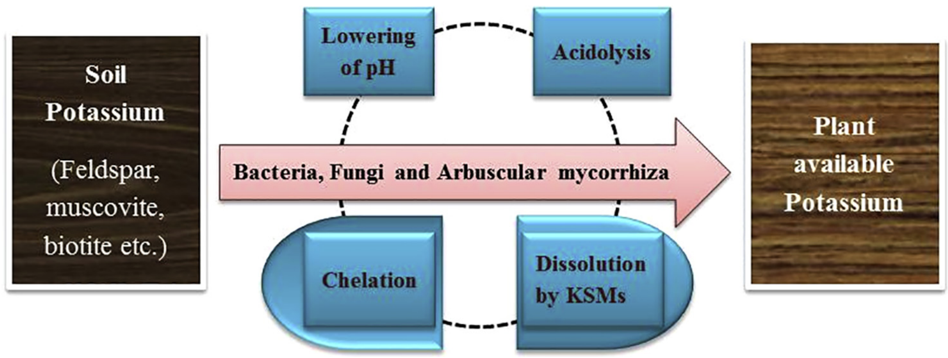

Fig. 3. Potential K-solubilizing mechanisms of potassium solubilizing microbes.

5.1. Solubilization of K-minerals

There is very little information available on K solubilization by soil microflora (bacteria, fungi, algae, protozoa, nematode etc.). However, available reports indicate that these microbes adopted specialized mechanisms for K rock mineralization that may include redox reactions by the production of chelating molecules and organic acids for K weathering and for its maximum bio-availability (Lian et al., 2008; Uroz et al., 2009).

5.1.1. Mechanisms of K-solubilization by bacteria/rhizobacteria

The KSMs include primarily some fungi and bacteria, but bacteria play the central role in solubilization of K minerals, and widely known as potassium dissolving bacteria (KDB) or potassium solubilizing bacteria (KSB). The K solubilization by bacteria/rhizobacteria was studied by various researchers all over the world to unravel different mechanisms (Fig. 3) used by these microbes include (i) direct way of solubilization, (ii) indirect way of solubilization, (iii) polysaccharides secretion, and (iv) biofilm formation on mineral surfaces.

5.1.1.1. Direct method of solubilization. Microbes help in K solubilization through (i) strong organic acid production (Alexander, 1977; Han et al., 2006), (ii) acidolysis of the rhizosphere (Gerke, 1992) minerals, and (iii) carbonic acid based chemical weathering (Gadd, 2007; Park et al., 2009). These microbes excrete organic acids like oxalic, tartaric and citric acids (Song and Huang, 1988; Rajawat et al., 2016) and H^+ ions (Fig. 4), which lowers the pH of surrounding soil (Bennett et al., 1998). Exudation of organic acids is an important mechanism of K minerals (mica, biotite, muscovite, feldspar, illite and orthoclase) (Basak et al., 2016) solubilization through microbial-mediated acidification and protonation into plant available form (Goldstein, 1994; Sheng et al., 2008; Zarjani et al., 2013). Basically, these organic acids associated protons lower the pH of rhizosphere, and enhance solubility of essential cations such as Fe, K, and Mg etc. Further, microbial respiration, degradation of particulate and dissolved organic carbon can elevate the concentration of carbonic acid at mineral surfaces (Meena et al., 2014b; Basak et al., 2016), which react with minerals and lead to an increase in the rates of mineral weathering by a proton-promoted dissolution mechanisms. Among these, tartaric acid is the most important and its use as an agent for solubilization of K minerals is going up gradually (Zarjani et al., 2013; Meena et al., 2015c). Other organic acids like acetic, glycolic, lactic, propionic, malonic and fumaric acids etc., were also reported to be involved in solubilization of K-minerals (Wu et al., 2005; Meena et al., 2015d). Some of the organic acids that are commonly released by microbes and play a role in K solubilization process are included in Table 1. Organic acid molecules influence mineral weathering in three separate but linked steps known as triple action: (i) acids adhere to the mineral surface and extract nutrients from the mineral particles by electron transfer reaction; (ii) break the oxygen links, and (iii) chelate ions present in solution through their carboxyl and hydroxyl groups. The third mechanism indirectly accelerates the dissolution rate by creating gradient between cation and anion concentrations in the solution (Welch et al., 2002). Synergistic impacts of KSMs inoculation on crops have been reported by many investigators. Lin et al. (2002) observed that carboxylic acids and capsular polysaccharide excreted *B. mucilaginosus* and *B. edaphicus* solubilized feldspar and significantly enhanced plant growth and yield (Sheng and Huang, 2002; Meena et al., 2015a). Furthermore, *B. mucilaginosus* releases some polymers, low molecular weight ligands and mixtures of these (Malinovskaya et al., 1990), which can improve K solubilization (feldspar, muscovite and illite) from ~68 to 83% compared to control (Sheng and Huang, 2002).

5.1.1.2. Indirect method of solubilization. Instead of acidolysis or lowering of pH, microbes also solubilize K minerals through indirect method of solubilization like (i) chelation of the cations bound to K silicate (Song and Huang, 1988; Bennett et al., 2001), (ii) exchange reactions (Gerke, 1992) (iii) solubilization by direct attachment of KSMs on mineral surfaces (Figs. 3 and 4) (Uroz et al. 2009), (iv) metal complexing ligands (Basak et al., 2016), and (iv) release of phytohormones through microbes. Chelating ability of the organic acids is an important mechanism of solubilizing K minerals (Meena et al., 2014a, 2015a). Chelation is an indirect method of K solubilization from K bound minerals (Fig. 4). These efficient KSMs also have the ability of weathering minerals (phlogopite) through acid dissolution and aluminum chelation process of the crystal structure (Leyval and Berthelin, 1989; Abou-el-Seoud and Abdel-Megeed, 2012). The KSMs form metal–organic complexes with both Al and Si ions associated with K-minerals, and as result, K ion is released in solution (Song and Huang, 1988; Romheld and Kirkby, 2010). Addition of EDTA (0.05 M) to the medium containing insoluble K has the same solubilizing results as observed from inoculation with *Penicillium bilaii* (Sheng and He, 2006; Meena et al., 2015e; Prakash and Verma, 2016; Yasin et al., 2016).

Metal complexing ligands are another potential way to solubilize K through microbes. The efficient microbes, in addition to organic acids, exude high-molecular-weight organic ligands and polymers such as guluronic acid, mannuronic acid, and alginates, which form complexes with ions on the mineral surface to weaken the metal–oxygen bonding (Basak et al., 2016). On the other hand, ligands can form complexes with ions in the solution and directly affect the saturation state of solution. Further, these polymers can accelerate ion diffusion from the surface of mineral by producing slime layers containing polysaccharides and enzymes around the mineral surface. This process can result in increased contact between mineral surface and water (Lin et al., 2002; Meena et al., 2013) and enhance the solubilization of a number of minerals. These microbe-produced polysaccharides contain functional groups (−COO−) that form complex with mineral ions, changing the saturation state of solution and thus boost the

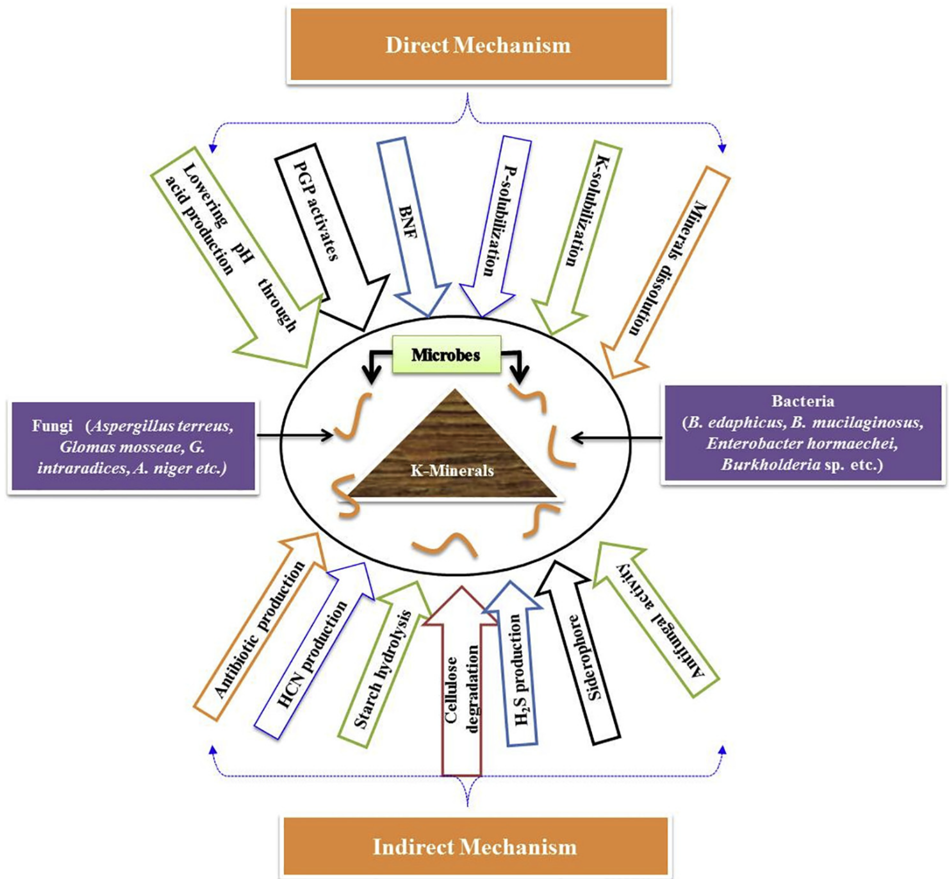

Fig. 4. Direct and indirect mechanisms of potassium solubilizing microbes for sustainable crop production.

Table 1
List of potassium (K) bearing minerals with chemical composition and K-contents.

Minerals	Chemical formula	K_2O (%)
Sylvite	KCl	63.09
Kalsilite	$KAlSiO_4$	29.75
Langbeinite	$2MgSO_4{\cdot}K_2SO_4$	22.71
Leucite	$KAlSi_2O_6$	21.56
Kainite	$KMgSO_4Cl{\cdot}3H_2O$	18.91
Carnallite	$MgCl_2{\cdot}KCl{\cdot}6H_2O$	16.94
Potassium feldspar	$KAlSi_3O_8$	16.91
Nepheline	$(Na,K)AlSiO_4$	15.67
Phlogopite	$K_2Mg_6Si_6Al_2O_{20}(OH)_4$	11.30
Muscovite	$KAl_3Si_3O_{10}(OH)_2$	10.88
Biotite	$K_2Fe_6Si_6Al_2O_{20}(OH)_4$	09.18

mobilization (Sheng et al., 2002). In addition, these microbial exudates (low molecular weight organic compounds) contain by products of metabolic processes, organic ligands, chelates and extracellular enzymes, which help in dissolution of K minerals (Malinovskaya et al., 1990) through pH manipulation of micro environment (Welch et al., 2002).

5.1.1.3. Polysaccharides secretion. Although, the mechanism of K release from silicate minerals is complex; microbes adopt many different ways to mobilize K in soil. Capsular exopolysaccharides (EPS) is another potential way by which rhizobacteria can solubilize K minerals. These microbe-produced EPS are strongly adsorbed by organic acids, and thus enhanced attachment to mineral surface occurs resulting in high concentration of organic acids on or around the minerals (Liu et al., 2012). Microbes such as *Bacillus, Clostridium* and *Thiobacillus* with the capacity to secrete metabolic intermediates or mucilaginous capsules containing of EPS showed higher biodegradation of feldspar and illite to release K^+ (De Graef et al., 2005; Sheng and He, 2006). Microbial EPS with high protein content (Du et al., 2008) stimulates the formation of bacteria-mineral complex where microbes excrete organic acids and resultant low pH enhances solubilization of K minerals and K bioavailability. Besides, EPS also have strong ability to adsorb organic acids (Lian, 1998). Consequently, micro environment where higher amount of organic acids is released, additional dissolution of the K minerals take place. Furthermore, EPS binds K^+ and SiO_2 that helps maintaining the equilibrium between soil solution and minerals eventually enhancing K^+ release and bioavailability (Lian et al., 2002). More specifically, in the K deficient soils microbial community having capability to solubilize K minerals release organic acids, extracellular enzymes and polymers, which participate in mineral degradation and enhance solution bio-available K^+ (Meena et al., 2016a). Rhizobacteria attack minerals to use them as an energy source and a nutrient of interest. During the interactions, other nutrients may also come into solution due to bio-weathering processes (Xiao et al., 2012).

Mineral solubilization is principally attributed to redox reaction, as in nutrient deficient conditions, bacteria transfer electron to metal groups on mineral surfaces resulting in destruction of metal. Bacteria usually contain many multiheme cytochromes in outer membrane surfaces of cells, which allow proteins to transfer electrons easily as and when contact with mineral oxides occur (Fredrickson and Zachara, 2008; Uroz et al., 2009).

5.1.1.4. Biofilm formation. Biofilm formation is a potential but least studied mechanism of K reserve mobilization. Biofilm is a very early step in plant–microbe interaction in which bacterial cells are stuck to abiotic/biotic surfaces. In biofilm, cells are fixed within a matrix of self-produced extracellular polymers that are junk proteins, DNA and polysaccharides. Higher microbial population in biofilms offers the opportunity to achieve improved biochemical reactions compared to single and dual cultures (Nagaraju et al., 2017). Certain microbial strains form a biofilm on the rhizospheric mineral surfaces and release organic acids, metabolites, and drops the pH that help in K mineral solubilization and uptake by plants (Balogh-Brunstad et al., 2008). It is concentrated microbial community on the root-hypha-mineral interface, which is protected by self-produced extracellular polymers (Gadd, 2007). These rhizobacterial communities have a tremendous phylogenetic and metabolic diversity for their ability to adapt and colonize in extreme environments due to exo-polysaccharide layer in which they extract inorganic nutrients and energy directly from the mineral surfaces and help in weathering of minerals. Basically, these primary proteins, extracellular polymers, and polysaccharides exudate by the microbes serve as a catalyst and help in mobilization of nutrients from complex mineral structures (Meena et al., 2016a). Further, biofilms provide shelter to microbes against unsafe environmental effects, protect from heavy metals, antibiotics, other cations, nutrients and pathogens. A large body of evidence suggests that biofilms may result in mineral weathering and nutrient uptake by plants through root hairs (Basak and Biswas, 2009).

5.1.2. Solubilization of K by fungi

Role of fungi in K solubilization is more pronounced through organic acid production and uptake through the root system to contribute to plant biomass enhancement. Some fungi such as *Aspergillus, Penicillium, Fusarium* and *Aspergillus niger* play a pivotal role in K solubilization and uptake. Fungi produce organic acids, especially oxalic, citric and gluconic acid, similar to rhizobacteria, which leads to deterioration of clay silicates, mica and feldspar (Vassileva et al., 2000). As reported by Hu et al. (2006), oxalic acid caused dissolution of feldspar in growth media whereas tartaric and oxalic acids were involved in mobilizing illite and gluconate, and promoting dissolution of albite, quartz and kaolinite (Argelis et al., 1993). Besides, fungi mineralize K through chelating reaction of mineral elements, acid hydrolysis, and secretion of insoluble macromolecules and polymers that play significant role to release K from K minerals (Lian et al., 2008). Furthermore, fungi exert direct bio-physical forces which can fracture K mineral to decrease particle sizes and create more reactive surfaces (Xiao et al., 2012). Fungi add acids to rhizospheric soil and help with dissolving silicate rock powders by mycorrhizae, which release fixed nutrients in soil (Leyval and Berthelin, 1989). Instead of acid production, some rock eating ectomycorrhizal fungi excrete low molecular weight organic compounds through hyphal tips that forms microscopic tunnels within K minerals (feldspar and hornblende) and significantly enhance the rate of mineral weathering in soil (Van Schöll et al., 2008).

Lopes-Assad et al. (2006) investigated the K mineral (ultramafic rock) solubilization ability of two strains of *Aspergillus niger* (CCT4355 and CCT911), and reported that fungal strains significantly enhance the titratable acidity and decrease the pH, which enhance K solubilization in soil. Acidity induced in the inoculated zone indicated that *A. niger* can exude organic acids, which solubilize the K minerals (Vassileva et al., 2000). Lian et al. (2007) also reported very similar findings and revealed that thermophilic fungus (*Aspergillus fumigatus*) enhanced K solubilization when inoculated onto K bearing minerals. Biofertilizer preparation by utilizing beneficial fungi is another positive and emerging aspect pertaining to sustainable agriculture (Priyadharsini and Muthukumar, 2016; Raghavendra et al., 2016; Yadav and Sidhu, 2016).

In addition, yeast also has the ability to mobilize K from silicate minerals. However, despite the known ability of yeasts to produce organic acids, there are only a few studies on K solubilization through yeast. In this regard, Rosa-Magri et al. (2012) conducted a study on yeast and reported that strong acids released from yeast (*Torulaspora globosa*) could solubilize the alkaline ultramafic rock and release as much as ~38% of total K in the medium within fifteen days. In line of these studies, Mohamed et al. (2017) conducted another study on solubilization of muscovite mica with soil yeasts in the presence of maize. Results showed that yeast *Pichia anomala* and *Rhodotorula glutinis* had strong ability to solubilize K minerals as well as providing significant plant growth enhancements (~14% increment in roots and ~23% increment in shoots). In another work, Sangeeth et al. (2012) investigated K solubilization efficiency of *Paenibacillus glucanolyticus* in the presence of black pepper. According to their findings, soil inoculated with strain of *Paenibacillus glucanolyticus* showed ~37 to 68% increase in tissue dry mass and live bacterium grew 1.25–1.85 fold higher compared to uninoculated soil.

5.2. Plant growth promotion (PGP) activities

The KSMs promote plant growth through various direct and indirect growth promotion mechanisms. In soil, inoculation with KSMs enhance nutrient uptake, promote K solubilization, organic matter decomposition and many other functions (Kloepper et al., 1991). Through direct mechanisms, microbes play a vital role in N_2-fixation, P-solubilization, production of plant growth hormones (auxin, cytokinins, ethylene, IAA and GA_3) (Sheng and Huang, 2001), organic acid production and K solubilization (Alexander, 1977; Sheng and Huang, 2001; Park et al., 2003). In indirect mechanisms, microbes enhance plant growth by production of siderophores, antibiotics, H_2S, antifungal compounds, starch hydrolysis, and cellulose degradation (Meena et al., 2014b). Through these beneficial mechanisms, KSMs in most cases also promote plant growth (Lian et al., 2002). Higher nutrient uptake and plant growth promotion is usually attributed to plant growth hormones, which are produced in soil and plant rhizosphere, and are beneficial to root growth (Kloepper et al., 1991). The K solubilization from K mineral is the main characteristic of KSMs, which significantly enhance the fertility status of soil and eventually promote plant growth (Rajawat et al., 2012). Utilization of KSMs for growth promotion is a sound technique and has the ability to restore unproductive soils (Basak and Biswas, 2012; Rajawat et al., 2012).

Several studies evaluated the impact of KSMs on plant growth and K minerals solubilization. Inoculation of *Bacillus mucilaginosus* in nutrient limited soil showed positive response on growth and yield of eggplant. Furthermore, maximum K release and uptake was observed in soil amended with K mineral and *B. mucilaginosus* (Han and Lee, 2005). According to the findings of Ramarethinam and Chandra (2006), *Frateuria aurantia* belonging to the family *Pseudomonaceae* considerably enhanced K solubilization and plant growth upon inoculation. They reported that K solubilization and PGP activities in this study were due to secretion of organic acids and enzymes produced by KSMs. These microbes are capable for releasing organic acids that influence K release from structural compounds. In addition, different types of amino acids, vitamins and plant growth promoting substances such as gibberellic acid (GA_3) and indole-3-acetic acid (IAA) are released, which help plants attain better growth (Ponmurugan and Gopi, 2006; Singh et al., 2015). High auxin production was observed in the presence of *B. edaphicus* NBT strain, which ultimately enhances plant growth. The strain NBT has high potential to solubilize K and was found to maximize growth of cotton and rape (Sheng and Huang, 2001).

Inoculation of K solubilizing strain (*Penicilium oxalicum* CBPS-3F-Tsa) resulted highest K solubilization, secretion of enzymes, hormones and organic acids in microbial suspension (Park et al., 2003). Inoculation with KSMs enhanced N and P uptake together with K partly because of hormones, enzymes and organic acid exudation in root interface. This occurred due to microbial action, and KSM colonized roots contributed to boosting growth (Kloepper et al., 1991). *Azotobacter chroococcum* A-41 is another K-solubilizers, plant growth and yield promoting strain (Fig. 4). Plant growth promotion by this strain is attributed to the N_2-fixing and K solubilizing ability in addition with phyto-hormone production (Vessey, 2003). Phyto-hormones released from KSMs directly enhance (Fig. 2) plant growth and yield through production of lateral roots and absorbent root hairs in the rhizosphere, which facilitate nutrient uptake from soil away from the plant (Patten and Glick, 1996). Other than direct effect, KSMs also enhance plant growth through indirect effect by releasing nutrients in soil solution from the mineralization of rocks, which are available to plants (Patten and Glick, 1996).

Instead of a single inoculation of KSMs, few studies have documented the effect of co-inoculation or a consortium of KSMs and PGPMs. In a greenhouse study, it was observed that co-inoculation of N_2-fixing *A. chroococcum* A-41 with K solubilizing *B. mucilaginosus* enhanced growth and nutrient uptake of sudan grass compared to single inoculations (Basak and Biswas, 2012). Findings from this experiment showed NFB + KSB could be a promising and alternative strategy for releasing K from structural compounds, supplying part of required N and thereby maintaining soil sustainability. As microbe-mediated release of nutrients is relatively slow, they alone are not able to meet the nutrient requirement of plants for their optimum growth and development.

KSMs also enhance plant growth by indirect mechanism through disease suppression and providing resistance against insect pests and diseases. Through combined beneficial effects of making nutrients more available and improving plant vigor, these microbes strengthen plants and thus enable them to fight against diseases. For example, some microbes release K, aluminum and silicon through weathering of minerals and secrete phyto-hormones, which strengthen the defense mechanism by providing resistance against diseases and other external stresses, enhance plant growth (Lian et al., 2002), plant nutrition and competitiveness (Fig. 4). Rhizobacteria like *Azospirillum*, *Bacillus*, *Pseudomonas*, *Enterobacter* were used in many studies (Boelens et al., 1993) for their beneficial effects on plant growth, yield and disease resistance (Kloepper and Beauchamp, 1992; Hoflich et al., 1994). Therefore, it is imperative to isolate more species of mineral solubilizing rhizobacteria (MSR) to enrich the pool of microbial species to contribute to ecological and agricultural sustainability (Verma et al., 2015b; Rawat et al., 2016; Saha et al., 2016a).

6. Factors affecting activity of potassium solubilizing microbes

Microbes are living entities that are abundant and diverse in dynamic soil systems. As conditions in soil are changeable, there are a number of factors that affect microbial survival in soil. Any adverse change in these factors can severely affect microbial activity in soils. Some of the important factors are pH, oxygen concentration, carbon sources, temperature and bacterial strain, which are used to solubilize K mineral (Sheng and Huang, 2002).

These microbes need food and higher level of energy for their survival. They obtain their food from different carbon (C) sources. Without a C source, rate of multiplication slows and ultimately, they show reduced activity or activity may even cease. In the case of KSMs, lacks of food sources reduce their rate of K solubilization. Decomposition of organic matters in soil is the major C source for these microbes. In general, higher K solubilization and higher microbial diversity is observed in the presence of a labile food source (Meena et al., 2016a). KSMs in soil require specific temperature for maximum K solubilization. Maximum K mineral solubilization ($\sim 49\,mg\,L^{-1}$) was reported as temperature reached 25–30 °C (Meena et al., 2016a). Sheng and Huang (2002) also found similar results, and reported an increase in K solubilization from ~84 to 127% in 7 days at 28 °C temperature.

Soil pH is another important factor, which affects survival and diversity of microbes in soil. Most suitable pH reported for microbial growth and survival was in the neutral range. Microbial growth was highest at pH 7, but pH > 7 caused decrease in solubilization of K due to fixation of K at high pH (Meena et al., 2016a). However, Sheng and Huang (2002) reported that for a higher microbial activity, optimum growth conditions required to release $\sim 35\,mg\,L^{-1}$ K in 7 days at 28 °C in the pH range from 6.5 to 8.0. Similarly, Badr (2006) reported that neutral pH was the most suitable for maximum microbial activity. A large body of literature also indicated that KSMs not only solubilize K-but are also capable of P solubilization (~ 490 to $758\,mg\,L^{-1}$) at pH range of 6.5–8.0, which is suitable for microbial survival in soil–plant system.

In addition to these soils and environmental factors, K solubilization was also affected by type of K mineral, structure and composition of minerals (Liu et al., 2012). Different types of K minerals are present in soil; each with specific characteristics, different structural arrangement and resistance against K solubilization. In a study conducted to determine the solubilization of different type of K minerals (illite and feldspar) by *B. edaphicus* (KSMs), illite showed highest solubilization as compared to feldspar when both were used as a K source (Sheng and He, 2006). However, K bioavailability was also dependent upon soil type, plant type and soil and environmental factors (Vessey, 2003; Sheng, 2005). This effect is likely due to structural variation of minerals as some minerals are easily solubilized and release K, while others are complex in structure and resist solubilization. In addition to specific minerals, a suitable microbial strain is also very important for highest microbial activity and K solubilization (Sindhu and Dadarwal, 2000). Suitable strains can enhance K bioavailability for amelioration of K deficient soils in areas where K deficiency is a significant limiting factor for optimum plant growth. Availability of oxygen is also a very important limiting factor because KSMs are aerobic in nature so, presence of oxygen is necessary for maximum solubility and K availability. Many investigators reported a clear decline in microbial growth and activity in an oxygen limiting environment, which also affected K availability in soil for plants (Verma et al., 2015a; Saha et al., 2016b; Sharma et al., 2016; Shrivastava et al., 2016).

7. Potential of potassium solubilizing microbes for crop production

Potassium is one of the important and essential nutrients, and plays a critical role in plant growth and production. A large body of literature indicate that inoculation of seeds with KSMs as well as seedling treatment significantly enhanced seedling vigor, germination percentage, K uptake by plants, plant growth and yield under both greenhouse and field conditions (Basak and Biswas, 2010; Singh et al., 2010; Youssef et al., 2010; Awasthi et al., 2011; Zhang et al., 2013). The beneficial effect of KSMs inoculation has been observed on a range of crops (Table 2) including wheat (Sheng and He, 2006), sorghum (Badr, 2006), cotton and rape (Sheng, 2005), sudan grass (Basak and Biswas, 2010), chili (Ramarethinam and Chandra, 2006), pepper and cucumber (Han et al., 2006), tomato (Lin et al., 2002) and khella (Hassan and Hamad, 2010).

Aleksandrov (1985) for the first time observed a combined effect of organo-minerals and silicate bacteria on plant growth and yield of wheat and maize. Furthermore, many field experiments conducted on multiple crops such as maize, wheat, rice, groundnuts and forage crop have shown that KSMs could significantly decrease the use of both synthetic and organic fertilizers (Xie, 1998; Singh et al., 2010; Sindhu et al., 2014; Zeng et al., 2012). These microbes also take part in the synthesis of chlorophyll by taking part in various enzymatic activities (Senthurpandian et al., 2008; Meena et al., 2014b). These beneficial microbes enhance plant growth not only directly but also indirectly through root enlargement, hormone production, P solubilization as well as through enhancing the total chlorophyll and carotenoid contents (Youssef et al., 2010; Singh et al., 2010; Awasthi et al., 2011; Jayaganesh et al., 2011; Basak and Biswas, 2012; Zhang et al., 2013).

These efficient KSMs have been isolated from different crop rhizosphere i.e. wheat (Zhang et al., 2013), common bean (Kumar et al., 2012), rice (Muralikannan and Anthomiraj, 1998), tea, black pepper (Sangeeth et al., 2012), potato (Abdel-Salam and Shams, 2012), minerals feldspar (Sheng et al., 2008), Iranian soils (Zarjani et al., 2013), mica core of Andhra Pradesh (Gundala et al., 2013), biofertilizers

Table 2
Organic acids produced by potassium solubilizing microbes.

Microbes	Organic acids	References
Bacillus mucilaginosus, B. edaphicus	Citric, tartaric, oxalic acids	Malinovskaya et al. (1990); Sheng and Huang (2002)
Enterobacter hormaechei	Oxalic acid, citric acid,	Prajapati and Modi (2012)
B. megaterium, E. freundii	Citric, gluconic acids	Meena et al. (2014a)
B. mucilaginosus	Citric, oxalic, tartaric acids	Song and Huang (1988); Friedrich et al. (1991); Bennett et al. (1998)
B. mucilaginosus, B. edaphicus	Carboxylic acids, capsular polysaccharide	Lin et al. (2002); Sheng and Huang (2002)
B. mucilaginosus	Oxalate, citrate acids	Sheng and He (2006)
Paenibacillus mucilaginosus	Oxalic, tartaric, citric acids	Hu et al. (2006); Liu et al. (2012)
Clasdosporium sp.	Oxalic, citric, gluconic acids	Argelis et al. (1993)
B. megaterium, Pseudomonas sp.	Malic, lactic, lactic, oxalic acids	Meena et al. (2016a)
B. mucilaginosus	Citric, oxalic, tartaric acids	Basak and Biswas (2010)
B. mucilaginosus, B. edaphicus	Citric, tartaric, oxalic acids	Malinovskaya et al. (1990); Sheng and Huang (2002)
A. niger	Citric acid	Nahas et al. (1990); Vassileva et al. (2000)

(Zakaria, 2009), soil of Tianmu Mountain, Zhe-jiang Province of (China) (Hu et al., 2006), and valencia orange (Shaaban et al., 2012; Sindhu et al., 2016; Velázquez et al., 2016).

To assess the effects of KSMs in hydroponics, a study on wheat and maize was conducted by evaluating the solubilizing ability of *B. mucilaginosus, A. chroococcum*, and *Rhizobium* sp. in a phytotron growth chamber. According to results, KSMs significantly enhanced the K content, plant biomass, crude protein and chlorophyll content in both crops (maize and wheat). It was also reported that *B. mucilaginosus* showed significantly higher solubilization and uptake of K than *A. chroococcum* and *Rhizobium* sp. (Singh et al., 2010). Sheng and He (2006) conducted a pot experiment on wheat in yellow brown soil with lower K contents to evaluate the mobilization of K through a wild-type strain NBT of *B. edaphicus*. Higher shoot, root growth and NPK contents were observed in treatments, which were inoculated with bacterial strain compared to non-inoculated (See Table 3).

Similar to KSMs' indirect effect of solubilizing other nutrients some other microbes also contribute to solubilization of K minerals. For example, Si solubilizing microbes solubilize Si as well as K. Likewise, Muralikannan and Anthomiraj (1998) showed a significantly higher rice yield (~17%) and soil organic matter contents (Zahra et al., 1984) through inoculation of soil with silicate solubilizing bacteria *B. cirulans* (solubilize K in addition to Si). Furthermore, 1.04 $t\,ha^{-1}$ increments in wheat yield was documented in response to inoculation of KSMs in eroded soil as compared to normally eroded uninoculated soil (Mikhailouskaya and Tcherhysh, 2005). Due to co-inoculation of K and P bearing minerals with KSMs significant enhancement of K (~41, 93 and 79%), P (~71, 110 and 116%) and dry matter yield (~48, 65 and 58%) of sorghum plant in three different textured soils i.e. clay, sandy and calcareous soils, respectively (Badar et al., 2006) was obtained. Sugumaran and Janarthanam (2007) conducted a study and found that soil inoculated with *B. mucilaginosus* significantly enhanced oil content (~35%) and dry matter (~25%) of groundnut, and increased P and K contents from ~7 to 9 $mg\,kg^{-1}$ and ~87 to 99 $mg\,kg^{-1}$, respectively, in soil compared to an uninoculated control. Soil inoculated with *B. edaphicus* NBT, a well-known K solubilizer, solubilized insoluble K, enhanced root/shoot growth, influenced K mineral (illite) solubilization, bioavailability and uptake in cotton and rapeseeds. A significant

Table 3
Effect of potassium solubilizing microbes on crop growth, yield and nutrient uptake.

Crops	Microbes	Effect on crops	References
Black pepper	*Paenibacillus glucanolyticus*	Enhanced K-uptake and dry weight in inoculated plants	Sangeeth et al. (2012)
Cotton	*B. edaphicus*	Improved plant growth and yield	Paau (1989)
Egg plant	*B. mucilaginosus* KCTC 3870	Increased P and K uptake	Han and Lee (2005)
Eucalyptus	Ectomycorrhizal fungi (UFSC-Pt22 and UFSC-Pt186)	Enhanced N, P, K content and plant growth	Alves et al. (2010)
Lettuce/tomato	*Pseudomonas putida* and *P. fluorescens*	Increased root and shoot growth	Hall et al. (1996); Glick et al. (1997)
Maize	*A. chroococcum, B. megaterium, B. mucilaginosus*	Increased growth and uptake of N, P and K	Wu et al. (2005)
Maize/wheat	*B. mucilaginosus, Azotobacter chroococcum*	Higher K-mobilization, root shoot growth and yield	Singh et al. (2010)
Okra	*Enterobacter hormaechei, Aspergillus terreus*	Increased root, shoot growth and K-uptake	Prajapati et al. (2013)
Peanut/sesame	*Bacillus pasteurii*	Significant increase in K availability	Youssef et al. (2010)
Rapeseed	*B. edaphicus* NBT	Increased root and shoot growth	Sheng (2005)
Sudan grass	*A. chroococcum* A-41	Enhanced biomass and yield	Vessey (2003); Kloepper et al. (1991)
Sudan grass	*Bacillus mucilaginosus*	Higher biomass yield, uptake and % K-recovery, increased root-shoot growth	Basak and Biswas (2009)
Sudan grass	*Bacillus mucilaginosus*	higher biomass accumulation and nutrient acquisition	Basak and Biswas (2010)
Switch grass	*Arbuscular mycorrhizae*	Increased plant height, root and shoot weight, root length and P, N contents	Clark et al. (1999)
Tea	*Pseudomonas putida*	Tea quality parameters like theaflavin, thearubigin, highly polymerized substances, total liquor colour, were improved	Bagyalakshmi et al. (2012)
Tobacco	*Enterobacter cloacae, Klebsiella variicola*	Inoculation improved plant dry weight and enhanced nutrient uptake	Zang and Kong (2014)
Tomato	*Pseudomonas* sp.	P and K-solubilizers significantly improved tomato yield	Lynn et al. (2013)
Valencia orange trees	*Bacillus circulans*	Inoculation significantly improved leaf K content, fruit weight and yield	Shaaban et al. (2012)
Wheat	*A. chroococcum*	Increased crop productivity and nutrient uptake	Kapulnik et al. (1985, 1987), Kloepper et al. (1989, 1991)
Wheat	*Bacillus* sp.	Increased grain yield and disease resistances	Kloepper et al. (1991)

increase (~26–30%) of K content was observed when an insoluble K source (eliot) was inoculated with a bacterial strain NBT (Sheng, 2005). Furthermore, strain *B. edaphicus* NBT enhanced P and N contents in both soil and plants, and was also able to colonize roots of cotton and rapeseeds (Sheng, 2005). The co-inoculation of P and KSMs significantly boosted the available P and K from ~12 to 21% and ~13 to 15%, respectively. Supanjani et al. (2006) reported that soil inoculation with KSMs increased the plant's photosynthetic rate by ~16% and leaf area by ~35% than that of the control.

Different types of fungi were also very active in solubilization of K minerals. The arbuscular mycorrhizae (AM) released protons (H^+) or CO_2 and many different types of organic acids or compounds, which helped in K mineral solubilization (Meena et al., 2014a). Instead of K, AM also significantly enhanced N, Ca and Fe concentration in plant leaves and fruits (Wu et al., 2005; Jones et al., 2009; Veresoglou et al., 2011; Yousefi et al., 2011). The scanty information of macronutrient increase or decrease was documented in AM inoculated plants (Clark and Zeto, 1996), but in cases of K nutrient, it was dependent upon plant growth, soil condition as well as some other climatic factors (Clark and Zeto, 2000). Alves et al. (2010) reported that mycorrhizae-colonized plants had significantly higher plant height, root length, shoot dry weight, K and P contents after 90 days of inoculation compared to control because AM enhanced root length and nutrient uptake ability. The higher K acquisition was reported in AM inoculated switch grass grown in acid soil compared to Mg and Ca (Clark et al., 1999). Furthermore, K solubilizing fungi namely *Aspergillus niger* and *A. terreus*, which were isolated from various K rich soils could solubilize insoluble K minerals (potassium aluminum silicate and feldspar), and showed the highest available K in liquid medium because of acidic nature of fungi. The concentration of trace elements was also enhanced through acid production by fungi (Mirminachi et al., 2002).

8. Role of potassium solubilizing microbes in disease and stress resistance in crops

Plants are exposed to many abiotic and biotic stresses such as chilling, drought, high light intensity, nutrient limitations, heat, diseases, reactive oxygen species {(hydroxyl radical (OH^-) and superoxide radical (O_2^-)} (Cakmak, 2005). A large body of evidence suggests that improvement of K status of plants can greatly enhance plants' resistance against stress, disease and insect attack (Rehm and Schmitt, 2002). It promotes root growth and enlargement, stem strength, and provide resistance against cold and water stress. Potassium is directly involved in plant strength, crop quality, and improves overall plant productivity (Cakmak, 2005). Potassium also strengthens plant defense system, and it is important for the survival of crop plants under environmental stress conditions such as chilling, drought and high light intensity.

Applications of KSMs significantly enhance K content in plants, nutrient uptake and disease resistance (Kloepper et al., 1991). Plants inoculated with KSMs (*B. mucilaginosus*) showed increased solubilization of K mineral, IAA, N, P uptake and photosynthesis, which eventually improved growth of plant (Han and Lee, 2005). Rhizospheric microbes have many beneficial effects on plant growth. For example, *Frateuria arrange,* a bacterial strain of *Pseudomonas* family, which was isolated from agriculture soil showed higher potential for K mineral solubilization along with higher resistance against stress (cold and water stress) (Cakmak, 2005; Ramarethinam and Chandra, 2006). The solubilization behavior, which is generally observed in microbes, is due to the variation in their capacity of producing enzymes and organic acids can reflect specific characteristics of KSMs. These efficient microbes in soils can improve nutrient uptake, plant growth, root growth and enlargement, plant competitiveness, and enhance resistance against external biotic and abiotic stresses. Some associative bacterial species such as *Bacillus*, *Enterobacter*, *Pseudomonas* and *Azospirillum* have also been used in a number of studies due to their involvement and benefit on plant growth mechanism (Kloepper and Beauchamp, 1992; Hoflich et al., 1994).

9. Commercialization of potassium solubilizing microbes

Microbes present in the rhizospheric soil have multiple functions such as N_2-fixation, P and K solubilization, siderophore production and other PGP activities that promote plant growth and development. However, these microbes often are not present in high number to fulfill plant requirements. Farmers are not familiar with K deficiency because of hidden hunger of K in plants and are reluctant to replenish the depleted soils due to higher prices of K fertilizers. Moreover, K fertilizers do not give a visual response as that of urea in plants. In the past, soil available K reserves were enough for crop requirement, and also irrigation water contained K but current scenario is quite different. In order to feed ever increasing world population, high yielding varieties and extensive agriculture is being practiced, which cause depletion of all nutrients, especially K because plant require higher K compared to other nutrients. Although soils K reserves are large, these are in mineral form (mica, illite, biotite etc.), which are not bioavailable. The solubilization of these reserves can play a critical role in maintaining soil fertility and making agriculture sustainable. Solubilization of these nutrients from mineral sources can be best achieved through microbes. However, efficient indigenous microbes in soil are not enough. Isolation of these microbes followed by mass production for augmentative use as biofertilizers and biological inoculants has the potential to mitigate K deficiency in the future.

Although, in some countries of the world, these products are extensively used especially in China and Korea because their significant large production areas of cultivated soils are deficient in bioavailable K and is considered a major limiting factor for sustainable food security (Xie, 1998). Therefore, use of KSMs as biofertilizers can be a better strategy to improve crop production and can be used to reduce synthetic fertilizer demand and thereby supporting environment friendly agriculture (Sheng et al., 2003). These biofertilizers were used in tea for K solubilization and growth production. These KSMs based biofertilizer has higher potential for solubilization of K minerals and synthetic K fertilizers muriate of potash (MOP). However, solubilization index showed that biofertilizer formulation performed better for MOP compared to K minerals. It was also observed that glucose and ammonium nitrate supplementation supported MOP availability than other mineral K sources. Considering the economic crises of tea cultivators as a case study, it appears that use of KSB containing biofertilizers in combination with synthetic K fertilizers may be an economically feasible eco-friendly option. Regardless of the original discovery of plant association of a microbe, these products can be used for other plants. It is encouraging to note that biofertilizers containing multiple microbes are currently present in market. A few examples are P solubilizers (*Bacillus megaterium*), N-fixer (*Azotobacter chroococcum*), arbuscular mycorrhizal fungi (*Glomus mosseae* and *Glomus intraradices*) and K-solubilizers (*Bacillus mucilaginous*) (supplied by V-mark Resources, Hong Kong). According to Wu et al. (2005) biofertilizers were better option for promotion of growth and yield of maize and enhancing soil sustainability. Consequently, it is important to search for more species of microbes and genes, which can solubilize K minerals, and make them available to growers as commercial products. As more nutrient solubilizing products become available in the market in the future, those should provide better solution for crop growth and provide more benefit to agriculture (Liu et al., 2012).

10. Concluding remarks and prospects

Agricultural soils continue to be depleted of nutrients, especially K. Higher prices of K fertilizers and less awareness of farmers about this deficiency worsens the situation. Utilization of naturally present but not bioavailable K sources is critical to sustainable agriculture. Rhizospheric microbes significantly contribute to solubilization of