Potassium and Its Role in Sustainable 17
Agriculture

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Abstract

Apart from two major components nitrogen and phosphorous, potassium is the third essential macronutrient required for the growth and metabolism of plant, and its deficiency in plants causes poorly developed roots, slow growth, low resistance to disease, delayed maturity, small seed production and lower yields. The concentration of soluble K in soil is very small as maximum part of K exists in insoluble form. Silt, clay and sand are important components of soil in earth and biggest reservoir of potassium. Most common deposits of potassium are feldspar and mica. The available K level in soil dropped in the last decade due to rapid development of agriculture and application of imbalanced fertilizers. Potassium is released when these minerals are slowly weathered, or, alternatively, it can be solubilized by some beneficial microorganisms and made available for plants. Several bacterial and fungal strains have been identified for their ability of high potassium solubilization. Various species of Pisolithus, Cenococcum, Piloderma, Bacillus, Paenibacillus, Acidithiobacillus, Pseudomonas, Burkholderia, Aspergillus and Clostridium have been reported to release large amount of potassium from different minerals and enhance the productivity of many crops. Co-inoculation of PSMs and KSMs in conjunction with direct application of rock P and K minerals into the soil has been reported to increase N, P and K uptake, photosynthesis and the yield of plants grown in P- and K-limited soils. Thus, identification of microbial strains capable of solubilizing potassium minerals can rapidly conserve our existing resources and escape environmental pollution hazards caused by heavy application of chemical fertilizers.

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17.1 Introduction

Potassium (K) is a soft, silver-white metal, light in its pure form that reacts very violently with water. It is commonly called potash (K_2O) , a term that has been derived from an early production technique where K was leached from wood ashes and concentrated by evaporating the leachate in large iron pots (Mikkelsen and Bruulsema [2005\)](#page-15-0). Soils contain varying quantities of K-bearing minerals that constitute a major K reserve. The K reservoir in the earth crust is associated with primary alumina silicates that are the most abundant K-bearing minerals such as K feldspar, mica, biotite, muscovite and nepheline. The secondary alumina silicates, however, comprise hydrous mica (illite) as well as a continuum of micaceous weathered or inherited products, viz. mixed-layer phyllosilicates (Bertsch and Thomas [1985](#page-13-0)). McAfee [\(2008](#page-15-0)) described feldspar and mica ranging from 90 % to 98 % as the most common soil components of potassium. The potassium content of Indian soils varies from less than 0.5 % to 3.00 % (Mengel and Kirkby [1987](#page-15-0)). Some of the mineral sources available in India containing $3-14\%$ K₂O are glauconitic sand, feldspar, muscovite and nepheline syenite (Indian Minerals Yearbook [2011\)](#page-14-0). Out of various feldspars, potassium feldspar is the most common one and contains up to 13 % $K₂O$ (Rao et al. [1998\)](#page-16-0). Micas are important for plant nutrition because they represent a major source of K, whereas the K in biotite acts as a good fertilizer for plants (Arnold [1963\)](#page-12-0).

17.1.1 Forms of Potassium

Potassium is available in four forms in the soil which are K^+ ions in the soil solution, an exchangeable cation tightly held on the surfaces of clay minerals and organic matter, potassium

fixed by weathered micaceous minerals and potassium present in the lattice of certain K-containing primary minerals. All forms of potassium are linked with each other. The amounts of exchangeable and readily available potassium do not provide the rate at which the non-exchangeable or fixed potassium can move into the exchangeable form. These are the reasons why some soils may have a relatively low level when tested and yet supply enough potassium for relatively high crop yields. It has been hypothesized that the lack of crop response on these soils may be attributed to K release from non-exchangeable soil K, particularly from K feldspars (Rehm and Sorensen [1985](#page-16-0)).

17.1.1.1 Soluble Potassium

Soluble potassium is the most available form but its contribution to total K is very small. According to a report of During [\(1984](#page-13-0)), it ranged from 3 to 30 μg/ml in most soils of New Zealand. This type of potassium does not form any chelates, complexes or ion pairs in the soil. Plants take up most of their potassium directly in this form and so deplete it very rapidly in soil.

17.1.1.2 Exchangeable Potassium

Exchangeable K is defined as the fraction that occupies sites in the soil colloidal complex (Malavolta [1985\)](#page-15-0). It is a major bioavailable form of K in the soil, usually $0.1-2\%$ of total potassium, i.e. between 10 and 400 ppm (Schroeder [1974\)](#page-16-0). The amount of K^+ held by clay minerals at exchange sites depended on kinetic as well as thermodynamic factors (Parfitt [1992\)](#page-16-0).

Release of non-exchangeable K to the exchangeable form occurred when levels of exchangeable and soluble K were decreased due to crop uptake or leaching and perhaps by increase in microbial activity (Sparks et al. [1980;](#page-17-0) Sparks [2000\)](#page-17-0). Hence, the amount of the exchangeable K concentration determines the effectiveness of resupply. The exchangeable K is more related to the type of clay and its net negative charge. It was found that the exchangeable K levels of allophanic soils were relatively small, whereas soils with large amounts of vermiculite or mica had greater amounts of exchangeable K (Parfitt [1992](#page-16-0)). Potassium in this form is mostly contained by minerals as feldspar and mica. For optimal nutrition of a crop, the replenishment of a K-depleted soil solution was affected predominantly by the release of exchangeable K from clay minerals (Sheng and Huang [2002\)](#page-16-0).

17.1.1.3 Fixed Potassium

Fixed K is held between the layers of micaceous clay minerals and not readily accessible for exchange with other solution cations. The K⁺ present in the wedge, edge, step and crack positions can be referred to as fixed K. Potassium in this form is temporarily trapped between the expanding layers of some clay minerals and most likely between structural layers in the soil of micas, intergraded hydrous micas (e.g. illites) and vermiculites or in the wedge zones during edge weathering of the micas (Kirkman et al. [1994](#page-14-0)). A fixed form of potassium in soils which is high in feldspars and volcanic glass where the K is structurally bonded is slowly available to plants over time and cannot be replaced by ordinary cation exchange process. This would contribute little to plant growth, because of the low levels or absence of micaceous 2:1 clay minerals (Fieldes and Swindale [1954](#page-13-0)).

17.1.1.4 Structural Potassium

Potassium within a soil also exists as structural potassium and is variously known as mineral K, unweathered K, native K, matrix K or inert K. It constitutes the largest amount of the total K in most soils (Metson [1980](#page-15-0)). It is mostly bound covalently within the crystal structure of the K-bearing minerals such as micas (biotite and muscovite), feldspars (orthoclase and microcline) and volcanic glasses (acidic and basic) (Metson [1968\)](#page-15-0), and it only becomes available upon long-term weathering. Biotite and basic volcanic glasses were found to weather easily, whereas feldspars and acidic volcanic glass weathered slowly (Fieldes and Swindale [1954\)](#page-13-0). Generally, highly weathered soils from humid and tropical areas have much less structural potassium remaining than newer soils or soils from cold arid climates.

17.2 Potassium as Fertilizer

Glauconite sand contains around $4-8\%$ K₂O and has been used as a source of potash fertilizer worldwide (Majumder et al. [1995](#page-15-0); Yadav et al. [2000](#page-17-0)). The need for potash in fertilizer can be determined by plant analysis and soil testing.

17.2.1 Potassium Chloride

It is a common source of fertilizer, and for the most part, it is mined as sylvite ore (KCl, the potassium analogue of halite, or rock salt, NaCl), mixed with NaCl, beneficiated to remove some of the contaminants and sold. It is highly soluble; hence, excessive rate can cause salt damage to plants. Further, KCl may also be the result of crystallization from brine, either from solution mining of KCl ore or precipitation from hypersaline waters, e.g. Searles Lake and Dead Sea, often with carnallite $(KCIMgCl₂)$ as an intermediate precipitate. The final form of KCl from crystallization processes is white crystals. Typical fertilizer analysis of KCl consists of 60–63 % $K₂O$ and 46 % Cl.

17.2.2 Potassium Sulfate

Potassium sulfate has ~5 % market share and basically constitutes $48-53\%$ K₂O and 17–18 % S. It is found rarely in pure form. This fertilizer is used particularly for horticultural crops in which chloride uptake is a problem, as in tobacco plant.

17.2.3 Potassium Magnesium Sulfate

This is the primary K fertilizer produced by German and French mines from langbeinite ore and historically was called 'double manure salts'. The analysis comprises $20-22\%$ K₂O with secondary nutrients like S (21–22 %) and Mg (10–11 %). Potassium magnesium sulfate is a good source of K when there is also a need for magnesium and sulfate in plant nutrition, though excess K is expected to induce magnesium deficiency.

17.2.4 Potassium Nitrate

In this fertilizer the formulated forms of potassium are KCl and nitric acid with 44 $\%$ K₂O and 13 % N. It is expensive for agronomic use, mostly applied for horticulture and greenhouses. It was also known as saltpetre to the ancients and recognized by Glauber in the seventeenth century as the 'principle of vegetation'. Besides abovecited fertilizers, potassium phosphate (KH_2PO_4) and potassium thiosulfate $(K_2S_2O_3)$ are also available. Kelp meal, plant residues and wood ash, which contain K mainly as a carbonate (K_2CO_3) , hydroxide (KOH) and rock powder, e.g. granite and minerals such as alunite, orthoclase, microcline, etc., are some other sources of potassium sold as K fertilizer.

17.3 Functions of Potassium in Plants

Potassium is a major nutrient element found in the soil which is required by plants in greater amounts. Being essential or vital nutrient for plant growth, potassium (K^+) plays an important role in plant regulatory development including osmoregulation, plant-water relation and internal cation/anion balance. It also has substantial effect on enzyme activation involved in the formation of organic substances, protein and starch synthesis, respiratory and photosynthetic metabolism (Lauchli and Pfluger [1979;](#page-14-0) Wyn Jones et al. [1979](#page-17-0); Marschner [2010\)](#page-15-0), stomatal movement and water relations (turgor regulation and osmotic adjustment) by increasing protein production in plants (Marschner [1995](#page-15-0)). Enzyme activation is also needed to metabolize carbohydrates for the manufacture of amino acids and proteins and tolerance of external stress such as frost, drought, heat and light. Potassium also functions in triggering the growth of young tissues and cell enlargement and, hence, improves early growth. Besides, potassium is important during plant ontogeny and in improving plant quality and oil content in plants. Hence, large amount of potassium is required to maintain plant health but it often receives less attention than N and P in many crop production systems. The crop yield can be positively and negatively influenced by favourable and unfavourable environmental conditions. Unfavourable environmental conditions which would create potentially damaging physiological changes within plants are known as stresses (Shao et al. [2008](#page-16-0)). Potassium has also been involved in various physiological functions related to plant health and resistance to biotic and abiotic stresses such as diseases, pests, drought, salinity, cold, frost and waterlogging (Wang et al. [2013\)](#page-17-0) However, suitable application of potassium can improve insect and disease resistance in plants. The protective role of K^+ in plants suffering from drought stress has been well documented (Pier and Berkowitz [1987;](#page-16-0) Sen Gupta et al. [1989](#page-16-0)). There are major challenges for agriculture to enhance crop yields and to stabilize plant development and yield formation under biotic and abiotic stress conditions (Reynolds et al. [2011](#page-16-0)).

17.3.1 Biotic Stress Resistance

Biotic components such as weeds caused the highest potential loss $(\sim 32 \%)$, followed by animal pests (18 %), fungi, bacteria (15 %) and viruses (3 %) (Oerke and Dehne [2004\)](#page-16-0). Recently, it was seen in K-deficient soil that plants were more susceptible to infection than those plants having adequate supply of K (Wang et al. [2013\)](#page-17-0) and also the rate of rice borer infestation was greatest when there was no supply of K, but decreased rapidly as the K concentration increased (Sarwar [2012\)](#page-16-0). It was found that the use of K in fields extensively decreased the occurrence of fungal diseases by 70 %, bacterial by 69 %, viral by 41 %, insect and mite infestation by 63 % and nematodes by 33 % (Perrenoud [1990\)](#page-16-0). The synthesis of high-molecular-weight compounds (such as proteins, starch and cellulose) was markedly increased in K-sufficient plants, thus lowering the concentrations of lowmolecular-weight compounds, such as soluble sugars, organic acids, amino acids and amides in the plant tissues which were generally responsible for the development of infections and insect infestations. Thereby, plants were protected from diseases and pest attacks in K-sufficient plants (Marschner [2012\)](#page-15-0). Adequate K also increased phenol concentrations, which could also play a significant role in plant resistance (Prasad et al. [2010\)](#page-16-0).

17.3.2 Abiotic Stress Resistance

Abiotic stresses can cause major damage to the crops as compared to yield losses from biotic stress (Oerke [2006](#page-16-0)). Major abiotic factors are drought stress (low moisture, aquaporins and water uptake, osmotic and stomatal regulation, detoxification of reactive oxygen species, etc.), salt stress, cold stress and waterlogging stress. The use of potassium triggers many plant activities, whereas depletion of potassium uptake can cause problem for plant growth. Potassium to a great extent contributes to the survival of the plants exposed to various abiotic stresses. It was documented by Wang et al. [\(2013](#page-17-0)) that abiotic stress factors such as heat, cold, drought and salinity had a huge impact on world agriculture, and they might reduce average yields by $~50\%$ for most major crop plants. Increased application of $K⁺$ has been shown to enhance photosynthetic rate, plant growth and yield and drought resistance in different crops under water stress conditions (Sharma et al. [1996](#page-16-0); Tiwari et al. [1998;](#page-17-0) Yadav et al. [1999;](#page-17-0) Egilla et al. [2001\)](#page-13-0).

17.3.2.1 Drought and Low Moisture Stress

Association between K stress and plant drought resistance has been demonstrated by many workers. Drought can be defeated by plants by inducing deeper rooting, larger absorption surfaces and greater water retention in plant tissues, which can also be overcome by application of K fertilizers with other nutrients like phosphorus and nitrogen (Kirkby et al. [2009\)](#page-14-0). Sufficient amounts of K enhanced the total dry mass accumulation of crop plants under drought stress/low-moisture conditions in comparison to lower K concentrations (Egilla et al. [2001\)](#page-13-0). Similar findings were documented by Lindhauer [\(1985](#page-15-0)) that not only plant dry mass was increased but also leaf area and water retention in plant tissues under drought-stressed conditions improved. It was found that plants that were continuously exposed to drought stress could form reactive oxygen species, which caused leaf damage (Cakmak et al. 2005; Foyer et al. [2002;](#page-13-0) Oerke and Dehne [2004\)](#page-16-0). Wang et al. [\(2013](#page-17-0)) found a close relation of K in physiological and molecular mechanisms of plant drought resistance. For the period of drought stress, root growth and the rate of K^+ diffusion in the soil towards the root got restricted and depressed the plant resistance as well as K absorption.

Aquaporins and Water Uptake

Potassium is also involved in plant-water relations by regulating the osmotic potential and hydraulic conductivity of membranes and altering water permeability (Heinen et al. [2009;](#page-14-0) Maurel and Chrispeels [2001](#page-15-0)). Aquaporin is water along with K^+ ions which moves through specific channel protein present in the plasma and intracellular membranes of cells (Maathuis et al. [1997;](#page-15-0) Steudle [2000\)](#page-17-0). K^+ is found in the plant cell in two distinct compartments, the cyto-sol and the vacuole (Leigh [2001\)](#page-15-0), hence transported through plant cell membranes with the help of specific protein channels (Maathuis et al. [1997](#page-15-0)). Under drought stress conditions, aquaporin gene expression could be regulated (Tyerman et al. [2002](#page-17-0); Lian et al. [2004\)](#page-15-0) to help the plants to maintain their water balance (Kaldenhoff et al. [2008](#page-14-0)). During water stress, roots regulated their water and ion uptake capacities by modifying PIPs (plasma membrane intrinsic proteins) and K^+ channel at the transcription level to cope with the water deficiency (Smart et al. [2001](#page-17-0); Galmes et al. [2007;](#page-14-0) Cuellar et al. [2010](#page-13-0)). Kanai et al. ([2011\)](#page-14-0) also observed close coupling between aquaporin activities and K channel transporters. They found that aquaporin activities might have been suppressed by K deficiency and resulted in a reduction of root hydraulic conductance and water supply to the growing stem for diameter expansion and the leaf for transpiration.

Osmotic and Stomatal Regulation

Under drought stress condition, the maintenance of enough water levels is important for plant survival; hence, osmotic regulation is the most important trait involved in maintaining high cellular turgor potential and water retention in response to drought stress. An adequate amount of K may help osmotic adjustment, which maintains higher turgor pressure, relative water content and lower osmotic potential, thus improving the ability of plants to tolerate drought stress (Kant and Kafkafi [2002;](#page-14-0) Egilla et al. [2005\)](#page-13-0). Stomata are essential to control plant water loss via transpiration and quick stomatal closures are needed to survive during stressed conditions. Stomatal closure is preceded by rapid release of K^+ from the guard cells into the leaf, thus improving the ability of plants to tolerate drought stress (Kant and Kafkafi 2002). When K⁺ is deficient, the stomata cannot function properly and water losses from plant may reach damaging levels (Gething [1990](#page-14-0)).

Detoxification of Reactive Oxygen Species (ROS)

Generally, drought stress or K-deficient plants induce ROS, e.g. superoxide radical (O'₂), hydrogen peroxide (H_2O_2) and hydroxyl radical ($^{\text{t}}$ HO), production (Cakmak [2005](#page-13-0)). Production of ROS is mainly responsible for impairment of cellular functions and growth depression in stress conditions. K requirement for drought-stressed

plants could be related to the role of K in enhancing photosynthetic $CO₂$ fixation and transporting photosynthates into sink organs and inhibiting the transfer of photosynthetic electrons to O_2 , thus reducing ROS production (Cakmak [2005\)](#page-13-0). Besides the photosynthetic electron transports, nicotinamide adenine dinucleotide phosphate (NADPH)-dependent oxidase activation represents another major source for production of ROS in plant cells by a number of biotic and abiotic stress factors. Furthermore, abscisic acid has also been shown to be effective in increasing H_2O_2 and O_2 ⁻ accumulations in roots or leaves (Lin and Kao [2001](#page-15-0); Jiang and Zhang [2001\)](#page-14-0). Hence, maintaining an adequate K nutritional status critical for plant osmotic adjustment and for mitigating ROS damage as induced by drought stress.

17.3.2.2 Salinity Stress

Salinity is another major abiotic stress that affects major part of the total land area on earth. Saline soils generally had higher concentrations of Na⁺ than K⁺ and Ca²⁺ which resulted in passive accumulation of $Na⁺$ in root and shoot (Bohra and Doerffling [1993](#page-13-0)). Due to the accumulation of salt, water uptake by plant roots in soil became difficult thus disturbing water balance, while high concentrations of salts in plant tissue were found to be toxic (Wang et al. [2013\)](#page-17-0). Salinity inhibited seed germination and plant growth, affected the leaf anatomy and physiology of plants and, thereby, influenced plant-water relations, photosynthesis, protein synthesis, energy production and lipid metabolism (Parida and Das [2005\)](#page-16-0).

17.3.2.3 Cold Stress

Cold stress inhibited plant growth and development and resulted in reduced crop productivity (Wang et al. [2013\)](#page-17-0). Devi et al. ([2012\)](#page-13-0) noticed that in *Panax ginseng*, a high K^+ concentration activated the plant's antioxidant system and increased the levels of ginsenoside-related secondary metabolite transcripts, which are associated with cold tolerance. Thus, cold stress might have destroyed photosynthetic processes and reduced the efficacy of antioxidant enzymes, resulting in ROS accumulation (Mittler [2002;](#page-15-0) Xiong et al. [2002;](#page-17-0) Suzuki and Mittler [2006\)](#page-17-0). Potassium improved plant survival under cold stress by increasing antioxidant levels and reducing ROS production (Cakmak [2005](#page-13-0); Devi et al. [2012\)](#page-13-0).

High concentrations of K^+ protect plant cell against freezing by lowering the freezing point of the cell solution. The plasma membrane is the prime site which is mainly affected when changes in temperature occur, and membrane fluidity is reduced by cold stress resulting in changes of fatty acid unsaturation and the lipidprotein composition of the cell membrane (Wang et al. [2006](#page-17-0)). Maximum growth response and chilling resistance in tomato, eggplant and pepper plants with the addition of K^+ were associated with increase in phospholipids, membrane permeability and improvement in biophysical and biochemical properties of cell (Hakerlerker et al. [1997\)](#page-14-0). Hence, higher K tissue concentrations reduced chilling damage and increased cold resistance, thereby increasing yield production (Mengel [2001](#page-15-0); Kant and Kafkafi [2002\)](#page-14-0).

17.3.2.4 Waterlogging Stress

Waterlogging, a serious obstacle for sustainable agriculture development, affected approximately 10 % of the global land area (Setter and Waters [2003\)](#page-16-0). The main biological consequence that plant encounters during waterlogging stress is the respiration of roots, and microorganisms further deplete the residual oxygen, hence making the environment hypoxic (i.e. oxygen levels limit mitochondrial respiration) and later anoxic (i.e. respiration is completely inhibited). It resulted in a severe decline in energy status of root cells which affected important metabolic processes of plants (Bailey-Serres and Voesenek [2008;](#page-12-0) Wegner [2010\)](#page-17-0). To overcome this difficulty, application of K could efficiently offset the adverse effects of waterlogging on plants. It was reported that K supplement under waterlogging not only increased plant growth, photosynthetic pigments and photosynthetic capacity but also improved plant nutrient uptake as a result of higher K^+ , Ca^{2+} , N, Mn^{2+} and Fe^{2+}

accumulation (Ashraf et al. [2011\)](#page-12-0). Exogenous application of K in soil and as foliar spray alleviated the adverse effects of waterlogging on cotton and many other plants such as corn (Welch and Flannery [1985;](#page-17-0) Csatho [1991\)](#page-13-0), rice (Datta and Mikkelsen [1985\)](#page-13-0), wheat (Beaton and Sekhon [1985](#page-13-0); Khurana and Bhaya [1990\)](#page-14-0) and oilseed rape (Sharma and Kolte [1994](#page-16-0)). There are major challenges for agriculture to enhance crop yields and to stabilize plant development and yield formation under biotic and abiotic stress conditions (Reynolds et al. [2011\)](#page-16-0).

17.4 Deficiency of Potassium

There are several factors that lead to the insufficient supply of nutrients in soil and as a result plant has to face deficiency. In addition, the presence of extreme amounts of reduced substances in poorly drained soils is also responsible for retarded root growth and reduced K uptake (Fairhurst et al. [2007\)](#page-13-0). Fundamentally, K^+ is water soluble and highly mobile and transported to the xylem in plants (Lack and Evans [2005\)](#page-14-0). It acts as regulator in plants since it is constituent of 60 different enzyme systems of drought tolerance and water-use efficiency. K deficiency, also known as potash deficiency, occurs widely in plants and has a strong impact on plant metabolism. A plenty of deficiency symptoms have been reported which include chlorosis, poor growth, reduced yield and poor fibre quality with the increased susceptibility to diseases (Amtmann et al. [2008](#page-12-0)) and pests (Amtmann et al. [2006;](#page-12-0) Troufflard et al. [2010\)](#page-17-0). It also affects photosynthesis process and plant growth; hence, purple spots may also appear on the leaf undersides. Besides, older leaves change from yellow to brown, leaf tips and margins dry up, root oxidation power declines, younger leaves decolourize, and root length and density reduce causing reduction of nutrient uptake and cytokine production in roots. Moreover, K-deficient plants are highly light sensitive and very rapidly become chlorotic and necrotic when exposed to high light intensity (Cakmak [2005](#page-13-0)). Potassium deficiency also inhibits evaporation which causes the temperature in the leaves to rise and results in burning of cells, which mainly occurs on the edges of the leaves. Stressed plants may be more sensitive to the cold injury. Sometimes rust-brown spots may appear in the leaf if K deficiency is severe, and leaves often turn or curl radially on the top and entire leaves become necrotic and eventually fall off. Flowering will be severely inhibited which ultimately affects crop production.

The reasons for potassium deficiency could be insufficient fertilization, excessive 'table salt' (sodium) in the root environment, unfavourable soil structure (e.g. sandy soils) and formation of depletion zones around roots (Kayser and Isselstein [2005;](#page-14-0) Moody and Bell [2006](#page-15-0); Andrist-Rangel et al. [2007](#page-12-0)). Effects of K deficiency on plants depended on specific crop type such as corn becoming small in size and showing low yield and tomatoes exhibiting uneven fruit ripening, whereas leaves of cotton plants turned reddish brown and then black, appeared scorched and eventually fell, and yield and quality of forage crops were adversely affected [\(www.ncagr.gov\)](http://www.ncagr.gov/). To overcome the deficiency, the prevention and cure can be achieved at great extent by adding potassium-specific fertilizer, e.g. potassium carbonate, rock potash, potassium nitrate, potassium sulfate, etc. Thus, study of potassium uptake and strategies to enhance uptake in plants is necessary.

17.5 Pathways and Mechanisms for Potassium Uptake

Plant cannot acquire nutrient directly unless it is present in available or dissolved form or released by weathering. There are several processes that contribute to the availability of potassium in the soil. Besides, the release of K from the rocks and minerals requires weathering over long periods of time, although calcinations of rocks can break the K out of the structure but makes the K more expensive than that from the evaporite ores. In addition to plant uptake of K from the soil solution, some of the exchangeable potassium on the soil colloids is also absorbed directly by roots. A plant root possesses a negative charge and

attracts the positively charged potassium (K^+) which is held on the clay mineral surfaces and edges. However, potassium uptake of plants can be increased by using potassium solubilizers as bioinoculants which further increased the crop productivity (Shanware et al. [2014\)](#page-16-0). Lian et al. ([2008\)](#page-15-0) reported that there were three major reaction pathways utilized by Aspergillus fumigatus to release potassium from potassium minerals which were acid hydrolysis, secretion of insoluble macromolecules and polymers bound in the cell membrane and direct biophysical forces which could split mineral grains.

It was demonstrated that potassiumsolubilizing microorganisms have the capacity to dissolve K from insoluble minerals (Alexander [1985\)](#page-12-0). Potassium-solubilizing bacteria are able to solubilize rock K mineral powder, such as micas, illite and orthoclases through various processes such as acidolysis, enzymolysis, capsule absorption and complexation by extracellular polysaccharides (Avakyan [1984;](#page-12-0) Rozanova [1986;](#page-16-0) Malinovskaya [1988;](#page-15-0) Malinovskaya et al. [1990](#page-15-0); Friedrich et al. [1991;](#page-13-0) Ullman et al. [1996](#page-17-0); Welch et al. [1999](#page-17-0)). Mechanisms involved in degradation of potassium-bearing minerals can be divided into direct (bacterial cell wall) and indirect (bioleaching, mineral weathering, microbial weathering and mechanical fragmentation) mechanisms.

17.5.1 Bacterial Cell Wall

Prokaryotes have various cell wall types which secrete one or more metabolic products that react with ions or compounds in the environment resulting in the deposition of mineral particles. Bacterial surfaces such as cell walls or polymeric materials (exopolymers) exuded by bacteria, including slimes, sheaths or biofilms, and even dormant spores, acted as important sites for the adsorption of ions and mineral nucleation and growth (Konhauser [1998;](#page-14-0) Beveridge [1989;](#page-13-0) Banfield and Zhang [2001;](#page-12-0) Bäuerlein [2003](#page-13-0)). In gram-negative bacteria, the layers external to the bacterial cell wall that may be involved in mineral nucleation include S-layers, capsules,

slimes and sheaths. S-layers are acidic and possess a net negative charge, thereby having an affinity for metal cations (Southam [2000](#page-17-0)). In some cases, capsules are also known to form in response to the presence of metal ions (Appanna and Preston [1987\)](#page-12-0).

17.5.2 Bioleaching

The process of removal of soluble material from the rocks in solution by percolating water is termed as leaching. Halite (NaCl) and sylvite (KCl) are highly water soluble, while carbonates and sulfates are sparingly soluble. Bioleaching microbes are mainly Thiobacillus ferrooxidans, T. thiooxidans and Leptospirillum ferrooxidans.

17.5.3 Mineral Weathering

The weathering reactions contribute to nutrient cycling (Huntington et al. [2000](#page-14-0)). Chemical weathering of bedrock releases inorganic nutrients such as Ca, Mg, K, Fe and P, which are then cycled through the saprolite, soil and vegetation. Inorganic nutrients were cycled by microorganisms via uptake, release, biomineralization, oxidation and reduction (Berner and Berner [1996](#page-13-0)). Microorganisms also contributed to mineral weathering and soil formation by secreting organic acids and other ligands such as siderophores as indicated by many researchers (Richter and Markewitz [1995;](#page-16-0) Kalinowski et al. [2000](#page-14-0); Liermann et al. [2000,](#page-15-0) [2005](#page-15-0); Richter and Oh [2002\)](#page-16-0). Within the rooting zone, plants take up mineral nutrients, which are recycled back into the soil when plants get decomposed.

During weathering, physical, chemical and biological forces act on the parent materials and break them down into finer fractions, largely sand-, silt- and clay-size particles. This breakdown results in the release of several chemical elements, including potassium, and the formation of different clay minerals. Most of the total potassium inherited from the parent material during the soil-forming processes will be in the non-exchangeable and exchangeable forms. The

relative amounts of sand, silt and clay fractions found in a soil depend on the kind of parent material (sandstone, limestone, shale or mica) from which the soil was derived. Potassium fixation and release is greatly influenced by the relative amounts of these fractions and the kinds of clay minerals present in the soil. Mineral dissolution studies with cultures of bacteria and fungi showed a dramatic increase in the dissolution rates of feldspar, biotite, quartz, apatite and other minerals (Berthelin and Belgy [1979;](#page-13-0) Callot et al. [1987](#page-13-0); Thorseth et al. [1995](#page-17-0); Ullman et al. [1996](#page-17-0); Barker et al. [1997;](#page-13-0) Paris et al. [1996\)](#page-16-0).

17.5.4 Microbial Weathering

The known and potential mechanisms of microbial weathering included redox reactions through the production of organic acids which led to weakening of chemical bonds in minerals for promoting mineral dissolution (Banfield et al. [1999;](#page-12-0) Harley and Gilkes [2000\)](#page-14-0) and chelating molecules for mineral degradation (Uroz et al. [2007,](#page-17-0) [2009;](#page-17-0) Lian et al. [2008](#page-15-0)). Bacteria produced a wide range of low-molecular-weight organic acids such as citric, malic, oxalic, succinic and tartaric acid (Jones [1998;](#page-14-0) Neaman et al. [2005\)](#page-16-0). Han and Lee ([2005\)](#page-14-0) concluded in a study that KSB solubilized potassium rock through production and secretion of organic acids. Similar were the observations of Prajapati and Modi ([2012\)](#page-16-0), which attributed the solubilization to reduction in pH due to organic acids. Few other reports are also available for feldspar solubilization by Bacillus mucilaginosus and Bacillus edaphicus due to acid production (Malinovskaya et al. [1990;](#page-15-0) Sheng and Huang [2002\)](#page-16-0). In addition to organic acids, microorganisms (such as bacteria, algae, fungi and protozoa) used carbonic acid formed from carbon dioxide to attack the mineral surface, promoting the chemical weathering of rocks and minerals (Gadd [2007](#page-13-0); Park et al. [2009\)](#page-16-0).

Microbes played a key role in the weathering of major type of rocks, releasing various elements they needed as nutrients (Calvaruso et al. [2006\)](#page-13-0). Many rock-inhabiting fungi were

melanized, and melanin pigmentation conferred extra-mechanical strength to the hyphae to penetrate the rock surface and crevices (Dornieden et al. [1997;](#page-13-0) Sterflinger and Krumbein [1997\)](#page-17-0) and also offered protection from metal toxicity (Gadd [1993\)](#page-13-0). Fungi have been reported from a wide range of rock types, including rocks from extreme environments (Staley et al. [1983;](#page-17-0) Nienow and Fridman [1993;](#page-16-0) Sterflinger [2000;](#page-17-0) Etienne and Dupont [2002;](#page-13-0) Gorbushina [2007\)](#page-14-0). In an experimental study conducted by Puente et al. [\(2004](#page-16-0)), fluorescent pseudomonads and bacilli were found to weather igneous rock, limestone and marble.

17.5.5 Biofilm

Biofilm helps to accelerate weathering of minerals like biotite and anorthite. Biotite weathering occurs in two stages: by oxidation within the rindlet zone and by alteration to kaolinite within the saprolite. Biofilms and biocrusts were normally supposed to cause higher weathering rates due to biodegradation (Warscheid and Braams [2000](#page-17-0)). It was accepted that the microbial biofilms not only accelerated the weathering process but also regulated denudation losses by acting as a protective layer covering the mineral-water-hyphal/root hair interface in the mycorrhizosphere and rhizosphere of vascular plants. Besides, biofilm formation on mineral surface promoted the corrosion of potassium-rich shale and the release of K, Si and Al in the bacteria-mineral contact model (Li-yang et al. [2014](#page-15-0)).

17.5.6 Mechanical Fragmentation

Fragmentation of the mineral caused by root activity increases the reactive surfaces, so having direct positive effect of the bacteria on mineral weathering. Mechanical fragmentation of rock particles also occurred when there was extension of hyphae (unique for fungal organisms) into the interior of minerals to acquire nutrition (Jongmans et al. [1997\)](#page-14-0).

17.6 Potassium-Solubilizing Microorganisms (KSMs)

Potassium is the third major essential macronutrient for plant growth and development. It constitutes \sim 2.5 % of the lithosphere but actual soil concentrations of this nutrient vary widely ranging from 0.04% to 3.0% (Sparks and Huang [1985\)](#page-17-0). Plants absorb K only in soluble form from soil, and its availability to crop plants is generally as low as 90–98 % of total K in soil in the unavailable mineral forms (Sparks [1987](#page-17-0)) such as feldspar and mica (McAfee [2008](#page-15-0)). The addition of chemical fertilizers causes environmental pollution and has many deteriorating impacts such as global warming, alteration of soil microbial diversity, etc. Moreover, they also influence soil-plant dynamics with its microbial distribution (Meena et al. [2013](#page-15-0); Maurya et al. [2014\)](#page-15-0).

Microorganisms on solid and liquid medium were tested, and it was observed that bacterium Enterobacter hormaechei (KSB-8) was more viable in liquid broth as compared to solid medium containing carrier lignite, while fungus Aspergillus terreus (KSF-1) was good at both liquid and solid medium (Kalawati and Modi 2014). Rhizosphere microorganisms play an important role in solubilization of bound form of soil minerals and enhancing the availability of plant nutrients in the soil. Increasing the bioavailability of phosphorus (P) and potassium in soils with inoculation of plant growth-promoting rhizobacteria (PGPR) singly or in consortium with or without rock materials has been reported by many researchers (Lin et al. [2002](#page-15-0); Sahin et al. [2004](#page-16-0); Girgis [2006](#page-14-0); Eweda et al. [2007](#page-13-0); Jha et al. [2012](#page-14-0); Meena et al. [2015b;](#page-15-0) Singh et al. [2015\)](#page-17-0), which may lead to increasing P uptake and plant growth. The mould A. niger has been well documented for its ability to solubilize P in rocks due to organic acid production, especially citric acid (Nahas et al. [1990;](#page-16-0) Vassileva et al. [1998](#page-17-0); Jain et al. [2014](#page-14-0)).

Different microorganisms are used to supply different kind of nutrients in the soil such as symbiotic and non-symbiotic nitrogen-fixing

bacteria which can supply nitrogen to plants by fixing the atmospheric nitrogen and converting the nitrogen into ammonium ion. Bacillus megaterium and Pseudomonas sp. are the most common phosphate-solubilizing bacteria that are used as a biofertilizer to solubilize phosphorus in soil. Solubilization of potassium from aluminosilicate minerals has also been observed by some fungi (Wallander and Tonie [1999;](#page-17-0) Glowa et al. [2003](#page-14-0)). It was proposed by Yuan et al. ([2000\)](#page-18-0) that ectomycorrhizae could mobilize potassium from clay minerals and thus enhanced its uptake by plants. Further, Yuan et al. [\(2004](#page-18-0)) studied the effect of four fungal strains, Pisolithus XC1, Pisolithus sp., P. microcarpus and Cenococcum geophilum SIV, collected from the roots of eucalyptus on the degradation of phlogopite and vermiculite; the results revealed that all four strains were able to weather the mineral phases and release elemental K. Moreover, Glowa et al. [\(2003\)](#page-14-0) evaluated the ability of fungus *Piloderma* in extracting potassium from biotite, microcline and chlorite and found that the fungus species was able to acquire potassium from all three minerals, out of which biotite was more biodegradable (Meena et al. [2014a](#page-15-0), [2015a\)](#page-15-0).

Muentz ([1890\)](#page-15-0) showed the first evidence of microbial involvement in solubilization of rock potassium. Since then a diverse group of soil microflora has been reported to be involved in the solubilization of insoluble and fixed forms of K into available forms, which can easily be absorbed by plants (Li et al. [2006](#page-15-0); Gundala et al. [2013;](#page-14-0) Zarjani et al. [2013](#page-18-0)). A wide range of potassium-solubilizing bacteria (KSB), namely, Bacillus edaphicus, B. circulans, Paenibacillus spp., Acidithiobacillus ferrooxidans, Pseudomonas spp., Burkholderia spp., etc., have been reported to release potassium from K-bearing minerals in soil (Sheng et al. [2008;](#page-16-0) Lian et al. [2002;](#page-15-0) Rajawat et al. [2012;](#page-16-0) Liu et al. [2012;](#page-15-0) Basak and Biswas [2012;](#page-13-0) Singh et al. [2010](#page-17-0)).

KSB such as Bacillus mucilaginosus solubilized potassium rock and stimulated plant growth through synthesis of growth-promoting substances via their biological activities.

Similarly, silicate-solubilizing bacteria were found to dissolve potassium, silicon and aluminium from insoluble minerals (Aleksandrov et al. [1967](#page-12-0)). KSB have capacity to dissolve K from insoluble minerals (Alexander [1985](#page-12-0)). Many microorganisms in the soil are able to solubilize 'unavailable' forms of 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 the K into solution (Groudev [1987](#page-14-0); Friedrich et al. [1991;](#page-13-0) Ullman et al. [1996;](#page-17-0) Bennett et al. [1998](#page-13-0)). Therefore, the application of K-solubilizing microorganisms (KSMs) is a promising approach for increasing K availability in soils (Zahra et al. [1984;](#page-18-0) Vandevivere et al. [1994;](#page-17-0) Barker et al. [1998;](#page-13-0) Meena et al. [2014b;](#page-15-0) Kumar et al. [2015](#page-14-0)).

KSMs can be isolated from many sources in in vitro conditions using different media. Prajapati and Modi ([2012\)](#page-16-0) isolated 14 bacterial strains from samples collected from ceramic industry using feldspar on a solid media, out of which five strains showed higher potassium solubilization. Recently, Parmar and Sindhu [\(2013](#page-16-0)) used Aleksandrov medium supplemented with mica to isolate 137 K-solubilizing bacteria from soil samples collected from wheat rhizosphere. Among isolated strains, 20 strains were found to solubilize potassium from mica. The amount of K released by the strains ranged from 15 to 48 mg L^{-1} . Further examination for optimization of conditions for K release revealed that maximum solubilization occurred with glucose as carbon source at $25 \degree$ C temperature and 7.0 pH. Potassium solubilization was maximum when KCl was used as potassium source, followed by K_2SO_4 , and least solubilization was found in mica powder. It was suggested that efficient potassium-solubilizing bacterial strains could be further exploited for plant growth improvement under field conditions. Sheng [\(2005](#page-16-0)) used sucrose minimal salt medium with illite as K source for the isolation of B . *edaphicus* strain NBT from rhizosphere soil of cotton. Wu et al. ([2005\)](#page-17-0) used the same medium with glass powder for the growth of B. mucilaginosus, a vigorous K solubilizer. Further, it was found to have great K-releasing capability and could promote the release of potassium through weathering of silicate minerals (Hu et al. [2006;](#page-14-0) Lian [1998;](#page-15-0) Zhao et al. [2006,](#page-18-0) [2008\)](#page-18-0). Sangeeth et al. ([2012\)](#page-16-0) identified potassium-solubilizing bacterium, Paenibacillus glucanolyticus IISRK2, isolated from rhizosphere of black pepper plant. It was further evaluated for plant growth, and after the studies, it was documented that the strain efficiently promoted the shoot and dry matter of wheat plants promoting the overall plant growth. Commercially available microbial inoculants that are able to dissolve K from minerals and rocks not only enhance plant growth and yield but are also eco-friendly; microbes Aspergillus niger, Bacillus extorquens and Clostridium pasteurianum were found to grow on muscovite, biotite, orthoclase microclase and mica in vitro (Archana et al. [2013\)](#page-12-0).

17.7 KSM Role in Sustainable Agriculture

Potassium is an essential and major nutrient for crop production (Alfaro et al. [2003;](#page-12-0) Zhang et al. [2011](#page-18-0)). The role of potassium is well known for improving shelf life of crops and disease resistance (Khawilkar and Ramteke [1993\)](#page-14-0). Potassium is useful in agriculture land to increase crop yield as proper amount of potassium in soil can enhance root growth, improve drought resistance, activate many enzyme systems, maintain turgor pressure, reduce water loss and wilting, aid in photosynthesis and food formation, reduce respiration, prevent energy losses, enhance translocation of sugars and starch, produce grain rich in starch, increase protein content of plants, reduce waterlogging and retard crop diseases. Therefore, it is essential for the growth and metabolism of plants; the deficiency of potassium in plants causes poorly developed roots, slow growth and low resistance to disease, delayed maturity, small seeds and lower yields. With rapid development of agriculture or due to application of imbalanced fertilizers, available K level in soils has dropped. The concentration of soluble K is very small and the maximum part of K exists in insoluble form. Silt, clay and sand are biggest reservoirs of potassium and important component of soil. The most common component of potassium is feldspar and mica, and fortunately, India has the largest deposits of mica mines distributed in some districts of Bihar and Jharkhand. In such conditions the application of KSMs can be an alternative approach for increasing K availability (Krishnamurti and Huang [1988](#page-14-0); Prajapati and Modi [2014;](#page-16-0) Zhang and Kong [2014\)](#page-18-0).

It has been studied that by introducing potassium-solubilizing bacteria *B. mucilaginosus* and phosphate-solubilizing bacteria Bacillus megaterium var. phosphaticum, simultaneously, macronutrient (nitrogen, phosphate and potassium) uptake was increased in eggplant, pepper and cucumber leading to higher yields (Han et al. [2006](#page-14-0)). B. edaphicus strain was also examined for the growth promotion and increased potassium uptake on cotton and rape plants, and increased plant growth was observed in the soil treated with insoluble potassium with strain NBT. The shoot and root dry weight increased from 25 $\%$ to 33 $\%$ (cotton) and from 24 $\%$ to 27 % (rape), whereas K content was increased from 31 % to 34 % ($P < 0.05$) (cotton) and 28–31 % (rape) when the soil with insoluble K source and bioinoculant was compared to the uninoculated soil (Sheng [2005\)](#page-16-0). Experiments conducted with tobacco seedlings, inoculated with Klebsiella variicola strains JM3, XF4 and XF11, showed greater height and dry weight than uninoculated seedlings. The GL7 significantly increased plant dry weight. Inoculation with the strains JM3, GL7, XF4 and XF11 significantly increased seedling absorption of N, P and K. Seedlings exposed to K feldspar absorbed significantly more N and K than those not exposed to added K feldspar (Jhang and Kong 2014). Krishnamurthy (1990) reported that the potassium content in tobacco leaf was strongly and positively correlated with available K status in sandy and sandy loam soils.

Nowadays, biofertilizer is a substitute to chemical fertilizer to increase soil fertility and crop production in sustainable farming. The use of plant growth-promoting microorganisms, including phosphate-solubilizing and potassium-mobilizing bacteria as biofertilizers, was suggested as a possible solution to improve plant nutrient and production (Vessey [2003\)](#page-17-0). Beneficial microorganisms in the form of biofertilizers are applied on seeds/roots or in soil which mobilizes the availability of nutrients, especially N-P-K by their biological activity, thereby helping in the build-up of positive microflora and enhancing the soil health. The use of bioinoculants can also improve the physical properties and enhance water-holding capacity of soil. Moreover, microorganisms that are applied as biofertilizer can prevent nutrient leaching and lead to soil enrichment with nutrients. They are low in cost, compatible with long-term sustainability, and eco-friendly as compared to chemical fertilizers. Besides, the nutrient supply is constant and sustainable through these microorganisms' activities. Though the use of biofertilizer has gained momentum in recent years since chemical fertilizers are high in cost and can cause hazardous effect (Aseri et al. 2008), unfortunately not much attention has been given to the manufacturing of K biofertilizers.

17.8 Concluding Remarks

Potassium being the third major nutrient for plants is vital for plant growth. However, majority of potassium in soils is available in insoluble forms. Therefore, potassium-solubilizing microorganisms, the component of soil microbial community, play an important role in K solubilization to provide available form to plants. K solubilization benefits crop growth and improves soil fertility in an eco-friendly manner. Potassium-solubilizing strains are able to colonize the rhizosphere, promote crop yield and enhance plant stress response during stress conditions and K uptake. Unfortunately, very little attention has been paid to K-solubilizing microorganisms and K biofertilizers as most of the researches are focused on nitrogen and phosphorus biofertilizers. Hence, it is requisite to study the efficient K-solubilizing microorganisms to improve sustainable agriculture and to keep the soil productive.

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