
Role of Rhizosphere Microflora in Potassium Solubilization

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Abstract

The K^+ is not just the essential nutrient required to support optimal plant growth and yield, it is also an important signaling agent mediating a wide range of plant adaptive responses to abiotic and biotic stresses such as drought, salinity, oxidative stress, and apoptosis. The main source of K^+ for plant is soil which is taken up by the plant roots through the epidermal and cortical cells and transported to the shoot and distributed to the leaves. Movement of K^+ is facilitated by transport systems present in the cell membrane and the availability of which strongly determines crop yield. It is important to note that only a small percentage of the total K^+ of the soil exists in a form available for plant uptake. The remainder is in complex with other elements and organic matter, making it unavailable and even intensive agricultural practices is adding to K^+ deficiency in soil. It is already reported that large agricultural areas of world are deficient in K^+ availability which is a major concern today. In this connection, efforts to understand the K^+ uptake by plants and its solubilization from the K-bearing minerals such as waste muscovite, biotite, feldspars, orthoclase, illite, and mica have been undertaken. Recent investigations have shown that organic exudates of some microorganisms such as *Pseudomonas* spp., *Burkholderia* spp., *Acidithiobacillus ferrooxidans*, *Bacillus mucilaginosus*, *B. edaphicus*, *B. megaterium*, and *Aspergillus* spp., and even plant roots play a key role in releasing non-available K^+ from the minerals. The list of rhizosphere microflora with potassium solubilization is increasing, and hence the present chapter discusses the mechanism of K^+ solubilization and its role in signaling its uptake system in plants. Plant species effective in K^+ uptake and K^+ -solubilizing microbial populations may be further key factors that control the K^+ release from soil minerals.

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KeywordsPotassium solubilization • Rhizosphere microflora • K^+ uptake • Minerals**4.1 Introduction**

Sustainable agriculture is taking front seat for the next green revolution, and it is considered to be the best alternative for conventional agriculture, which is considered to be slow and failing to yield to the expectations of human beings in agricultural needs. Conventional agriculture also demands more inputs in terms of chemical fertilizers and pesticides which is converting the agricultural practice nonprofit for farmers (Kumar et al. 2015; Singh et al. 2015). Along with these, the steady increase in corporate farming-based conventional methods in the last few decades, which is primarily profit driven, has increased the destabilization of rural communities as well as increased the detrimental effects on both the farmland ecology and surrounding natural environments. The sustainable agriculture in turn is eco-friendly with fewer inputs to agricultural fields, and supply of important nutrients required for plant growth will be taken care by microbial activity. Microorganisms are supporting plant growth from the time immemorial as a component of soil and in continuous association with roots. This type of agriculture uses a special farming technique wherein the environmental resources can be fully utilized and at the same time ensuring that no harm was done to it. Thus the technique is environment friendly and ensures safe and healthy agricultural products.

Soil microorganisms in particular and microbial populations in general are instrumental in fundamental processes such as biogeochemical cycles that drive stability and productivity of agroecosystems. Even today there is a continuous investigation on the diversity, dynamics, and importance of these microbes in agricultural productivity (Singh et al. 2011).

Plants require several nutrients for its growth. These nutrients are usually supplied through chemical fertilizers which contain inorganic salts of the macronutrients such as nitrogen,

phosphorus, and potassium. Fertilizers having only one of these three nutrients are termed as straight fertilizers such as superphosphate, ammonium nitrate, and muriate of potash (a source of potassium), where as fertilizers that contain two or more mineral nutrients are referred to as compound fertilizers or mixed fertilizers used in combinations such as 10:14:10, which refers to the effective percentages of N, P_2O_5 , and K_2O , respectively, in the fertilizer. Among these, potassium is an essential plant nutrient required in large amounts by plants and hence referred to as a macronutrient. The common fertilizer sources of K^+ are KCl, $K_2SO_4-2MgSO_4$, KNO_3 , and K_2SO_4 .

K is available mainly in minerals such as feldspar, mica, and clays such as montmorillonite, vermiculite, and illite. Biotite is also known as a mica-type mineral containing K, Fe, and Mg. However, of immediate concern to crop production is the portion of this nutrient that is in an exchangeable (available) form available for plant use. ~72 % of India's agricultural area needs immediate K fertilizers for increased crop production. 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 (Meena et al. 2014a).

K and N are absorbed by plants in larger amounts than either magnesium or calcium. Among these K plays an important role in numerous plant functions such as nutrient absorption, respiration, transpiration, and enzyme activity. K is unique because it does not become part of plant compounds, but remains in ionic form in the plant; it remains in plant residues after harvest and in manure which is quickly returned to the soil by water leaching through both the components. Once released to the soil, understanding its availability to plants is actually a mystery even to modern science. Even though effects of K on plants growth and yield are well known, but exactly why and how it happens is not

completely understood (Xie 1998). Hence deficiency in plant-available P and K is still considered to be a major limiting factor to food production in many agricultural soils.

4.2 Sources of K in Soil

Soil is a primary source of several mineral nutrients including potassium. The continental crust comprises of potassium 2.1 % along with other elements. It is a cation generally bound to the surface of soil particles which is negatively charged. Addition of a cation such as potassium K^+ can displace another cation such as calcium (Ca^{2+}) from its binding on the surface of the soil particle and make it available for uptake by the root.

The total K^+ content of soils frequently exceeds 20,000 ppm. Most of K component of soil minerals is not available for plant growth. Due to large differences in soil parent materials and the effect of weathering of these minerals in different agricultural fields, the amount of K^+ supplied by soils to plants also varies. Therefore, the need of K^+ in a fertilization program varies for different agriculture production system.

K is available in soil such as unavailable, slowly available or fixed, and readily available or exchangeable. Several factors such as soil type, temperature, wetting and drying cycles, pH, aeration, moisture and even complex interactions of soil mineralogical and textural factors, and biological processes determine how readily structural or fixed K^+ in soil minerals may become available for crop uptake (Hinsinger and Jaillard 1993; Hinsinger et al. 1993; Wang et al. 2000). Typically 98 % of all soil K^+ is found in K-feldspars and phyllosilicates (Andrist-Rangel et al. 2010). The exact mechanism by which some of these factors influence the reactions required for release of K in soil is not clearly understood.

The imbalance in the potassium is generally caused by crop removal, fixation, and leaching. Aside from the contributions of rainwater, atmospheric deposits, and the recycling of elements contained in falling leaves and dead roots, soil minerals (primary and secondary minerals)

constitute the main reservoir of inorganic nutrients for the long-lasting functioning of these ecosystems. In fact a fertile soil is distinguished from an infertile soil not by the fact that it contains more NPK but by the fact that the nutrients present in the soil are liberated with greater rapidity in the fertile than in the unfertile soil.

In most virgin soils, plants rely totally on the soluble and exchangeable K pools for their requirements. The unavailable form is contained in unweathered or slightly weathered minerals and is not available to plants. This accounts for 90–98 % of the total potassium in soils. Along with this after prolonged periods of agricultural production and removal of produce, pools of potassium in soil are slowly depleted. Once depletion of exchangeable potassium occurs, plants rely on the release of fixed potassium to recharge the exchangeable and soluble pools. However in many soils, the size of the fixed potassium pool, or the rate at which it is released, is insufficient to meet plant demand. This is particularly the case where intensive, high-yielding production systems are established.

4.3 Rhizosphere Microflora

Rhizosphere is the zone of soil surrounding a plant root where the biology and chemistry of the soil are influenced by the root exudates such as amino acids, organic acids, carbohydrates, sugars, mucilage, and proteins (Lugtenberg and Kamilova 2009). The ability of microorganisms in particular and rhizobacteria in particular to use these exudates as carbon source correlates with rhizosphere competence and also the microbial diversity around roots. The specific chemotoxicity between the root and its surroundings selectively decides the group of microbial flora to be colonized around the root, and hence these selected bacteria in turn may play an important role in plant growth promotion (Droge et al. 2012).

In turn, rhizosphere microorganisms play a significant role on plant growth by various mechanisms, namely, fixation of atmospheric nitrogen, utilization of 1-aminocyclopropane-1-

carboxylic acid (ACC) as the sole N source, production of siderophores, and production of plant growth regulators (hormones). Further, many microorganisms in serpentine soil are able to solubilize “unavailable” forms of heavy metal-bearing minerals by excreting organic acids (Rajkumar et al. 2009).

The intensification of mineral weathering in the rhizosphere can be attributed, in part, to root-associated fungal and bacterial communities. There is increasing evidence that the mineral weathering by soil fungi and bacteria affects ion cycling and plant nutrition (Toro et al. 1997; Wallander 2000; Calvaruso et al. 2006). Until recently, mineral-weathering ability to release P and K from apatite and biotite has been mainly documented in mycorrhizal fungi (Wallander 2000; Blum et al. 2002; Glowa et al. 2003). However, the presence of weathering bacteria was reported in the rhizosphere or rhizoplane of several plants, including desert plants (*Helianthus annuus jaegeri* and annual sunflower) (Goldstein et al. 1999), mangrove trees (Vazquez et al. 2000), and cactus (Puente et al. 2004).

These bacteria isolated from rhizosphere of different plants are characterized for their ability to solubilize minerals. *Sphingomonas* spp. and *Collimonas* spp. isolated from oak-*Scleroderma citrinum* mycorrhizosphere, *Pseudomonas* spp. isolated from forest soil (Calvaruso et al. 2009; Uroz et al. 2007), *Rahnella* spp. isolated from rhizosphere of soybean, *Rhizobium* spp. isolated from agricultural soil (Kim et al. 1998), *Azospirillum* spp. isolated from rhizosphere of sugarcane (Rodriguez et al. 2004), *Acinetobacter* spp. isolated from rhizosphere of soybean, *Burkholderia* spp., and *Enterobacter* spp. (Vassilev et al. 2006) are reported to solubilize the soil minerals (Meena et al. 2013, 2014a, b; Maurya et al. 2014).

It is well documented that the production of siderophores in the rhizosphere greatly contributes to the growth-promoting effect of bacteria on plants. Siderophore-producing bacteria *Variovorax paradoxus*, *Flavobacterium* spp., *Rhodococcus* spp., *Ralstonia* spp., *Arthrobacter* spp., *Stenotrophomonas* spp., and *Pseudomonas* spp. isolated from rhizosphere of *Brassica juncea* (Belimov et al. 2005); *Pseudomonas* spp., *Serratia*

marcescens, and *Streptomyces* spp. isolated from different rhizosphere soil (Kuffner et al. 2008); *Microbacterium* spp., *S. liquefaciens*, *P. tolaasii*, *P. fluorescens*, *Ralstonia taiwanensis*, *Agrobacterium tumefaciens*, *Paracoccus* spp., and *Cellulomonas* spp. isolated from rhizosphere of perennial Gramineae grasses (Dell'Amico et al. 2005); and *Methylobacterium mesophilicum*, *M. extorquens*, *Methylobacterium* spp., *Burkholderia terricola*, *Okibacterium fritillariae*, *Rhodococcus fascians*, *Rhodococcus* spp., and *Microbacterium* spp. isolated from rhizosphere of *Thlaspi goesingense* (Idris et al. 2004) need to be evaluated for its capacity to solubilize K as they are already reported to be associated with metal-contaminated rhizosphere.

4.4 Potassium-Solubilizing Microorganisms (KSMs)

Evolution studies have proved that stones can be considered as a primary ecosystem which are rich in several minerals and are supplied to the plants through effective microbial mineral-leaching abilities due to its extraordinary adaptive capacity through simple gene regulation. These pioneer microbes will release the inorganic nutrients/minerals required for the establishment of other organisms including plants (Banfield et al. 1999). Even to date, it has been accepted that lichens are the first weathering pioneer organisms in both types of ecological successions, whereas now the list also includes bacteria from different genera such as *Anabaena* spp., *Bradyrhizobium* spp., *Burkholderia* spp., and *Collimonas* spp. (Mannisto and Haggblom 2006; Seneviratne and Indrasena 2006; Gorbushina 2007).

Nowadays, several bacteria including KSMs play an essential role in the environment by contributing to the release of key nutrients from primary minerals that are required not only for their own nutrition but also for that of plants. Fundamentally, KSB is a heterotrophic bacterium which obtains their energy and cellular carbon from preexisting organic material. Thus, they are important in the formation of humus in soil, the cycling of other minerals tied up in

Table 4.1 Potential potassium-solubilizing microorganisms

Potassium-solubilizing microorganisms	References
<i>Penicillium frequentans</i> , <i>Cladosporium</i> spp.	Argelis et al. (1993)
<i>Paenibacillus mucilaginosus</i>	Liu et al. (2012) and Hu et al. (2006)
<i>Aspergillus niger</i> , <i>Penicillium</i> spp.	Sperberg (1958)
<i>B. megaterium</i> , <i>Pseudomonas</i> spp., <i>B. subtilis</i>	Taha et al. (1969)
<i>B. megaterium</i> , <i>E. freundi</i>	Taha et al. (1969)
<i>Arthrobacter</i> spp., <i>Bacillus</i> spp., <i>B. firmus</i>	Bajpai and Sundara (1971)
<i>Aspergillus fumigatus</i> , <i>Aspergillus candidus</i>	Banik and Dey (1982)
<i>Pseudomonas aeruginosa</i>	Sheng et al. (2003) and Badar et al. (2006)
<i>B. mucilaginosus</i>	Vandevivere et al. (1994), Welch and Ullman (1999), Sheng and He (2006), and Zakaria (2009)
<i>Pseudomonas</i> spp.	Krishnamurthy (1989)
<i>Pseudomonas</i> spp., <i>Burkholderia</i> spp., <i>Acidithiobacillus ferrooxidans</i> , <i>Bacillus mucilaginosus</i> , <i>Bacillus edaphicus</i> , and <i>Bacillus megaterium</i>	Sheng et al. (2002)
<i>Bacillus edaphicus</i>	Sheng and He (2006)
<i>A. fumigatus</i>	Teng and Lian (2007)
<i>Bacillus globisporus</i>	Sheng et al. (2008)
<i>Pseudomonas</i> , <i>Burkholderia</i> , <i>Acidithiobacillus ferrooxidans</i> , <i>Bacillus mucilaginosus</i> , <i>Bacillus edaphicus</i> , <i>B. circulans</i> and <i>Paenibacillus</i> spp.	Sheng (2005), Lian et al. (2002), Li et al. (2006), and Liu et al. (2012)
<i>Pseudomonas chlororaphis</i> and <i>Bacillus megaterium</i>	Yu et al. (2012)
<i>Bacillus altitudinis</i>	Huang et al. (2013)
<i>Bacillus</i> spp.	Gundala et al. (2013)
<i>Buttiauxella izardii</i> , <i>Enterobacter cancerogenus</i> , <i>Burkholderia ubonensis</i> , <i>E. hormaechei</i> , and <i>Burkholderia pyrrocinia</i>	Ruangsanka (2014)
<i>Klebsiella variicola</i> , <i>Enterobacter cloacae</i> , <i>E. asburiae</i> , <i>E. aerogenes</i> , <i>Pantoea agglomerans</i> , <i>Agrobacterium tumefaciens</i> , <i>Microbacterium foliorum</i> , <i>Myroides odoratimimus</i> , and <i>Burkholderia cepacia</i>	Zhang and Kong (2014)

organic matter, and the prevention of buildup of dead organic materials. Besides, the KSB are aerobic bacteria which play an important role in maintaining soil structure by their contribution in the formation and stabilization of water-stable soil aggregates (WSA). In addition, Gram-positive bacteria can produce substance that stimulates plant growth or inhibit root pathogens (Zakaria 2009). Moreover, KSB are able to solubilize rock K mineral powder, such as micas, illite, and orthoclases (feldspar) through production and excretion of organic acids or chelate silicon ions to bring the K into solution (Ullman et al. 1996; Bennett et al. 1998; Meena et al. 2015a, b; Singh et al. 2015). Reports on KSMs are increasing and Table 4.1 summarizes the list of microorganisms in potassium mineral leaching and its solubilization.

4.4.1 Role of Earthworms' Gut Microflora in Mineralization of Soil Minerals

Even though earthworms are considered as main component of vermicompost, the role of its gut microflora is the degradation of complex polysaccharides and also helps in mineralizing soil minerals. Earthworms are an ecosystem's engineers, contributing to a wide range of nutrient cycling and geochemical processes in the ecosystem. Their activities can increase rates of silicate mineral weathering. Their intestinal microbes usually are thought to be one of the key drivers of mineral degradation mediated by earthworms, but the diversities of the intestinal microorganisms which were relevant with mineral weathering are unclear. The phylogenetic tree based on the 16S

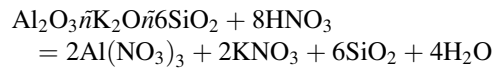
rRNA gene sequences of the clones obtained from the soil in which earthworms fed for 10 days revealed that the library contained sequences homologous to *Verrucomicrobia* (26.86 %); *Bacteroidetes* (24.30 %); *Proteobacteria* (12.8 %) including *Alphaproteobacteria* (0.26 %), *Betaproteobacteria* (0.77 %), *Gammaproteobacteria* (7.42 %), and *Deltaproteobacteria* (4.35 %); *Firmicutes* (2.05 %); *Actinobacteria* (0.52 %); and two unidentified OTUs. The results of the phylogenetic tree and homologous sequences indicated the presence of *Acidobacteriaceae* (*Acidobacteria*, *Acidobacteriales*), *Opitutae* group (*Verrucomicrobia*), *Flavobacterium* spp. (*Bacteroidetes*, *Flavobacteria*, *Flavobacteriales*, *Flavobacteriaceae*), *Sphingobacteriales* (*Bacteroidetes*, *Sphingobacteria*), and *Aquicella* spp. (*Proteobacteria*, *Gammaproteobacteria*, *Legionellales*, *Coxiellaceae*) (Liu et al. 2011). These group organisms need to be evaluated further for its efficacy in mineral weathering in general and K solubilization in particular along with siderophore-producing bacteria as already mentioned.

4.4.2 Transformation of Potassium by Soil Microbes

K is considerably less susceptible to effects of microorganisms in its relationships to plant development in soils. It belongs to a large group of elements in soil which are not affected in a great variety of ways, on account of the fact that they do not enter into organic combination to the extent of such elements as nitrogen or sulfur. Its entrance into organic compounds is more generally confined to replacing the hydrogen of the acid groups where it forms the salts of these acids. In plant residues a large portion of the K is present in inorganic form, occurring in the various fluids of the cells. Upon ignition of the organic substances, the potassium remains in the ash residue. Another factor appreciably limiting the capacities of microorganisms to affect the element is its stable character. It is not oxidized and reduced and consequently cannot be carried through the extensive series of changes common

to nitrogen, sulfur, and iron. The influence of microorganisms on such elements as potassium is confined to causing its solution from organic and inorganic substances and its assimilation in growth of the microbial cells. Considerable potassium becomes added to soils in the form of various organic and inorganic compounds. Stable manures, green manures, plant stubble, and microbial cells all contain K (Wang et al. 2000).

When these organic substances are decomposed by microorganisms in the soil, the potassium is liberated in forms available to higher plants. A small part of this K may be re-assimilated by the microbes which bring about the decomposition processes, thus part of the potassium may be temporarily removed from circulation. The ash of bacteria and fungi usually contains between 5 and 40 % of potassium calculated as K_2O . The inorganic forms of K added to the soil as fertilizers are generally soluble, but the minerals in the soil which contain potassium are quite insoluble. Solution of potassium from these minerals is accelerated by interaction with various acids produced by microorganisms, as shown in the case of orthoclase:



The products of nitrification and sulfur oxidation, as well as the carbonic acid produced by the microbial population in general, aid in such solution of potassium.

4.5 Role of Potassium in Plant Growth and Developments

The nature provides both organic and inorganic nutrients required for living organisms through soil. Some of these inorganic elements, such as sodium, potassium, calcium, and magnesium, are present in bulk because it is available in large concentrations.

Potassium, present in the form of cation K^+ within plants, plays an important role in the regulation of the osmotic potential of plant cells. Enzymes involved in respiration and

photosynthesis are activated by K^+ . Mottled or marginal chlorosis is the first observable symptom of potassium deficiency which is then develops into necrosis primarily at the leaf tips, at the margins, and between veins. These necrotic lesions may initially form at the leaf tips and margins and then extend toward the leaf base in many monocots. These symptoms will appear first on mature leaves than younger leaves because potassium can be mobilized more to the younger leaves. The leaves may also curl and crinkle. The stems of potassium-deficient plants may be slender and weak, with abnormally short internodal regions. In potassium-deficient corn, the roots may have an increased susceptibility to root-rotting fungi present in the soil, and this susceptibility, together with effects on the stem, results in an increased tendency for the plant to be easily bent to the ground (lodging).

When relating acute deficiency symptoms to a particular essential element, an important clue is the extent to which an element can be recycled from older to younger leaves. Some elements, such as nitrogen, phosphorus, and potassium, can readily move from leaf to leaf; others, such as boron, iron, and calcium, are relatively immobile in most plant species. If an essential element is mobile, deficiency symptoms tend to appear first in older leaves.

Maintenance of osmotic balance and for the generation of ionic gradients across membranes, Na^+ and K^+ (together with H^+ and Cl^-) which bind weakly to organic ligands, are ideally suited. In contrast, Mg^{2+} and Ca^{2+} with intermediate-binding strengths to organic ligands can play important structural roles and, in the particular case of Ca^{2+} , serve as a charge carrier and a trigger for signal transmission. Zn^{2+} not only plays a structural role but can also fulfill a very important function as a Lewis acid. Organic ligands which bind tightly with redox metal ions like iron and copper play an important role in oxygen transport besides participating in innumerable redox reactions.

The regulation of the flow of ions across cell membranes is absolutely essential for the functioning of living cells. Because of the hydrophobicity of cellular membranes, the

energetically driven preference of ionic species such as Na, K, Cl, H, and Ca to cross, never mind to find them preferentially on one side or the other of a biological membrane, would be impossible. Without ionic gradients, which maintain high concentrations of K^+ within the cell and low concentrations of Na^+ , cells would not be able to carry out their normal metabolic activities. This means, in simplistic terms, that some molecular machines must be able to distinguish between Na^+ and K^+ ions (presumably unhydrated, since the degree of hydration could make for difficulties in discrimination).

Another significant function of potassium is in the construction of the cuticle layer. This cuticle layer is the plant's first line of defense to disease and insect attack. Plants receiving adequate potassium nutrition have a stronger enzyme activity and are capable of withstanding more fungal attack. Increasing potassium will reduce the amount of disease both in the root and in the above ground parts of the plant.

In plants, hence potassium plays a vital role in a wide range of both biophysical and biochemical processes. It exists as a monovalent cation and does not participate in covalent binding; it functions to maintain charge balance. The preservation of cell turgor pressure is very sensitive to a limited K^+ supply. Indeed, due to its high mobility, K^+ is usually the principle cation that contributes to vacuole and cell expansion (Hamamoto and Uozumi 2014). Nonetheless, over a longer time scale, it can be replaced by Na^+ (Jeschke and Wolf 1988) and/or organic solutes, explaining the observed highly variable (10–200 mM) vacuolar K^+ levels. In contrast, cytoplasmic levels are relatively stable, near 100 mM. It is suggested that as total tissue K^+ concentration declines, the cytoplasm maintains a homeostatic concentration of K^+ to enable K^+ -dependent processes. Consequently, any initial changes in tissue K^+ concentrations are likely to be at the expense of vacuolar K^+ , with other solutes being diverted to the vacuole to maintain the osmotic potential.

Extent of turgor pressure (usually around 4 atm for *E. coli*) is determined by the concentration of intracellular solutes (glutamate, potassium). To establish cell turgor and maintain cell

electroneutrality, K^+ will act as a principle cation and > 70 enzymes in plants will utilize K^+ as a cofactor.

At the biochemical level, K^+ plays an important role in the activation of many enzymes, especially in protein and starch synthesis, as well as in respiratory and photosynthetic metabolism. Starch synthesis, for instance, has a requirement of about 50 mM K^+ for normal activity. In line with this level, most K^+ -requiring enzymes need about 10–50 mM of K^+ for optimal activity. Interestingly, these levels may be reduced by the substitution of other monovalent cations for K^+ . For example, Rb^+ , Cs^+ , and NH_4^+ are about 80 % as effective as K^+ at maintaining starch synthetase activity, while Na^+ is approximately 20 % as effective. Hence, in both biophysical and biochemical processes, K^+ may be the most efficient monovalent cation, although to a certain extent, it can be replaced.

4.5.1 Potassium Uptake in Plants

There are three families of plant K^+ transport systems that are active at the plasma membrane: the Shaker K^+ channel family, comprised of voltage-gated channels that dominate the plasma membrane conductance to K^+ in most environmental conditions, and two families of transporters, the HAK/KUP/KT K^+ transporter family, which includes some high-affinity transporters, and the HKT K^+ and/or Na^+ transporter family, in which K^+ -permeable members seem to be present in monocots only (Very et al. 2014).

A number of regulatory partners have been identified that control the targeting or the activity of plant Shaker channels at the plasma membrane. These include β -subunits (Zhang et al. 1999), 14-3-3 proteins (Sottocornola et al. 2006), different types of kinases (Xu et al. 2006; Zhao et al. 2013), phosphatase (Chérel et al. 2002; Lee et al. 2007), and SNAREs (Sutter et al. 2006; Honsbein et al. 2009).

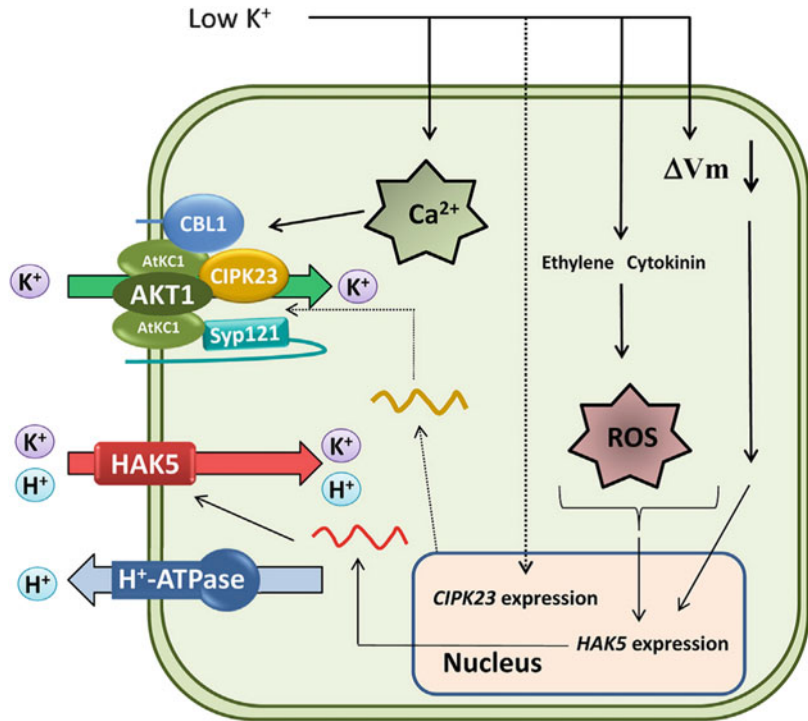
4.5.2 Potassium Deficiencies in Plants

Proteomic study of the plant response to potassium deficiency has revealed the overexpression of several proteins compared to normal K availability. HAK/KUP transporters at the tonoplast (Hamamoto and Uozumi 2014) are one such example, which are energized via coupling to the transtonoplast motive force. This transporter helps in the active transport of the K from the vacuole to the cytoplasm against concentration gradient (Walker et al. 1996). This indicates that the prolonged K starvation imparts additional energy burden on plants directly affecting the crop yield.

Sensing of and response to K^+ by the plant appear to be mediated by a number of different means. These include the cell membrane potential, reactive oxygen species (ROS), Ca^{2+} , hormones (ethylene, jasmonic acid, or cytokinins), and direct sensing of the environmental K^+ concentrations by K^+ channels. During K^+ starvation, there is a transcriptional upregulation of *Arabidopsis* HAK5 and its homologues from other plant species (Alemán et al. 2009; Martínez-Cordero et al. 2004; Nieves-Cordones et al. 2007; Wang et al. 2002) and repressed after K^+ resupply (Ahn et al. 2004; Armengaud et al. 2004; Gierth et al. 2005; Nieves-Cordones et al. 2008).

Hyperpolarization of the membrane potential is considered to be the first effects of root cells to K^+ deprivation (Amtmann et al. 2006). This suggests a role for the membrane potential in the regulation of this type of genes. In addition, AtHAK5 expression is dependent on reactive oxygen species (ROS) production and K^+ -deficient plants rapidly accumulate ROS (Hernandez et al. 2012; Shin et al. 2005; Shin and Schachtman 2004; Demidchik 2014). Initiation of the signal cascades which activates the K^+ uptake epidermal cells in the root tip is by a rapid accumulation of ROS at 24 h of K^+ starvation. After the accumulation of ROS, the activity of antioxidative enzymes such as superoxide dismutase, peroxidase, and ascorbate peroxidase, is increased, and oxidative damage resulted in

Fig. 4.1 K^+ sensing in plants: elements involved in low K^+ response of root cells (Nieves-Cordones et al. 2014)



prolonged K^+ starvation (Hernandez et al. 2012). ROS production in response to K^+ deficiency and modulation of AtHAK5 expression after K^+ starvation is mainly contributed by *Arabidopsis* class III peroxidase RCI3 (Kim et al. 2010). Ethylene inhibitors will block the production of ROS in K^+ -deficient plants, indicating that this hormone is involved in low K^+ signaling upstream ROS (Fig. 4.1).

4.6 Roles of KSMs in Agriculture

Soil erosion, crop uptake, runoff, and leaching will decrease the potassium content in soils (Sheng and Huang 2002). In these instances, potassium fertilizer must be applied to ensure healthy plant growth. The direct application of rock phosphate (RP) and potassium (rock K) materials is more agronomically useful and even environmentally feasible than soluble P and K (Rajan et al. 1996; Ranawat et al. 2009). It is also considered as cheaper sources of P and K, but they are not easily available to plants because of its slow release of

the mineral, and its use seems to be insignificant in present-day agriculture due to overemphasis on more yields at short time. In contrast, plant growth, nutrition, root growth pattern, plant competitiveness, and responses to external stress factors are improved by the application of P and K solubilizers (Vessey 2003; Sheng 2005; Setiawati and Handayanto 2010; Ekin 2010).

Increased availability and uptake of P and K by the maize plants grown on P- and K-limited soil by co-inoculating the PSB (*B. megaterium* var. *phosphaticum*) and KSB (*B. mucilaginosus* and *B. subtilis*) with direct application of RP and K materials [R+ (P+ K)] into the soil was reported by Abou-el-Seoud and Abdel-Megeed (2012). It was also observed that plant growth is increased by the co-inoculation of beneficial microorganisms.

Increasing the bioavailability of P and K in the soils may also be achieved by adding rock materials along with co-inoculation (Lin et al. 2002; Han and Lee 2005; Han et al. 2006), and it will also lead to increased P and K uptake and plant growth (Han et al. 2006; Chen et al. 2006; Eweda et al. 2007;

Jorquera et al. 2008; Sabannavar and Lakshman 2009).

The highest biomass and seedling height of *Zea mays* were observed by the use of biofertilizer containing arbuscular mycorrhizal fungus (*G. mosseae*), N fixer (*A. chroococcum*), P solubilizers (*B. megaterium*), and K solubilizers (*B. mucilaginosus*) (Wua et al. 2005). Maize and wheat plants which are inoculated with *B. mucilaginosus*, *A. chroococcum*, and *Rhizobium* spp. made a good source of K availability for plant growth from waste mica, which in turn acted as a source of potassium (Singh et al. 2010). Therefore, KSB are extensively used as biofertilizers in Korea and China as significant areas of cultivated soils in these countries are deficient in soil-available K (Xie 1998). Thus, application of KSB as biofertilizer for agriculture improvement can reduce the use of agrochemicals and support eco-friendly crop production under sustainable agriculture (Sheng et al. 2003; Sindhu et al. 2010).

According to Simonsson et al. (2007), a study was conducted on the release and fixation rates of K ($\text{kg ha}^{-1} \text{ year}^{-1}$) estimated in five long-term field experiments located on varying parent materials in South and Central Sweden, each having an array of K fertilizer application rates. The resulted estimates ranged from $65 \pm 07 \text{ kg ha}^{-1} \text{ year}^{-1}$ of K released from soil reserves to $85 \pm 10 \text{ kg ha}^{-1} \text{ year}^{-1}$ of K trapped by fixation. Release and fixation rates were highly dependent on the soil K balance, confirming that these are reversible processes that depend on plant uptake and fertilizer input. Soils, with a texture from sandy loam to clay, showed release rates approaching the net K output, when not K fertilized. These calculations carried out by them were based on accumulated K inputs and outputs from the soil during the 30 years and on changes in topsoil and subsoil exchangeable K.

It is estimated that 1 ha of soil may have anywhere between several tonnes to several hundred tonnes of K held in the structure of micas and K feldspars within the rooting zone (Sparks and Huang 1985). Of this, exchangeable K is traditionally believed to form a reserve that is available for

uptake by plants in the short term. The size of this pool may be a few hundred kg ha^{-1} , i.e., corresponding to the demand of just a few years of intense cropping. It has long been known that crops may also extract K from non-exchangeable sources on a time scale of only a few years (Gholston and Hoover 1948). Nonetheless, negative K balances (harvest > fertilization) may be a concern in agriculture, if release of fixed or structural mineral K from soil minerals does not compensate for nutrient offtake and losses. Indeed, negative field K balances are common in mixed systems with both livestock and arable farming, especially in organic farming systems, which mainly rely on on-farm nutrient recycling and internal sources (Oborn et al. 2005).

Recently *Frateruria aurantia*, a potassium-mobilizing bacteria (KMB) isolated from banana rhizosphere, has the ability to mobilize the elementary or mixture of potassium which can be easily absorbed by plants. It is estimated that 50–60 % of potash chemical fertilizers usage can be reduced by using *F. aurantia* as a biological inoculant. It belongs to the family *Pseudomonadaceae* and shown to have the extra ability to mobilize K in almost all types of soils especially, low K content soils, soils of pH 5–11, and it survived in the temperature up to 42 °C. Pindi and Satyanarayana (2012) proved that this KMB can be used as a biofertilizer and can be applied in combination with *Rhizobium*, *Azospirillum*, *Azotobacter*, PSM, etc.

4.7 Mechanism of K Solubilization by Soil Microflora

The soil is influenced by the biological weathering of minerals. Mineral weathering is more rapid in the rhizosphere than in bulk soil without roots. This intensification of the mineral-weathering process can be linked to the pH status of the rhizosphere, which is generally different to that of bulk soil (Fig. 4.2). This variation in pH and the mineral-weathering intensification can be due to the plants themselves: their growing roots might physically disrupt the mineral particles, exposing new surface areas to weathering,

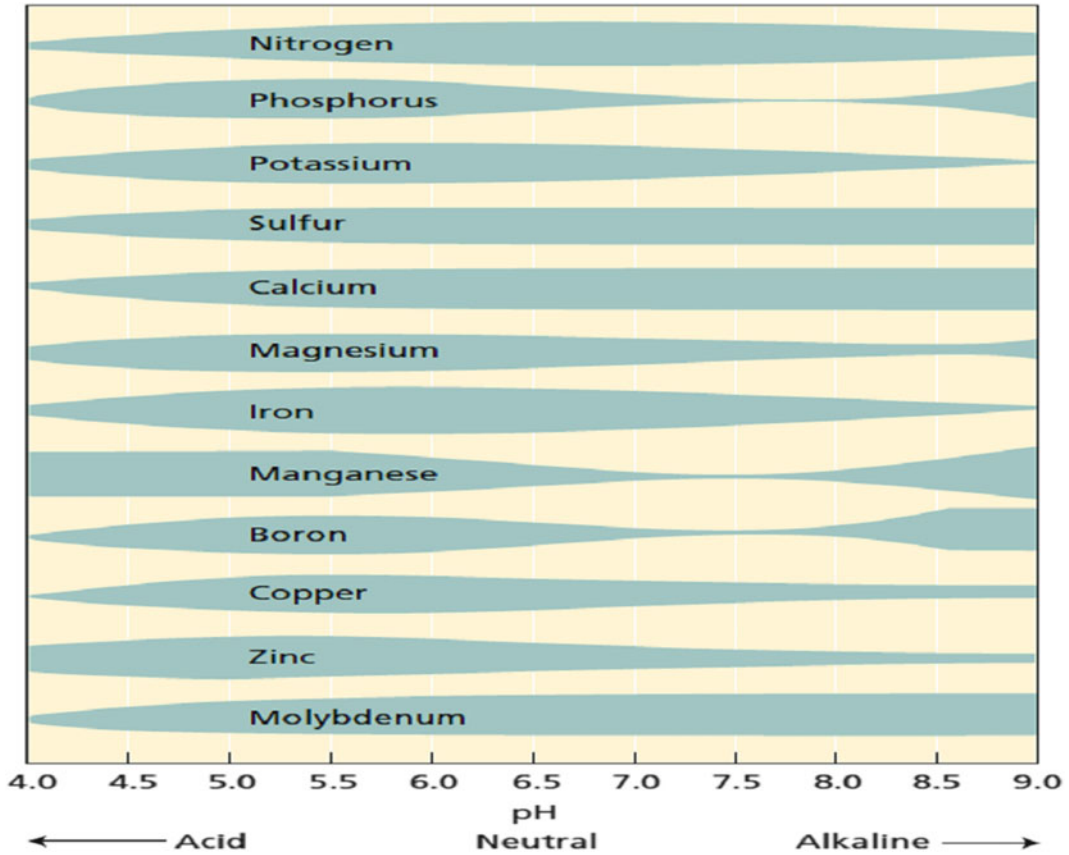
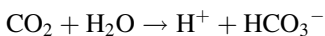


Fig. 4.2 Influence of soil pH on the availability of nutrient elements in organic soils. The width of the shaded areas indicates the degree of nutrient availability to the

plant root. All of these nutrients are available in the pH range of 5.5–6.5 (Lucas and Davis 1961)

and/or the exuded metabolites (such as organic acids and protons) might act directly on mineral-weathering kinetics (Barker et al. 1997).

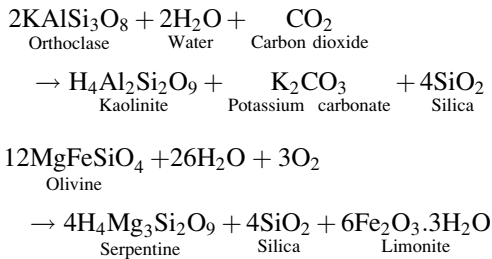
The protons associated with organic acid molecules decrease the pH of the solution and, therefore, induce the releasing of cations such as iron, potassium, and magnesium (Uroz et al. 2009). Major factors that lower the soil pH are the decomposition of organic matter and the amount of rainfall. Carbon dioxide is produced as a result of the decomposition of organic material and equilibrates with soil water in the following reaction:



This reaction releases hydrogen ions (H^+), lowering the pH of the soil. Microbial decomposition of organic material also produces ammonia and hydrogen sulfide that can be oxidized in the soil to form the strong acids such as nitric acid (HNO_3) and sulfuric acid (H_2SO_4). Hydrogen ions also displace K^+ , Mg^{2+} , Ca^{2+} , and Mn^{2+} from the cation-exchange complex in a soil. Leaching then may remove these ions from the upper soil layers, leaving a more acid soil. By contrast, the weathering of rock in arid regions releases K^+ , Mg^{2+} , Ca^{2+} , and Mn^{2+} to the soil, but because of the low rainfall, these ions do not leach from the upper soil layers, and the soil remains alkaline.

The monovalent cations such as potassium (K^+) can form electrostatic bonds with the carboxylic groups of many organic acids. Nonetheless, much of the potassium that is accumulated by plant cells and functions in osmotic regulation and enzyme activation remains in the cytosol and the vacuole as the free ion.

The chemical processes involved in the weathering of rocks are those of hydrolysis, oxidation, hydration, solution, and carbonation or carbonate formation. The following reactions illustrate the chemical changes involved in the weathering of orthoclase and olivine, two rock-forming minerals:



4.7.1 Role of Acids in Mineral Solubilization

B. mucilaginosus and *B. edaphicus* can generate polysaccharide and carboxylic acids, such as tartaric acid and citric acid, to solubilize K compounds (Lian et al. 2002). Using K-solubilizing microbes to increase the concentration of available K ions in the soil may mitigate K deficiency (Barker et al. 1998). New facultative alkaliphilic *Bacillus* spp. are isolated from mica mines of Nellore District of Andhra Pradesh, India. The analysis of the culture medium by high-pressure liquid chromatography identified gluconic acid as the main organic acid released by *Bacillus* spp. SVUNM9. This study is the first report on the isolation and characterization of indigenous KSB from mica ore (Gundala et al. 2013).

The release of potassium in accessible form from K-bearing minerals in soils has been reported by a wide range of bacteria, namely, *Pseudomonas*, *Burkholderia*, *Acidithiobacillus ferrooxidans*, *B. mucilaginosus*, *B. edaphicus*,

B. circulans, and *Paenibacillus* spp. (Sheng 2005; Lian et al. 2002; Li et al. 2006; Liu et al. 2012). These KSB were found to dissolve potassium, silicon, and aluminum from insoluble K-bearing minerals such as micas, illite, and orthoclases, by excreting organic acids which either directly dissolved rock K or chelated silicon ions to bring K into the solution (Bennett et al. 1998).

Solubilization of K and silicon from the silicate minerals by the KSMs resulted mostly from the action of organic acids. Gluconic acid seemed to be the most active agent for the solubilization of the three silicate minerals. Gluconic and acetic acids were likely involved in the solubilization of feldspar. The strain could be acid or alkali and salt tolerant and temperature resistant (Sheng et al. 2008).

The *B. altitudinis* strain could accelerate weathering of potash feldspar, change mineral surface morphology, and induce the formation of new mineral complex. The strain dissolved potash feldspar and significantly released more Si, Al, and Fe elements by producing more organic acids. Many bacteria and some spherical minerals were observed on the surfaces of the feldspar and the energy-dispersive spectrometry analysis showed that the new minerals contained more Fe. After 30 days, siderite might be the newly formed mineral identified by X-ray diffraction (XRD) in the mineral-weathering process (Huang et al. 2013).

KSB, such as *B. mucilaginosus*, increased K availability in agricultural soils and increased mineral content in plant (Sheng et al. 2002; Zakaria 2009). *B. mucilaginosus* increases the rate of dissolution of silicate and alumino-2 silicate minerals, and it releases the K^+ and SiO_2 from the crystal lattice primarily by generating organic acids (Vandevivere et al. 1994) and accelerates the dissolution of a variety of silicates by the production of extracellular polysaccharides (EPS) (Welch and Ullman 1999). The dispute about the mechanism by which *B. mucilaginosus* decomposes silicate minerals and releases K^+ and SiO_2 may have severely limited the use of the organism in agriculture as a form of biological K fertilizer. Polysaccharides strongly adsorbed the organic

acids and attached to the surface of the mineral, resulting in an area of high concentration of organic acids near the mineral (Liu et al. 2006).

4.8 Effect of KSMs on K Availability in Soils

Organic acids as explained earlier are considered to play an important role in bringing rock K (K-containing primary minerals) to solution through dissolution (Basak and Biswas 2009). In recent studies application of rock K along with the inoculation of KSMs to soil has yielded good results. Cotton, oilseed rape, pepper, cucumber, and Sudan grass resulted beneficial effects when KSMs along with mica were applied to the soil (Sheng et al. 2002; Han and Lee 2005, 2006). The exudates from the KSMs can also effectively increase the release of K from clay minerals. After a series of incubation trials carried out in the laboratory, it revealed that the application of inoculated feldspars into the soil enhances about 40–60 % of K solubility and plant K uptake (Han and Lee 2006; Basak and Biswas 2009; Abou-el-Seoud and Abdel-Megeed 2012). A less information is available on the field application of such methods, which is most likely due to difficulties in soil inoculation under field conditions. In order to evaluate the potential of such applications for agricultural production systems, we need more field studies that evaluate their effect on both soil as well as control conditions.

4.9 Future Approach for KSMs

The possible alternative to solve K deficiency in soil could be to fully exploit the reservoir of K present in the soil. Because minerals are present in a myriad of environments, more bacterial species with mineral-weathering ability, as well as additional molecular mechanisms involved in this process, will continue to be discovered in the future. The use of KSMs has several advantages over conventional chemical fertilizers in agriculture such as the following (a) microbial products are eco-friendly compared

to chemical fertilizers which have a residual effect in the soil; (b) microbial products or microbes will not accumulate in the environment; (c) due to less generation time, repeated inoculation to field is not required; and (d) KSMs are not considered harmful to ecological processes or the environment.

There are many questions which need to be addressed in the future about the application of microorganisms to enhance K solubility in soil. Along with this more studies are needed to identify additional microbial genes, enzymes, and metabolites involved in mineral weathering such as metagenomic analysis of the different agricultural soil. It is also possible to develop methods combining molecular and isotopic approaches, such as stable-isotope probing of nucleic acids, to identify mineral-weathering organisms and quantify their relative contributions.

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