Noushina Iqbal
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Preface

Nutrient deficiency is a common problem in agricultural crops affecting plant growth and yield. It is required for various physiological and biochemical processes, and the deficiency up-regulates signalling molecules or phytohormones to initiate a cascade of reaction that increases nutrient uptake and helps in maintaining nutrient homeostasis. Neither deficiency nor excess of nutrients is good for plants, and therefore a proper balance is essential for maintaining their homeostasis and affecting plant performance. Among various factors affecting nutrient acquisition and maintaining its homeostasis in plants, hormones play a prominent role both under stress and non-stress conditions. Phytohormones may coordinate with each other to affect root system architecture that involves the root, environment and the hormones and eventually affects nutrient uptake.

Among nutrients, potassium (K^+) is one of the vital macronutrients required for plant growth and development and affects important cellular processes, like activation of enzymes, carbohydrate metabolism and synthesis of protein, cation–anion balance, water movement, osmoregulation and regulation of stomatal movement. Plants with K^+ deficiency show stunted growth and yellowing of leaf margins. It also plays a major role in adaptation to abiotic stresses. Upon exposure to abiotic stress, the K^+ homeostasis is disturbed and that induces the expression of K^+ transporters and regulates K^+ channel through a feedback mechanism to optimize its uptake. Interaction of K^+ occurs with different phytohormones and nutrients to counter abiotic stress conditions. The excess formation of reactive oxygen species, disturbances of photosynthetic apparatus, reduction in photosynthetic products and disturbances in ion homeostasis results in reduced growth and yield. Several studies have focussed on reduction in K^+ content under abiotic stress and alleviation of stress by supplementation of potassium. This book *Role of Potassium in Abiotic Stress* deals with interaction between potassium either alone under control conditions or its interaction with different nutrient and phytohormones under abiotic stress condition to initiate defence and tolerance under varied stresses.

The first chapter deals with the general role of potassium and gives a detailed account of role of K in photosynthesis process followed by a description of the role of K in plant growth and yield.

In the second chapter, a detailed role of K in adaptation to various abiotic stresses to reduce the damage to plants is focussed. Proper use of K^+ with other nutrients helps to achieve sustainable productivity and quality of crops and guarantee nutritional food security for animals and humans. The chapter will elaborate our existing knowledge on the application of K in combating various abiotic stress and the mechanism involved.

Chapter 3 is an elaboration of Chap. 2 with the involvement of the molecular mechanism involved in abiotic stress tolerance induced by K. It provides an insight into the molecular strategies associated with the potassium uptake and homeostasis during different abiotic stress conditions.

Chapter 4 talks about soil potassium availability and the role of microorganisms in influencing potassium availability to plants. The study reported focusses on recent research on nutrient use efficiency and the incessant growing gap between the use and supply of nutrient. Therefore, efforts are needed to ensure the nutrient requirement of plants and enhance the nutrient use efficiency. Hence, the application of microbial inoculants is of great significance in promoting the agriculture productivity.

Chapter 5 is interesting and discusses the involvement of phytohormones in different abiotic stress-regulating K content. This chapter is an attempt to study the synergistic role of potassium and phytohormones and their crosstalk in reducing the stress conditions and making the plants feel better. These types of interactions could be helpful in nutrient uptake and also promote transport and utilization of nutrient and in reversing the ill effect of stress.

Plant growth regulators (PGRs) are well known to sense the K^+ deficiency in plants and further trigger the complex signalling networks between PGRs and other signalling molecules. Chapter 6 focusses on the emerging trends in phytohormone-assisted K^+ regulation, their uptake, transportation, relocalization and molecular aspects under abiotic stress condition.

Chapter 7 focusses on a single stress drought and discusses the effects of drought on plant growth and various physiological parameters; role of K in maintaining the various aspects of plant metabolism and how K is responsible for mitigating the adverse effects of drought on plants by altering various physiological and biochemical mechanisms.

Chapter 8 is about the role of potassium in heavy metal stress tolerance. The chapter discusses about the role of K^+ in reducing oxidative stress, enhancing protein content, proline and secondary metabolites like phenols, flavonoids synthesis as well as improved antioxidant enzymes activity under heavy metal stress.

While in Chap. 9, salt stress alleviation strategies to maintain K^+ homeostasis in plants is discussed.

Chapter 10 is an elaboration of mechanism involved in salt tolerance. It discusses the involvement of potassium in ion homeostasis, signalling and changes in transcriptomes and metabolomes enduring salinity stress. Actually, the pathways undertaken during ionic stress, osmotic stress and ROS accumulation are intricately entwined to target the restoration of K^+ homeostasis in the cytosol required for the stability of cellular membranes, protein structures and function and thereby essentially contributing to the survival of plants during salt stress.

Chapter 11 discusses the involvement of potassium as a potent modulator of plant responses under changing environment. In this chapter, data related with the role of potassium-mediated regulatory functions against abiotic stresses, its possible molecular mechanisms for regulation of various physiological processes under changing environment and its role in conferring tolerance against abiotic stresses is explained together with the crosstalk of potassium with various phytohormones under stress and stress-free conditions.

Chapter 12 is a very interesting and informative chapter that discusses potassium involvement in abiotic stress with major emphasis on potassium transporters and molecular mechanisms involved. Potassium uptake is regulated by the high-affinity and low-affinity K^+ uptake systems in plants. At molecular level, it has been demonstrated that this system in different environmental conditions has directly involved in the potassium use efficiency (KUE) of crops. Transcriptional profiles data on crops under potassium deficit can reveal the role of this macronutrient in plants and the potential correlation with the main abiotic stresses. In this chapter, the role of potassium in plants under different abiotic stress conditions and the expression profiles of the genes for K^+ transporters is reviewed.

Chapter 13 discusses a completely different and less explored involvement of K in regulating nitric oxide synthesis which affects potassium and nitrogen homeostasis in plants for salt tolerance. It focusses on the synthesis of NO with emerging role of K and N nutrients under salt stress. The synthesis of NO and its effects on plant growth, morphology and plant metabolism are discussed. The physiological and molecular mechanisms of K and N function with NO in plant salt stress resistance are reviewed. This study summarizes a vital role of NO synthesis in modulating the homeostasis of K and N and its nutrition in plants and highlights the future needs for research about the role of K and N with NO synthesis under salt stress in agriculture.

The compilation of chapters would definitely provide very informative knowledge about potassium which is a vital macronutrient with plethora of functions in plants.

In view of this, it is critical to understand the role of essential and beneficial nutrients in minimizing the harmful effects of abiotic stresses and their mode of action in physiological and molecular processes by which these nutrients affect tolerance of plants against different environmental stresses.

New Delhi, India

Noushina Iqbal
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Editors and Contributors

About the Editors

Noushina Iqbal did her master's and Ph.D. from Aligarh Muslim University, Aligarh, and then she worked as a Post-Doctoral Fellow in Jamia Hamdard, New Delhi (UGC-DS Kothari PDF) and recently she has been doing another PDF (SERB-DST NPDF) from Jamia Hamdard as Principal Investigator. During her Ph.D. she received the UGC-BSR Fellowship for meritorious student and worked on an UP-CST-funded research project. She also got the prestigious Senior Research Fellowship (SRF) by CSIR. She has more than 30 peer-reviewed international publications and has attended conferences and seminars. She has authored one book and edited three books. Her research papers have lots of citation and have a high impact factor. She is also a life member of Indian Society for Plant Physiology. Dr. Noushina is also review editor of Frontiers in Plants Science section Crop and Product Physiology. Her research interest focuses on but not limited to the role of various phytohormones and nutrients in combating abiotic stress tolerance.

Shahid Umar is Professor and Head of the Department of Botany, School of Chemical and Life Sciences, Jamia Hamdard, New Delhi. He did his M.Phil. and Ph.D. from Aligarh Muslim University, Aligarh. He has 30 years of teaching experience and has successfully guided 40+ M.Sc. dissertation and supervised 16 thesis and 3 more under progress. He has received the IPI-FAI International Award (2003) instituted by International Potash Institute (IPI) (Basel, Switzerland) and Fertilizer Association of India for the significant contribution towards potassium nutrition management for improvement of crop yield and quality. Felicitation from for fruitful cooperation with IPI during International Symposium on balanced fertilization for sustainable crop productivity (2006) and again in 2009 felicitation from IPI for fruitful cooperation with IPI during International Symposium on balanced fertilization for sustainable crop productivity (OUAT, Bhubaneswar, Orissa). He has successfully completed 5 research projects as Principal Investigator mainly involving potassium and has published more than 100 papers in peer-reviewed international journals. He has edited eight books and has membership of various bodies.

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Role of Potassium in Plant Photosynthesis, Transport, Growth and Yield

Jyoti Rawat, Neha Pandey, and Jyoti Saxena

Abstract

Potassium (K) is the most abundant element next to nitrogen (N) and phosphorus (P) which is largely required by the plants. It is involved in many physiological processes such as photosynthesis, enzyme activation within the plant, translocation, and regulation of opening and closing of the stomata. Deficiency or inadequate supply of K results in a drop of photosynthetic carbon assimilation which ultimately stunts growth and reduces yield of the plants. K-deficient plants show symptoms like brown or yellow edges along with their leaves. K as biofertilizer is seen to increase crop yield and enhance productivity of protein- and starch-rich grains. It also helps to improve immunity against change of weather and protects against oxidative stress and diseases. However, studies on the effect of K deficiency in plant growth promotion, photosynthesis and K uptake are limited. The current review gives a detailed account of role of K in photosynthesis process followed by a description of the role of K in plant growth and yield.

Keywords

Potassium · Photosynthesis · Plant growth promotion

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1.1 Introduction

Nutrient deficiencies in plants are widespread throughout the most agricultural regions in the world especially in developing countries where fertilizers may not be affordable (Snapp et al. 2001). In an agricultural segment, the low availability of potassium (K) for many crops grown in areas naturally low in K, is a global concern. Agricultural production is limited due to a variety of abiotic stresses such as drought and salinity that drastically reduce the quality and quantity of the produce. K is a chief macroelement next to nitrogen (N) and phosphorus (P) for the survival and proper functioning of living organisms. It plays an important role in cell expansion, maintains turgor pressure in plants, aids in cellular osmoregulation, helps in opening and closing of stomata, and activates more than 60 enzymes (Hawkesford et al. 2012). It has been noticed that plants under drought stress have a higher internal need for K (Cakmak 2005; Wang et al. 2013). In this case more K was required for CO_2 fixation during photosynthesis, protection of chloroplasts against oxidative damage, alteration of the associated modifications in carbohydrate metabolism, and regulation of stomatal opening and hydric relations (Cakmak 2005). Besides, K affects the activity of nicotinamide adenine dinucleotide phosphate (NADPH) oxidases and retains photosynthetic electron transport activity which helps to reduce reactive oxygen species (ROS). There is a vast diversity of K^+ transporters in plant cells which are involved in physiological and developmental processes.

Soil fertilization is the most common method of providing essential nutrients to plants. When K supply is inadequate, a reduction occurs in exchangeable or plant-available soil K which is indicative of a loss of K from the soil-plant system (Xie and Zhou 2012). K is relatively abundant in the earth's crust and represents around 2.1% by weight. It is not found free in nature and is mined as potash (KOH), sylvite (KCl), carnalite, and langbeinite. About 90–98% of K in soil exists in the form of insoluble K minerals such as feldspar and mica (McAfee 2008). However, as a chemical fertilizer, K has been used in fields since the nineteenth century. The use of fertilizers and organic amendments are the oldest methods to improve the productivity of plants. This chapter summarizes the importance of K in plant physiology and transport, its role in photosynthesis and effect of K addition on plant growth and yield.

1.2 Role of Potassium in Plants

Potassium is vital for several biochemical and physiological processes and is accountable for the growth and development of plants with respect to the necessary nutrients. K has an important role in the translocation of water, essential nutrients, and other substances from the roots through the stem to leaves. It is involved in numerous metabolic and biochemical processes in plant cells (Rengel and Damon 2008; White 2013) including regulatory and transport mechanisms (Adams and Shin 2014). Therefore, it is needed in large quantities for the proper growth and reproduction of plants as stated below:

1. K has substantial effect on enzyme activation, protein synthesis, photosynthesis, stomatal movement, and water relations (turgor regulation and osmotic adjustment) in plants (Marschner 1995).
2. K also plays a mitigating role in various abiotic stresses such as drought, salinity, metal toxicity, high or chilling temperatures etc. Increased application of K has been shown to enhance photosynthetic rate, plant growth, yield, and drought resistance in different crops (Yadav et al. 1999; Egilla et al. 2001; Pervez et al. 2004). K-fed plants maintained higher leaf water potential, turgor potential, and relative water content and lower osmotic potential as compared to untreated plants of *Vigna radiata* (Nandwal et al. 1998), maize (Premachandra et al. 1991), and wheat (Sen Gupta et al. 1989) grown under water stress conditions.
3. Adenosine triphosphate (ATP) is an important source of energy for many chemical processes that take place in plants. K triggers the activation of biochemical enzymes important for the generation of ATP. It regulates the movement of water and other salts in plant tissues and cells (osmoregulation) and contributes to the cationic-anionic balance, the movement of water, and the transfer of energy. Also, the absorption of water by the roots of plants and its loss through the stomata are affected by K.
4. K plays an important role in the activation of many enzymes related to plant growth. The synthesis of protein and starch in plants also requires K. It facilitates carbohydrate metabolism and enzyme activation and is required at almost every step of the process; the enzyme responsible for the process is also activated by K.
5. There is a correlation between phytohormones and K; they interact with each other and with other signaling molecules which regulate biochemical processes and metabolism exerting physiological responses related to almost all characteristics of plant growth and development and improving stress tolerance (Wang et al. 2013). Genes regulated by auxins control proteins that affect transcriptional repressors of stress responses in plants. Abscisic acid (ABA) influences the expression of genes that modulate complex stress-sensitive regulatory networks. The functions of a number of other hormones including cytokinin, ethylene, jasmonic acids, gibberellic acid, and salicylic acid have been documented for their ability to confer abiotic stress tolerance.

1.3 Potassium Deficiency in Plants

Irrespective of its availability in soils, K deficiency can occur frequently, and the symptoms start from the lower leaves and progress towards other vital parts of the plants. It also causes abnormalities in plants that affect reproduction and growth. Plants absorb K^+ from soil through root cells. Thus, roots are the primary organs that are most likely to affect the K^+ content of plants (Hsiao 1973; Wang and Wu 2013). K^+ content (<10 g kg^{-1} dry weight) will cause deficiency symptoms in most species beginning with chlorotic interveinal areas on older leaves that become necrotic with progression of the deficiency and in case of adverse conditions death of lateral and terminal meristems (Marschner 1995; Epstein and Bloom 2005). When plants are deficient in K, they show stunted growth and yellowing of the leaf edges, a poor root system, and reduced yields. Also, the number and size of leaves are reduced. K deficiency affects stomatal conductance, increases mesophyll resistance, and decreases the activity of ribulose-1, 5-bisphosphate carboxylase/oxygenase (RuBisCO) in plants, thus lowering overall photosynthetic rate (Zhao et al. 2001). Lack of K fertilizer also increases the susceptibility of plants to various diseases and pest infestations and makes them vulnerable under various stressful conditions. Since K is an important growth catalyst, its deficiency or insufficiency can lead to slow growth or underdeveloped roots and stems. Low resistance to ecological changes and reduced availability of K will directly lead to less fluid circulation and nutrient transfer in plants. This will make the plants directly sensitive to changes in temperature. An investigation was done to study the role of shoot and root in the regulation of premature leaf senescence induced by K deficiency in cotton (*Gossypium hirsutum* L.), in two contrasting cultivars (CCRI41, a more susceptible cultivar to K deficiency, and SCRC22, a less susceptible cultivar) (Li et al. 2012).

1.4 Potassium Transport in Plants

K is also available through fertilizers in the form of K_2O. The bioavailability and uptake of K by plants from the soil varies according to different factors. The rate of respiration by plants is largely the determining factor for proper uptake and transport of K by plants. Its uptake is dependent on sufficient ATP. K is absorbed in the form of K^+ ions from the soil solution by epidermal and cortical cells of the roots. Once K^+ is inside the root symplast, it may be stored in vacuoles where it fulfills osmotic functions or is transported to the shoot via xylem (Pardo and Rubio 2011). In turn, shoot cells may also supply stored K^+ for redistribution via phloem. In this transit from the soil to the different plant organs, K^+ crosses various cell membranes through K^+-specific transport systems. Coordinated operation of different transport systems within the plant to secure K^+ uptake from the soil and delivery to the different plant organs requires complex K^+ sensing and signaling mechanisms.

Uptake and distribution of K^+ in plant cells is carried out by a variety of transporter proteins categorized into several families with varied structures and transport mechanisms that comprise the channel families shaker-like voltage-dependent, the tandem-pore (TPK), the two-pore channels (TPC) (Hedrich 2012), the carrier-like families KT/HAK/KUP (Nieves-Cordones et al. 2014; Li et al. 2018), HKT uniporters and symporters (Hamamoto et al. 2015), and cation-proton antiporters (CPA). The CPA family is the largest one and includes the NHX, CHX, and KEA antiporters (Sze and Chanroj 2018) (Fig. 1.1).

The high-affinity K^+ transporter (HAK5, AKT1) and nonselective cyclic nucleotide-gated ion channels (CNGC) contribute to K^+ nutrition although in different ranges of substrate concentrations from low to high availability, respectively. The outward exit of K^+ through the rectifying GORK channel facilitates fine adjustment of the electrical potential of the plasma membrane and allows

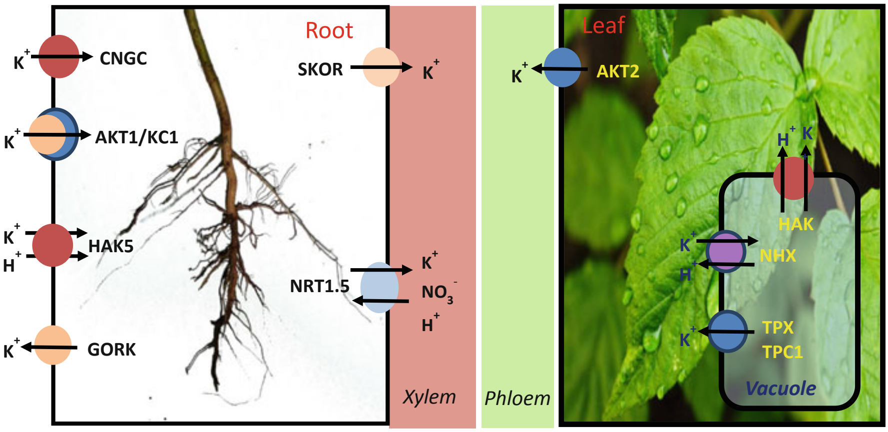

Fig. 1.1 Transporters involved in K^+ uptake by roots and interorgan partition

repolarization in circumstances that promote depolarization, such as salinity stress. In the root stele, the SKOR canal that is rectified outward releases K^+ into the xylem vessels for the supply of nutrients to the shoots. The nitrate transporter, NRT1.5, facilitates the loading of K^+ into the xylem by electrical coupling with other selective K^+ transporters or by acting directly as a K^+/H^+ antiporter. In aerial tissues a network of K^+ pulse channels and KT/HAK/KUP carriers allow uptake of K^+ entering green cells. K^+ is stored within vacuoles by NHX exchangers and released into the cytosol through TPK and TPC1 channels and probably also by KT/HAK/KUP carriers at the tonoplast level (the vacuole is omitted in cells of the root for simplicity). The K^+ channel from the plasma membrane outward, AKT2, releases K^+ into the phloem to return K^+ to the root and facilitate photosynthetic loading into the phloem sap.

1.5 Importance of Potassium in Photosynthesis

Potassium regulates the opening and closing of the stomata and improves the photosynthesis by regulating the absorption of CO_2. It plays a crucial role in the photosynthesis and the resulting translocation and metabolism of carbohydrates which ultimately increases crop yield and improves grain quality (Pettigrew 2008; Zorb et al. 2014; Lu et al. 2016). Also, K controls photosynthesis by intercepting sunlight. Leaf area and sunlight interception were significantly reduced when K was below the level required by the plants (Bednarz et al. 1998). K is an essential component for the proper development of plants. It is important in photosynthesis in regulating the responses of plants to light through the opening and closing of stomata.

The regulation of stomata during photosynthesis is a vital event that governs the process of continuous photosynthesis and is significantly moderated by the amount of K retained in the plant (Marschner 2012). The rate of photosynthesis in plants increased with the enhanced use and export of photoassimilates. The evidence showed that the level of sucrose in the leaves was increased several times when the plants received a sufficient level of K (Zhao et al. 2001). Furthermore, photosynthetic CO_2 uptake and the use of photoassimilates were reduced due to K deficiency accelerating ROS production from plants and ultimately accelerating rapid photooxidative damage (Waraich et al. 2012). Thus, the most significant function that K plays in regulation of stomatal opening is to balance the entry of CO_2 and the elimination of H_2O vapor from the intercellular spaces. However, the amount of CO_2 entering the intercellular spaces represents the amount of photosynthetic production in the leaf. K is also essential in the activation of the ATP synthase enzyme, thus contributing to the process of photosynthesis. Shingles and McCarty (1994) suggested that ATPase performance was the best when the plant's K content was at an optimal level. However, molecular identification of K^+ transporters involved in photosynthetic regulation has increased the apparent importance of K in plants. Recent studies have revealed the important roles of three K^+ efflux anti-stressors; AtKEA1/2/3 were involved in photosynthesis and development of primary chloroplasts in *Arabidopsis*. AtKEA1 and AtKEA2 were located in the inner envelope membrane of chloroplasts, while AtKEA3 was found in the thylakoid membrane (Kunz et al. 2014). Chloroplast development and the rate of photosynthesis were significantly damaged in the triple mutant, AtKEA23, resulting in stunted growth of mutant plants (Kunz et al. 2014; Dana et al. 2016). AtKEA1 and AtKEA2 showed a polar distribution in small and dividing plastids which regulated the development of chloroplasts as reported by Aranda-Sicilia et al. (2016). AtKEA3, an H^+/K^+ antiporter, mediated the exit of H^+ from the thylakoid lumen to the stroma by H^+/K^+ exchange and regulated the proton driving force through the thylakoid membranes. Therefore, it regulated photosynthesis and photosynthetic acclimation in fluctuating light environments (Armbruster et al. 2014; Wang and Wu 2017). Singh and Reddy (2017) pointed out that K deficiency limited *Glycine max* growth more than photosynthetic processes. Li and his team (2013) found 25% reduction in the contribution of N/K to strawberry (*Fragaria*×*ananassa* Duch), which was also associated with a higher foliar intercellular CO_2 concentration than control plants. Therefore, in case of K deficiency, the causes of decrease in the photosynthetic rate might be due to reduction in the conductance of the mesophyll caused by anatomical alterations of the leaves that led to the decrease in the surface of the chloroplast per unit of leaf area (Battie-Laclau et al. 2014; Lu et al. 2016). Additionally decrease in stomatal conductance and chlorophyll concentration could also be another reason for the drop in photosynthetic rate (Weng et al. 2007; Martineau et al. 2017).

1.6 Potassium Fertilizers and Importance of Potassium in Agriculture

The long-term addition of chemical fertilizers not only deteriorates environment but also leads to global warming alteration of soil pH and microbial diversity and adverse effects on consumers' health (Meena et al. 2013; Maurya et al. 2014). Due to the application of unbalanced fertilizers in agriculture fields, the level of K available in soils has decreased. The soluble K concentration in the soil is very low because a maximum part of K exists in insoluble form. Feldspar and mica are major deposits of K on the earth, whereas in soil K is found mainly in the form of silt, clay and sand. It is released when these minerals are slowly altered, or alternatively, it can be solubilized by certain beneficial microorganisms and made available to plants.

Potassium is mandatory for most of the biochemical and physiological processes influencing plant growth and metabolism (Wang et al. 2013). It is majorly used in hydroponics to improve root growth and enhance drought tolerance. It also enhances the building of cellulose, thus reduces lodging. Moreover, K plays a significant role in enhancing crop quality; therefore, it is also used as a constituent in artificial fertilizers. It has been well documented that crop yield and production of grains rich in starch and protein content are increased by using NPK fertilizers. Since K present in agricultural soil is chemically bound with insoluble mineral form and is not available to the crops, various sources of K are being made depending upon their requirement. Scherer (2005) reported manufacturing and applications of different sources of K fertilizers. Potassium chloride is the cheapest and most commonly available K fertilizer; potassium nitrate (also referred to as nitrate of potash) is also formed by the reaction of potassium chloride with a nitrate source. This fertilizer is used particularly for horticultural crops in which chloride uptake is a problem as in tobacco plant. Subsequently, potassium sulfate is produced when potassium chloride reacts with sulfuric acid that contains sulfur and potassium. In addition to the fertilizers listed above, potassium phosphate (KH_2PO_4) and potassium thiosulfate ($K_2S_2O_3$) are also available. Kelp meal plant residues and wood ash containing K, mainly in the form of carbonate (K_2CO_3), hydroxide (KOH), and rock powder, e.g., granite, and minerals such as alunite, orthoclase, microcline, etc. are other sources of potassium that are sold as K fertilizers (Rawat et al. 2016). Although K fertilizers have great significance, they can cause fertilizer injury to plants or seeds when placed too close to the plants. Therefore, application of K fertilizers in a band approximately 3 inches to the side and 2 inches below the seeds prevents the fertilizer injury to the plants and is called the band placement process.

Potassium fertilizer is widely used to reduce insect invasion and disease incidence in many host plants. Additionally, potassium fertilizers may help to improve plants' immunity to weather changes, various diseases, and injuries caused by nematodes. William and Smith (2001) reported the significance of K fertilizer in reducing the diseases called stem rot and aggregate sheath spot (AgSS), and negative correlations were found between the percentage of K in leaf blades and disease severity. K has a positive influence on fruit quality, yield, and stress tolerance of plants (Abbasi et al.

2016; Shen et al. 2016; Huang et al. 2016; Li and Chen 2017). In a study, it was observed that nodulation, nitrogenase activity, and dry matter yield increased with incremental K supply in broad beans, grown at moisture level of only 1/4 of field capacity (Abd-Alla and Wahab 1995).

1.7 Potassium-Solubilizing Microorganisms (KSMs) and Their Role in Crop Productivity

Microbes have played a key role in weathering of rocks and releasing various elements that they needed as nutrients (Calvaruso et al. 2006). Prajapati and his co-worker (2012) isolated 14 bacterial strains from samples taken in the ceramic industry using feldspar in solid medium of which 5 strains showed substantial potassium solubilization. Potassium-solubilizing bacteria (KSB) are capable of solubilizing K rock mineral dust such as micas, illite, and orthoclases through various processes such as acidolysis, enzymolysis, capsule absorption, and complexation with extracellular polysaccharides (Avakyan 1984; Rozanova 1986; Malinovskaya 1988; Malinovskaya et al. 1990; Friedrich et al. 1991; Ullman et al. 1996; Welch et al. 1999). The mechanisms involved in the degradation of potassium minerals can be divided into direct (bacterial cell wall) and indirect mechanisms (bioleaching, mineral alteration, microbial alteration, and mechanical fragmentation) (Rawat et al. 2016). The mechanisms of microbial corrosion included redox reactions through the production of organic acids that led to the weakening of chemical bonds in minerals to promote the dissolution of minerals (Banfield et al. 1999; Harley and Gilkes 2000) and chelating molecules for the degradation of minerals (Uroz et al. 2007, 2009; Lian et al. 2008). Bacteria produced a wide range of low molecular weight organic acids such as citric, malic, succinic, oxalic and tartaric acids (Jones 1998; Neaman et al. 2005). Han and Lee (2005) concluded in a study that KSB solubilized potassium rock through the production and secretion of organic acids. The observations of Prajapati and Modi (2012) were similar which attributed solubilization to the reduction in pH due to organic acids. Few other reports are also available on the solubilization of feldspar by *Bacillus mucilaginosus* and *Bacillus edaphicus* by acid production (Malinovskaya et al. 1990; Sheng and Huang 2002). In addition to organic acids, microbes used carbonic acid formed from carbon dioxide to attack the mineral's surface promoting the chemical weathering of rocks and minerals (Gadd 2007; Park et al. 2009). Many rock-dwelling fungi have been melanized, and melanin pigment has conferred extra-mechanical strength on hyphae to penetrate rock surfaces and crevices (Dornieden et al. 1997; Sterflinger and Krumbein 1997) which in turn offered protection against the toxicity of metals (Gadd 1993).

The beneficial microorganisms in the form of biofertilizers are applied to the seeds/roots or in the soil which mobilizes the availability of nutrients through its biological activity, thus contributing to the accumulation of beneficial microflora and improving the health of the soil. Commercially available microbial inoculants that are able to dissolve K from minerals and rock, not only enhance plant growth and yield but are also eco-friendly. *Aspergillus niger*, *Bacillus extorquens*, and *Clostridium pasteurianum* were found to grow on muscovite, biotite, orthoclase, microcline, and mica in vitro (Archana et al. 2013). Supanjani et al. (2006) showed that bacteria that dissolved K (as well as bacteria that solubilized phosphate) also increased photosynthesis of hot pepper (*Capsicum annuum* L.) by approximately 16% and leaf area by approximately 35% as compared to control plants. Besides, the biomass and the fruit yield of the treated plants were higher by 23% and 30%, respectively than the control. Recently, Prajapati and his team (2013) isolated K-solubilizing bacterial strain of *Enterobacter hormaechei* and fungal strain of *Aspergillus terreus* and studied their effects and nutrient uptake on okra (*Abelmoschus esculentus*) in K-deficient soil using pot experiments. *E. hormaechei* increased the growth of the roots and shoots of the plant, and both microbes were able to mobilize K in the okra plants when the feldspar was incorporated into the soil. Likewise, Han et al. (2006) studied the effect of KSB, *Bacillus mucilaginosus* on pepper and cucumber plants. A remarkable work by Bagyalakshmi and her team (2012) showed that the inoculation of tea plants with KSB (*Pseudomonas putida*) led to the improvement in productivity and absorption of nutrients by the plants. Traits of tea quality such as theaflavin, thearubigin, highly polymerized substances, total liquor, colour, caffeine, briskness, leaf colour, and flavor indices were found to be greatly improved in the treated plants. A few species of *Bacillus* have been identified as KSB biofertilizer to provide K in the soil during cultivation (Meena et al. 2016). Parmer et al. (2016) reported that among all their isolated strains, two most efficient *Bacillus* species, namely, *B. licheniformis* and *B. subtilis*, had K solubilization potentials of 46.37μg ml^{-1} and 42.37μg ml^{-1}, respectively. However, Badr (2006) reported that a strain of *B. mucilaginosus* solubilized only 4.29μg K ml^{-1} in broth medium supplemented with muscovite mica. Previous work has reported the beneficial effect of KSB inoculation on the growth of various crops, namely, cotton and rapeseed (Sheng 2005), bell pepper and cucumber (Han et al. 2006), khella (Hassan et al. 2010), sorghum (Badr et al. 2006), wheat (Sheng and He 2006), tomato (Lin et al. 2002), chilli (Ramarethinam and Chandra 2005), Sudan grass (Basak and Biswas 2009), and tobacco (Zhang and Kong 2014). In a study, the application of isolated *B. pseudomycoides* in combination with MW (mica waste) significantly increased the availability of K in the soil, which in turn facilitated the absorption of K by tea plants (Pramanik et al. 2019). The yield and quality of soybean (*Glycine max* (L.) Merr.), an important oil crop and the source of high-quality plant protein for humans, has been limited in the K-deficient fields (Yin and Vyn 2004; Abbasi et al. 2012).

1.8 Conclusion

Potassium is important in physiological and stressful environments for the survival of plants. The appropriate use of K with other nutrients contributes to the achievement of sustainable crop production and quality and to the maintenance of animal and human nutritious food security. Maintaining an optimal nutritional status of K is essential for the resistance of plants to biotic and abiotic stress. During most abiotic pressures, essential physiological processes including photosynthesis are significantly impaired leading to a rise in toxic ROS in plant cells. However, an adequate supply of stressed K plants will decrease the output of ROS and improve the condition of the plants. KSMs are capable of mobilizing bounded K from soil thus, can be used as K-based biofertilizers. These fertilizers also control water requirement for crops throughout the growth period. Balanced fertilization and efficient use of K along with supplementary nutrients not only contribute to the growth, yield, and quality of sustainable crops but also improve plant-soil health and reduce environmental risks.

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Potassium Role in Plants' Response to Abiotic Stresses

2

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Abstract

Among the plant nutrients, potassium (K^+) is one of the vital elements required for plant growth and physiology, along with nitrogen (N) and phosphorus (P). K^+ is a cation present in plants in concentrations ranging from 50 to 150 mM in the liquid parts, the cytoplasm, and the vacuole. The concentration of K^+ in the cytoplasm is usually constant about 50 mM, while the concentration in the vacuole may vary quite substantially. It is a component of the plant structure, but also has a regulatory function in several biochemical processes related to protein synthesis, carbohydrate metabolism, and enzyme activation. Numerous physiological processes depend on K^+, such as stomatal regulation and photosynthesis. In recent decades, K^+ was found to provide abiotic stress tolerance mechanisms, e.g., enzyme activation, protein synthesis, photosynthesis, stomatal movement, turgor regulation, and osmotic adjustment. It also functions in plant signaling systems which assist in defending some stresses by activating antioxidant defense systems. K^+ accumulation in plants before stress events such as water deficiency, lodging, cold stress, and salinity stress is a survival strategy for the plant. K^+ is needed at high concentrations inside the plants from early stages of vegetative growth phase. High internal K^+ concentration can reduce extreme sudden environmental events like cold, frost, late season rains, salinity stress, and heat waves. The whole structure of proteins and protein activity need high concentrations of K^+ in the cytosol for optimum plant functions. Yet, to survive osmotic stress and unusual physical burden, prior accumulation of K^+ was shown

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to reduce the damage to plants. Proper use of K^+ with other nutrients helps to achieve sustainable productivity and quality of crops and guarantee nutritional food security for animals and humans.

Keywords

Potassium · Abiotic stress · Tolerance

2.1 Introduction

Abiotic stress is defined as environmental conditions that decrease crop growth and yield below optimum levels (Asada et al. 2000). It hampers plant productivity by changing plant growth patterns and physiological responses (Asada et al. 2000). Most cultivated crops undergo abiotic stress or combination of more than one kind of stress through their growth cycle (Asada et al. 2000). Combination of different stresses is becoming more common, for example, drought and high temperature are the most common stress combination (Asada et al. 2000), while in arid and semiarid regions, salinity and high temperature stresses may occur at the same time. These complex stresses generate changes in cropping patterns, crop agricultural practices, and, sometimes, the extinction of plant species (Asada et al. 2000; Vranová et al. 2002).

Food production must be increased by up to 100% by the year 2050 to meet the nutritional needs of the increasing world population (Asada et al. 2000). The area of agricultural lands is very limited and has been declining all over the world; thus, the desirable increases in food production must be achieved on the already cultivated land. However, there is a global decrease in soil productivity and fertility due to degradation and intensive use of soils without consideration of proper soil-management practices (Asada et al. 2000; Vranová et al. 2002). Insufficient and unbalanced mineral nutrient supply and reduced soil fertility are distinct problems, leading to a decrease in global food production, particularly in the developing countries. It is estimated that about 60% of cultivated soils have growth-limiting difficulties associated with mineral deficiencies and toxicities (Asada et al. 2000).

To sustain food security, there is a great need to minimize the harmful effects of abiotic stresses on crop production. Part of the solution can be achieved with balanced supply of mineral nutrients and maintaining soil fertility. This chapter deals with K^+ roles in reducing the negative effects of abiotic stress on crop production.

2.2 Potassium in the Soil

Potassium (K^+) contains an average of 2.6% of the earth's crust, making it the seventh most abundant element and the fourth most abundant mineral nutrient in the lithosphere (Asada et al. 2000; Vranová et al. 2002). K^+ is a vital element of plant

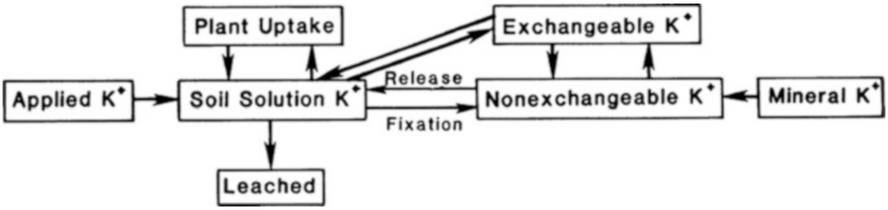


Fig. 2.1 Dynamics between the various K phases in soil, from Bertsch and Thomas (1985)

nutrition and is the second largest nutrient assimilated by plants after nitrogen (Asada et al. 2000). The amount of K^+ in a given soil reflects the parent materials of the soil, weathering degree, and volume of K fertilizer added, minus losses due to crop removal, soil erosion, and leaching. Crop removal and fertilization are highly important factors in cultivated soils. Cultivating practices used around the world have a strong effect on K^+ levels in soils. Any time the crop vegetative portion is removed; a large increase in K^+ is expected to be removed as well. In some livestock operations, manure is returned to the soil, which significantly reduces the loss. Where this is not the case, K^+ removal is so large that even the best endowed soils cannot withstand the loss forever (Asada et al. 2000; Vranová et al. 2002).

Potassium availability and spatial distribution in agricultural soils are affected by many agro-environmental factors (Biehler and Fock 1996; Cakmak 2000). However, not all K forms are readily available for plants. It is commonly recognized that K^+ occurs in soil in four forms: water soluble, exchangeable, non-exchangeable, and structural (Asada et al. 2000). There is a dynamic equilibrium reaction among the K^+ different forms that control the release and/or fixation of K^+ according to soil biogeochemical properties and processes (Asada et al. 2000; Vranová et al. 2002). Hence, soil K^+ form distribution is affected by different agro-environmental factors, such as soil parent materials (Biehler and Fock 1996; Cakmak 2000), soil weathering degree (Asada et al. 2000), topography (Asada et al. 2000; Vranová et al. 2002), and nutrient balance (Bertsch and Thomas 1985).

The readily available K^+ for plant nutrition exists in the soil solution. K^+ concentration in the soil solution is very low at any time; therefore, the replacement of the solution from other K-bearing phases is of great importance in determining a soil's K fertility status. Once K^+ is released to solution, it diffuses into the roots to ensure normal plant uptake. This diffusion process is reliant on several factors, such as soil water content, tortuosity of the diffusion path, temperature, K^+ diffusion coefficient in water, and K^+ concentration gradient. Plants take up relatively high amounts of K^+, thus rapidly reducing the K^+ concentration in the root zone (Fig. 2.1) (Biehler and Fock 1996; Cakmak 2000). K cycle in the soil is shown in Fig. 2.2.

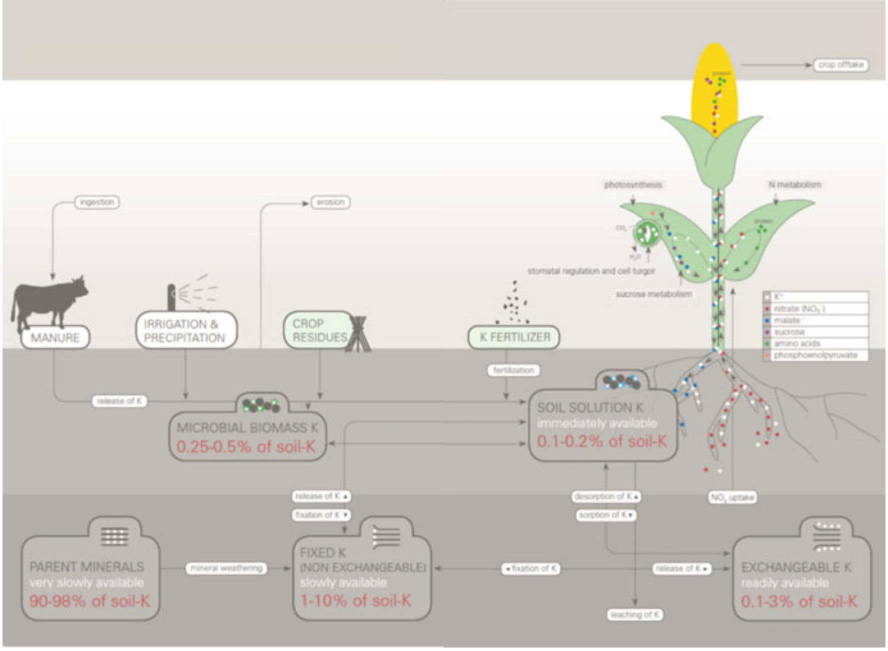


Fig. 2.2 K cycle in soil (IPI website: https://www.ipipotash.org/)

2.3 Potassium Role in Plants

Potassium is an essential nutrient and the most abundant cation in plants. K^+ is a unique plant nutrient as it occurs solely in the free ion form (Asada et al. 2000). In sufficiently supplied plants, K^+ may make up about 6% of plant dry matter or concentrations of around 200 mM (Asada et al. 2000; Vranová et al. 2002). Highest K^+ concentrations are found in young developing tissues and reproductive organs indicative of its high activity in cell metabolism and growth. K^+ activates numerous enzymes including those involving energy metabolism, protein synthesis, and solute transport (Biehler and Fock 1996; Cakmak 2000). Other processes where K^+ is found to be involved include stomatal movement, osmoregulation and cell extension, photosynthesis, and phloem loading and transport and uptake (Cakmak 2000; Choi et al. 2002). K^+ is needed in the plant cells for maintaining transmembrane voltage gradients for cytoplasmic pH homeostasis and in the transport of inorganic anions and metabolites (Asada et al. 2000). K^+ is the dominant cation in long-distance transport within the xylem and phloem saps, neutralizing inorganic and organic anions, giving high K^+ mobility throughout the whole plant (Asada et al. 2000; Vranová et al. 2002). K^+ uptake and accumulation by plant cells is the main driving force for cells' osmotic expansion (Biehler and Fock 1996; Cakmak 2000).

The most common symptom of K^+ deficiency is chlorosis along leaves edges, also known as leaf margin scorching. Chlorosis occurs first in older leaves, due to the high rate of K^+ allocation from mature tissues to developing tissues. First, the growth rate is decreasing (known as hidden hunger), and only later chlorosis and necrosis appear in the older leaves. Because K^+ is required in photosynthesis and protein synthesis, K^+-deficient plants will have slow and stunted growth. In some crops, stems become weak and lodging incidences increase. Seed and fruit size and their production quantity are reduced. Plants with K^+ deficiency demonstrate turgor decrease and become flaccid under water stress, especially during midday hours (Choi et al. 2002; Cakmak 2000).

Potassium also contributes to the survival of plants exposed to various abiotic stresses (Asada et al. 2000). Potassium plays vital roles in contributing to the survival of crop plants under environmental stress conditions and many physiological processes, such as protein synthesis, energy transfer, enzyme activation, photosynthesis and translocation of photosynthates into sink organs, osmoregulation, stomatal movement, phloem transport, cation-anion balance, and stress resistance and reducing excess uptake of ions such as Na and Fe in saline and flooded soil (Asada et al. 2000; Vranová et al. 2002).

2.4 Potassium Role in Response to Abiotic Stress

Increasing events of drought and other abiotic stresses rising from loss of soil fertility and global warming will require a specifically high supply of K^+ for crop stress reduction (Biehler and Fock 1996; Cakmak 2000). During their evolution, plants have developed a wide range of tolerance mechanisms to cope with a variety of stressed conditions. Increasing evidence suggests that mineral nutrients play a vital role in plant stress tolerance (Cakmak 2000; Choi et al. 2002). Out of all these mineral nutrients, K^+ plays a particularly important role in plant growth and metabolism, and it significantly contributes to plant survival under various biotic and abiotic stresses. The importance of K^+ fertilizers to the establishing crop production and quality is known. As a result, potash consumption has increased dramatically in most areas of the world (Asada et al. 2000).

2.4.1 Drought

Most crops will be exposed to water shortages at some point during their growing season, resulting in numerous harmful effects on plant growth. Drought stress mitigation is therefore an essential aspect of crop management (Asada et al. 2000; Vranová et al. 2002). Maintaining sufficient K^+ status in the plant is vital for drought adaptation (Biehler and Fock 1996; Cakmak 2000), and there is increasing evidence that plants under drought conditions have a higher internal K^+ requirement (Cakmak 2000; Choi et al. 2002). Simultaneously, plants' K^+ uptake is significantly decreased by drought stress (Marschner et al. 1996). This reduction is due to both decreased K^+

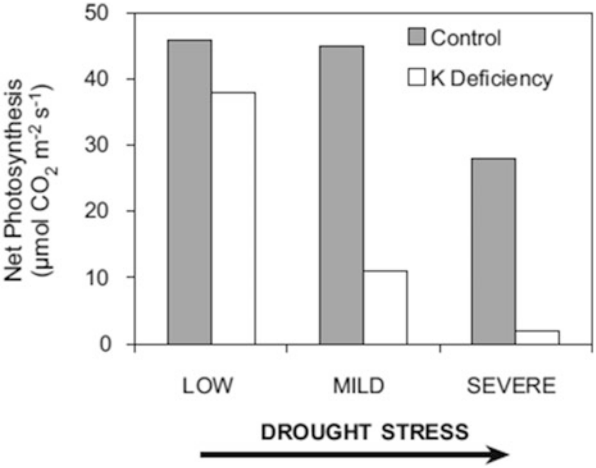


Fig. 2.3 Net photosynthesis of wheat leaves subjected to varied drought stress and K supply, from Cakmak (2000)

mobility in the soil and reduced transpiration rate and impaired activity of root membrane transporters (Asada et al. 2000).

The reason for the enhanced need for K^+ by plants suffering from abiotic stresses is related to the fact that K^+ is required to maintain photosynthetic CO_2 fixation. High K^+ has also been linked to maintaining optimum pH values in the chloroplasts' stroma and optimal function of photosynthetic mechanisms (Asada et al. 2000; Vranová et al. 2002). Water-stressed chloroplasts were showing increased K^+ leakage, resulting in additional photosynthesis suppression (Fig. 2.3) (Biehler and Fock 1996; Cakmak 2000). When water-deficit stressed plants were supplied with higher than optimum quantities of K^+, they were able to maintain efficient photosynthetic activity (Cakmak 2000; Choi et al. 2002) and contained higher K^+ concentrations compared to plants which received optimal quantities of water (Marschner et al. 1996). This can be explained by K's ability to maintain CO_2 assimilation rates by regulating stomatal function and balancing cell water relations (Asada et al. 2000).

Potassium accumulation plays a crucial role in osmotic regulation, contributing on average between 35% and 50% of the cell osmotic potential in crops (Asada et al. 2000; Vranová et al. 2002). Biehler and Fock (1996) and Cakmak (2000) reported that in wheat, differences in shoot K^+ content were 84% of the difference in osmotic adjustment among K-sufficient genotypes, while in plants lacking K^+ fertilization, K^+ accumulation in leaves was only 17–28% of osmotic adjustment. K fertilization was found to increase osmotic adjustment and improved water relations in a wide range of crops (Cakmak 2000; Choi et al. 2002).

The K^+ status of the plant also influences on the plant's ability to extract water from the soil. Plants supplied with sufficiently amounts of K^+ can utilize the soil moisture more effectively than K^+-lacking plants (Marschner et al. 1996). K^+ application was found to enhance cell elongation, the key of plant growth. Cell elongation is initiated by wall relaxation, leading to osmotic potential-driven water uptake and turgor-driven cell expansion (Asada et al. 2000). Enhanced cell expansion and growth set up a pressure gradient between the root and its surrounding which increases water uptake (Asada et al. 2000; Vranová et al. 2002), which might help the plant keep drawing water when the soil is getting dryer.

2.4.2 Cold Stress

Temperature is an important factor determining plants' geographical distribution in an optimal environment for their survival and development (Biehler and Fock 1996; Cakmak 2000). Cold stress (<20 °C) occurs when low temperatures affect cellular macromolecules, which results in slowing down of metabolism, cell membrane solidification, and losing membrane functions (Cakmak 2000; Choi et al. 2002). Abrupt changes in the plant's environment result in slower growth and reduced yield due to resource shifting from reproductive processes to metabolic process, in order to attain tolerance (Marschner et al. 1996). Cold stress symptoms include wilting, chlorosis, leaf expansion, and growth reduction (Marschner and Cakmak 1989), which may further develop to necrosis, reduced development of reproductive components, and hindered seed and pod development in sensitive species (Asada et al. 2000). The combination of all these mentioned factors ultimately leads to crop yield reduction.

Plants perform better when exposed to cold stress, when their K concentration is in the range of what Asada et al. (2000) and Vranová et al. (2002) described as "luxury consumption concentration range." Biehler and Fock (1996) and Cakmak (2000) proposed that K^+ accumulation by plants before stress initiation is not luxury but rather an "insurance strategy" to enable the plant to survive an unexpected environmental change (abiotic stress). Lack of K^+ in the early developmental stages of plant growth will affect the entire structure of the plant and may lead to lodging and frost damage in a higher ratio than expected from a healthy plant (Cakmak 2000; Choi et al. 2002). When temperatures decline (frost or chilling event), it causes a sudden change in the membrane fluidity. This change differs from cell to cell and dependent on the relative composition of various phospholipids (Marschner et al. 1996). In general, low temperature stress has an effect on the membrane lipid fluidity and thus modifies the membrane structure (Marschner and Cakmak 1989).

The balanced fatty acid ratio is involved as well in reducing plants' chilling sensitivity. High ratio between unsaturated and saturated fatty acids in the cell membrane makes the tissue more tolerant to low temperatures (Asada et al. 2000). Asada et al. (2000) and Vranová et al. (2002) showed that additional K^+ in tomatoes, eggplants, and peppers led to maximum growth response and chilling tolerance. This response was associated with phospholipid increase, membrane permeability, and improving cells' biophysical and biochemical properties. Biehler and Fock (1996) and Cakmak (2000) studied the effect of increasing K^+ concentration on yield and chilling damage in the carnations. Stem brittle incidence percentage increased 5–6 weeks after cold night events (>8 °C), followed by clear sunny days. When K^+ concentration in the irrigation water was increased, the weekly loss of broken

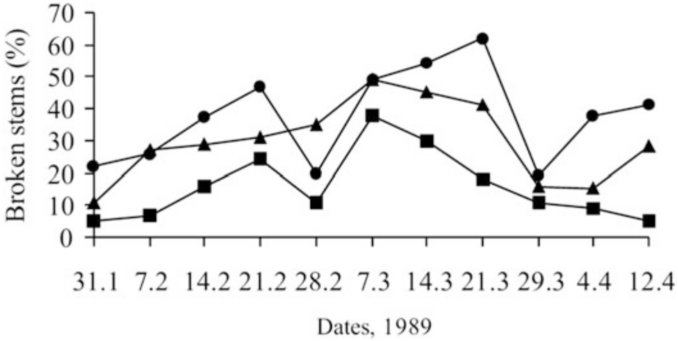
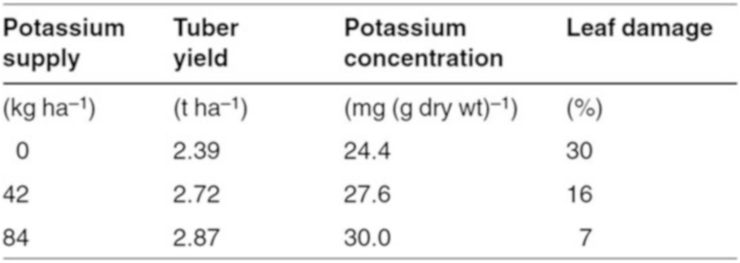


Fig. 2.4 Broken stems of carnation cv. White candy during the growing season on three on levels of K^+ in irrigation water: filled circle 93; filled triangle 252; filled square 378 g K^+ m^{-3}. Source: Yermiyahu and Kafkafi (1990)



Potassium supply	Tuber yield	Potassium concentration	Leaf damage
(kg ha⁻¹)	(t ha⁻¹)	(mg (g dry wt)⁻¹)	(%)
0	2.39	24.4	30
42	2.72	27.6	16
84	2.87	30.0	7

Fig. 2.5 Potassium supply influence on tuber yield, potassium concentration of leaves, and leaf frost damage in potato. Adapted from Asada et al. (2000)

stems was lower (Fig. 2.4). Likewise, Cakmak (2000) and Choi et al. (2002) reported that high K applications could alleviate cold-induced yield reduction and increases in leaf damage in potato plants under field conditions (Fig. 2.5). K-deficient potato plants might be more vulnerable to frost; Marschner et al. (1996) reported that application of K^+ at high rates can efficiently increase frost tolerance of some frost-sensitive potato genotypes. Nitrogen (N) and K effect on two rice cultivars' spikelet sterility induced by low temperature at the reproductive stage was studied by Marschner and Cakmak (1989). Increasing the K^+ supply and the K:N ratio in the leaves reduced the spikelet sterility in one of the tested rice cultivars, but the effect was not clear in the second cultivar. The different response of the rice cultivars to chilling effects might be because they differ in the fatty acid composition of their root membranes.

High K^+ content inside cells can increase frost tolerance by regulating osmotic and water potential of the cell sap and decreasing electrolyte leakage caused by low temperatures (Asada et al. 2000; Vranová et al. 2002). Cold stress can also cause photooxidative damage to chloroplasts as a result of impairments in photosynthetic carbon (C) metabolism. Under cold stress, the absorbed light energy surpasses the chloroplast capacity to utilize it in CO_2 fixation; instead, the excess energy is used to activate O_2 to reactive oxygen species (ROS) (Biehler and Fock 1996; Cakmak 2000).

The main processes damaged by cold stress are the photosynthetic electron transport, rubisco activity, stomatal conductance, and CO_2 fixation (Cakmak 2000; Choi et al. 2002). These cellular processes are also being negatively affected by K deficiency. Thus, when K supply is insufficient, low temperature-induced photooxidative damage can be worsened, leading to a further reduction of plant growth and yield. Supplying plants with high amounts of K may protect them against oxidative damage caused by cold stress (Marschner et al. 1996). To summarize, high concentration of K in the tissue can decrease chilling damage and increase cold tolerance, resulting in increased yield production. Frost damage is negatively correlated to K concentration and can be significantly reduced with K fertilization (Marschner and Cakmak 1989). High frost damage was observed in potatoes growing in soils with available K concentration of ≤ 114 ppm. This concentration might be the critical available K level for frost damage formation in potatoes and also can be used for K fertilizer recommendations (Grewal and Singh 1980).

2.4.3 Salinity Stress

Salinity stress is one of the major abiotic stresses that impact almost every aspect of plant physiology and biochemistry, resulting in yield reduction (Barnes et al. 1995). Thus, it is a serious threat to agricultural productivity, especially in arid and semiarid regions (Asada et al. 2000). It has been estimated that 20% of total cultivated and 33% of irrigated agricultural lands worldwide are afflicted by salinity. Moreover, salinized areas are increasing at a rate of 10% annually. Additionally, brackish water is often used for irrigation, especially in dry climates, due to intensive use of scarce water resources, further increasing salinization of soils and groundwater (Asada et al. 2000; Vranová et al. 2002).

Sodium (Na^+) and K nutrition impairment is a great indicator of salt-stressed plants. Thus, K:Na ratio is considered a useful way to estimate salt tolerance in plants (Biehler and Fock 1996; Cakmak 2000). Plants' ability to maintain high K^+ cytoplasmic levels is vital for their survival in saline environments (Cakmak 2000; Choi et al. 2002). In saline soils, Na^+ concentration is usually higher than K^+ and calcium (Ca^{2+}), which can create a passive accumulation of Na^+ in the plant (Marschner et al. 1996). High Na^+ levels can cause to Ca^{2+} relocation from the root membranes, changing their integrity and eventually affecting the selectivity of K^+ uptake (Marschner and Cakmak 1989). Potassium uptake is regulating K^+ xylem loading (Barnes et al. 1995), suggesting that salinity interferes with K^+ translocation from the roots to the shoot, which results in a lower K^+ shoot content and a higher K^+ root content (Asada et al. 2000). Salinity inhibitory effects on K^+ uptake and relocation were found to be stronger when the K^+ concentration in the nutrient solution was low (Asada et al. 2000; Vranová et al. 2002). Sodium toxicity happens as a result of Na^+ competing with K^+ for enzyme activation and protein biosynthesis. Yet, it is not the

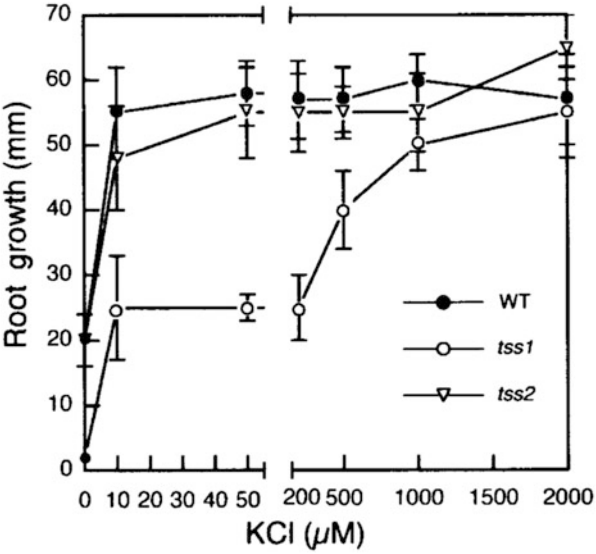


Fig. 2.6 tss1 mutants with hypersensitivity low potassium. From Borsani et al. (2001)

absolute concentration of Na^+ by itself but rather the K^+: Na^+ ratio in the cytosol that controls the cells' metabolic capability and ultimately the plant's ability to survive in saline environments (Biehler and Fock 1996; Cakmak 2000). Numerous studies stated that the cytosolic K^+:Na^+ ratio plays an important role in salt tolerance of plants (Cakmak 2000; Choi et al. 2002).

In breeding, selecting genotypes with high K:Na ratios can be a solution to minimize the negative effects on plants growing in saline soils (Marschner et al. 1996). A wheat mutant was found to have high capability to accumulate K in the shoot. This mutant showed higher tissue hydration, seed germination, and seedling growth under growing NaCl concentrations, compared with other wheat genotypes (Marschner and Cakmak 1989). Arabidopsis mutant lines showing hypersensitivity to NaCl were found to be hypersensitive to low K supply as well. The high salt sensitivity was associated with very low capacity of the plants to take up K from the growth medium, showing again the importance of K nutrition in salt tolerance (Barnes et al. 1995). Similarly, tomato salt-hypersensitive mutants were found to have malfunctioning K uptake and had a reduced K nutrition (Fig. 2.6) (Zhao et al. 2001). Asada et al. (2000) reported that salinity effect on the growth of maize plant was dependent on K^+ concentration in the growth medium. Salinity had no effect on root dry weight, but low K^+ concentration in the nutrient solution reduced shoot dry weight significantly. Asada et al. (2000) and Vranová et al. (2002) reported similar responses found in spinach. The differences in shoot growth between plants growing in low and high salinity levels were decreased as a response to an increasing K^+ concentration. Shoot/root ratio was lower when plants grew in 100 mmol/L NaCl, but the effect was significant only when the K^+ concentration in the nutrient solution was low. These results highlights that sufficient K nutrition has a crucial role in

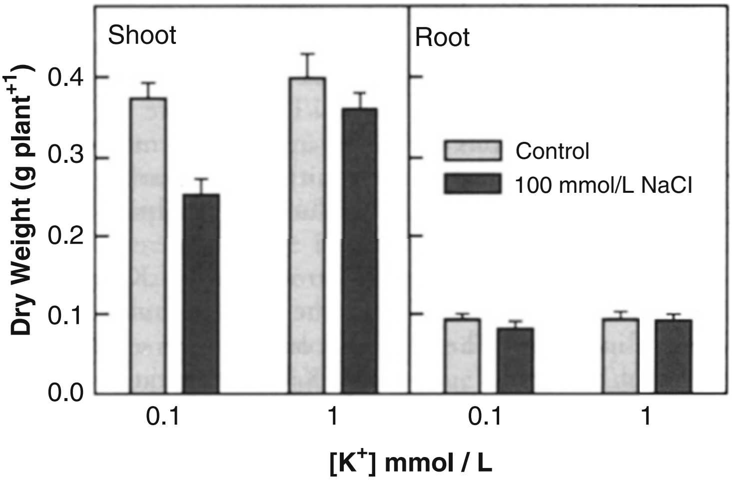


Fig. 2.7 NaCl and potassium concentration effect on shoot and root dry weight of 19-day-old maize plants. Each column represents the mean of four replicates. The error bars represent the standard error ($n = 4$) (Marschner et al. 1996)

alleviating the detrimental effects of salinity in plants (Biehler and Fock 1996; Cakmak 2000) (Fig. 2.7).

2.4.4 Heat Stress

High temperature stress occurs when the temperature is higher than what was defined as temperature optimum range for plants (Marschner and Cakmak 1989). Heat stress is a major environmental factor which poses limitations on plant growth, metabolism, and productivity all over the world. Plant growth and development include many biochemical responses which are sensitive to temperature (Barnes et al. 1995). Heat stress has a negative impact on different plant processes (e.g., growth, development, physiological) and yield (Zhao et al. 2001). Figure 2.8 is showing the cell signaling associated with low K levels in plants. One of the major heat stresses results in excess production of ROS, which later causes an oxidative stress. Plant responses to heat stress are dependent on the degree and exposure to the stress and the plant type.

Potassium plays an important role in plant tolerance to heat stress. K^+ helps to activate numerous physiological and metabolic processes, e.g., photosynthesis, respiration, and nutrient homeostasis. Additionally, K^+ enhances plant tissue's water potential, which aids in plant tolerance to high temperature stress (Asada et al. 2000). Potassium functions as an osmolyte and assists in maintaining and regulating stomatal conductance and thus preventing cell damage (Asada et al. 2000; Vranová et al. 2002). ROS production was seen in plants with K^+ deficiency, which happened via photosynthetic electron transport pathways and NADPH oxidizing

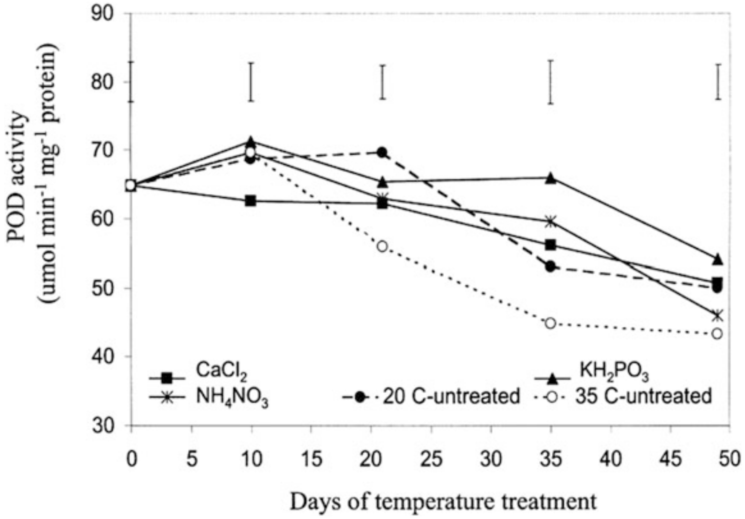


Fig. 2.8 Cell signaling associated with low potassium levels in plants (Zhao et al. 2001)

enzymatic reactions (Biehler and Fock 1996; Cakmak 2000). K^+ protects plants by assisting protein synthesis, participating in numerous enzymatic reactions and carbohydrate biosynthesis, and improving plant cells' water use efficiency. Under heat stress conditions, wheat heat tolerance was improved with potassium orthophosphate (KH_2PO_4) foliar application, which protected the leaves from damage (Cakmak 2000; Choi et al. 2002).

When losing significant K^+ quantity from the chloroplast, a decrease in photosynthesis is noticed. Applying K^+ in this case can assist plant cells to become more resilient to the heat stress by strengthening the photosynthetic capability. Foliar K^+ applications lead to increased photosynthate accumulation and translocation, and dry matter as well. Marschner et al. (1996) observed a decline in hydrogen peroxide activity after 21 days of heat stress, after applying foliar KH_2PO_3 and other nutrients (Fig. 2.9), as part of improved response to heat stress. Heat stress can cause leaf senescence associated with oxidative stress caused by ROS production (like hydrogen peroxide). Reducing ROS overproduction during stress can reduce damage done to cellular components like lipids, protein, DNA, and RNA (Marschner and Cakmak 1989).

2.4.5 Potassium and Lodging

The definition of lodging is stem dislocation from their standing position. Lodging can be partially reversible or permanent, depending on the bending degree. Lodging is more common to occur in cereal crops. There are two kinds of lodging: (1) stem lodging is defined as lower culm internode bending (Marschner et al. 1996; Zhao

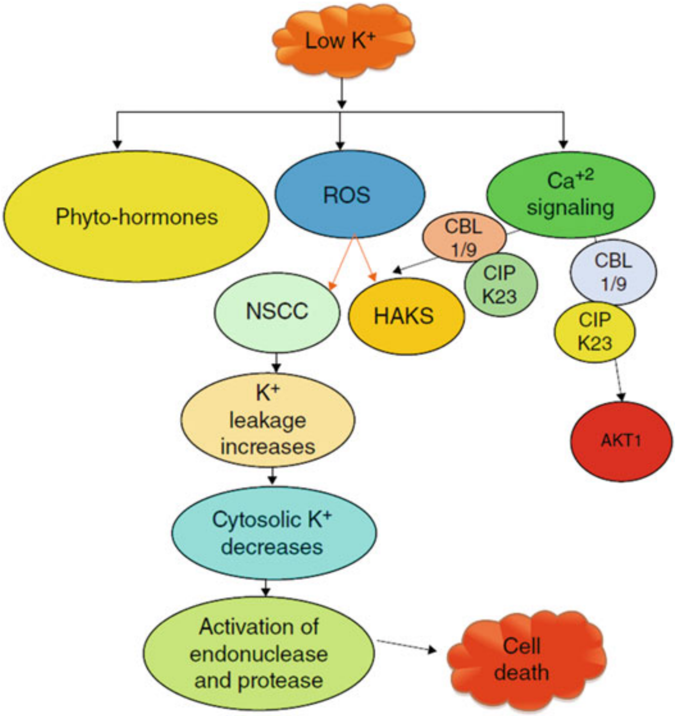


Fig. 2.9 Effect of nutrient foliar application on hydrogen peroxide activity in bentgrass. Bars indicate LSDs ($P = 0.05$) for treatment comparisons at a given day (Barnes et al. 1995)

et al. 2001) and (2) root lodging is defined when the plant is leaning from the crown due to insufficient root growth (Asada et al. 2000). Lodging loss is critical in heading and early grain development stages. Lodging is affected by combined effects of plant type and nutrient management and environmental and soil conditions (Asada et al. 2000; Vranová et al. 2002). Lodging causes yield reduction and financial costs. For example, severe lodging happens once in 3–4 years in the UK and might result in yield losses in cereal crops and oilseed rape of 25–75%, depending on the lodging timing during the growing season (Biehler and Fock 1996; Cakmak 2000). Lodging also affects yield quality, as lodged crop grains are less likely to meet bread-making quality. The estimation for the UK is that lodging can lead to financial losses of 170 M £ in a severe lodging year (50 M £ on average), as a result of yield loss, lower grain quality, and higher grain drying costs (Cakmak 2000; Choi et al. 2002). Lodging increases the risk of mycotoxin development in the grain (Marschner et al. 1996), which can be dangerous to animals and humans.

The stem diameter of K-deficient plants is smaller, which makes the plant more vulnerable to lodging. When K supply is insufficient, sclerenchyma fiber cells and woody parenchyma cells create thin and poorly lignified cell walls which decrease stem diameter (Marschner and Cakmak 1989). Barnes et al. (1995) reported that

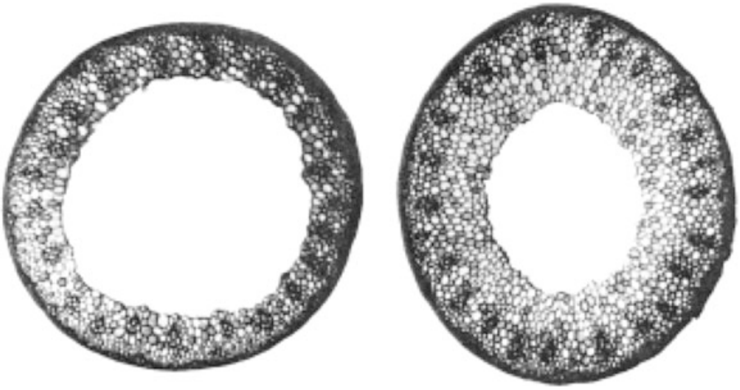


Fig. 2.10 Cross section of wheat internode with low (*left*) and high (*right*) K^+ nutrition (Kant and Kafkafi 2002)

optimal K nutrition elevated the thickness of sclerenchyma tissue layers in rice. Wheat internode cross section (Fig. 2.10) shows that plants which received more K^+ have developed thicker stalk wall. Improved stem stability and thickness can be related to delayed aging of the pith parenchyma, and activation of general defense mechanism when K supply is optimal (Zhao et al. 2001). Adding K^+ decreased senescent stalks and stalk lodging percentage in corn grown on K-deficient soils (Marschner et al. 1996; Zhao et al. 2001). Welch and Flannery (1985) reported that applying K^+ increased crushing strength and skin.

Potassium deficiency increases both transpiration and respiration rate and reduces photosynthesis, starch accumulation, and cell wall substances, e.g., holocellulose, which affect stem strength in rice. Potassium content in the culm basal part is highly correlated with the stem breaking strength, suggesting that adequate amount of K^+ is related to lignification of vascular bundles and sclerenchyma cells, and strengthening culms, thus increasing the plant lodging resistance (Datta and Mikkelsen 1985). Increasing K^+ dose from 50 to 200 kg ha^{-1} reduced total lodging percentage (Fig. 2.11) (Melis and Farina 1984). Lodging resistance is mainly ruled genetically, and sufficient K application further reduces the likelihood of lodging in different crops (Parks 1985).

2.4.6 Potassium and Iron Toxicity

Iron (Fe) toxicity happens when the soil solution contains high concentrations of reduced iron (Fe^{2+}) (Becker and Asch 2005). Iron toxicity is more common in flooded soils and may result in low productivity in affected soils. Because rice is a major crop growing in flooded soils, most of the research is focused on Fe toxicity in this crop. Fe^{2+} toxicity symptoms occur with uptake of high Fe^{2+} concentrations, translocating them to the leaves and producing toxic oxygen radicals harming cellular structures and afflicting physiological processes (Wu et al. 2017; Onyango

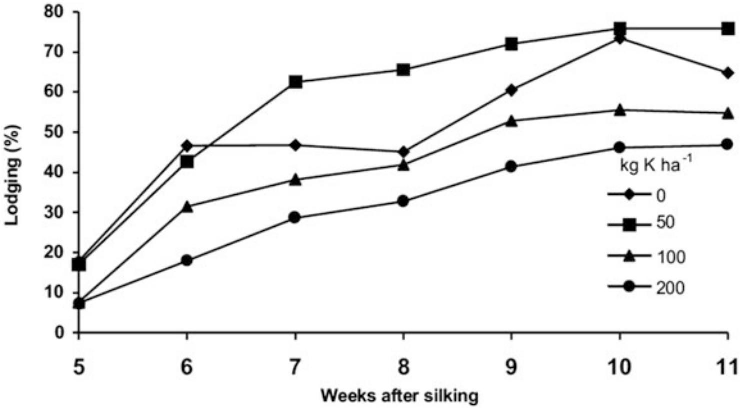


Fig. 2.11 K^+ application effect on lodging in a susceptible maize cultivar (Melis and Farina 1984)

et al. 2019). Consequently, browning symptoms, like bronzing, appear on the leaves, leading to reduced active leaf area and yield. Bronzing developed mostly in older leaves, which transpire more (Suriyagoda et al. 2017).

Potassium application was reported to reduce Fe^{2+} concentration in rice plants and improve their growth (Yamauchi 1989; Sahrawat 2004). Applying K fertilizer is improving rice root's oxidizing power and lateral root formation and decreases primary root growth suppression (Fig. 2.12) (Trolldenier 1988; Li et al. 2016). Furthermore, sufficient K supply decreased Fe^{2+} translocation from roots to shoots (Li et al. 2001) (Fig. 2.13). Under K deficiency conditions, low-molecular-weight metabolite exudation from roots was increased, encouraging the activity of Fe-reducing bacteria in the root zone (Trolldenier 1988). though, by improving K nutritional status, cannot abolish Fe toxicity completely (Ramírez et al. 2002). Furthermore, high K levels in the soil solution might cause a negative effect on bioavailability of other nutrients (Suriyagoda et al. 2020).

2.4.7 Potassium and Light-Induced Cell Damage

During photosynthesis, ROS are being produced mostly by chloroplasts, e.g., superoxide radical ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), and singlet oxygen ($^1O_2$) (Asada et al. 2000). ROS production in the chloroplasts is especially high when plants are experiencing environmental stresses (Asada et al. 2000; Vranová et al. 2002). ROS are highly toxic, causing damages to the membranes and chlorophyll degradation, leading to leaf chlorosis and necrosis development. Under optimal growing conditions, about 20% of the total photosynthetic electron flux is directed to molecular O_2, creating $O_2^{\cdot-}$ and other $O_2^{\cdot-}$ driven ROS (Biehler and Fock 1996; Cakmak 2000). If there is a limiting factor (such as stress) on the absorbed light energy utilization in carbon fixation, the electron flux to O_2 is increased, leading to large ROS accumulation in the chloroplasts. Then, excitation energy is being

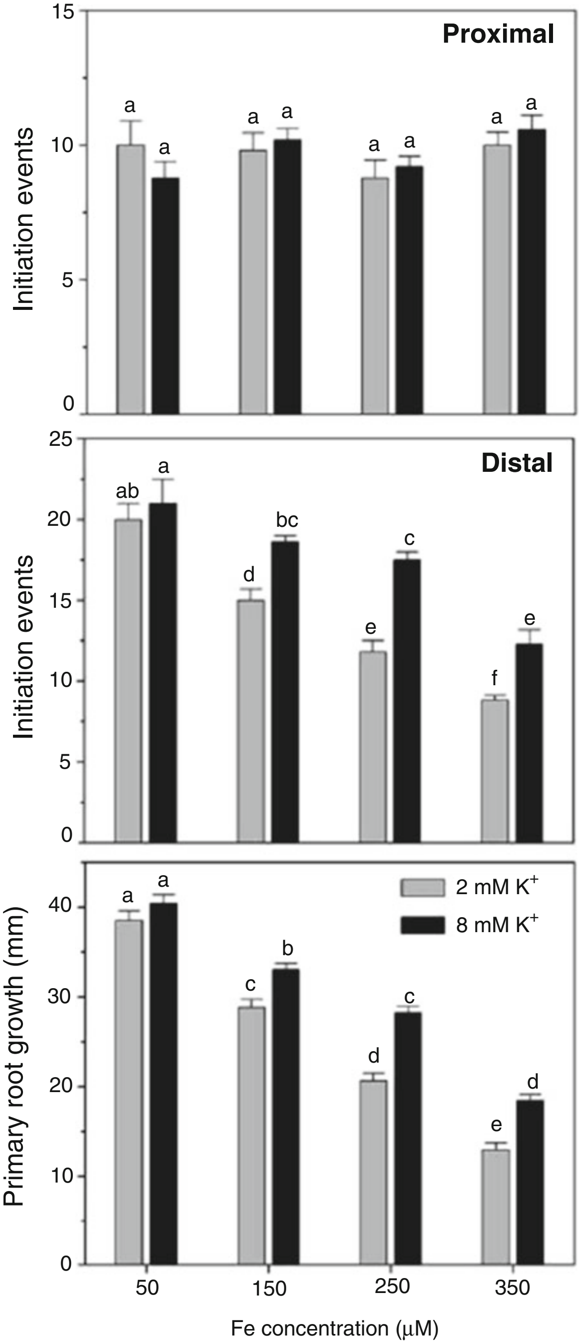


Fig. 2.12 Exogenous K^+ effect on primary root growth and lateral root formation in Arabidopsis under excess Fe. Values are the means ± SE, $n \geq 4$. Different letters represent means statistically different, $P < 0.05$ (Li et al. 2016)

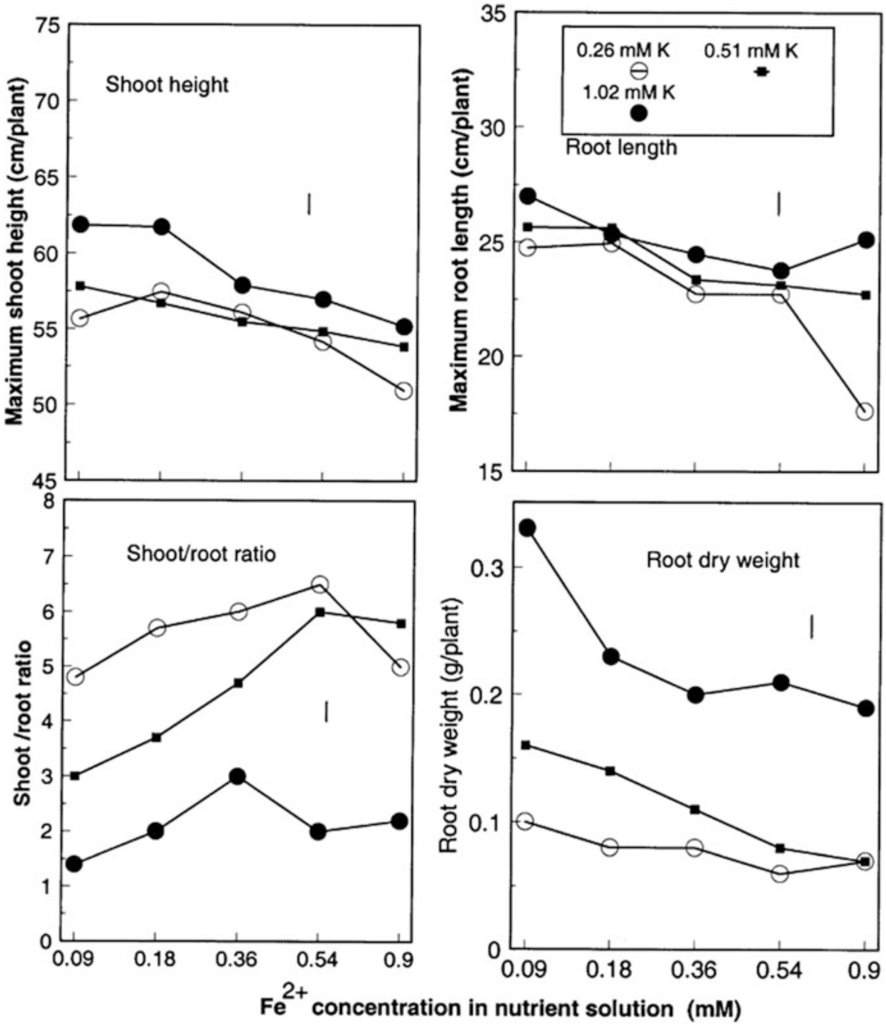


Fig. 2.13 Fe^{2+} level effects on shoot and root growth of hybrid rice under three potassium concentrations. Data are means of three replications. The bars are LSD5%, $P < 0.05$ (Li et al. 2001)

relocated to O_2 to form extremely toxic $^1O_2$. ROS production in the chloroplasts turns more noticeable when stressed plants are exposed to high light intensity, which result in photooxidative damage to the chloroplasts (Cakmak 2000; Choi et al. 2002).

Potassium-deficient plants are highly sensitive to intense light. When K supply is low, leaf chlorosis and necrosis will appear in plants growing under high light intensity, but not when growing under low light intensity (Marschner et al. 1996). Partial shading of K-deficient leaves can prevent leaf chlorosis and necrosis

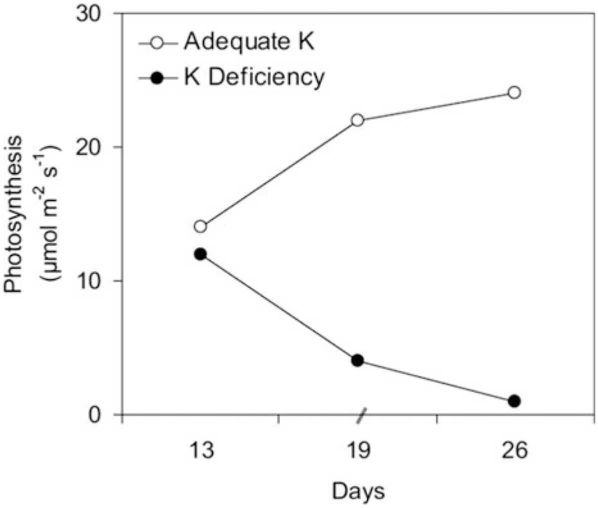


Fig. 2.14 Photosynthesis rate in leaves sufficient and deficient of potassium supply (Cakmak 2000)

development as well. The strong effects of high light intensity on the appearances of chlorosis were not correlated with K concentrations in leaf tissues; the concentrations were similar in shaded and nonshaded leaves with sufficient and deficient K supply (Marschner and Cakmak 1989). These support the concept that photooxidative ROS-induced injury to the chloroplasts has a crucial role in the presence of leaf symptoms typical to K deficiency. There are few explanations for high sensitivity to increasing light intensity in K-deficient plants. K is important to maintain photosynthesis and associated processes.

When plants are exposed to elevated atmospheric CO_2 and O_3 concentrations, the negative impact of K deficiency on photosynthesis is becoming more distinct (Barnes et al. 1995), suggesting that plants require more K when growing in CO_2-enriched conditions. Reduced photosynthesis due to K deficiency (Fig. 2.14) seems to be connected to decreased stomatal conductance, higher mesophyll resistance, and lower activity of the enzyme ribulose bisphosphate carboxylase (Zhao et al. 2001). Maintaining a high rate of photosynthesis at is also reliant on the export and use of photoassimilates inside the plant. When K supply is sufficient, there is a significant increase in sucrose concentration in source leaves and a noticeable decrease in roots when K is insufficient (Marschner et al. 1996; Zhao et al. 2001). Enhanced ROS production is inevitable due to impairment of photosynthetic CO_2 fixation and decreased photoassimilate utilization under K deficiency, which then cause photo-oxidative damage. Increased severity of leaf chlorosis under K deficiency was related to higher activity of enzymes involved in H_2O_2 detoxification and its utilization in oxidative processes (Fig. 2.15) (Cakmak 1994). In K-deficient leaves, there is an increase in H_2O_2 detoxification capacity, suggesting that ROS production is enhanced in K-deficient leaves on the account of CO_2 fixation. Plants exposed to high light intensity might have larger K necessities at physiological levels compared

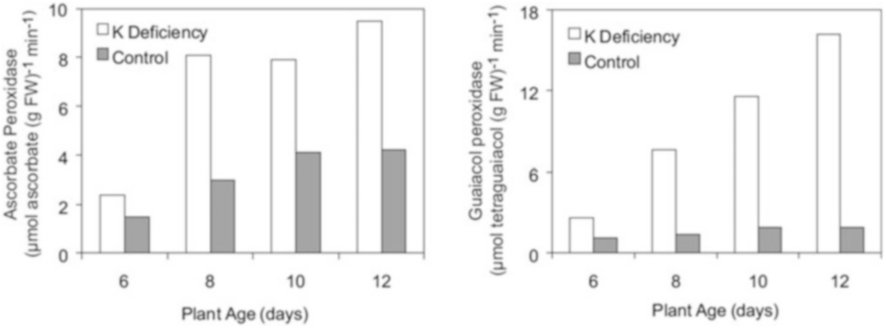


Fig. 2.15 Ascorbate peroxidase and guaiacol peroxidase activity in leaves of bean (*Phaseolus vulgaris*) plants over 12 days of growth in nutrient solution with 2000 µM and 50 µM potassium (redrawn from Cakmak 1994)

to plants grown under low light intensity. Higher K supply under high light intensity is required for efficient absorbed light energy utilization in photosynthetic CO_2 fixation and photosynthate transport to sink organs (Cakmak 2005).

2.5 Conclusions

Potassium deficiency is a crucial nutritional problem, which affects crop yield production and quality. Keeping optimal K nutritional status is vital for plant tolerance to biotic and abiotic stresses. Effective K usage and balanced fertilization combined with other minerals will contribute to sustainable crop growth, yield, and quality, will impact plant health, and decrease environmental risks. Though additional research is needed to fully understand the role of K in whole-plant stress response mechanisms, as they are complex (Fig. 2.16). K is required in high concentrations inside plants, from early developmental vegetative stages. High internal K^+ concentration was found to reduce extreme and sudden environmental events like low and high temperature, salinity, drought, and high light intensity stresses. The entire protein structure and protein activity require high K^+ concentrations in the cytosol for optimal plant functions.

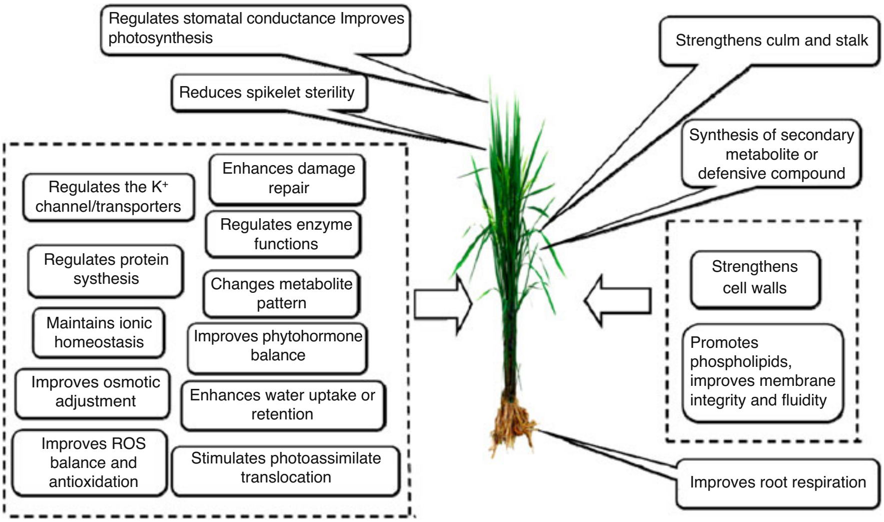


Fig. 2.16 Potassium roles in resisting all stresses (Wang et al. 2013)

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Molecular Approaches to Potassium Uptake and Cellular Homeostasis in Plants Under Abiotic Stress

3

Dhriti Kapoor, Priyanka Sharma, Upma Arora, Vandana Gautam, Savita Bhardwaj, Pardeep Atri, Neerja Sharma, Puja Ohri, and Renu Bhardwaj

Abstract

Intracellular potassium (K^+) homeostasis is an essential requirement for the optimum processing of plant metabolism and overall functioning of plants. It is regulated by K^+ ion uptake, efflux, and intracellular and long-distance translocation, which is arbitrated by a great amount of K^+-selective and nonselective channels and transporters placed at both plasma and vacuolar membranes. Various abiotic stresses like drought, salinity, water-logging stress, etc. led to drastic deterioration of intracellular potassium homeostasis. These stresses aggravate a K^+ channel and transporter expression along with the posttranslational control of their actions and optimization of K^+ absorption and consequently cause programmed cell death. Though there are certain specialized approaches which

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regulate the action of K^+ channels and transporters by membrane potential, cytosolic Ca^{2+}, reactive oxygen species, polyamines, plant growth regulators, and gasotransmitters are related to the adaptive plant responses to the unfavorable environment. Therefore, this chapter mainly provides an insight into the molecular strategies associated with the potassium uptake and homeostasis during different abiotic stress conditions.

Keywords

Potassium homeostasis · K+ channels and transporters · Plant growth regulators · Reactive oxygen species

3.1 Introduction

Oxidative burst caused by various abiotic stresses, for instance drought, salinity, temperature, heavy metal stress, etc., caused severe loss to plant productivity globally, and plant response to a combination of different environmental stresses is unlike to the response developed by the plant to individual stress (Fahad et al. 2017). These abiotic stresses in combination or alone caused imbalances in the redox cell homeostasis due to the generation of a plethora of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2), superoxide ($O_2^{\bullet -}$), and radicals (Kaur et al. 2018). For the normal functioning of the plant metabolism and their survival, plants require water (H_2O) and essential mineral nutrients; however, to maintain the cellular homeostasis under stress conditions, plant genome stimulates expression of different sets of genes to ensure availability of nutrients and H_2O (Mitra 2018). In this context, level of intracellular potassium (K^+) homeostasis is altered by various abiotic stresses. K^+ after N and P is the third most required essential macronutrient by plants for their healthy life span (Srinivasarao and Kundu 2017).

Plants contain 2–10% of K of their dry weight, and cytoplasmic K^+ amount is approximately 100 mM; however, vacuole may have 20–200 mM of K^+ (Gierth and Mäser 2007), and apoplastic amount of K^+ may vary between 10 and 200 mM and may increase up to 500 mM (White and Karley 2010; Wang et al. 2013). Several cellular proteins especially membrane proteins which are often called transporters and channels are beneficial in K^+ uptake from the outer environment and transport it to various plant tissues, and the upregulation of the K status decreases the ROS generation in plants. K decreases the activity of nicotinamide adenine dinucleotide phosphate (NADPH) oxidases and regulates the photosynthetic electron transport activity which helps to reduce ROS (Hasanuzzaman et al. 2018). There are two types of K^+ transporters on the basis of their affinity for K^+: one is high-affinity transporters which are active at low concentration of external K^+, and the other one is low-affinity channels which are active at high concentration of external K^+ (Wang and Wu 2013).

Intracellular K^+ homeostasis is recognized as a beneficial essential macronutrient for the normal functioning of plant metabolism ultimately, overall plant productivity and its essentiality are related to its multiple roles in plants like enzyme activation, osmoregulation, maintenance of cell turgor pressure, regulation of membrane polarization, and cytoplasmic pH regulation (Barragán et al. 2012), some others are regulation of cell elongation, stomatal movements, tropisms, phloem solute transport, ion balancing, photosynthesis process functioning, protein synthesis, carbohydrate translocation, and metabolism, and as most of these processes are directly involved in plant adaptation to hostile environment, K^+ uptake, transport, and homeostasis play a vital role in strengthening plant tolerance to abiotic stresses (Shabala and Pottosin 2014). Over 50 different cytoplasmic enzymes are regulated by K^+; therefore, impairment of the K^+ homeostasis caused by different stresses results in severe damage to plant metabolism both in root and leaf tissues (Almeida et al. 2017).

3.2 Potassium Uptake and Transport Under Abiotic Stress Conditions

Potassium (K^+) is an essential macronutrient for the growth, development, and metabolic processes of plants. It is an obligatory element and rich cation in plant cells which plays a prime role in physiological processes, viz., photosynthesis, transportation, and stomatal and signal regulation (Clarkson and Hanson 1980). It also has a modulatory function in key biochemical channels related to carbohydrate, sugar, and energy metabolism and protein and enzyme activation (Marschner 2012). Potassium is a chief fertilizer complex in physiological, biochemical, and metabolical vibrant processes to augment plant growth, physiology, development, yield, quality, and environmental adversity tolerance. Furthermore, these cations play principal osmotic functions, i.e., cellular turgor, maintenance of cytosolic pH, and membrane potential along with the proton motive force in plant system (Maathuis 2009; Marschner 2012). Potassium is also considered as a foremost macronutrient in tolerance to abiotic stresses, i.e., osmotic, drought, salinity, temperature, etc. Thus to maintain a resistance against adverse stresses, plants advance energy for the uptake of K^+ ions and their distribution throughout the plant (Amtmann et al. 2008; Sharma et al. 2013).

Potassium is predominantly absorbed through roots into the xylem sap and transported aboveground to plant parts by transpiration-driven mass flow process (Wegner 2015) (Fig. 3.1). Plants take up potassium either in the form of a cation (K^+) or salt form, viz., KNO_3, KCl, K_2CO_3, etc., from soils. Among these, KCl is the most routinely used for agronomic crops (Kafkafi et al. 2001). The uptake of K^+ by root system depends on the properties of the soil like texture, pH, organic, alkalinity, and moisture content of soil. A few soluble forms of K compound, namely, K silicate minerals, also exist in certain soils at a very low concentration. Thus, microorganisms like fungi and bacteria accelerate solubility of K and play a key role in transformation to soluble forms via exchange, acidification, and chelation methods (Masood and Bano 2016). However, in sandy soil circumstances, potassium is given in the form of foliar spray. But, the efficiency of the foliar application is

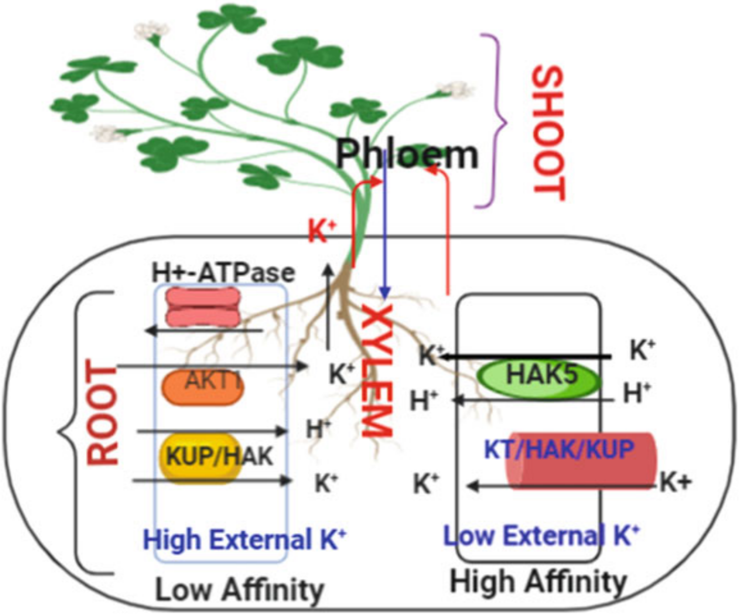


Fig. 3.1 Overview of potassium uptake and transport in plants under the influence of various transporters and proteins

dependent on the absorption, penetration, and sufficient leaf area capacity into leaves (Ling and Silberbush 2002; Hasanuzzaman et al. 2018).

Potassium is taken up from the soil through xylem and translocated to different cellular compartments from the external surroundings which requires many proteins called transporters and channels which are present at the surface of the cell membrane (Fig. 3.1). Potassium is highly mobile in plants, and its translocation takes place through both xylem (root to shoot) and phloem (from source to sink). In the whole translocation process from the soil to the different plant organs, K^+ transverse numerous tissues cell membranes via specific K^+ membrane transport systems (Fig. 3.1). For the effective transportation and uptake of K^+ via various plant tissues to cellular compartments, a coordinated molecular mechanism of sensing, signalling, and protein channels are primarily processes.

Potassium ion uptake in different plant parts shows dual-affinity mechanism on the basis of their affinity for K^+. It can be classified as high affinity where K^+ uptake is mediated by K^+ transporters at a low concentration of external K^+ and low-affinity K^+ uptake mechanism facilitated mainly by K^+ channels that are active at a higher concentration, usually at more than 0.3 mM external K^+ (Wang and Wu 2013; Cherel et al. 2014) (Fig. 3.1). Over the past few years, progression in molecular approaches and their advanced implementations enhanced the understanding and involvement of high-affinity and low-affinity transporters in diverse crop species including *Oryza sativa*, *Hordeum vulgare* L., *Capsicum annuum* L., and *Arabidopsis* *thaliana* (Pyo et al. 2010; Wang and Wu 2013; Nieves-Cordones et al. 2014; Hasanuzzaman et al. 2018).

Therefore, K^+ uptake from soil and translocation into cellular compartments are accomplished through numerous membrane transporter proteins and channel families, viz., Shaker family channels include the tandem-pore K (TPK), voltage-dependent, and two-pore channels (TPC) (Hedrich 2012), cation-proton antiporter transport families include CHX, NHX, and KEA antiporters (Sze and Chanroj 2018), and the carrier transport families are KT/HAK/KUP, HKT uniporters, and symporters (Hamamoto et al. 2015; Li et al. 2018a) (Fig. 3.1). All these transporters and channels have difference in their energetic coupling, affinity, and selectivity for uptake and transport of K^+ in plant cells (Ward et al. 2009; Sharma et al. 2013). The pH and voltage potential gradients caused by H^+-ATPase gated energy for K^+ influx across the cell membrane of root cells in apoplasmic solution are appropriate at less than 1 mM K^+ (Maathuis and Sanders 1994). H^+/K^+ symporters, such as NHXs and CHXs, mediate this process and play an important function in K^+ homeostasis in vacuolated plant cells (Leidi et al. 2010; Barragán et al. 2012). The efficiency of K channels and transporters might be enriched by overexpressing their underlying genes or enhancing their protein activity. The increasing expression of genes encoding high-affinity systems plays an important role in K^+ influx when K^+ is in short supply (Shin and Schachtman 2004; Wang et al. 2015).

It is important to uphold normal growth of plants by taking an optimal amount of K^+ via high-affinity K^+ transporter uptake system in roots from the soil (Cherel et al. 2014; Ragel et al. 2019). So, K^+ carrier transporters might be grouped into four major families like KT/HAK/KUP, CHX, Trk/HKT, and KEA (Liang et al. 2020). These channels and transporter proteins play a vital action to strengthen tolerance mechanism in plants to various abiotic stresses, viz., salt, temperature, drought, heavy metal, etc. (Bose et al. 2014; Song et al. 2015). The KT/HAK/KUP-gated transporters are the leading potassium ion transporter families. These plasma membrane transporter proteins mediated K^+ uptake over a broad range of concentrations. For the homeostasis maintenance of ions in plants, numerous K^+ transporters have been recognized in relation to their functions either influx or efflux from the cellular compartments and within the whole plant (Grabov 2007; Liang et al. 2020).

Over a few years, KT/HAK/KUP membrane transporters have been enumerated in diversified annual crop species like barley, rice, maize, weeds, tomato, pear, and Arabidopsis (Vallejo et al. 2005; Zhang et al. 2012; Song and Su 2013; Han et al. 2016; Li et al. 2018b). In *Arabidopsis thaliana* comprehensively 71 K^+ membrane transporters and protein channels have been documented for the distribution of potassium ions (Wang and Wu 2013; Sharma et al. 2013).

The transportation of potassium ions from soil to cellular compartments is carried out via enormous genes. These genes are virtually grouped into different transporter and channel families, viz., Shaker-type K^+-gated channels, antiporter K^+/H^+ genes, pore K^+ channels, KUP/HAK/KT transporters, HKT transporters, cyclic nucleotide-gated channels, and glutamate receptors (Anschütz et al. 2014). Thus, the interplay of biomarker genes has a putative role in K^+ influx and K^+ efflux in plants.

Wang and Wu (2013) confirmed that channels and transporters encoded by different genes have diverse functions to redox homeostasis in plants. At root level, the K^+ uptake is primarily mediated by two proteins, AKT1 and HAK5, since these two proteins are expressed in the roots which have high-affinity transporters to mediate adequate K^+ uptake for plant growth (Pyo et al. 2010; Li et al. 2014; Yang et al. 2014) (Fig. 3.1).

These K^+ transporters and channels are considered not only as the major components for uptake and translocation of K^+ but also as potential K^+ sensors for plant responses to K^+ deficiency. Still, the regulatory mechanisms of many K^+ transporters and channels remain unknown. Hence, forthcoming investigations should give consideration to functional characterization of these membrane channels and transporters and to the regulatory mechanisms of these components. Analyzing the molecular approaches among various channels and transporters to potassium uptake is also an important task, one that would benefit our understanding of the complex signalling network for plant responses under abiotic stress.

3.3 Potassium Homeostasis Under Abiotic Stress Conditions

Potassium (K^+) is an essential plant nutrient, and despite of the fact that most of the soils are rich in potassium, yet the demand for K fertilizer is increasing owing to the lesser amounts of bioavailable forms of K^+ to plants and the leaching and runoff from the upper soil layers, contributing to K^+ deficiencies in agricultural soils. Potassium is one of the vital structural elements in plants as well as it regulates several physiological and biochemical processes in cells and organs like carbohydrate metabolism, photosynthesis, protein synthesis, enzyme activation, and stomatal movements.

3.3.1 Potassium and Abiotic Stress Tolerance in Plants

Recent research outcomes credit potassium to provide abiotic stress tolerance in plants. K helps to regulate the osmotic balance under salt stress conditions and also maintains the ion homeostasis. It helps the plants to adapt themselves to water deficiency by regulating the stomatal opening under drought stress conditions. K has also been reported to enhance antioxidant defense system of plants, thus providing them oxidative stress protection under various environmental adversities. Potassium retains the photosynthetic electron transport activity by reducing the activity of nicotinamide adenine dinucleotide phosphate (NADPH) oxidases leading to ROS alleviation. The molecular mechanisms of K-induced abiotic stress tolerance in plants might include an insight into the cellular signalling provided by this element alone or in association with other signalling molecules and phytohormones (Hasanuzzaman et al. 2018).

3.3.1.1 Salinity Stress

A high concentration of soluble salts in the soil refers to as high soil salinity where NaCl is the most soluble and widespread salt. Saline soils show an electrical conductivity (EC) of 4 dS/m (corresponding to approximately 40 mM NaCl) and significantly reduce the growth and yield of most crops. Salinity is often considered as an intrinsic problem in coastal areas and river deltas, but excessive use of irrigation with poor-quality water and insufficient drainage in inland areas lead to the buildup of secondary salinization of the soil surface (Thomson et al. 2010). Salinity poses two major threats to plants:

1. Osmotic stress due to excess solutes outside the roots that reduces the soil water potential and hence water absorption affecting cell turgor and expansion, promoting biosynthesis of ABA, lowering stomatal conductance, hampering carbon assimilation and biomass production, and thus decreasing the yield (Munns and Tester 2008)
2. The ionic stress due to excessive influx of sodium ions (Na^+) and/or chloride (Cl^-) ions into the plant leading to interruption of metabolic processes and inducing tissue necrosis and early leaf senescence (Roy et al. 2014)

Salinity stress inhibits plant root growth due to osmotic effect and ion toxicity which decreases nutrient uptake and translocation, especially that of potassium K^+ (Wang et al. 2013), which is a vital macronutrient that plays essential functions related to cellular metabolism like osmotic regulation, turgor maintenance, enzyme activation, regulation of the membrane potential, protein synthesis, and cytoplasmic homeostasis (Almeida et al. 2017). Decrease in K^+ content was observed in the roots and shoots of *Vigna subterranea* (L.) Verdc due to salinity stress, while increase in Na^+ concentration has been reported by Taffouo et al. (2010).

Sodium exhibits a strong inhibitory effect on K^+ uptake by cells via inhibiting K^+ transporters, i.e., AKT1 (hyperpolarization-activated inward-rectifying K^+ channel) (Fuchs et al. 2005) and HAK5 (carrier-type HUP/HAK/KT transport) (Nieves-Cordones et al. 2010), that are present in the plasma membrane of root cells. Further, K^+ leakage occurs due to salinity-induced membrane depolarization and decreased membrane integrity. Na^+ competes with K^+ for major binding sites in enzymatic reactions and cellular metabolism like protein synthesis and ribosome functions due to similarity in their physicochemical properties, i.e., ionic radius, ion hydration energy, etc. (Marschner 1995; PPI 1998). Activity of over 50 different cytoplasmic enzymes that require K^+ for functioning is inhibited by Na^+ ions. Hence, the disruption of the K^+ homeostasis and higher Na^+ concentrations are toxic for cell metabolism and lead to severe metabolism impairment, both in root and leaf tissues. However, exogenous potassium application has been shown to positively affect the plant root and shoot growth during salinity stress (Saida et al. 2014). Fayez and Bazaid (2014) found that the shoot fresh weight and height of the *Hordeum vulgare* plants under 150 mM NaCl stress improved when treated with potassium. Similar results have been reported by Amjad et al. (2016) in *Solanum lycopersicum* under 75 mM NaCl stress, Merwad (2016) in *Beta vulgaris* cultivars, and Chakraborty et al. (2016) in peanut (*Arachis hypogea* L.) under salt stress. Thus, maintaining the cytosolic K^+ contents at a constant level is important for plant metabolic processes (Flowers et al. 2015; Shabala et al. 2016).

Maintaining the cellular K content above a certain threshold and maintaining a high cytosolic K^+/Na^+ ratio are crucial for plant growth and salt tolerance. Mansour (2014) has associated the increased P-ATPases activity with salt stress tolerance and has attributed this to the repolarization of the NaCl-induced depolarized plasma membrane. This significantly reduces Na^+ influx via depolarization-activated NSCCs and through depolarization-activated outward-rectifying K^+ channels (e.g., GORK) (Adams and Shin 2014) and also NSCCs (Sun et al. 2009), which help to restore higher K^+/Na^+ levels (Sun et al. 2009). The higher P-ATPase activity under salt stress also energizes the active transport that excludes Na^+ from root cells, a process dependent of the SOS1 Na^+/H^+ antiporter (Gaxiola et al. 2007). High-affinity potassium transporters (HKT) have been shown to mediate Na^+-specific transport either channel-like Na^+ uniport (class I or HKT1 group) or Na^+-K^+ symport (class II or HKT2 group) which have vital roles in plant Na^+ tolerance (Su et al. 2015). Generally, dicot species have only a few HKT genes in their genomes preferably encoding class I HKT proteins, whereas monocots have multiple HKT genes of both classes (Suzuki et al. 2016; El Mahi et al. 2019). Figure 3.2 represents the integrative model of action of various factors involved in potassium homeostasis (Assaha et al. 2017).

3.3.1.2 Drought Stress

Drought stress is one of the main factors limiting yield in many crops. Preserving K^+ homeostasis and maintaining a high cytosolic K^+/Na^+ ratio are important strategies of the plants for coping with drought stress (Scoffoni et al. 2017). H^+-ATPase in the plasma membrane of mesophyll cells maintains membrane potential to regulate K^+ transmembrane transport (Falhof et al. 2016). Lower drought resistance has been observed in transgenic *Arabidopsis* (plasma membrane H^+-ATPase mutants aha1–6 and aha1–7) due to membrane depolarization-induced higher K^+ efflux (Yan et al. 2015). Increased root hair cell plasma membrane H^+-ATPase was associated with drought stress tolerance in oats (*Avena sativa* L.) (Gong et al. 2010) and wheat seedlings (Liu et al. 2005). The exogenous supply of potassium however provides drought stress tolerance as has been observed in olive (Benlloch-González et al. 2008) and sunflower leaves (Benlloch-González et al. 2010). An external supply of K_2CO_3 has been reported to significantly increase shoot potassium content and improve drought resistance in the drought-tolerant variety SN16 relative to the intolerant variety JM22 (Wei et al. 2013). Presence of potassium in adequate amounts in plants facilitates in improving the ability of plants to tolerate drought stress by maintaining high turgor pressure and low osmotic potential through osmotic adjustment (Egilla et al. 2005) Plasma membrane-located AKT/KAT K^+ uptake channels like Os-AKT1 (Li et al. 2014) and AtAKT1 are activated by plasma membrane hyperpolarization (Daszkowska-Golec and Szarejko 2013). Drought stress management requires the hydraulic uncoupling of guard cells from the surrounding mesophyll cells (Becker et al. 2003), and Shaker-like

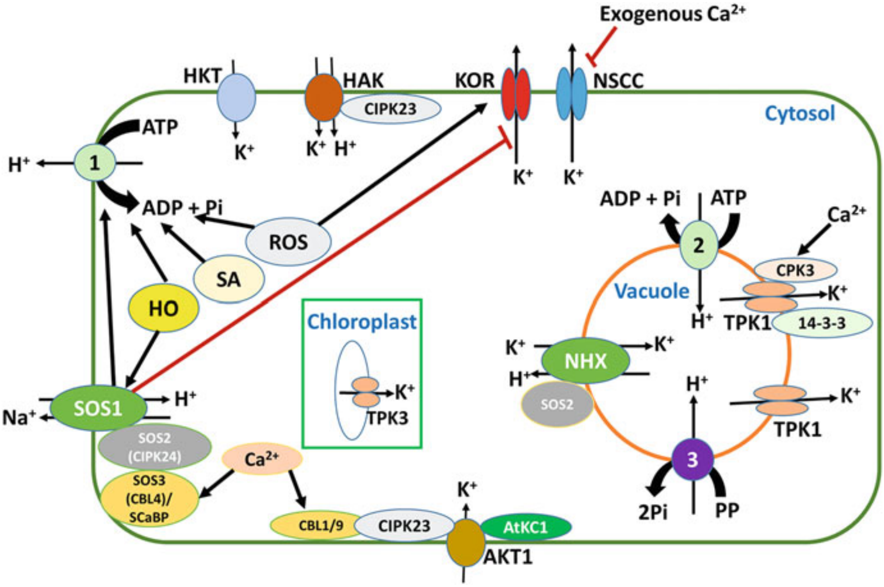


Fig. 3.2 PM H^+-ATPases are at the center of K+ uptake under salt stress and low-K+ conditions. The activity of SOS1 (salt overly sensitive 1), SA (salicylic acid), HO (heme oxygenase), and ROS (reactive oxygen species) contributes in stabilizing the membrane potential, by regulating the activity of H^+-ATPase. This stable membrane potential is favorable for K+ uptake by HAK and AKT1 which are sensitive to membrane depolarization. Membrane depolarization by ROS will lead to K+ efflux through NSCCs (nonselective cation channels) and KORs (K+ outward-rectifying channels), but application of exogenous Ca^{2+} and the activity of SOS1 can alleviate this condition. In the vacuole, the tonoplast two-pore K+ channels (TPK1) are important in replenishing lost cytosolic K+ from vacuolar pools, while in the chloroplast, thylakoid localized TPK3 is essential in regulating membrane potentials and protein gradients that drive ATP synthesis and the dissipation of excess energy during light photosynthetic reactions, thus enhancing plant fitness. Red lines indicate inhibition, while black arrows indicate activation (modified after Assaha et al. 2017)

depolarization-activated outward-rectifying K^+ (GORK in Arabidopsis) channels at the guard cell plasma membrane plays a crucial role in this process.

The organic osmolyte production especially proline is also increased by exogenous supply of K under drought conditions. Pro accumulation plays a highly protective role in the plants exposed to drought stress, and it is involved in osmotic adjustments (Teixeira and Pereira 2007). Several studies have revealed an increase in Pro through K application, e.g., in *Oryza sativa* (Pandey et al. 2004), *Brassica napus* (Din et al. 2011), *Triticum aestivum* (Jatav et al. 2012), *Zea mays* (Zhang et al. 2014), and *Gossypium hirsutum* (Zahoor et al. 2017) under drought stress conditions. The external application of potassium has also been found to enhance root growth that increases the root surface area under drought conditions, which ultimately enhances the water uptake by plant cells (Römheld and Kirkby 2010). Under drought conditions, excess ROS production in plants leads to excessive cellular lipid peroxidation, leading to an increase in the cellular membrane permeability followed by

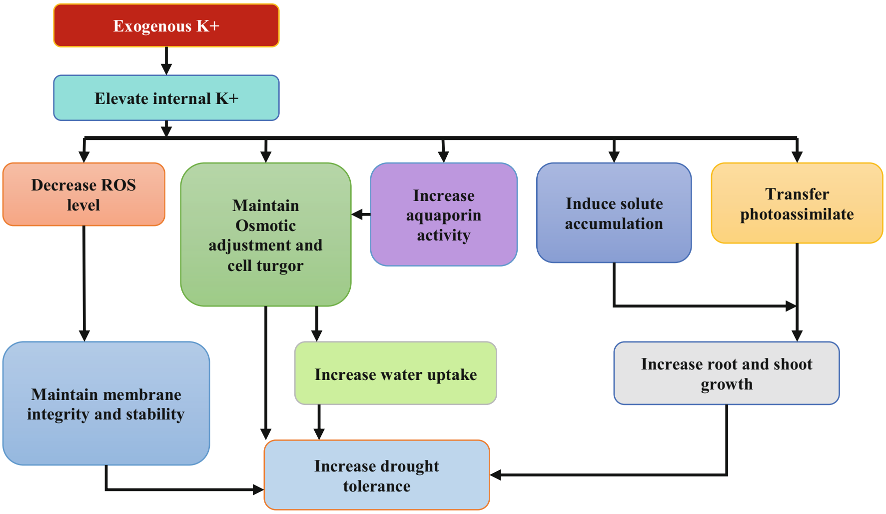


Fig. 3.3 Role of potassium under drought stress (modified after Hasanuzzaman et al. 2018)

enhanced electrolyte leakage (EL) and malondialdehyde (MDA) content (Fazeli et al. 2007). Soleimanzadeh et al. (2010) reported significant decrease in MDA content under water shortage conditions in sunflower (*Helianthus annuus* L.) on adequate supply of K which clearly indicates the role of K in mitigating oxidative stress. A relationship between the aquaporin activities and the K channel/transporter has been demonstrated by Kanai et al. (2011). The results of the study showed K deficiency to significantly alter the K+-channel activity, resulting in a variation in the root hydraulic conductance and signal transduction with consequent changes in the aquaporin activity. Thus, the reduction in the root hydraulic conductance and water supply for transpiration was suppressed under K deficiency. Guo et al. (2007) observed a positive correlation between water uptake and K absorption in their work on common bean (*Phaseolus vulgaris* L.). Potassium was found to mediate the xylem hydraulic conductance resulting in maintenance of cell turgor, stomatal movements, and sufficient gas exchange as part of the drought adaptations as these events helped to maintain water balance in plants (Oddo et al. 2011). Drought-stressed plants commonly experience xylem cavitation, and increased K^+ availability has been observed to reduce its occurrence (Trifilò et al. 2011). Figure 3.3 illustrates the involvement of K in plant tolerance under drought stress.

3.3.1.3 Extreme Temperature Stress

Plants suffer from extreme temperature stress at the temperature more than the optimum temperature for plant growth and development. Extreme temperatures disrupt various biochemical reactions and plant metabolisms (Hasanuzzaman et al. 2013). K plays a significant role in coping with temperature stress as it helps to activate the various physiological and metabolic processes such as photosynthesis, respiration, and nutrient homeostasis.

High Temperature Stress

Potassium plays a significant role in increasing the tissue water potentiality that assists in high temperature stress tolerance. It has been observed that plants accumulate various types of osmolytes to overcome the damage caused by the heat stress, and potassium is suggested to work as an osmolyte that helps to maintain stomatal conductance and prevent damage (Azedo-Silva et al. 2004). K-deficient plants produce ROS under stress conditions, and such plants have been found to be benefitted by supplementation with adequate amounts of K that helps plants by supporting protein synthesis, stimulating various enzymatic reactions, assisting in carbohydrate production, and increasing the WUE (Cakmak 2005). Foliar application of K has been shown to alleviate the heat stress in wheat plants by preventing leaf damage, increasing the photosynthetic ability, and enhanced translocation and accumulation of photosynthates (Dias and Lidon 2010).

Chilling/Freezing Stress

Chilling/freezing stress causes dehydration and loss of apoplastic water and downregulation of K-regulated mechanisms such as photosynthesis and carbon assimilation, metabolism, and phloem activity. Such freezing-induced dehydration can be ameliorated by adequate supply of K that adjusts the osmotic potential (Wang et al. 2013) and leads to better ROS defense ultimately resulting in greater stress tolerance (Farooq et al. 2008).

3.3.1.4 Stress Due to High Light Intensity

High light intensity causes photooxidative damages and rapid leaf chlorosis leading to impaired photosynthesis (Choi et al. 2002). In cases of severe stress, the photosynthetic ability, RuBisCO activity, quantum yield, and electron transport are disrupted (Lu et al. 2017). The damage to plant system in terms of enhanced leaf chlorosis, decreased photoassimilate utilization, and phloem translocation has been correlated with the insufficient amounts of K in plants facing high light intensity stress (Schumann et al. 2017). Hence, plants receiving high light intensity show requirement of K in a great quantity to utilize the absorbed high light for CO_2 fixation, and source-sink relation.

3.3.1.5 Stress Due to Waterlogging

At least 10% of the global agricultural land has been affected by waterlogging which is an important barrier for crop production as the root zone of waterlogged plants faces a severe shortage of oxygen supply (hypoxia or anoxia). This disrupts the respiration process in roots leading to energy shortage in the cells. Plants growing in waterlogged soils face a “physiological drought” that causes reduction in stomatal conductivity by severalfold (Ou et al. 2011, Polacik and Maricle 2013), thus affecting nutrient delivery to the shoot. Increase in the xylem sap osmolality during prolonged flooding and root growth arrest due to hypoxia result in a significant reallocation of root K^+ toward the shoot. Due to reduced root capacity to take up K^+, the roots experience a severe K^+ deficiency. Shoot potassium content also decreases severalfold in plants exposed to prolonged waterlogging (Smethurst et al. 2005, Board 2008).

Hence, the key mechanism to save the plants growing in waterlogged condition is avoiding K loss, at the time of hypoxia or anoxia (Teakle et al. 2013). Several researchers have reported the effect of exogenous K application for ameliorating the adverse effects of waterlogging. Higher application of K to soil or foliage has been found to increase plant height, photosynthetic capacity, chlorophyll content, and greater nutrient uptake in cotton plants (Ashraf et al. 2011) and improvement of nonstructural carbohydrates (NSC) contents, photosynthetic pigment content, and higher antioxidative activity as well as lower lipid peroxidation in rice plants (Dwivedi et al. 2017). It also results in a temporary upregulation of H^+-ATPase activity reducing K^+ loss via KOR channels.

Elemental soil toxicity due to the changes in the soil redox potential also contributes to the negative impact on root K^+ homeostasis under flooded condition (Khabaz-Saberi and Rengel 2010; Shabala 2011). Zeng et al. (2013) observed a massive increase in the amount of available Mn and Fe in the soil solution often to above toxic levels within a few days of onset of waterlogging. Other reports also show similar patterns of soil elemental toxicity, e.g., a fivefold increase in Fe content in waterlogged *Eucalyptus nitens* plants reported by Close and Davidson (2003), and fivefold increase in root Fe level in waterlogged lucerne reported by Smethurst et al. (2005). Elemental toxicity leads to production of ROS species, causing lipid peroxidation, damage to DNA and proteins, pigment breakdown, and impairment of various enzymatic activities. Hydroxyl radicals, the most reactive and detrimental among ROS, activate both K^+-selective outward-rectifying (Demidchik et al. 2010) and nonselective K^+ permeable (Zepeda-Jazo et al. 2011) channels, resulting in a massive K^+ leak from the cytosol. In addition to elemental toxicity of waterlogged soils due to inorganic phytotoxins like Fe^{2+}, Mn^{2+}, and H_2S, the organic substances like ethanol, acetaldehyde, various short-chain fatty acids, and phenolics have also been found in significant abundance in waterlogged soils as a result of anaerobic metabolism in both plants and rhizosphere microorganisms (Armstrong and Armstrong 1999, Shabala 2011). These secondary metabolites have detrimental effects on K^+ uptake and accumulation, both at the whole plant and cell-specific levels (Pang et al. 2007). TEA^+, a known blocker of voltage-gated Shaker-type K^+ channels, has been found to strongly inhibit net K^+ efflux induced by physiological concentrations of hydroxybenzoic and acetic acids in barley roots (Pang et al. 2007). Although the K^+ leakage in flooded roots is certainly detrimental for overall plant nutrition and is responsible for K^+ deficiency in crops grown in waterlogged soils, it might also play a possible beneficial role in aerenchyma formation by eliminating cortical cells via PCD mechanism (programmed cell death) that seems to get triggered by the increased caspase-like activity in K^+-depleted cells (Shabala and Pottosin 2014).

3.3.1.6 Heavy Metal Stress

Rapid industrialization has led to increase in the heavy metal contamination of agricultural soils worldwide (Hasanuzzaman and Fujita 2012). The plants growing in such soils experience deleterious effects on their growth and development. Heavy metal toxicity causes major disturbances and alterations in the physiological and metabolic processes like uptake of essential nutrients, stomatal mechanism, membrane functions, photosynthesis, activities of various enzymes, and reduction of the water potential and generation of excess ROS (Emamverdian et al. 2015). Hence, remediation of these contaminants in soils or increasing plant tolerance or resistance to heavy metal stress is a matter of utmost concern for plant scientists. Among various other strategies implied for enhancing plant stress tolerance, using K as a plant protector against metal toxicity is quite promising as K plays a crucial role in the activation of several enzymes, synthesis of various proteins, photosynthetic activity, osmoregulation, stomatal movement, transfer of energy, phloem transport, cation-anion balance, and stress resistance (Wang et al. 2013). Potassium has been reported to play a significant role in ameliorating Cd-induced oxidative damage in broad bean (*Vicia faba* L.; Siddiqui et al. 2012). Song et al. (2015) have also provided the evidence that K helped in mitigating the Zn toxicity in peach plants by improving the photosynthesis and antioxidant defense system and maintaining plant nutritional balance.

3.3.2 Potassium-Induced Abiotic Stress Signalling

The K content of the soil does not remain constant over the growing period of a crop due to the varying environmental conditions. Fluctuations in the K^+ availability are sensed by plant roots, and when they sense K deficiency, a series of events occurs in the plant at the molecular level to cope with this condition. Under K-deficient conditions, two distinct Ca^{2+} signals get induced that are read by CBL1/9. The calcium sensors CBL1 and CBL2 regulate CIPK23 (a protein kinase) that activates the K^+ transporter AKT1 by phosphorylation (Behera et al., 2017). Potassium channels such as NSCC and GORK are very sensitive to ROS, and this is the primary reason for the K pool reduction in the cytosol under stress conditions (Demidchik 2014). Phytohormones such as ethylene, auxin, cytokinin, and JA are also involved in low K-induced signalling processes involving the regulation of high-affinity K^+ transporter HAK5 transcription and expression (Schachtman 2015). The involvement of microRNAs in plant nutrient homeostasis has also been reported in many studies, and the gene chip overexpression of OsmiR399 has been found to increase the plant nutrient contents including the contents of K^+ (Hu et al. 2015). It is suggested by various authors that a complex pathway induced by K signalling might be involved in ensuring the optimum K level in the plants. Figure 3.4 depicts the signalling components including the Ca^{2+} signalling, ROS, microRNA, membrane potential, and phytohormones involved from signal perception to adaptive responses (Wang and Wu 2013; Wang and Wu 2017).

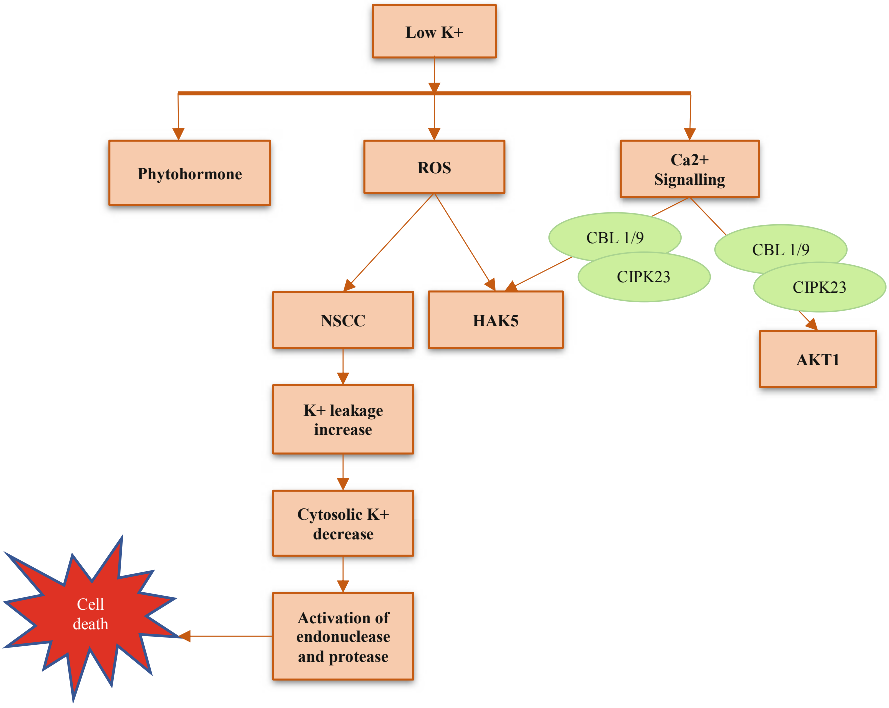
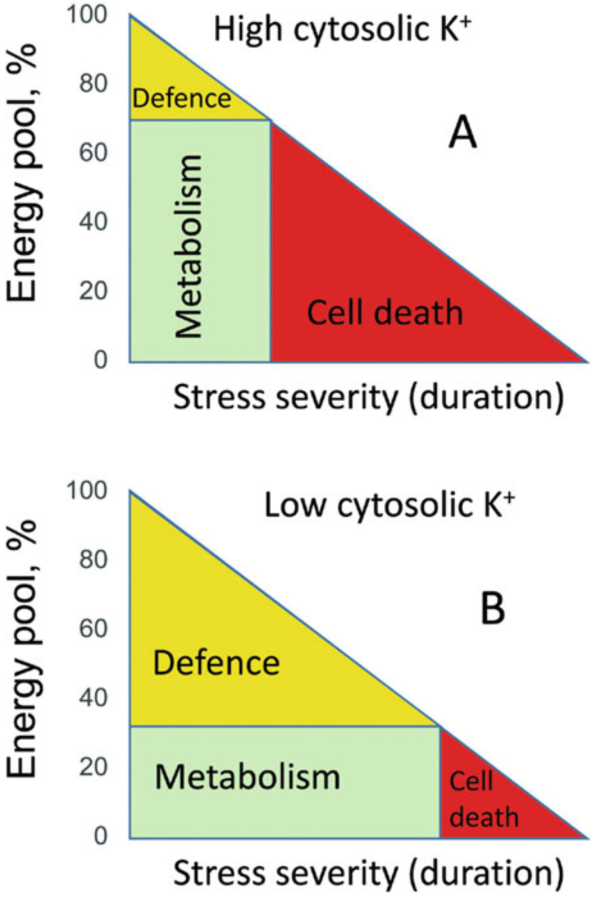


Fig. 3.4 K-induced signalling in the plants. *ROS* reactive oxygen species; *NSCC* nonselective cation channel; *HAK5 and AKT1* K^+ transporter; *CBL1/9* calcineurin B-like proteins; *CIPK23* A protein kinase (modified after Hasanuzzaman et al. 2018)

Cytosolic potassium homeostasis and the ability of various tissues to retain potassium under stress conditions are considered important for stress tolerance in plants, but recent studies suggest that stress-induced K^+ efflux might also mediate growth and development under various adverse environmental conditions and can be further considered as a switch between metabolic and defense responses. The physiological rationale behind it is that K^+ is known to be an activator of a very large number (>70) of metabolic enzymes (Anschütz et al. 2014). Under control conditions, when cytosolic K^+ concentrations are high, the major bulk of available energy is directed toward cell metabolism as the enzymes regulated by K are active. When plants are confronted by stress conditions, the available energy diminishes as ATP production declines, and a large pool of ATP is redirected toward defense reactions. With stress progression and increase in stress severity and stress duration, the amount of energy available for defense is quickly reduced to zero, and the cell dies. To avoid or delay the cell death, cell metabolism needs to be shut down to prevent the competition for energy between metabolic and defense responses. It is suggested that the cell uses K+ efflux as a metabolic switch and decreases the cytosolic $[K^+]$ to subthreshold levels to inactivate numerous metabolic reactions, allowing a redistribution of the ATP pool toward defense responses (Fig. 3.5).

Fig. 3.5 K^+ as a metabolic switch for plant defense under stress conditions (modified after Shabala 2017)



GORK channels—guard cell outward-rectifying K^+ channels (Véry et al. 2014)—play an important role in stomatal closure, and disruption of GORK K^+ efflux might be viewed as the "metabolic switch" inhibiting energy-consuming anabolic reactions and saving energy for adaptation and repair (Demidchik 2014). The whole process seems to be tightly controlled. K^+ efflux from the root must be confined to a relatively small root region so that the overall root potassium nutritional status is not compromised. The root apex is the most appropriate zone for this role as the cells in this zone are metabolically active and show much higher sensitivity to stress factors. It has an overall rate of K^+ loss 10 -30 times higher compared to mature zone cells, and have less negative membrane potential. Moreover, it reflects lower H^+-ATPase activity, thus depending more on K^+ efflux as a means of restoring membrane potential. However, underdeveloped xylem tissue in this region and changes in the radial K^+ fluxes will have no implications for long-distance K^+ transport to the shoot and the overall volume of cells in the apex being much smaller as compared with the bulk of the root, hence such signalling by K^+ loss

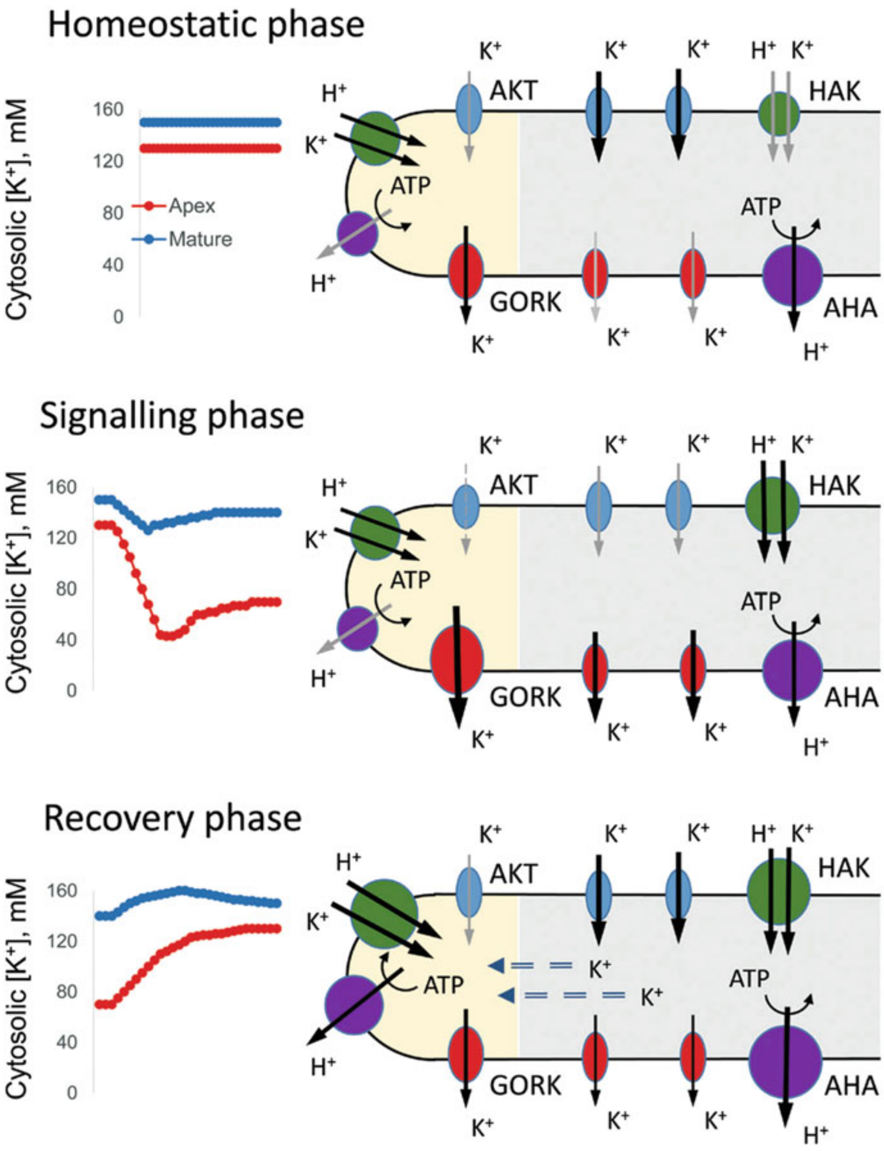


Fig. 3.6 Cytosolic [K$^+$] signalling (modified after Shabala 2017)

will not affect the overall K$^+$ nutrition (Shabala et al. 2016). The correlation between potassium and PCD events implies that a prolonged decrease in the cytosolic K$^+$ level may be detrimental to cell viability, and, hence, signalling via K$^+$ efflux should only be transient along with addition of brief cytosolic K$^+$ spikes and Ca^{2+} and ROS messengers that would signal and shape plant adaptive stress responses. Figure 3.6 represents a model for cytosolic [K$^+$] signalling (Shabala 2017). The three phases depicted include:

1. Homeostatic phase (before stress)—cytosolic [K^+] is maintained at a constant level in both zones. Higher metabolic demand for K^+ and 10–15 mV less negative membrane potential in the apex maintain slightly higher cytosolic potassium levels. The optimal cytosolic [K^+] levels are maintained in the mature zone by low-affinity K^+ uptake mediated by AKT channels along the electrical gradient provided by H^+-ATPase. In the root apex due to less negative membrane potential, a small but constant K^+ leak via GORK channels occurs that needs to be compensated by the high-affinity K^+ uptake mediated by HAK transporters.
2. Signalling phase (onset of the stress)—depolarization of membrane potential in the apical zone to very low levels triggers a massive K^+ efflux via GORK channels that is further exacerbated by the increase in GORK transcripts. This efflux partially restores the membrane potential and switches the cell's operation from metabolic to defensive mode. Mature root cells also lose some K^+ but to a lesser extent resulting in more-negative membrane potential initially.
3. Recovery phase (after stress)—plant cells in both zones recover K^+ loss due to stress-induced activation of H^+-ATPase. To enable the root apical cells to regain optimal [K^+], some K^+ obtained by mature zone cells is redirected via symplast pathway to the apex.

The complex pathway of the reactive oxygen species-calcium-hormone signalling network is held responsible for sensing K^+ deficiency in plants, and the elucidation and comprehensive understanding of these signalling pathways help in developing the genetic approaches using K^+ transporters to increase K^+ use efficiency (KUE) in plants under stress (Srivastava et al. 2020).

3.4 Factors Controlling Intracellular K^+ Homeostasis in Plants

3.4.1 ROS

ROS are important regulatory agents in plants (Møller et al. 2007). By the onset of various stresses, the accumulation of ROS occurs in the cell, which has a destructive effect on the action of ion transporters, especially K^+ ion in the cell (Shabala and cuin 2008; Demidchik et al. 2010). The ratio of K^+ declined under abiotic stress (salt stress) which involves the formation of ROS. The ROS is elevated which leads to the activation of K^+ permeable for nonselective cation channel (NSCC) and guard cell outward-rectifying K^+ (GORK) channel. Thus, the potassium ion efflux from cytosol and its content was reduced (Anschütz et al. 2014), which in turn interrupt the homeostasis of cytosolic Na^+-K^+ ratio (Hauser and Horie 2010). Cytosolic K^+ homeostasis was maintained by exhausting the vacuole K^+ pool that results in turgor loss, and osmotic adjustment is done by synthesizing the organic osmolytes which leads to scavenging of ROS to retain the K^+ ion in cytosol (Cuin et al. 2003; Shabala et al. 2006). It also activates the endonuclease and protease which leads to programmed cell death (Anschütz et al. 2014) as shown in Fig. 3.7.

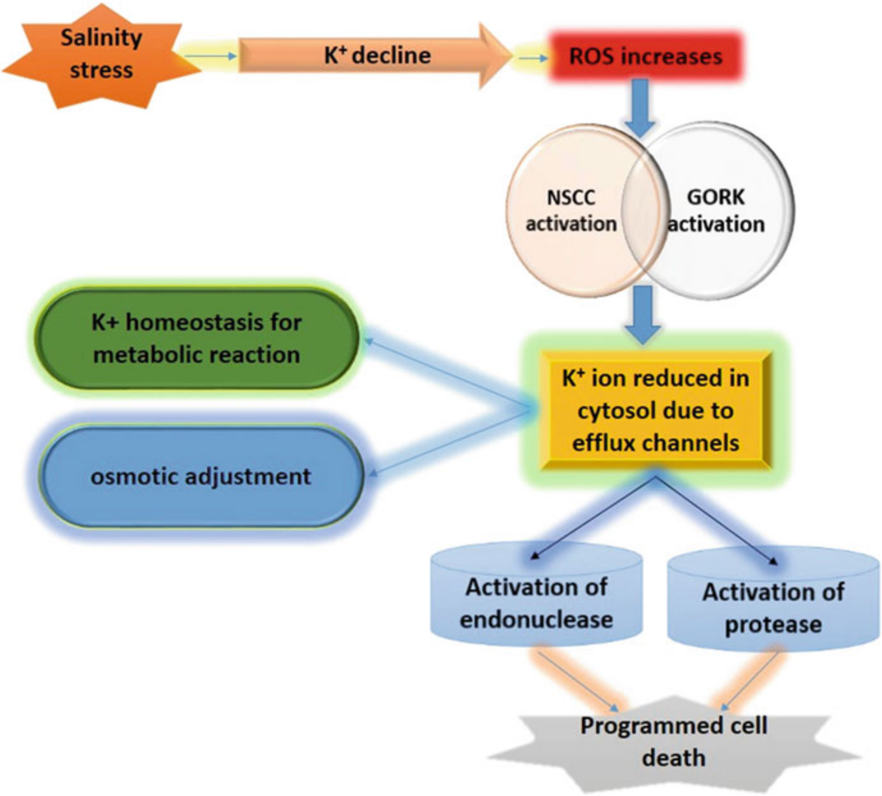


Fig. 3.7 Model represents the role of ROS to maintain the K^+ ion homeostasis in plants

3.4.2 Polyamines

Polyamines are the most important component in cells (Pegg 2016) which involve the role of polyamines in protein synthesis, cell division, etc. (Baronas and Kurata 2014; Handa et al. 2018). Ion transporter is also affected by polyamines like Spd, Spm, and Put (Roy et al. 2005). Inward rectifying of K^+ channels (KIRC) is blocked by Spm during salt stress (Liu et al. 2000). NSCC and K^+ efflux are also blocked by Spm under salt stress (Shabala et al. 2007). In barley seedling, the reduction of K^+ efflux was observed by blocking VI-NSCC under the influence of exogenous spermidine during salinity stress (Zhao et al. 2007). Zhao et al. (2007) reported that Na^+ accumulation is declined in roots which maintain a high level of K^+ ions in shoots by affecting the Na^+ and K^+ currents in root cells by exogenous application of polyamine. In guard cells the inward K^+ current is inhibited by the application of extracellular and intracellular polyamine (Liu et al. 2000). Vacuole K^+ channel is affected by polyamines by inhibiting vacuolar NSCCs that increase K^+/Na^+ selectivity in tonoplast (Hamamoto et al. 2008). Prevention of the leakage of Na^+ ion helps in restocking of cytosol with K^+ through vacuolar K^+ channels under the

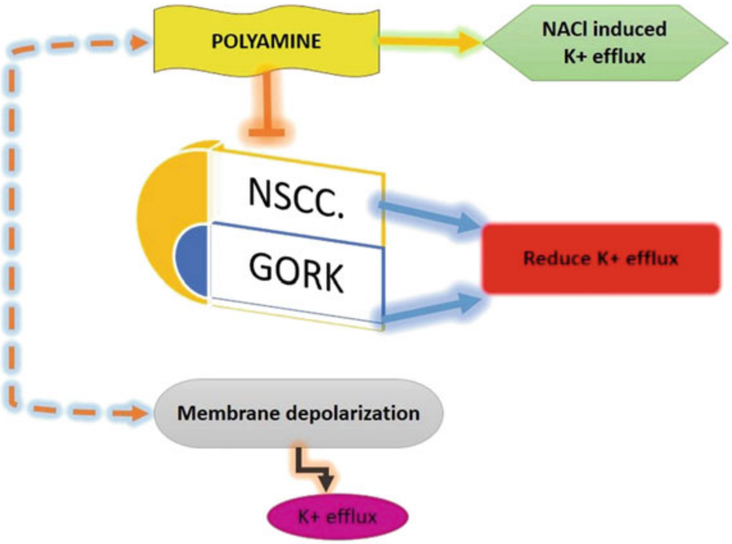


Fig. 3.8 Model represents the role of polyamine to control the K^+ ions in plant cells

influence of polyamine (Zepeda-Jazo et al. 2008). Exogenous application of polyamine in pea mesophyll inhibited the VI-NSCC and reduced the loss of the K^+ ions by decreasing the salt inducing membrane depolarization (Shabala et al. 2007). The role of PAs involves inhibition of NSCC and GORK to reduce K^+ efflux by depolarization of potentials (Zepeda-Jazo et al. 2008). Depending on the growth condition and root zones, PAs improved NaCl-induced K^+ efflux (Pandolfi et al. 2010). Activation role of PAs includes the induction of the depolarization of plasma membrane (Ozawa et al. 2010) which affects the transporter and generates driven force for the K^+ efflux (Pottosin and Dobrovinskaya 2014) as shown in Fig. 3.8.

3.4.3 Plant Growth Regulators

There is a positive influence of K on the synthesis of plant hormones (Ashley et al. 2006). Alterations in auxin localization, its concentration, and its sensibility result in inhibition of lateral root growth under prolonged K^+ shortage (Hafsi et al. 2014) and many auxin-associated gene responses to K^+ deficiency in rice (Ma et al. 2012). MYB77, which is an *Arabidopsis* transcription factor, maintains the low K-dependent decline of the lateral root density through auxin signal transduction (Shin et al. 2007). GORK (guard cell outward-rectifying K^+) channel activity and its expression level are expressively enhanced by elevated amounts of abscisic acid (ABA) and jasmonic acid and the expression of SKOR (stelar K^+ outward rectifier) which is a K^+ channel that is prevented by ABA during drought stress (Ragel et al. 2019). *AtPP2CA* involved in ABA signalling interacts with GORK and reduces its functioning independently from the phosphorylation status of the GORK protein

(Lefoulon et al. 2016), and this *PP2C* not only regulates K^+ channel activity by ABA signalling but also regulates SKOR activity. Cytokinins' dependent and independent mechanisms maintain the HAK5 channel expression under low-K conditions, and in *Arabidopsis*, cytokinins also regulate HAK5 gene expression negatively under K starvation (Nam et al. 2012). OPEN STOMATA 1 (OST1), a crucial kinase in ABA signalling, phosphorylates K^+ uptake transporter 6 (KUP6) in guard cells, and kup2 kup6 kup8 and kup6 kup8 GORK triple mutants (KUP2 and KUP8 are homologs of KUP6) display hypersensitivity to water deficit conditions as a result of defects in ABA-induced stomatal closure (Osakabe et al. 2013), showing that KUP6 and its homologs are involved in ABA signalling.

Ethylene is associated with the low-K signalling pathway by triggering the generation of ROS in roots, then altering root hair and primary root growth, and stimulating HAK5 expression in *Arabidopsis* (Jung et al. 2009). Low level of K^+ in roots improved the amount of ethylene and the H_2O_2 level by mediating the expression of ethylene biosynthetic and signalling-related genes, and also of ROS metabolism-associated genes, and then, both ethylene and ROS escalated the transcription of *HAK5* in *Arabidopsis* and tomato (Ródenas et al. 2018). Ethylene and ROS also stimulate the transcription of *HAK5* under K-deficient environments (Schachtman 2015). Jasmonic acid is also involved in triggering comprehensible expression of a HAK5 in response to K^+ deficiency, and it regulated the expression of rice K^+ transporter (Chen et al. 2016). Augmented amounts of JA, 12-oxo-phytodienoic acid (OPDA), and hydroxy-12-oxo-octadecadienoic acids (HODs) were found through K-deficient environments in addition with the escalation of the 13-lipoxygenase (LOX) cascade, acknowledging the transcript phase of numerous biosynthetic enzymes with K association (Troufflard et al. 2010). Gene expression of K^+ and its availability is decreased in the CORONATINE INSENSITIVE1 (*coi1*–16) mutant which is an important protein of JA signalling. However, K^+ deficiency triggered the JA synthesis which enhanced the tolerance against pathogens and insects to the wild-type plants (Armengaud et al. 2010). Polyamines regulate stomatal movement by activating the K^+ channel of the guard cell membrane, therefore showing that polyamines have important association with K at the cellular level (Liu et al. 2000).

3.4.4 Gasotransmitters

Gasotransmitters are the gaseous signalling molecules, for example, carbon monoxide (CO), nitric oxide (NO), nitrous oxide (N_2O), and hydrogen sulfide (H_2S), which vary from the usual signalling molecules due to their distinctive modes of action (Mustafa et al. 2009). Gasotransmitter accumulation has been reported to be enhanced in plants under the influence of abiotic stress conditions as the gasotransmitters increase stress tolerance in plants by regulating the action of numerous antioxidant enzymes (Yao et al. 2019). Gasotransmitters have been observed to provide cytoprotection for the potassium channel of mitochondria (Walewska et al. 2018). CO has been reported to regulate the number of ion channels of cell through the calcium-activated K^+ as well as voltage-activated K^+ receptors not only during normal conditions but also during pathogen infestation (Jaggar et al. 2005; Dallas et al. 2011; Duckles et al. 2015; Wilkinson et al. 2009). However, the mechanisms of actions behind modulation of the ion channels through carbon monoxide are not yet fully discovered; some studies suggest that sensitivity to CO is imparted toward certain ion channels through protein cofactors (Wilkinson and Kemp 2011). Similarly, in the plasma membrane, H_2S has a variety of effects on the action of diverse potassium channels (Zhong 2010). In the HEK293 cells, hydrogen sulfide-mediated S-sulfhydration targets the Cys43 in the Kir6.1 subunit of the K_{ATP} channel and subsequently activates the ion channel (Mustafa et al., 2011). Further, it was observed that hydrogen sulfide also affects the activities of other Kir channels, i.e., Kir2 and Kir3 (Ha et al. 2018; Tang et al. 2005).

3.5 Regulation of K^+ Uptake and Cellular Homeostasis by Molecular Approaches

The potassium transport systems (channels and transporters) are more complex and encoded by large gene families. The transport systems of same family are expressed into various tissues. This complex K^+ sensing and signalling mechanism plays a role in the regulation of potassium ion uptake from the soil and transfer to different plant organs.

3.5.1 Regulation by NHX Transporters

It is genetically demonstrated that NHXs are involved in regulation of K^+ homeostasis in Arabidopsis (Rodríguez-Rosales et al. 2008; Leidi et al. 2010; Bassil et al. 2011). Under control growth conditions, a single knockout mutant *AtNHX1* displayed an altered phenotype including smaller cells and smaller leaves associated with altered K^+ homeostasis. This is due to lower K^+/H^+ and Na^+/H^+ antiport activity (Apse et al. 2003; Sottosanto et al. 2004). AtNHX1 and 2 mutants showed reduction in rapidly elongating organs such as flowers, filaments, and hypocotyls of etiolated seedlings. In root and leaf cells of the double mutant, the vacuolar K^+ content was about one-third of that from wild-type cells. The double mutant was highly sensitive to external K^+ (*nhx1nhx2* mutant has higher K^+ cytosolic content), and this may indicate that these vacuolar NHX antiporters are the main moderators of cytosolic K^+ uptake into the vacuole. It is also proposed that fluctuation of K^+ content is essentially promoted by the activity of vacuolar NHX proteins (Bassil and Blumwald 2014). Stomatal movements require bidirectional K^+ fluxes across the guard cells' plasma and tonoplast membranes. Disruption in K^+ accumulation in guard cells may affect the guard cell osmoregulation and stomatal movement (Andrés et al. 2014). Hence, it is suggested that NHX1 and NHX2 are the main transporters mediating K^+ uptake to the vacuole.

3.6 Regulation of HAK/KUP/KT Transporters

3.6.1 Transcriptional Regulation

Transcriptional regulation is a universal mechanism for different plant species in response to K^+-deficient stress (Wang and Wu 2013). Work with the DmHAK5 transporter showed that co-expression of the corresponding cRNA with that of CBL9/CIPK23 (but not DmHAK5 alone) brings about inward K^+ in Venus flytrap and Rb^+ currents in *Xenopus* oocytes that were invigorated by low external pH (Scherzer et al. 2015). Salt bladders of the halophyte *Chenopodium quinoa* that store salts to very high concentrations express a HAK-like activity and selective K^+ uptake that was reliant on acidic external pH and by the CIPK23/CBL1 kinase module of *Arabidopsis* (Böhm et al. 2018). HAK1-like transporters are subject to complex transcriptional and posttranslational regulations; still research have been carried out almost exclusively in *Arabidopsis* AtHAK5 (Jung et al. 2009; Rubio et al. 2014; Ragel et al. 2015). In rice, adding NaCl in the external solution upregulates expression of OsHAK1 at high-K^+ condition but downregulates its expression at low-K^+ concentrations (Chen, et al. 2015). Furthermore, it has been commonly examined that the expression of *HAK1*-like genes is also regulated by other ions, particularly $NH4^+$, NO^{3-}, Na^+, and Pi and not always in the same way (Nieves-Cordones et al. 2019). For example, the transcriptional expression of HAK5 in both tomato (cv. Micro-Tom) and Arabidopsis was also regulated by nitrate (NO^{3-}) or phosphate (Pi) supply in response to low K^+, but these regulations had no effect on the root K^+ uptake rate of roots (Rubio et al. 2014) (Meng et al. 2016). It is shown that the expression of HAK5, RAP2.11 (encoding a transcriptional regulator of HAK5 (Kim et al. 2012)), and ANN1 (Laohavisit, et al., 2012) in the roots of nrt1.5 (a nitrate transporter) mutant is downregulated by NO^{3-} starvation. The results suggest that on one hand HAK5, probably as well as other high-affinity K^+ transporters, may be regulated transcriptionally or posttranscriptionally by low-K+ signal, while on the other hand, HAK5 may be involved in unknown functions related to plant NO^{3-} and Pi deficiencies (Rubio et al. 2014). The root cell activity can be changed by growth medium containing NH^{4+}, NO^{3-}, Na^+, and Pi. Thus, the effect of the salt stress and mineral inadequacy on transcriptional expression of certain HAK/KUP/KT genes may be linked with variations in the root cell membrane potentials (Rubio et al. 2014).

3.6.2 Regulation by Transcription Factors

The target sequences of many transcription factors (TFs) have been identified in the *AtHAK5* promoter, and out of them ARF2 (auxin response factor 2) is described as a negative regulator of *AtHAK5* transcription (Zhao et al. 2016). When K^+ ions are present in large quantity, then channel-mediated K^+ transport would be more favorable than cotransport (symport) through AtHAK5, and therefore AtHAK5 should be close (Zhao et al. 2016). Under such situations, within the AtHAK5 promoter, ARF2 binds to AuxREs (auxin-responsive elements) and represses transcription.

Under K^+ deficiency, ARF2 is phosphorylated by a kinase and removed from the promoter and alleviates the repression on ATHAK5 transcription. Other transcription factors such as RAP2.11 bind to the ethylene-responsive element (ERE) and the GCC box of the *AtHAK5* promoter, and its expression is upregulated by ethylene signalling, reactive oxygen species production, and calcium signalling (Kim et al. 2012). When K^+ is again provided, ARF2 becomes dephosphorylated and represses the expression of *AtHAK5* (Zhao et al. 2016). Thus, it is evident that regulation of the activity of TFs acting on *AtHAK5* promoter (positively or negatively) is important to learn cooperatively the aggregation of the transcripts (Santa-María et al. 2018).

Potassium channels: These channels are further subdivided into two channels: voltage-independent potassium channels and voltage-dependent channels:

3.7 Voltage-Independent Potassium Channels

3.7.1 Tandem-Pore Potassium Channels

These channels consist of six members, five tandem-pore channels (TPK1–TPK5), and a single subunit (KCO3) in *Arabidopsis thaliana* that resulted from chromosome segment duplication of a tandem-pore channel gene and subsequent partial deletion. All TPK/KCO channels are located at the vacuolar membrane and interact with 14-3-3 proteins (GRFs), showing regulation at the protein level. Cytosolic C-terminal part of these channels contains 1–2 Ca^{2+} binding, and N-terminal contains binding sites for 14-3-3 proteins. TPK channels are much dependent on Ca^{2+} ions which might be important for channel regulation (Latz et al. 2007a).

It has been proposed that TPK channels are involved in the K^+ ion homeostasis of plant cells by providing controlled intracellular potassium transport from and into organelles. Recently the patch-clamp technique has revealed a mechano-sensitive nature of TPK channels recommending a role in osmoregulation. TPK1 has characteristics of K^+-selective channels from *Vicia faba* specified in vivo with selectivity for potassium over sodium ions (Bihler et al. 2005; Gobert et al. 2007; Latz et al. 2007b). It was shown that TPK activity depends on cytosolic pH with probability of 6.7, decreasing 20–30% at physiological pH 7.5–7.8. Also, it has the highest affinity for calcium ions including calmodulin protein. It has been reported that TPK1 participates in K^+ release from vacuole during stomatal closure, seed germination, and radicle growth (Gobert et al. 2007). There is higher abundance of *TPK5* in senescent leaves and petals at mRNA levels (Voelker et al. 2010). TPK activity was observed in root cortex, vascular tissue, mesophyll cells, guard cells, and pollen grains using promoter-reporter gene (GUS) fusion (Czempinski et al. 2002).

3.7.2 Plant Kir-Like Channels

First Kir channels were identified from genome sequence databases by searching TPK1-related sequences in *Arabidopsis*. At biochemical level, KCO3 could be determined as a stable dimer (Rocchetti et al. 2012). The plants having mutant KCO3 gene show reduced growth under osmotic stress; hence, KCO3 gene plays an important role in osmoregulation. But the changed plant phenotype can be accomplished by expressing a mutant *KCO3* gene with an inactive pore region. These results showed that the KCO3 serves its function independently to its ability to transport potassium ions under osmotic stress (Rocchetti et al. 2012). Thus, the above considerations revealed that these channels should be restored into the TPK family, instead of being expressed as a separate channel family.

3.8 Voltage-Dependent K^+ Channels

These are the first Shaker-like, voltage-gated (VG) channels (AKT1) which are involved in nutrient uptake (Hirsch et al. 1998). The plant voltage-gated channels are phylogenetically related to animal Shaker channels and also include functional domains (Jegla et al. 2018). Four α-subunits of VG channels surround a central aqueous pore for K^+ permeation. Each subunit (contains six transmembrane segments, i.e., S1–S6) can be divided into two different modules: a voltage-sensor domain (consists of four α-helices) contains positively charged residues that moves within the membrane in response to voltage which ultimately results in opening and closing of the channel. The physiological function and effect of plant *Shaker* channels on the plant are described in the following sections.

3.8.1 Regulation of AKT1 Channel

AKT1 is an inward-rectifying potassium channel involved in low and high potassium uptake in plants and is regulated by the protein kinase complex which consists of the kinase CIPK23 and one of the two alternative calcium-dependent regulatory subunits CBL1 and CBL9 (Li et al., 2006; Xu et al. 2006). AIP1, a 2C-type protein phosphatase (CIP kinases), was shown to bind and inactivate AKT1 (Lee et al. 2007). In principle, it is evidenced that phosphorylation/dephosphorylation regulates the activity of AKT1 channel, but it should be noted that no phosphorylation of AKT1 by CIPK23 and dephosphorylation by AIP1 have been revealed conclusively (Hashimoto et al. 2012). Instead it is suggested that mutual interaction of four components, CIPKs, CBLs, PP2Cs, and AKT1, inhibits the phosphorylation activity of the kinase and to dephosphorylate AKT1 (Lan et al. 2011). It is also indicated that CBL10 directly binds AKT1 and reduces its activity in a concentration-dependent and CIPK-independent manner (Ren et al. 2013). The phosphorylation-dephosphorylation system of CBL gives a strong regulatory network for the plant to respond to a wide range of environmental variations (Kudla et al. 2010).

3.8.2 Regulation via Heteromerization

Another regulatory subunit of Kin *Shaker*-like channels that alters the functionality of AKT1 is AtKC1. AtKC1-D increased the inhibition of AKT1 channel activity and confined K^+ leakage through AKT1 under low-K^+ conditions, thereby increasing the tolerance to nutrient stress (Wang et al. 2016). It is demonstrated that AtKC1 shifts activation threshold of AKT1 toward more-negative values and prevents K^+ efflux through AKT1 under unfavorable conditions (Duby et al. 2008). It is established that at higher K^+ concentrations, the pore of AKT1-AtKC1 heteromers collapses than that of AKT1homomers. Hence, heteromers comprise a more suitable obstructive K^+ passage in the unfavorable outward direction.

3.9 Conclusion and Future Prospective

Intracellular K homeostasis is essential for the proper functioning of cultivar metabolic apparatuses and genotypes including development. The indispensability of K is due to its multifaceted appearance in genotypes such as stabilizing cell turgor pressure, cell expansion, opening and closing of stomata, osmotic adjustments, solute translocation in phloem, maintenance of membrane polarization, optimal photosynthetic activity, and many more. As many of these aspects are straightforwardly associated with plant acclimatization to adverse ecological situations, therefore K absorption, translocation, and homeostasis appear important to counteract abiotic factors. Our perception to the significance of K uptake strategy and its cellular homeostasis under stress environments has elevated substantially in recent years. Exposure to abiotic factors caused noteworthy interruption to intracellular K homeostasis which ultimately leads to huge K^+ outflow. An intricate gene regulatory apparatus was found in cultivars to confirm K uptake and to uphold K^+ homeostasis in plants under abiotic stress circumstances. Novel crop cultivars, which can absorb more K under hostile ecological circumstances and produce yield which is sufficient to fulfill the demands of human and animal, need to be developed. It is apparent that more studies, at both genetic and entire genotypic levels, are required to understand the mechanism of K homeostasis, its signalling, and regulators that alter their functioning.

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Soil Potassium Availability and Role of Microorganisms in Influencing Potassium Availability to Plants

4

Samina Mazahar and Shahid Umar

Abstract

The availability of potassium in soils is of prime importance in maintaining the balance between nutrient use efficiency and sustainable agriculture. The potassium-solubilizing microorganisms (KSMs) play a significant role in the solubilization of fixed K. The site for solubilization and mineralization is the rhizospheric region and is referred to as biological hotspot. A range of bacterial and fungal strains are efficient K solubilizers regulating the nutrient flow by converting the insoluble K into its soluble forms and as a result show effective interaction between soil and plant system. Hence KSMs promote plant growth and yield, lessen the use of agrochemicals and reduce environmental pollution caused by leaching and over-fertilization. According to recent research on nutrient use efficiency, there will always be an incessant growing gap between the use and supply of nutrient, and so efforts are needed to ensure the nutrient requirement of plants and enhance the nutrient use efficiency. Hence the application of microbial inoculants is of great significance in promoting the agriculture productivity. More studies are needed for the identification of such new microbial strains and also understanding their mechanism of application to the agricultural lands.

Keywords

Potassium-solubilizing microorganisms (KSMs) · Microbial inoculants · K solubilization · Nutrient use efficiency · Rhizospheric zone

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4.1 Introduction

Potassium is one of the most dynamic plant nutrients responsible for various vital activities of plants. It enhances the antioxidant and phenolic composition (Khayyat et al. 2007) and triggers the regulation of several metabolic processes such as photosynthesis, protein synthesis, enzyme activation (Schwarz et al. 2018), osmoregulation, cation-anion balance, energy transfer and many other vital activities (Hasanuzzaman et al. 2018) such as providing resistance against plant diseases, pests and stresses (Gurav et al. 2018). The utilization of K and its uptake are known to interact with the availability and uptake of various other nutrients. It is present abundantly in the agricultural fields and also applied as synthetic and natural fertilizers; however only 1–2% of it is available to the plants, and the rest is in bound forms with other minerals and therefore unavailable to plants (Meena et al. 2016). The unavailability of nutrient K is due to the strong affinity with exchange sites of clays. However the plant K demand varies with plant species, cultivars, yield and also the plant growth stage. During the vegetative stage, plant K demand is high, and hence the uptake can reach up to 10 kg/ha/day and above (Ramamurthy et al. 2017).

The interaction between the plant-soil and microorganism has gained significant importance in the recent years. According to Zhao et al. (2016), microorganisms can make nutrients available to plant by different mechanisms. The microbes are abundantly present in the soil and are in an association with the plants. They function as efficient biofertilizer agents for improving the agricultural productivity, protecting the environment and improving the soil fertility (Meena et al. 2016). Microorganism plays a central role in ion cycling and enhancing the availability of insoluble potassium by solubilization and mineralization. Hence the rhizospheric zone has become a biological hotspot in the soil (Singh et al. 2017).

The microorganism solubilizes the insoluble potassium to soluble forms and promotes plant growth and yield (Meena et al. 2014b). The K solubilization is carried out by a large number of saprophytic bacterial and fungal strains. The rhizospheric microorganisms are contributing to the biological and physiochemical parameters of soil through their useful activities and also suppress the activities of various pathogens and improve the soil nutrient and structure (Meena et al., 2014b). There are various functions of rhizospheric bacteria such as storage and release of nutrients, its mobilization and mineralization, decomposition of soil organic matter, exudation of various soluble compounds and K solubilization (Abhilash et al. 2013). Hence they are the crucial component of sustainable agricultural ecosystem (Meena et al. 2016).

4.2 Potassium Level in Soil

Soil is the source of nutrient and energy for all the living beings, and so maintaining a balance between the uptake and assimilation of nutrients is an important criterion in maintaining the soil health and also reducing environmental pollution. Among the major nutrients, potassium is the third important macronutrient required by plants and serves as one of the main pillars of balanced fertilization. It is absorbed by roots and translocated in the plant as positive cation (K^+) (Meena et al. 2016). Recent study suggests the net negative NPK balance as 19% N, 12% P and 69% K; this negative balance is due to the reason that plants lose an average of 1.5 times more K than N. Further the K applied as fertilizers are comparatively lower than that of N or P (Gurav et al. 2018), and the K status of the Indian soil is rated as medium to high. However the available K levels in the Indian soil range less than 0.5–3.00%, and hence poor correlation exists between the total and available soil K, and so the K fertility status of the soil remains unspecified (Meena et al. 2014b).

For maintaining the optimum K level and enhancing the soil fertility, frequent application of K is required by the use of K-rich fertilizers (Patra et al. 2017). The K status of the soil also varies depending upon the soil type in different agro-ecological regions (such as laterite soil, alluvial soil, red soil, medium and deep black soil) and the management practices involved (Srinivasarao et al. 2011). Depending on the type of soil, nearly 98% of total soil K is found in unavailable forms (Meena et al. 2016).

Recent research by scientists from the Indian Institute of Soil Science, Bhopal, and Tamil Nadu Agricultural University suggests that most parts of the country are categorized under low and medium K fertility level than the high and very high K category (Dey et al. 2017). This is because the K present in the soil remains in its insoluble bound form and hence is unavailable to plants. The current scenario of nutrient balance suggests that there will always be a continuous growing gap between the nutrient use and supply and therefore efforts are needed to ensure the nutrient requirement of plants and enhance the nutrient use efficiency.

4.3 Potassium-Solubilizing Microorganisms (KSMs) in the Soil

The mobilization of K in soil is affected by many environmental factors including the soil parameters such as physiochemical properties, pH along with the occurrence of a diverse group of microorganisms such as rhizospheric bacteria and mycorrhizal fungi and the plant root exudate composition (Meena et al. 2016). These potassium-solubilizing bacteria are ubiquitous in its distribution, and hence they vary in number from diverse soil type. The insoluble and fixed forms of K become available in its soluble form by the process of mineralization carried out by the potassium-solubilizing microorganism (KSMs) and hence are easily absorbed by plants. The KSMs are an indigenous rhizospheric microorganism and show efficient interaction between soil and plant. The insoluble forms of K like feldspar, mice and various others are solubilized into organic acids, capsular polysaccharides and siderophores by these microorganisms (Singh et al. 2017).

There are numerous members of KSMs such as *Bacillus edaphicus*, *Bacillus mucilaginosus*, *Bacillus circulans*, *Paenibacillus* spp., *Pseudomonas*, *Acidithiobacillus ferrooxidans*, *Burkholderia* (Meena et al. 2014a, b; Kumar et al. 2015), *Arthrobacter* spp. (Zarjani et al. 2013), *Enterobacter hormaechei* (Prajapati et al. 2013), *P. frequentans*, *Cladosporium* (Argelis et al. 1993), *Aminobacter*, *Sphingomonas*, *Burkholderia* (Uroz et al. 2007), *Paenibacillus glucanolyticus* (Sangeeth et al. 2012). These microbial strains are known to be actively involved in the K-solubilization process and release potassium from potassium-bearing minerals in the soil which is easily available to plants. Arbuscular mycorrhizae improve the solubility of mineral form of potassium by releasing the protons, CO_2 and organic acid anions such as citrate, malate and oxalate (Meena et al. 2014b) and hence significantly enhance the potassium, nitrogen, calcium and iron content in plant leaves and fruits (Veresoglou et al. 2011; Yousefi et al. 2011).

Increase in the K uptake in the maize crop was observed when the inoculants of *G. intraradices* and *G. mosseae* (species of arbuscular mycorrhizal fungi) were applied in soil on the weight basis (Wu et al. 2005). Some strains of potassium-solubilizing fungi (KSF) such as *Aspergillus niger* and *Aspergillus terreus* were found in soil samples rich in K, and both the species also showed the highest available K level in liquid medium when two insoluble forms of K such as potassium aluminium silicate and feldspar were used, based on their morphological features and colonies (Prajapati et al. 2012). However solubilization and acid production on both insoluble potassium sources were highest in *A. terreus* (Meena et al. 2016). Therefore KSMs promote the availability of nutrients and enhance the plant growth under field conditions.

4.4 Potassium-Solubilizing Mechanism

Plants generally take up the nutrients in its soluble forms, and there are several mechanisms that contribute to the availability of K in the soil and to the plants. The K-solubilization mechanism involves the solubilization and mobilization of unavailable forms of potassium compounds due to the production of various types of organic acids. Various studies suggest that K solubilization and the release of organic acids by the K-solubilizing strains improved the growth of plants (Meena et al. 2014b). The solubilization of structural K compounds by abundantly naturally occurring KSMs is widespread under in vitro conditions (Zarjani et al. 2013) and also under field and greenhouse condition (Prajapati et al. 2013; Parmar and Sindhu 2013).

Weathering is involved to release the K from the minerals and rocks, and that takes a longer time; however calcinations of rocks can break the structure and release K, but this is more expensive than evaporite ores (Rawat et al. 2016). The K solubilization and uptake can be enhanced by the bioinoculants and rhizospheric microorganism which produce organic acids and provide potassium and other minerals and hence enhance the crop productivity. However the K-solubilization efficiency varies with the nature of the potassium-bearing minerals and aerobic conditions (Uroz et al. 2009). Significant levels of fixed K are present in the biomass of the rhizospheric microorganism present in the soil and are potentially available to plants (Girgis 2006). Also the K released from the minerals was affected by oxygen, pH and the bacterial strain used (Sheng and Huang. 2002).

Table 4.1 Potassium-solubilizing microorganisms (KSMs) involved in the production of various organic acids in different strains (adapted from Meena et al. 2014b)

K-solubilizing microorganism	Predominant organic acids
Penicillium frequentans, *Cladosporium*	Oxalic, citric, gluconic acids (Argelis et al. 1993)
Paenibacillus mucilaginosus	Tartaric, Citric, Oxalic (Liu et al. 2012; Hu et al. 2006)
Pseudomonas spp.	Tartaric, Citric (Krishnamurthy 1989)
Aspergillus fumigatus, *Aspergillus candidus*	Oxalic, tartaric, citric, oxalic (Banik and Dey 1982)
B. megaterium, *Pseudomonas* sp., *B. subtilis*	Lactic, malic, oxalic, lactic (Taha et al. 1969)
B. mucilaginosus	Oxalate, citrate Sheng and He (2006)
Arthrobacter sp., *Bacillus* sp., *B. firmus*	Lactic, citric (Bajpai and Sundara 1971)
B. megaterium, *E. freundii*	Citric, gluconic (Taha et al. 1969)
Aspergillus niger, *Penicillium* sp.	Citric, glycolic, succinic (Sperberg 1958)
Pseudomonas aeruginosa	Acetate, citrate, oxalate (Sheng et al. 2003; Badar et al. 2006)

Three major reaction pathways are employed in the K-solubilization mechanism by potassium-solubilizing fungi *Aspergillus fumigatus* such as acid hydrolysis, secretion of insoluble macromolecules and polymers bound in the cell membrane along with direct biophysical forces which may possibly split the mineral grains (Lian et al. 2008). The potassium-solubilizing bacteria (KSB) involve various mechanisms like capsular absorption, acidolysis, enzymolysis and complexation by extracellular polysaccharides and solubilize rock K mineral powder such as orthoclases, illite and micas (Welch et al. 1999).The mechanism involved by KSMs in K solubilization is achieved by enhancing chelation of the cations bound to K, lowering the pH and acidolysis of the surrounding area of microorganism (Meena et al., 2014b). The protons and organic acids are released by the KSMs by lowering the pH of the medium (Zarjani et al. 2013).

Table 4.1 shows the list of potassium-solubilizing microorganisms (KSMs) which produces different organic acids in different strains and helps in the solubilization of insoluble potassium into its soluble form. The techniques involved in the detection of the organic acids produced by KSMs are high-performance liquid chromatography (HPLC) and enzymatic methods (Zhang et al. 2013). According to Liu et al. (2006), the chelating ability of different organic acids is also important as it is observed that the addition of 0.05 M EDTA into the medium has the same solubilizing effect as compared to the inoculation with *Penicillium bilaii*.

Mechanisms involved in the solubilization of K-bearing minerals can be done by various ways and are grouped into direct (bacterial cell wall) and indirect process involving mineral weathering, microbial weathering, bioleaching and mechanical fragmentation (Rawat et al. 2016).

4.4.1 Direct Method

4.4.1.1 Bacterial Cell Wall

The cell wall of prokaryotes secretes various metabolic products that reacts with ions and compounds and results in mineral deposition (Rawat et al. 2016). The cell wall of bacteria includes slimes, biofilm or sheath and dormant spores which acts as main sites for mineral nucleation, ion adsorption and growth (Banfield and Zhang 2001; Bauerlein 2003). In Gram-negative bacteria, the mineral nucleation in the layer external to the bacterial cell wall includes capsules, S-layer, slimes and sheaths, where the S-layer is acidic and has a net negative charge possess affinity towards the metal cation (Southam 2000). Also direct absorption of some of the exchangeable K occurs in the soil colloids directly through the roots which are negatively charged and hence are attracted towards the positively charged potassium ions (K^+) present on the surface of the clay mineral and the edges (Rawat et al. 2016).

4.4.2 Indirect Method

4.4.2.1 Microbial Weathering

Microbial weathering includes redox reaction during the production of organic acids due to which the chemical bonds of minerals weaken promoting mineral dissolution (Harley and Gilkes 2000) and also chelates molecules for mineral degradation (Uroz et al. 2009). Although among all the KSMs only two of the microbial strains such as *B. edaphicus* and *B. mucilaginosus* are highly capable of mobilizing and solubilizing K (Meena et al. 2016). These KSMs solubilize the potassium, aluminium and silicon from their insoluble K-bearing forms such as micas, illite and orthoclases through excreting organic acids by either chelating the silicon ions or by directly dissolving the K present in the rocks (Zhang and Kong 2014).

Hence these microbes are of significant importance in the weathering of rocks and release of important nutrients needed by plants.

4.4.2.2 Mineral Weathering

In mineral weathering the inorganic minerals are translocated by microorganism through processes such as uptake, release, biomineralization, oxidation and reduction (Berner and Berner 1996), and all the physical, chemical and biological forces act on the parent material and break them in fine fractions such as sand, silt and clay (Rawat et al. 2016). The availability of nutrients in plants increases due to the conversion of the insoluble K like mica, feldspar, biotite and feldspar into the soil solution form by the organic and inorganic acids. However the different types of organic acids produced by KSMs differ with different organisms (Meena et al. 2016). The organic acids produced by the microorganism in the solubilization of feldspar and illite are oxalic acid, citric acid, malic acid, succinic acid, gluconic acid, 2-ketogluconic acid, oxalic acid and tartaric acids (Sheng and He 2006). The most frequent agent of mineral K solubilization seems to be tartaric acid (Zarjani et al. 2013). The other organic acids which are identified as K solubilizers are propionic, malonic, succinic, acetic, lactic, citric, glycolic, oxalic and fumaric acids (Wu et al. 2005).

Microorganisms contribute to the mineral weathering and soil formation by releasing organic acids and ligands such as siderophores (Liermann et al. 2000, 2005). Inorganic nutrients are released by the chemical weathering of bedrock such as Ca, Mg, K, Fe and P which are cycled through the soil, saprolite and vegetation. Plants absorb the mineral ions in the root zones which are recycled back into the soil with the death and decomposition of the plant. Also the ratio of silt, sand and clay depends on the nature of parent material such as shale, limestone or mica from which the soil is derived and hence significantly influences the potassium fixation and its release (Rawat et al. 2016).

4.4.2.3 Bioleaching

Leaching is the process of removal of soluble materials present in the rocks in solution by percolating water. *Leptospirillum ferrooxidans*, *Thiobacillus ferrooxidans* and *T. thiooxidans* are some of the important bioleaching microbes. Among the minerals the carbonates and sulphates are sparingly soluble, whereas halite (NaCl) and sylvite (KCl) are highly water soluble (Rawat et al. 2016).

4.4.2.4 Mechanical Fragmentation

Mechanical fragmentation caused by the activity of the root increases the reactive surface and hence has direct positive influence of the bacteria on mineral weathering (Rawat et al. 2016). The rocks also undergo mechanical fragmentation when the microorganism is a fungus, and the hypha penetrates the interior of the minerals to derive the nutrition.

4.4.2.5 Biofilm

Microbial biofilm accelerates the weathering process of minerals. According to Warscheid and Braams (2000), the biofilms and biocrusts cause higher weathering rates due to biodegradation. Biofilm has multiple functions as it regulates the denudation losses by acting as a protective layer covering the root hair interface or the mineral-water-hyphae in the mycorrhizosphere and rhizosphere of vascular plants (Rawat et al. 2016). Besides it causes the weathering of minerals like biotite and anorthite, and also the biofilm formation on mineral surface promotes the corrosion of K-rich shale and the release of K along with Si and Al in the bacterial-mineral contact model (Li-yang et al. 2014).

4.5 Potassium-Solubilizing Microorganism (KSMs) Affecting Growth and Yield of Plants

Various studies suggest that inoculation with KSM produced beneficial effect on growth and yields of different plants as shown in Fig. 4.1 (Meena et al. 2015; Ahmad et al. 2016; Anjanadevi et al. 2016; Bakhshandeh et al. 2017; Xiao et al. 2017). Application of KSM is an alternative approach for increasing the unavailable K in its available and soluble forms to the plants. Microorganism applied as biofertilizer can prevent nutrient leaching and also add to soil enrichment. These beneficial microbes translocate the available nutrients and hence help in creating a positive microflora increasing fertility and enhancing soil health. Hence by the application of bioinoculants, the soil physical properties and the water-holding capacity can be improved. Various researchers suggest that KSMs can improve the agricultural productivity, lessen the use of agrochemicals (Prajapati et al. 2013) and reduce over-fertilization and environmental pollution caused by leaching.

4.6 Future Perspective

The potassium-solubilizing microorganism is an important and beneficial component of soil microflora, playing a central role in K solubilization and availability of soluble K to plants. Hence KSMs promote soil fertility, enhance crop growth and

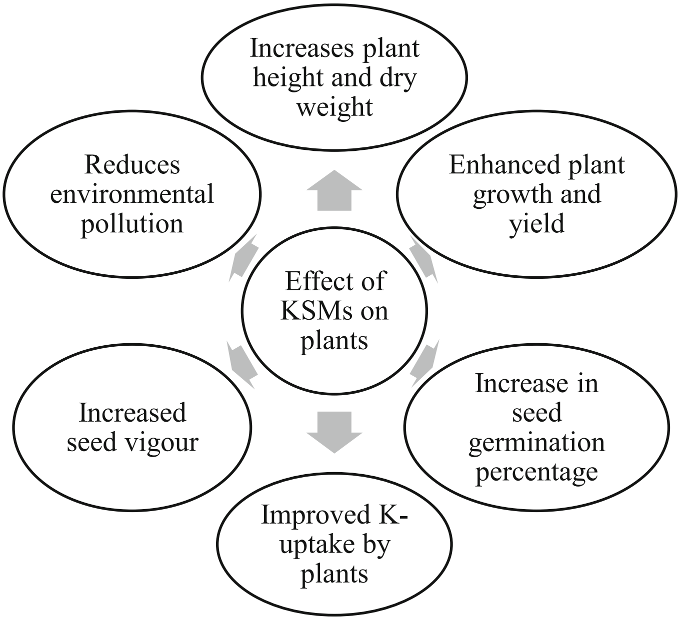

Fig. 4.1 Effect of KSM inoculation on seeds and seedlings of different plants

yield and prevent over-fertilization, nutrient leaching and environmental degradation. Hence more research should be conducted in relevance to the existence and role of KSMs in increasing the K-use efficiency and agricultural productivity and reducing the use of agrochemicals. Further the biochemical basis of such microbial interaction should also be studied, and various biotechnological applications should be employed to further improve the K-solubilizing efficiency of these microorganisms. Also more studies are needed for its application in agricultural fields besides in vitro and greenhouse condition so that application of KSMs can become a common practice along with the application of fertilizers and hence enhance the nutrient use efficiency and also the agricultural productivity.

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5

Crosstalk of Potassium and Phytohormones Under Abiotic Stress

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Abstract

Abiotic stress adversely affects plant growth and productivity and leads to the production of increased reactive oxygen species (ROS) that leads to oxidative stress. In order to avert this stress, numerous regulators such as phytohormones and potassium are applied. Potassium is added to soil as fertilizer and is generally added together with nitrogen and phosphorus. It is an important macronutrient in plants and occurs as the cation K^+. It is involved in the regulation of the osmotic potential of plant cells. It affects the enzyme activity, protein synthesis, photosynthesis, stomatal movement, and water relation. Phytohormones are employed to minimize the ill effect of stress. The current review is an attempt to study the synergistic role of potassium and phytohormones and their crosstalk in reducing the stress conditions and increasing plant adaptability. These types of interactions could be helpful in nutrient uptake and also promote transport and utilization of nutrient and in reversing the ill effect of stress.

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5.1 Introduction

Potassium (K) is a key macronutrient along with nitrogen (N) and phosphorus (P) (Fageria 2016; Hasanuzzaman et al. 2018). Potassium is involved in growth and development of the plant by inducing numerous biochemical and physiological processes, and also promotes synthesis of protein, carbohydrate metabolism, and activation of enzyme (Ma et al. 2012; Hasanuzzaman et al. 2018; Naciri et al. 2021). Potassium minimizes the level of different stress such as salinity, drought, metal toxicity, high temperature, or chilling temperatures (Wang et al. 2013). Under K-deficit conditions, plants exhibit stunted growth and yellowing of leaves. Potassium is a macronutrient that remains as a soluble ion in the cell sap but not incorporated into organic matter. In the plant body, K is the most abundant comprising up to 1/10 of a plant's dry weight (Leigh and Wyn Jones 1984). It performs critical functions within the plant body which includes enzyme activation, turgor generation, cell expansion, osmotic balance, an electric potential of membranes, and root growth (Hawkesford et al. 2012; Sustr et al. 2019).

Potassium is present in the earth's crust where it exists in insoluble forms such as rocks and silicate minerals. It is the main cation essential for plant growth and adaptation to the environment in plant cells (Luan et al. 2017; Zhang et al. 2018). In plant cells, it is present in abundance and is mainly involved in neutralization of charges, pH homeostasis, and control of the electrical membrane potential (Sharma et al. 2013). In cytosol, K^+ is not replaced by any other cation such as Na^+, because the latter affects H-bonding at the protein surface more than K^+ (Collins 1997), whereas the vacuolar K^+ up to some extent can be replaced by Na^+ (Leigh and Wyn Jones 1984; Benito et al. 2014). It was reported that K^+ decreases the level of stress exposed to high light intensity, chilling, and drought (Waraich et al. 2012). Halford and Hey (2009) reported that combined drought and high temperature tolerance were governed by potassium.

Apart from plant growth and productivity, K^+ maintains plant cell turgor, osmotic adjustment (Waraich et al. 2012), and aquaporin protein function (Wang et al. 2013) under drought conditions. Exogenous K supply increases root growth which in turn increases the root surface area under drought conditions, and ultimately leads to enhanced water uptake by plant cells (Egilla et al. 2005). Like other environmental stresses, salinity also adversely affects plant growth and development by decreasing the water use efficiency of plant. Salinity inhibits plant growth, and germination of seed interferes leaf anatomy and physiology of plants, thereby affecting plant metabolism (Parida and Das 2005; Fatma et al. 2021). Increasing the NaCl concentration in *Vigna subterranea* (L.) reduced content of K^+ in the studied parts (roots and shoots) that hinder K^+ uptake and translocation from the roots to the shoots (Toffouo et al. 2010). Merwad (2016) studied that external application of K can have a positive impact on yield and nutrient of most of the *Beta vulgaris* cultivars grown under salt stress. Heat stress affects various biochemical processes and the plant metabolism (Hasanuzzaman et al. 2013a, b). Under high temperature stress, K behaves as osmolyte to protect plants from heat damage and improve stomatal conductance (Azedo-Silva et al. 2004). However, in K-deficient plants, photosynthetic electron transport pathways as well as NADPH oxidizing enzyme reaction produce ROS (Cakmak 2005).

During chilling or freezing stress, in plants processes associated with K like phloem activity, photosynthesis, and carbon assimilation are downregulated. Seeds treated with KCl in *Triticum aestivum* under cold stress scavenges ROS for better performance (Farooq et al. 2008). K application adjusts the osmotic potential and decreases dehydration caused by cold stress that loses apoplastic water (Wang et al. 2013). K supply can remove frost damage in crop plants (Oosterhuis et al. 2013). K actively participates in hormone crosstalk and signaling. Maintaining a proper hormone level in plants indicates a competitive advantage to withstand adverse conditions. K provides cellular signaling alone or in combination with phytohormones and other signaling molecules (Hasanuzzaman et al. 2018). Reports show that in *Zea mays* and beans, exogenous application of K and cytokinin promotes stomatal opening and recovery in photosynthetic rate, depending on the plant species and dosage (Metwally et al. 1998; Rulcová and Pospíšilová 2001). In *Zea mays* exogenous application of GA increases the K content in cytoplasm and plastids. Several enzymes also required for the functioning of GA in plant body which may be activated by univalent cations as cofactors at specific concentrations for that purpose only K would work better in plant cells (Evans and Sorger 1966). Research has shown the accumulation of nonvalent cations K and sodium likely to play a major part in the stomatal movement in light (Fischer and Hsiao 1968; Sawhney and Zelitch 1969). The current review is an attempt to study the synergistic role of K and phytohormones and their crosstalk in reducing the stress conditions and making the plants feel better. These types of interactions could be helpful in nutrient uptake and also promote transport and utilization of nutrient and in reversing the ill effect of stress.

5.2 Potassium in Abiotic Stress Tolerance

Different environmental problems such as water deficiency, extreme temperatures, salinity, flooding, soil acidity, and pathogenic infections are increasing by using intensively natural resources due to increasing world population. These stresses significantly affect crop yields and decrease their rate well below the potential maximum yields (Cakmak et al. 2005; Ahanger and Agarwal 2017a; Aslam et al. 2021). The decrease in maximum crop yields with abiotic stress factors varies between 54% and 82% (Bray et al. 2000). Most of the fall in yield production is caused by abiotic stresses resulted from drought, salinity, high or low temperatures, excess light, inadequate mineral nutrient supply, and soil acidity.

Plants have adopted numerous mechanisms for their survival under abiotic stress conditions. It is well developed that mineral nutrient status of plants is involved in enhancing the tolerance in plants to stressful environment (Marschner 1995; Ahanger and Agarwal 2017b). Among the mineral nutrients, K^+ plays a vital role in the survival of crop plants under environmental stress conditions (Pandey and Mahiwal 2020). Potassium is necessary for regulating photosynthesis, photosynthate translocation, enzyme activation, and minimizing excess uptake of ions such as Na and Fe in saline and flooded soils (Marschner 1995; Mengel and Kirkby 2001).

5.2.1 Potassium and Salt Tolerance

Plants have adopted numerous strategies to reduce salt stress, such as reduced Na^+ uptake, activating Na^+ into the vacuole (Hasegawa et al. 2000; Yang et al. 2012; Khan et al. 2021). K^+ maintains cell turgor and osmotic adjustment. Vacuole and the cytosol in plant cells are the two important sites of K. Cytosolic K^+ concentrations are essential for plant metabolism and are maintained at a constant level, while vacuolar K^+ concentrations may vary dramatically (Walker et al. 1996).

Intracellular K^+/Na^+ levels are key determinants of salt tolerance as Na^+ and K^+ compete for enzyme activation and protein biosynthesis, resulting in Na^+ toxicity. The cytosolic K^+/Na^+ ratio determines the metabolic competence of a cell and, ultimately, the ability of a plant to survive under saline conditions. It is only the cytosolic K^+/Na^+ ratio that has been repeatedly named as a key determinant of plant salt tolerance (Gorham et al. 1991; Gaxiola et al. 1992; Dvořak et al. 1994; Maathuis and Amtmann 1999; Cuin et al. 2003; Colmer et al. 2006). The optimal cytosolic K^+/Na^+ ratio can be maintained either by restricting Na^+ accumulation in plant tissues or by preventing K^+ loss from the cell. Volkov et al. (2003) made comparisons between *Arabidopsis* and its salt-tolerant relative *Thellungiella halophila*, and he found that the latter is capable of increasing mesophyll K^+ content under saline conditions, while *Arabidopsis* shows a "classical" decline. This suggests that mechanisms are taking place within mesophyll cells to improve ionic changes, protecting and maintaining their photosynthetic and metabolic activity under saline conditions. Recently it has been shown that improving tissue K^+/Na^+ ratios by externally applied divalent cations enables normal leaf photochemistry in plants, even under high (100 mM) salinity conditions (Shabala et al. 2005). Under saline conditions, membrane depolarization occurs that promotes uptake of Na^+ from soil and favors K^+ efflux via depolarization-activated outward-rectifying K^+ channels (Shabala 2006). On the other hand, isotonic mannitol solution causes significant membrane hyperpolarization, resulting in increased K^+ uptake (Shabala et al. 2000; Shabala and Lew 2002). K application showing an enhancement in the osmolyte accumulation protects nitrogen metabolism and reduced Na/K ratio in *Triticum aestivum* under salt stress (Ahanger and Agarwal 2017a, b), and ion homeostasis was maintained by K to regulate the osmotic balance on salt exposure (Hasanuzzaman et al. 2018).

5.2.2 Potassium and Drought Tolerance

The crops grown in arid and semiarid regions face a major issue in plant growth and crop production in soil water availability. Drought inhibits photosynthesis and ultimately decreased crop yield via ROS accumulation (Foyer et al. 2002; Oerke and Dehne 2004; Cakmak 2005; Ahmed et al. 2021) and, ultimately, leads to decrease yield of crop. Root growth and the rates of K^+ diffusion in the soil toward the roots were both reduced by drought stress. K at low concentrations can interfere the plant resistance to drought stress and absorption of K.

In order to improve stress tolerance in plants, deep rooting can be induced by placing deep K^+ fertilizer in association with other mineral nutrients such as N and P, which both have root signaling functions (Kirkby et al. 2009). Sufficient amounts of K can increase under drought stress the accumulation of dry mass in crop plants when compared to K at low concentrations under drought stress (Egilla et al. 2001). K is key element for the translocation of photoassimilates in root growth (Römheld and Kirkby 2010). The appropriate increase in K supply under K-deficient conditions promotes root growth and was found to increase the root surface area that was exposed to soil as a result of increased root water uptake (Römheld and Kirkby 2010). Plants when subjected to well-defined K nutrition improved the water retention capacity, leaf area, and dry mass under drought stress (Lindhauer 1985). Bajji et al. (2002) studied that maintenance of membrane integrity and stability under drought stress is also essential for plant drought tolerance. Moreover, maize plants and sugarcane with higher K applications showed greater adaptation to water stress (Premachandra et al. 1991; da Silva et al. 2017). An adequate K supply is necessary for increasing the drought tolerance by increasing root elongation and maintaining stability of cell membrane. Specific channel proteins known as aquaporins found in plasma and intracellular membranes maintain proper plant water relations (Heinen et al. 2009). The expression of aquaporin gene expression can be regulated under drought stress conditions (Tyerman et al. 2002; Lian et al. 2004) to help plants maintain their water balance (Tyerman et al. 2002; Galmes et al. 2007; Kaldenhoff et al. 2008) and regulates stomatal opening and under drought and adapt plants under these conditions (Hasanuzzaman et al. 2018) showing the role of K^+ in aquaporin function under drought stress.

Under drought-stressed conditions, K-treated plants experienced significant increase in the synthesis of osmolytes and significant increase in growth under water stress conditions. Plants accumulating greater K were able to counteract the water stress-induced changes by maintaining lower Na/K ratio in *Triticum aestivum* under polyethylene glycol 6000 to induce osmotic stress (Ahanger and Agarwal 2017b). Potassium application alleviated drought stress of all maize hybrids grown under field conditions. The performance of maize hybrids was maximum under potassium application at 75 kg ha^{-1} than at 50 kg ha^{-1} KCl (Ul-Allah et al. 2020).

5.2.3 Potassium and Low Temperature Stress

Cold stress is a major abiotic stress that confines plant dispersal and agricultural yield in hilly areas (Mahfoozi et al. 2006). Cold stress alters metabolic activities via oxidative stress and affects plant growth and development and thus limits crop productivity. Devi et al. (2012) studied in *Panax ginseng* that increased K^+ exposure on yield and cold tolerance and concluded that a high K^+ concentration triggers the antioxidant metabolism and enhanced the levels of ginsenoside-related secondary metabolite transcripts. Cold stress disrupts with photosynthetic processes and reduces the effectiveness of antioxidant system that induces ROS accumulation (Mittler 2002; Xiong et al. 2002; Suzuki and Mittler 2006). K increases antioxidant levels and reduced ROS production, and hence helps in improving plant survival under cold stress (Cakmak 2005; Devi et al. 2012). K-deficient plants show greater frost damage which is related to water deficiency caused by the chilling stress and interfere with uptake of water and cellular dehydration (Zhu 2001). An adequate K supply can effectively increase frost resistance (Kant and Kafkafi 2002; Römheld and Kirkby 2010). Moreover, a well-managed cytosolic K^+ concentration is also essential for enzyme activities that are involved in regulating frost resistance (Kant and Kafkafi 2002). Low-, medium-, or high-potassium condition was used, increased K nutrition in *Plantago major* increased photosynthetic efficiency, and sorbitol is a protective solute that accelerates cold acclimation (Ho et al. 2020).

5.2.4 Potassium and High Temperature Stress

When the temperature is greater than the optimum, plants suffer from high temperature stress. Extreme temperatures affect various biochemical processes and the plant metabolism, which are highly concerned with the temperature (Hasanuzzaman et al. 2013a, b). Potassium supplementation is a better option for the plants grown in extreme temperature as it regulates various physiological and metabolic processes such as photosynthesis, respiration, and nutrient homeostasis, and it enhances the tissue water capability, which helps in high temperature stress tolerance. Plant avoids high temperature stress by producing a variety of osmolytes to minimize the damage caused by the stress. Potassium behaves as an osmolyte, by maintaining stomatal conductance to prevent damage from stress. In K-deficient plants, both photosynthetic electron transport pathways and the NADPH oxidizing enzyme reaction produce ROS (Cakmak 2005). The foliar spraying of potassium orthophosphate helps in increasing the heat tolerance of wheat by preventing leaf damage, under heat stress conditions (Dias and Lidon 2010). A significant decrease in K from the chloroplast affects the rate of photosynthesis. During these stress conditions, exogenous application of K helps the plant to tolerate the heat stress by enhancing the photosynthetic ability in wheat. Also, an increase in the translocation and accumulation of photosynthates as well as the dry matter of plant is observed by foliar application of K. These factors are related to stress resistance and ultimately help to increase plant yields (Meshah 2009).

5.2.5 Potassium and Metal Toxicity/Metalloids

Metal toxicity contamination in soil is drastically increasing with time because of rapid anthropogenic activities which has produced numerous headaches in global agriculture (Hasanuzzaman and Fujita 2012). Metal/metalloid toxicity is responsible for the generation of excess ROS that the decrease the uptake of other essential nutrients disrupts the stomatal structure, changes in membrane functions, and photosynthetic inhibition, downregulating the activities of several important enzymes, the reduction of the water potential (Chibuike and Obiora 2014; Emamverdian et al. 2015; Asgher et al. 2018; Asgher et al. 2020). Application of K was effective against Cd toxicity by increasing the activity of antioxidant enzymes and solute that ultimately increased plant growth and chlorophyll a fluroscence (Siddiqui et al. 2012; Naciri et al. 2021). Increased K supply (10 mM) alleviated Zn (2 mM) and increased photosynthesis, antioxidant defense systems, and plant K(+) nutritional status. The transcript levels of KUP K^+ uptake) genes involved in K^+ acquisition, transport, and homeostasis were upregulated following under K^+ application with Zn toxicity in peach seedlings (Song et al. 2015). Table showing the role of potassium under different stresses (Table 5.1).

5.3 Potassium and Mineral Nutrient Crosstalk in Abiotic Stress Tolerance

Different nutrients play different roles in overcoming plants to various types of environmental stresses. Among all the nutrients, N, P, and K play an important role in coping various types of stresses, by bringing about some changes in plant metabolism and various physiological processes. In this section we will discuss how K and other nutrients in combination help in removing stress by adapting different strategies of tolerance.

Under drought conditions an adequate supplementation of K can apparently enhance the organic osmolyte production especially proline (Zain et al. 2014). When plants are exposed to drought stress, proline accumulation plays a highly protective role in plants, and it is involved in maintaining osmotic balance of cells (Teixeira and Pereira 2007). In several studies, it was found that K application in *Oryza sativa* (Pandey et al. 2004), *Brassica napus* (Din et al. 2011), and *Triticum aestivum* under normal and drought stress conditions improved osmolyte production for plant defense (Jatav et al. 2012). Zhang et al. (2014) also observed that in *Zea mays*, cultivars treated with K show increase in proline content under drought conditions. Potassium supplementation improves the osmotic adjustment and upgrades the plants' ability to withstand drought stress, while N absorption and utilization by plants under water stress are very critical for plant growth and productivity. Nitrogen affects carbon distribution and improves leaf growth by accumulating soluble sugars such as starch (Rufty et al. 1988). Supplementation of N as fertilizers or in other forms is associated with the water absorption ability of roots from soil. When water level inside the plant body decreases below a threshold level, it favors stomata closing which resulted in reduced transpiration and water transport through the plant. Toth et al. (2002) and Vos and Biemond (1992) reported reduction in leaf production, individual leaf area, and total leaf area under N-deficient conditions.

Phosphorus is the second most deficient plant nutrient present in low concentration in soils as compared to N and K, and is applied to plants as fertilizer. Total P

Table 5.1 Showing the role of potassium under different stresses

Plant name	Potassium concentration	Stress type	Parameters studied	Response	References
Triticum aestivum	0.2 mM	Water stress	Net photosynthesis rate	Increased photosynthesis rate is observed	Pier and Berkowitz (1987)
Tomato	310 ppm	Cd	Chlorophyll a fluorescence	Increased chlorophyll a fluorescence	Naciri et al. (2021)
Triticum aestivum	KNO_3 6 mM	Salinity stress	Radicle growth	Positive effect on root radicle	Zheng et al. (2008)
Helianthus annuus	100 kg ha^{-1}	Drought stress	Oxidative stress	Positive effect in mitigating oxidative stress	Soleimanzadeh et al. (2010)
Zea mays	KCl 50 kg ha^{-1} 75 kg ha^{-1}	Drought	Grain yield	Steady increase in grain yield	Ul-Allah et al. (2020)
Ricinus communis	KCl 0.4 mM–1 mM	Cold stress	Phloem exudate	Increase in rate of phloem exudate	Mengel and Haeder (1977)
Prunus persica	10 mM	Zn^{2+} toxicity	Antioxidant system	Promotes ROS scavenging	Song et al. (2015)

concentration in surface soils varies from 0.005% to 0.15% (Havlin et al. 2007). P deficiency is mainly correlated with leaf-growth rate (Kirschbaum and Tompkins 1990), and it affects the photosynthetic rate per unit area. During P-deficit conditions, plants accumulate starch which indicates that photosynthates cannot be used for plant growth (Fredeen et al. 1989). Pilbeam et al. (1993) reported reduced uptake rate of nitrates and its assimilation by the nitrate reductase in P-deficient environment. However, under stress conditions like drought, the application of P as fertilizer can improve plant growth (Ackerson 1985; Studer 1993; Garg et al. 2004), which is attributed due to higher stomatal conductance (Brück et al. 2000), good rate of photosynthesis (Ackerson 1985), higher cell-membrane stability, water relations (Sawwan et al. 2000), and drought tolerance.

Calcium (Ca) earlier was considered important only for cell wall structure, but since the discovery of calmodulin, it has become clear that Ca is not just a macronutrient but also a major controller of plant metabolism and development (Poovaiah and Reddy 2000; Aslam et al. 2021). Calcium is involved in minimizing the stress during injury (Palta 2000). It has been found that Ca plays a crucial role in activating the plasma membrane enzyme ATPase which is required to pump back the nutrients that were lost in cell damage to recover from drought (Palta 2000). Ca also has a role to play in freeze injury tolerance. Calmodulin, a calcium-binding protein, controls the metabolic activities of plants and increases the plant growth under drought exposure.

Zinc (Zn) is an important micronutrient essential for plant growth and development. Among micronutrients, Zn plays an important role to drought stress which reduces the net photosynthetic rate of the plants. Zn deficiency symptoms such as stunted stems and chlorotic leaves were often observed in maize plants grown in the field (Liu et al. 1993; Liu 1996). In cauliflower, a reduction in photosynthesis induced by Zn deficiency was associated with a decrease in stomatal conductance, and intercellular CO_2 concentration (Sharma et al. 1994). In another mechanism, the activity of membrane-bound NADPH oxidase is reduced which in turn decreases the generation of ROS, and reduces photooxidation damage when Zn treatment is given, while the activities of SOD, POD, and CAT are enhanced indicating that Zn lowers the ROS generation and protect cells against ROS attack under water stress (Waraich et al. 2011).

Silicon (Si) is the second most abundant element in soil after oxygen. It is present in two major forms, silica and oxides of silicon, and both types exist in crystalline and/or amorphous forms such as quartz, flint, sandstone, opal, and diatomaceous earth's silicates. In soil solution, it occurs as silicic acid at concentration ranging from 0.1 to 0.6 mM, which is twofold higher than macronutrient P (Epstein 1999). Plants absorb most of Si in mono-silicic acid form. However, it is proved to be beneficial for better plant growth and development, especially in plants of Poaceae family (Shi et al. 2005). Silicon can improve plant growth and tolerance to biotic and abiotic stresses (Epstein 1999; Neumann and Niede 2001; Liang et al. 2007; Artyszak et al. 2021). Gao et al. (2004, 2006) reported that the addition of Si improved water use efficiency by limiting leaf transpiration and the water flow rate in the xylem vessel in maize. Si could facilitate water uptake and transport in

Sorghum bicolor (L.) in drought conditions (Hattori et al. 2005, 2007). Si helps in alleviating oxidative stress by regulating the activities of antioxidant enzymes under drought in potted wheat (Gong et al. 2005). Silicon nutrition enhances the antioxidant production and reduces ROS generation which in turn reduces the photooxidative damage and maintains the integrity of chloroplast membrane and enhances the drought tolerance in plants (Waraich et al. 2011; Bhardwaj and Kapoor 2021).

Evidence shows that ROS are major enhancers of salt-induced cell damage in crop plants. In several plant species, application of NaCl, even at low concentration, regulated the activities of antioxidative enzymes, which suggests a role of salt stress in ROS formation (Comba et al. 1998; Tsugane et al. 1999). Accordingly, salt stress-induced cell damage could be prevented by overexpression of superoxide dismutase (SOD) in chloroplasts of rice plants (Tanaka et al. 1999). Zinc ions are known to be strong inhibitors of NADPH oxidase. In bean and cotton root cells, Zn deficiency caused a significant increase in activity of NADPH-dependent $O_2^{\cdot-}$ production, and a resumed supply of Zn to Zn-deficient plants for 12 or 24 h caused a distinct reduction in the activity of $O_2^{\cdot-}$-generating enzymes (Cakmak and Marschner 1988; Pinton et al. 1994). Similarly, in tobacco cell cultures, salt-induced $O_2^{\cdot-}$ generation by NADPH oxidase was strongly inhibited by Zn (Kawano et al. 2002). Keeping in view the protective roles of Zn against ROS, it can be suggested that Zn ions protect salt-stressed plants not only from uptake of toxic ions across plasma membranes but also from removing attack of ROS. Like Zn, K is too a critical nutrient which impairs with salt-induced stress in plants. Under saline conditions, low concentration of K increased the toxicity of Na^+ in plant tissue. Thus, the K^+/Na^+ ratio decreased and led to ROS formation, which affects the stomatal closure and inhibits the plant's photosynthesis activity, and it promotes oxidative damage (Abd Elgawad et al. 2016). Higher production of ROS leads to cellular membrane damage during salt stress. Programmed cell death occurs as a result of K^+ leaks from the plant cells due to the activation of K^+ efflux channels (Shabala 2009). Exogenous application of K in a salt-growing medium provides salt tolerance via reduced ROS production in *T. aestivum* (Shirazi et al. 2001), *Z. mays* (Bar-Tal and Sparks 2004), and *O. sativa* (Cha-um et al. 2010) and increased antioxidant enzyme activities in *T. aestivum* such as SOD, CAT, and POD (Zheng et al. 2008). Jan et al. (2017) studied that antioxidants metabolism was increased by applying K under salt stress thus eliminated the ROS.

Sulfur has a variety of vital functions within the plant. Sulfur-containing compounds play an important role in plant stress defense. Glutathione synthesized under salt stress is correlated with tolerance to salinity (Noctor et al. 1998; Ruiz and Blumwald 2002; Kocsy et al. 2004), and the synthesis of GSH depends upon S supply and S assimilation. Under salinity stress, increased demand of GSH biosynthesis to induce salinity tolerance can activate enzymes of sulfur assimilation, and external sulfur supply may improve salinity tolerance through meeting out the demand for GSH synthesis.

5.4 Potassium Crosstalk with Phytohormones

Whereas the correlation between the phytohormone and the micro- and macronutrients is well studied, among all macronutrients, K actively participates in hormones crosstalk and signaling. Maintaining a proper hormone level in plants indicates a competitive advantage to withstand adverse conditions. K provides cellular signaling alone or in combination with phytohormones and other signaling molecules (Hasanuzzaman et al. 2018). Figure 5.1 shows potassium crosstalk with phytohormones. Gibberellic acid improved the uptake of potassium that increased auxin, cytokinin and decreased jasmonic acid. Low potassium induce jasmonic acid accumulation and decreased auxin and cytokinin level with stunted roots, stomatal disfunction, low photosynthetic rate, and stunted growth.

5.4.1 Role of K in Auxin Signaling

In the roots of *Arabidopsis thaliana*, auxin transport system requires K^+ transporter TRH1 for normal functions in root hair development and root gravitropism (Vicente-Agullo et al. 2004). The molecular mechanism of K crosstalk with auxin is also well demonstrated, and it has been confirmed that the genes involved in auxin biosynthesis were downregulated on K supply in K-deficient roots. Recently it has become clear that K uptake through K inward channels is required for growth, and the expression of K channel genes is a major target for auxin signal transduction (Christian et al. 2006). In hypocotyl region and leaves of *A. thaliana*, the voltage-dependent inward-rectifying shaker, K channels in *A. thaliana* 1 and 2 (KAT1 and

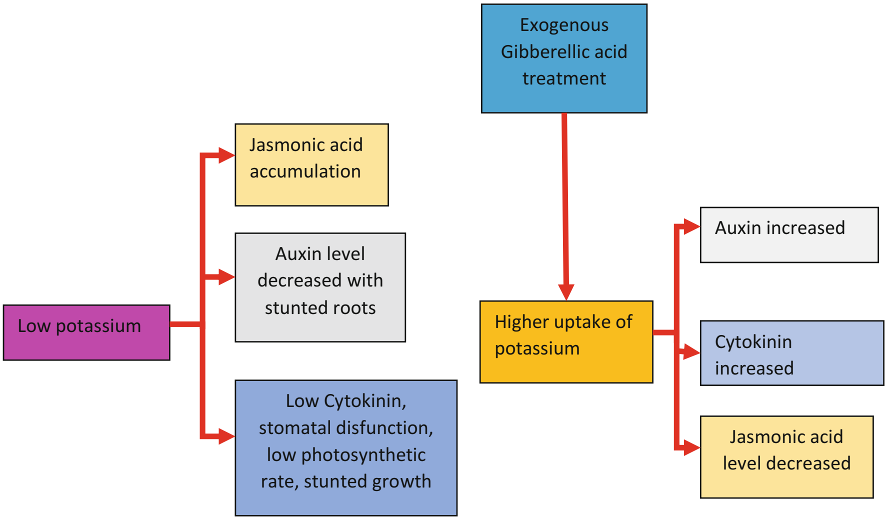

Fig. 5.1 Showing how K level crosstalk, the phytohormones, and the level of K impact plant growth

KAT2), and K transporter-like K transport 2, K uptake 2, and short hypocotyl 3 (KT2, KUP2, SHY3) are known to participate in auxin-induced cell expansion (Elumalai et al. 2002; Osakabe et al. 2013). Mutant lines for high-affinity K uptake in plants including athak5 (*Arabidopsis thaliana*) and oshak1 (*Oryza sativa*) have lesser K in tissues and show shorter roots as compared to wild-type genotypes in K scarcity conditions (Gierth et al. 2005; Qi et al. 2008). The stunted growth of roots in K-deficient plants is due to the low auxin concentration in plant tissues (Shin et al. 2007). The auxin signaling is affected by the low and high K concentrations in root apical meristem, the overexpression of genes responsible for uptake of K enhances root growth, so the auxin signaling machinery is affected by the low K stress (Shin et al. 2007). Bennett and Skoog (2002) and Waraich et al. (2011) reported that Zn influences auxin levels and increase in auxin levels due to Zn application regulates the root growth which in turn enhances drought tolerance in plants.

5.4.2 Role of K in Cytokinin Signaling

Macronutrient homeostasis had been controlled by the expression of some transporters which transport nitrate, phosphate, and sulfate, while the genes involved are regulated by cytokinin. The cytokinin level also decreases in the low K level. Literature showing that annual crops like *Zea mays* and beans reported that the exogenous application of K and cytokinin promotes stomatal opening and recovery in photosynthetic rate, depending on the plant species and dosage (Metwally et al. 1998; Rulcová and Pospíšilová 2001).

Besides this, it is also well documented that cytokinin may have a role in stomatal opening, and the turgor pressure in guard cells which is regulated by the uptake of K ions in guard cells (Incoll and Whitelam 1977). In perennial grass species "Kentucky bluegrass," it has been observed that 10μM cytokinin (6-BA) and 50 mM (KCl) K could enhance stomatal opening and photosynthetic efficiency after prolonged water-deficient conditions (Hu et al. 2013).

5.4.3 Role of K in Gibberellin Signaling

Gibberellic acid (GA) is known to regulate various developmental processes in plants starting from seed germination to fruit development, including cell and shoot elongation and a transition from bud to flowering (Davière and Achard 2013). GA plays all these functions in plant physiology with the integration of K ions and other solutes taken up by the plant through soil. Some studies show the combined role of K and GA in promoting hypocotyl elongation in light and show synergism (Guruprasad and Guruprasad 1988). In the dwarf line of *Zea mays*, exogenous application of GA increases the K content in cytoplasm and plastids. The change of ionic concentration after GA treatment is because of its involvement in a reaction sequence between the primary sites of action of GA at the membrane. Several enzymes also required for the functioning of GA in plant body which may be activated by univalent cations as cofactors at specific concentrations for that purpose only K would work better in plant cells (Evans and Sorger 1966).

5.4.4 Potassium and Abscisic Acids

There are many views from plant biologists regarding the hormonal control of stomatal behavior and gaseous exchange in plants. A few investigations from the past help us to investigate the role of abscisic acid as an inhibitor of stomatal opening in epidermal cells in intact leaves (Jones and Mansfield 1970; Mittelheuser and Van Steveninck 1971). The mechanism behind the opening and closing of stomata was not fully known; research has shown the accumulation of nonvalent cations K and sodium likely to play a major part in the stomatal movement in light (Fischer and Hsiao 1968; Sawhney and Zelitch 1969). Drought stress reduces yields of crop by triggering ABA and premature leaf senescence. The barley genotypes with a high K nutritional status in the flag leaf show superior drought tolerance by promoting ABA degradation. Flag leaf K concentration may thus represent a key trait for the selection of drought-tolerant genotypes (Hosseini et al. 2016)

5.4.5 Potassium Crosstalk with Jasmonic Acid

The significance of K in jasmonic acid signaling has been studied in the model system *Arabidopsis thaliana* with K-deficient/K-sufficient conditions; results obtained from experiments show that the K-starved plants are rich in phytohormone jasmonic acids, hydroxy-12-oxo-octadecadienoic acids (HODs), and 12-oxo-phytodienoic acid (OPDA), while the K-sufficient plants reported with low jasmonic acid content. K-deficient plants also resemble the one who has been attacked by herbivory in jasmonic acid content and the level of glucosinolate (Troufflard et al. 2010). Jasmonic acid also plays a role in the regulation of leaf senescence (He et al. 2002). And the leaf senescence is a slow process comprised of environmental cues (drought, salinity, heat, etc.) and mineral deficiencies such as nitrogen, K, and phosphorus. These nutrients need to be accumulated to sink organs before senescence (Quirino et al. 2000). Therefore, the previous studies have shown that the jasmonic acid enhances the leaf senescence at the transcriptional level by activation and upregulation of senescence-associated genes (Parthier 1990). The genes involved in the senescence are SAGs. Expression pattern of SAG genes (SAG12 and SAG13) in *A. thaliana* is induced by the deficiency of K in plants, while the jasmonic acid inhibitors abolished the expression of SAG genes by K deficiency (Cao et al. 2006).

Ethylene, which is another important plant hormone, assists in the progression of root morphology and stimulates ROS biosynthesis to tolerate a low K condition in Arabidopsis. Ethylene signaling is a component of the plant’s response to low potassium that stimulates the production of reactive oxygen species and is important for changes in root morphology and whole plant tolerance to low potassium conditions (Jung et al. 2009). Exogenously applied K and naphthaleneacetic acid (NAA) can interact significantly to increase the growth and yield of *V. radiata* (Hepper Doss et al. 2013). The grain yield and net return were recorded with N at 120 and K at 70 kg/ha in combination with GA_3 at 2.0 g/10 l (Kumar and Dawson 2013), and by applying K and SA to olive trees under salinity, all growth, yield, and fruits' physical and chemical properties, total chlorophyll, and proline contents in leaf and leaf nutrient uptake increased by increasing application of SA and potassium nitrate either separately or in combinations. The combination of the two treatments was the most effective (Abd-El-Rhman and Attia 2016).

5.5 Conclusion

Abiotic stress adversely affects plant growth and productivity and leads to the production of increased ROS that leads to oxidative stress. In order to avert this stress, numerous regulators such as phytohormones and potassium are applied. Potassium is added to soil as fertilizer and is generally added together with nitrogen and phosphorus. Potassium is an important macronutrient in plants and occurs as the cation K^+ involved in the regulation of the osmotic potential of plant cells. It has many effects on enzyme activation, protein synthesis, photosynthesis, stomatal movement, and water relation. Plant growth regulators are employed to minimize the ill effect of stress. The current review is an attempt to study the synergistic role of potassium and phytohormones and mineral elements and their crosstalk in reducing the stress conditions and making the plants feel better. These types of interactions could be helpful in nutrient uptake and also promote transport and utilization of nutrient and in reversing the ill effect of stress.

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Potassium (K^+) Regulation by Phytohormones Under Abiotic Stress

6

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Abstract

Potassium being the essential macronutrient is prerequisite in all the vital physiological and biochemical processes in plants. Metabolic machinery of plants mainly depends on the regulation of K^+ ion concentration which invariably affects the yield and quality of food crops. Intracellular K^+ concentration, uptake, efflux and transportation are typically regulated by the K^+ ion transporters and selective ion channels present on the vacuoles and plasma membranes. Under abiotic stress conditions, the membrane charge fluctuation disturbs the intracellular K^+ homeostasis. Among the plethora of signalling molecules, K^+ has emerged as a key component of the signal transduction pathway under hostile environmental conditions. Recent studies reveal that K^+ enhances the functioning of antioxidants to curtail the oxidative stressors in plants. K^+ also provides some signalling assistance in associations with the phytohormones. Plant growth regulators (PGRs) are well known to sense the K^+ deficiency in plants and further trigger the complex signalling networks between PGRs and other signalling molecules. This chapter focuses on the emerging trends in phytohormone-assisted

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K^+ regulation, their uptake, transportation, relocalization and molecular aspects under abiotic stress condition.

6.1 Introduction

Abiotic stressors are continuously challenging our cultivable crops from their germination up to growth stages and till the completion of their life cycles. Thus, in order to improve the food production, plants should adopt to be more resilient to these abiotic factors such as drought, waterlogging, salinity, temperature, etc. These stressor molecules disrupt the physiological and biochemical processes in plants which lead to low yields (Hasanuzzaman et al. 2013a). These stress factors either work independently or in a synergistic manner. One factor can promote the activity and duration of other associated factor, i.e. high temperature normally leads to drought, but on the other hand, high temperature and more intense light could favour the simultaneous occurrence of salinity and drought too (Jedmowski et al. 2015). Thus, improved agricultural practices should be adopted to counter these environmental challenges. One among them is the use of fertilizers in the fields to promote K^+ ion availability in field crops.

Potassium (K^+) among the most abundant cations in plant cells carries out various fundamental processes in plant system (Clarkson and Hanson 1980; Wang and Wu 2017). They are well known to operate pivotal physiological roles in the growth and development of crop plants like osmotic regulation, cell expansion, turgor pressure, pH homeostasis, regulation of membrane potential, etc. (Zörb et al. 2014; Isayenkov and Maathuis 2019). K^+ absorption from soil occurs through root epidermal cells which further enter the cortical cells and cytoplasm. K^+ is finally stored as K^+ pool inside the vacuoles as repository for future use under stress periods or starvation (Martinoia et al. 2012; Ahmad and Maathuis 2014). It is well observed that plant roots possess two K^+ accumulating and uptaken systems: (a) One among them is high-affinity transport system (HATS) which involves H^+/K^+ symporters at 0.25 mM low levels of external (K^+) concentrations, and (b) the second one is low-affinity system (LAS) works through K^+ ion channels at >0.50 mM high levels of external K^+ ions (Epstein et al. 1963; Nestrerenko et al. 2021).

Plant photosynthetic machinery requires K^+ as a key element after nitrogen (N). It contributes to about 10% of the plant's dry matter. Cytoplasmic K^+ ions trigger the activation of multiple enzymes required for the primary metabolic processes in plants. However, K^+-deficient plant cells observe the degradation of plasma membrane as well as of the chlorophyll pigments (Cakmak 2005). Therefore, reduced photosynthetic activities like CO_2 fixation further limit the mobilization and transportation of assimilates in the plant tissues (Waraich et al. 2012). Also, the K^+ deprivation in plants leads to interveinal chlorosis, reduced root growth, reduced leaf area and curling of leaf tips as observed (Hu et al. 2017).

Potassium plays an ameliorative role in plants through various regulatory pathways under multiple stresses like drought, temperature and waterlogging and under high light intensity (Zörb et al. 2014). K^+ associated regulatory mechanisms amplifies the activity of certain reactive oxygen species (ROS) degrading enzymes also they promote the activities of ATP synthases (adenosine triphosphate synthase). K^+ levels check the activities of membrane-bound H^+-ATPase pumps (Hasanuzzaman et al. 2018). With high levels of K^+ ions inside the plant cells, lowering of ROS molecules is observed under high temperature and drought stress. Also, they safeguard the photosynthetic electron transport chains (ETC) by lowering the nicotinamide adenine dinucleotide phosphate (NADPH) oxidase activity which further promotes the lowering in ROS molecules (Waraich et al. 2012).

From recent studies researchers have found that K^+ ions and phytohormones undergo specific interactions which involve various biochemical activities to surpass the unfavourable environmental conditions (Wang et al. 2020). A well-developed regulatory network between abscisic acid (ABA) and K^+ is found to occur during stomatal regulation under drought stress (Qi et al. 2018). K^+ is much explored as a plant nutrient, but data is lacking about its biological activities throughout the plant kingdom. However, a series of K^+ and phytohormone (ABA, cytokinin (CK), brassinosteroid (BR), ethylene (ET), indole acetic acid (IAA)) interactions and crosstalks are yet to be discovered with its molecular mechanisms under abiotic stress conditions.

6.2 Biological Functions of Potassium (K^+) in Plants (Seed Germination, Growth, Reproductive Development, Photosynthesis and Nutrient Balance)

The various macro- and micronutrients are the primary requirements for plants to complete the life cycle from germination of seed to the production of seeds (Wang et al. 2013). Along with nitrogen and phosphorus, K^+ is an essential macronutrient required for different biochemical processes like protein synthesis, carbohydrate metabolism, enzyme activation, ion homeostasis, regulation of cation/anion balance in photosynthesis, energy transfer and other different processes. The concentration of K in cytoplasm is found to be around 100 mM which is relatively high and stable, but the availability in soil is limited as most of the K is the part of mineral composition which is not readily available to plants. Different transporters and channels present in roots especially AKT1 and K/H symporter come into play and cope the low K^+ condition. Waraich et al. (2012) reported the ameliorative role of K^+ in plants under different abiotic stress conditions like temperature, metal, salinity, drought, high light intensity, etc.; under K^+-deficient condition, plant develops certain morphological and physiological abnormalities such as yellowing of leaf margins, stunted growth, lodging, poor root system and reduction in yield. In addition, K^+-deficient plants become more vulnerable to pest and disease infestation. In plants the photosynthetic electron transport activity is found to be well maintaining under K^+ upregulation whereas limits the nicotinamide adenine dinucleotide oxidase activity which further decreases the rate of generation of ROS in plants. Reduction in rate of CO_2 fixation and utilization and transport of photosynthetic assimilates is found to be associated with K^+ deficiency. Chlorophyll and membrane degradations are favoured under K^+-deficient conditions; further plant becomes more sensitive to light and shows symptoms like chlorosis and necrosis (Cakmak 2005).

6.2.1 Seed Germination

The role of K^+ salts in seed germination and emergence has been studied extensively. Potassium nitrate, potassium chloride and dipotassium hydrogen phosphate are some of the common forms of K^+ salt used in seed priming (Copeland and McDonald 2001; Mohammadi 2009). K^+ plays an important role in initiation of germination by promoting the imbibition and other related physiological processes. In cotton, use of KNO_3 manifests good result of germination as a priming agent. Similarly, osmopriming in rice with KNO_3 shows prominent result of percentage and rate of germination as well as other morphological features (Esmeili and Heidarzade 2012). These above findings provide ample evidence as a regulatory role of K^+ in seed germination.

6.2.2 Growth and Development

Potassium is an indispensable nutrient and plays an important role in growth and development. Excess or deficient levels of K^+ interfere with normal growth of plant. Therefore, it is important for plants to maintain the level of K^+ in growth medium as well as cellular level (Wang et al. 2013). Thus, for this reason application of K^+ fertilizers becomes crucial for plant growth. In mung bean, the application of different levels of K revealed maximum plant height at 90 kg SOP ha^{-1} and minimum at 0 kg ha^{-1} (Hussain et al. 2011). Similar results were obtained with potato plants. The different parameters of growth tend to increase with the increase in K^+ doses up to 150 kg ha^{-1} and minimum recorded at 0 kg ha^{-1} (Zelelew et al. 2016). Reduction in growth due to deficiency of K^+ at vegetative phase has also been reported in cotton (Gerardeaux et al. 2010). Moreover, reduction in root yield and biomass production in these cultivars of sweet potato grown under K-deficient soil has been reported (Tang et al. 2015). In leguminous plants, growth is linked with nodulation and level of K^+ ions and its ratio to N and P prominently govern the nodulation process. Plant growth and nodulation in legumes are related to one another, and ratio of different nutrients especially N, P and K determines its accomplishment (Divito and Sadras 2014).

6.2.3 Photosynthesis

Potassium has dramatic effect on rate of photosynthesis and translocation and metabolism of carbohydrates. K^+-deficient plant exhibited reduction in both size and number of leaves which in turn directly affect photosynthetic rate per unit leaf area and lead to subsequent reduction of photosynthates required for plant growth (Pettigrew 2008). K^+ controls the process of photosynthesis by interfering with sunlight requirement and leaf area exposed below its optimal level. K^+ is known to regulate stomatal aperture which is a key factor in photosynthesis operation. It becomes crucial to have a certain amount of K to obtain moderate rate of photosynthesis (Bednarz et al. 1998). Reduction in stomatal conductance coupled with lowering of RuBisCO activity under K^+ deficient has been noticed to decrease the rate of photosynthesis in plants. The utilization and export of photoassimilates are directly proportional to the rate of photosynthesis. Plant supplied with ample amount of K^+ is found to upsurge the sucrose level in leaves by several times (Zhao et al. 2001). Moreover, K^+ deficiency is found to elevate the rate of ROS generation which may cause photooxidative damage. This enhanced rate of ROS is triggered by low K^+ level through limiting the rate of CO_2 fixation and H_2O vapour removal from intercellular space (Waraich et al. 2012). K^+ helps in the photosynthesis process by activation of ATP synthase enzyme by regulating the amount of CO_2 entry and H_2O vapour removal from the intercellular space. The amount of photosynthate production is the outcome of how many molecules of CO_2 entered the intercellular space. Evidence suggested that K^+ assist in photosynthesis by activating ATP synthase whose activity is seen best at optimal K^+ level (Shingles and McCarty 1994).

The elucidated role of three K^+ efflux antiporters AtKEA1/2/3, located in the inner membrane of chloroplast and thylakoid membrane, in chloroplast development and photosynthesis and the subsequent damage upon mutation in AtKEA1/2/3 resulting in stunted growth strongly correlates with the role of K^+ (Kunz et al. 2014). Furthermore, the role of AtKEA1 and AtKEA2 in chloroplast development and AtKEA3 which is an H^+/K^+ antiporter that regulates the proton motive force by facilitating H^+ efflux in exchange of K^+ from thylakoid lumen to the stroma in turn regulate the process of photosynthesis (Wang et al. 2017).

6.2.4 Nutrient Balance

Potassium is a key regulator of nitrate reductase (NR) and starch synthetase which produces balanced protein and carbohydrate (Fageria 2016). In the absence of sufficient K^+ level even under abundant N supply, the different constituents of proteins such as amino acids, amides and NO_3 tend to accumulate in the cell resulting in low protein formation. K^+ imbalance is found to interrupt the translocation of hormones; enzymes; cations such Ca^{2+}, Mg^{2+}, NO_3 and PO43; as well as source-sink relationship (Coskun et al. 2017). The role of K^+ has also been seen in transport through xylem and phloem. Sterility in female flower part is found to be linked with Fe which has synergistic relationship with K^+ (Tewari et al. 2013). Iron (Fe) uptake has reduced when the plant faces Mo/K^+ scarcity, plant undergo sterility condition at the reproductive phase, while as upsurge in nodulation has reported with Mo application, results in further seed yields in lentils (Omer et al. 2016). Moreover, exogenous application of K^+ makes plant resistant to abiotic stresses, limits the uptake of harmful nutrients and improves the yields (Ganie et al. 2017).

6.2.5 Reproductive Balance

Potassium has an immense role from flowering to seed development. Elevated rate of pollen germination and pollen tube has been observed under exogenous application of K^+ in Arabidopsis (Fan et al. 2001). In some plants a link between yield and reproductive-vegetative ratio has been derived which shows higher vegetative growth over reproductive if the ratio of RVR is low and consequently reduction in yield observed (Makhdum et al. 2007). Delay in phenological development due to lowering of K^+ has been reported (Amanullah 2016). Many experimental works using splitting K^+ application showed that delay in phenological development such as delay in flowering and physiological maturity can be reversed by applying appropriate concentration of K^+. The application of basal dose of 90 kg ha^{-1} was found to improve the physiological maturity (Sadiq and Jan 2001). Similar results of physiological development in maize plant were observed (Asif and Anwar 2007). A positive relationship between K^+ and grain size and number has clearly indicated the role of K^+ in photosynthesis. In *Triticum aestivum* L., application of appropriate K^+ concentration has tremendous rise in rate of photosynthesis during the grain filling stage and helps in transferring food material to the developed grains. It has also a role in maximizing grain number and minimizes sterile grain. In *Oryza sativa*, percentage of sterility was reduced from 30.33% without K^+ to 22.60% in 100 kg K^+ ha^{-1} treated plants (Islam and Muttaleb 2016; Zou et al. 2007).

6.3 Potassium (K^+) Sensing, Transport and Assimilation in Plants

Potassium is among the most crucial macronutrients required by plants that helps in the regulation of various processes like membrane polarity, activation of enzymes, loading of sugars in the phloem and ion homeostasis (Adams Shin 2014; Dreyer 2014). Furthermore, various biological phenomena like photorespiration, photosynthesis and cell growth also depend on the availability of K^+ (Pettigrew 2008; Gattward et al. 2012; Pilon-Smits et al. 2009). Thus, for the optimal quality and yield of crops, the sufficient availability of K^+ is an important factor. So, to facilitate the uptake of K ions from external conditions and their transport to different tissues, various proteins, known as transporters or channels, are available on the cell membrane. To maintain the sufficient level of K^+, plants sense the availability of ions in their roots and switch on the machineries responsible for the uptake of ions. Various sensors and transporters involved in the uptake of K^+ ions remain unknown. Based on the K uptake capability, plants possess two K^+ uptake systems. One of them is a low-affinity K^+ uptake system that works under K^+-rich external conditions, and the other one is high-affinity K^+ uptake system (channels) that gets activated only under K^+ scarce external conditions.

Advancement in the molecular technologies has resulted in the identification of these K uptake channels in different species of plants. In Arabidopsis, 75 genes that are responsible for encoding proteins involved in uptake and transport of K^+ ions have been identified. Further, these genes can be classified into seven types, viz. high K transporters/HKT (1 gene), putative K^+/H^+ antiporters (6 genes), 2-pore K^+ channels like cyclic nucleotide-gated channel (CNGC) (6 genes), shaker-type K^+ channels (9 genes), KUP/HAK/KT transporters (13 genes) and glutamate receptors (Anschütz et al. 2014). The shaker-type transporters are further categorized into three types, viz. inward-rectifying, outward-rectifying and weakly rectifying channels. Inward-rectifying transporters are involved in low-affinity uptake process and get activated upon hyperpolarization of membrane. The inward-rectifying shaker receptors are expressed in the plasma membranes of root cells. These shaker-type receptors include AKT1 (ARABIDOPSIS K^+ TRANSPORTER1) in Arabidopsis, VvK1.1 in grapevine, LKT1 in tomato, OsAKT1 in rice and HvAKT1 in barley (Ros et al. 1999; Hartje et al. 2000; Fuchs et al. 2005; Boscari et al. 2009; Cuéllar et al. 2010). The other category is outward-rectifying transporters, which get activated after depolarization of membrane and are involved in intercellular or long-distance K^+ transport, and the last category is weakly rectifying transporters that perform dual function of influx and efflux (Wang et al. 2013). All these ion channels work in collaboration with other transporters and then respond to variations in the level of conductivity of K^+ ions (Very and Sentenac 2003).

For the growth of plant, K^+ uptake by plant root from the external source is regulated by two high-affinity transporter proteins HAK5 and AKT1; both these proteins have been found in the root of rice and *Arabidopsis*. In rice, Os-AKT1-mediated uptake of K^+ ion is regulated by two components, Os-CBL1 (calcineurin B-like protein 1) and CIPK23 (CBL-interacting protein kinase 23) (Jeanguenin et al. 2011; Wang et al. 2010). Similarly, for long-distance transport of K^+ ions, the outward-rectifying channels mediate the transport from stellar to the xylem. It has been proven experimentally also that a mutant lacking the SKOR (stellar outward rectifying) channel has reduced content of K^+ ion in the xylem sap. Moreover, the opening and closing of stomata also depends on the concentration of K ions in the guard cells. In guard cells, inward-rectifying channels, KAT1 and KAT2, mediate the uptake of K^+, and GORK (guard cell's outer rectifying K^+) channel mediates the release of K^+ ions from guard cells, ultimately leading to stomatal closure. Another channel NCC (non-selective cation channels) also helps in transfer of ions to the xylem sap. Furthermore, the influx or efflux of K^+ ions in tonoplast is facilitated by TPK1, TPK2, TPK3 and TPK5 (voltage-dependent K^+ channels) and Na^+ and K^+/H^+ antiporters like NHX1 and NHX2 (Bassil et al. 2011; Barragán et al. 2012) (Fig. 6.1).

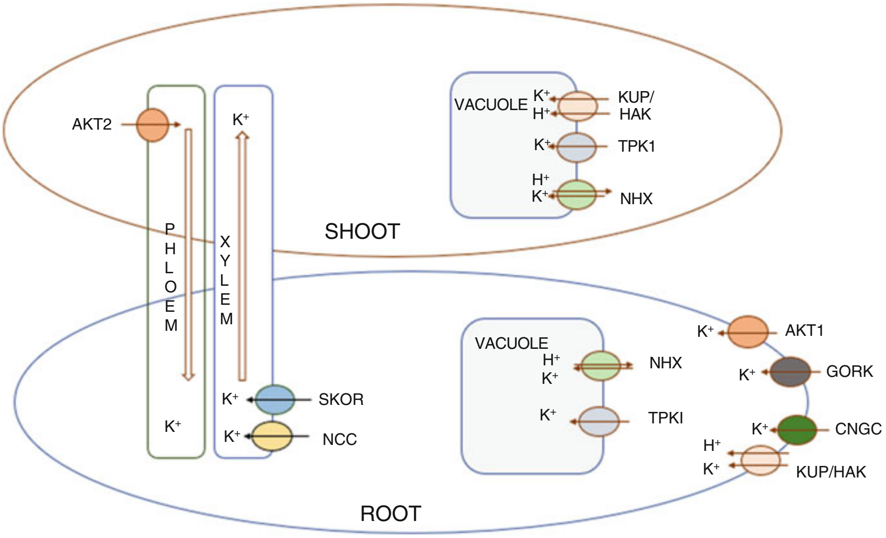

Fig. 6.1 Model depicting the uptake, transport and assimilation of K^+ from the external environment by plants with the help of various channels/transporters (modification after Hasanuzzaman et al. 2018)

6.4 Potassium (K^+) Transporters and Associated Mechanisms of Transport and Signalling

Out of the number of ions present in the plant cells, K^+ is one of the abundant ions. Its function largely revolves around keeping balance of electrical charge and sugar and nitrate transport, thereby helping in maintaining osmotic homeostasis, and also aids in activating enzymes and stabilizing proteins (Li et al. 2018). Therefore, a K^+-rich environment in the cells becomes highly essential for the proper functioning of several pathways. It has also been postulated that K^+ is also abundantly present in the earth's crust, but bioavailability for plants from soil solution is difficult because they are taken up only in the ionic forms by the plant roots (Grabov 2007). Hence, even though K has high concentrations in the bulk soil, its actual concentration at the root surface is very low (Grabov 2007). Hence, to fulfil the requirement, plants have a well-defined mechanism to acquire K from the soil and even the concentration gradients (Grabov 2007).

Initial studies have revealed that the plants have developed two mechanisms for the uptake of K in response to its variable concentrations in the soil. When the concentration of K in the external environment is high (>1 mM), the low-affinity transport system comes into play, while for low external K concentration, high-affinity transport system becomes active. For proper functioning, a concentration of K^+ has to be maintained between 100 and 150 mM in the cytosol, and it has been postulated that in natural ecosystems, soil solution K^+ concentration varies between

0.01 and 1 mM (White 2013; Li et al. 2018). Therefore, the major mechanism for K^+ acquisition adopted by plant roots is high-affinity transport system. However, for mobilization of K^+ ions inside the plant cells, both high-affinity and low-affinity transport systems may contribute (Li et al. 2018). Once taken up by the root system, its ions are translocated by transporters to cells of plant organs. Hence, both channels and transporters function in coherence to maintain the K^+ homeostasis inside the plant system. Experimental evidences have suggested that channels form a part of low-affinity transport system and the transporters are a part of high-affinity transport system (Pandey and Mahiwal 2020).

6.4.1 Transporters Associated with Root System (K^+ Sensing and Influx from Soil)

Several transport protein families are involved in providing K^+ nutrition to the plants. A voltage-gated channel ARABIDOPSISK^+TRANSPORTER1 (AKT1) is a shaker-type inward-rectifying K^+ transporter which is postulated to be involved in the key step of K^+ sensing (Adams and Shin 2014). These are involved in low-affinity K^+ uptake when the soil environment has sufficient K concentrations (Shin et al. 2017). These transporters are chiefly expressed in plasma membranes of the root cells in the outermost tissues (Daram et al. 1997; Hirsch et al. 1998; Ros et al. 1999; Spalding et al. 1999). The same family of transporters has also been reported in other plants such as rice (OsAKT1), barley (HvAKT1), tomato (LKT1) and grapevine (VvKT1) (Hartje et al. 2000; Fuchs et al. 2005; Boscari et al. 2009; Cuéllar et al. 2010). The AKT1 has been known to be regulated by CALCINEURIN B-LIKE PROTEINs (CBLs)-CBL-INTERACTING PROTEIN KINASE 23 (CIPK23) complexes (Wang and Wu 2013). It has been reported in studies that phosphorylation by CIPK23 is the key step which activates AKT1 and further it is able to form complexes with CBLs such as CBL1, CBL9 and CBL10 (Adams and Shin 2014). The deactivation of AKT1 occurs when AIP1 and AIP1H, the members of protein phosphatase 2C (PP2C) family, interact with CBL-CIPKs and cause inhibition of phosphorylation (Lan et al. 2011). The same study also reported that CBLs have the ability to interact with PP2Cs and inactivate them, and in turn activate AKT1.

After the K ions are sensed in the soil environment, the specific transporters present in the cells of the root surface are expressed to take up K ions. The most common transporter involved in K^+ uptake is suggested to be KT/KUP/HAK-type transporter (Adams and Shin 2014). These transporters present in plants are H^+:K^+ symporters which are high-affinity (cluster I) and/or low-affinity (cluster II) transporters (Grabov 2007). These were initially reported in barley (HvHAK1) where their function was identified as high-affinity K^+ transporters as their expression was induced in K^+ deficiency (Santa-María et al. 1997). Higher plants have been reported to have more members of the KT/KUP/HAK transporter gene family such as in *Arabidopsis*, 13 members have been reported, while in rice 17 members were reported (Rubio et al. 2000; Banuelos et al. 2002; Ahn et al. 2004; Adams and Shin 2014). The HAK5 transporters in Arabidopsis, rice and barley have been chiefly found to be localized in plasma membrane (Rubio et al. 2000; Banuelos et al. 2002; Gierth et al. 2005). As demonstrated in barley, the HIGH-AFFINITY K^+ TRANSPORTER5 (AtHAK5) in *Arabidopsis* was also induced in K^+ deficiency conditions leading to the uptake of K ions (Shin et al. 2017). Additionally, it has also been reported that AtHAK5 also gets induced with the deficiency of nitrogen and phosphorus, but the actual activation of the channel requires signal from low levels of K ions (Rubio et al. 2014). It has also been found that ammonium ions play a role in inhibition of HAK5 expression (Qi et al. 2008). The studies also indicate towards the post-transcriptional regulation of these high-affinity transporters (Shin et al. 2017). Interestingly, CIPK23, which is CBL-interacting kinase, has been shown to activate AtHAK5 in *Arabidopsis* and DmHAK5 in *Dionaea muscipula* (Shin et al. 2017). Apart from the above-mentioned high-affinity transporters, KUP2, KUP3 and KUP4 from *Arabidopsis* and HvHAK2 from barley were identified as low-affinity (cluster II) transporters, while KUP1 from *Arabidopsis* was identified as dual-affinity transporter (Quintero and Blatt 1997; Kim et al. 1998; Rubio et al. 2000; Ashley et al. 2006).

6.4.2 Transporters Associated with Leaves or Shoot System (K^+ and Long-Distance Transport)

After entering the plant system through roots, the K ions need to be translocated to various plant parts through the xylem. A type of shaker-type K^+ channels reported in *Arabidopsis* is STELAR K^+ OUTWARD RECTIFIER (AtSKOR) which plays a major role in long-distance transport inside the plants (Liu et al. 2006). These transporters are actively involved in distribution of K ions from roots to the shoots which also marks the first step in long-distance transport (Adams and Shin 2014; Shin et al. 2017). The studies have suggested that the C-terminal non-transmembrane region of SKOR plays a key role in intracellular K^+ sensing (Liu et al. 2006). These transporters were found to be negatively affected by ABA which indicates that water stress leads to lower K^+ ion transport within the plant system (Gaymard et al. 1998). After the K ions enter the xylem cells, they have to undergo efflux so that they are translocated into the xylem sap. For this step, plants show the presence of K^+ EFFLUX ANTIPORTERs (KEAs) which are H^+/K^+ antiporters (Yao et al. 1997; Mäser et al. 2001). In *Arabidopsis* however, AtKEA2 has been reported to be involved in maintaining cation and pH homeostasis in chloroplasts (Aranda-Sicilia et al. 2012).

Phloem loading of K ions is an imperative step and also requires specific transporters. A shaker-type inward-rectifying channel, KAT2, is associated with phloem loading (Adams and Shin 2014). In *Arabidopsis*, AKT2/3 and AtKAT2 both were found to accomplish phloem loading (Shin et al. 2017). The former channel, AKT2/3, belongs to the category of weakly voltage gated K^+ channels and is suggested to be regulated by Ca ions and extracellular protons (Hoth et al.

2001; Deeken et al. 2002; Ivashikina et al. 2005). Additionally, it has also been suggested that this transporter carries out phloem loading by causing the modification in phloem potential (Deeken et al. 2002). Along with phloem loading, AKT2/3 is also reported to function as K^+ efflux channel. For phloem loading and long-distance transport, these channels were observed to work in coordination with ABA-regulated channels and control K^+ current and membrane potential (Chérel et al. 2002). KAT2, on the other hand, has been found to be induced by the action of auxin and aids in maintaining the K^+ homeostasis inside the phloem (Philippar et al. 2004).

The long-distance transport of K^+ culminates when these ions reach the cells. However, for maintaining the appropriate concentrations inside the cells, influx and efflux constantly occur in and out of the vacuoles (Adams and Shin 2014). The tonoplast membrane of the vacuole possesses the NHX1 and NHX2 K^+/H^+ antiporters. These channels similarly function for Na^+ sequestration and thus serve as antiporters for Na^+ and also depend on Na^+ concentration (Venema et al. 2002; Rodríguez-Rosales et al. 2009; Barragán et al. 2012). Another antiporter, NHX3, is also reported to be present both in vacuolar membrane and endoplasmic reticulum and regulates K^+ deprivation tolerance (Liu and Xie 2010). Another efflux channels, TANDEM-PORE K^+ channels (TPK), have been found to participate in vacuolar K^+ movement (Shin et al. 2017). In *Arabidopsis*, AtTPK1 is regulated by Ca^{2+} and works in voltage-independent manner (Adams and Shin 2014). The functioning of stomata in terms of osmotic levels leading to opening and closing of guard cells is chiefly driven by K^+ levels. Studies have demonstrated that when H^+-ATPase gets activated, it causes the hyperpolarization of the membranes. This results in the activation of KAT1 and KAT2 which are inward-rectifying channels, thereby aiding in K^+ influx and ultimately causing stomatal opening. Conversely, when H^+-ATPase is inhibited, it causes depolarization of membrane which further leads to activation of GUARD CELL OUTWARD RECTIFIER K^+ (GORK), which is an outward-rectifying K^+ channel. As a result, K^+ efflux occurs and stomata close (Ache et al. 2000; Pilot et al. 2001; Schroeder et al. 2001; Lebaudy et al. 2010). It has been proven in studies that KAT1 is not affected by concentrations of K^+ in extracellular matrix; however, its N-terminus is sensitive to voltage changes (Marten et al. 1996; Marten and Hoshi 1998). KAT2 is responsible for stomatal opening and both KAT1 and KAT2 for a heteromer and form an inward K^+ channel (Pilot et al. 2001; Lebaudy et al. 2010). For efflux of K^+ ions from guard cells, ABA has the ability to depolarize the cell membrane of guard cells, and induce the expression of GORK (Ache et al. 2000; Becker et al. 2003).

6.5 Potassium Homeostasis

Potassium plays a very important role in influencing the production of crop and thus maintains the stability of the ecosystem. Due to leaching and runoff, K^+ is removed from the upper layers of soil, thus causing K^+ deficiency, and because of this deficiency, plant growth and productivity is decreased (Srivastava et al. 2020).

When there is K^+ deficiency, it is first of all detected by the epidermal cells and the root hairs which results in the initiation of series in plants (Schachtman and Shin 2007). The first response that occurs after K^+ deficiency is the hyperpolarization of root cell membrane along with extracellular acidification and extrusion of H^+ ions. These changes are due to increased activity of H^+-ATPases located at the plasma membrane which are responsible for pumping out of the H^+ ions from the cytoplasm to the apoplast (Wang and Wu 2010).

Potassium deficiency also leads to elevation in the level of Ca^{2+} ions which regulates the downstream signalling through CBL-CIPK complexes (Pandey et al. 2014). This complex has been well explained in *Arabidopsis* CBL1/9 (calcineurin B-like proteins) interaction with CIPK23 (CBL-interacting protein kinases) and targets the root plasma membrane for the phosphorylation of AKT1 (Arabidopsis K^+ transporter 1). The phosphorylated AKT1 helps in enhancing the uptake of K^+ activity (Xu et al. 2006). A type 2C phosphatase (AP2C1) has been found recently as an interactor of CIPK9. In *Arabidopsis* AP2C1 causes the dephosphorylation of CIPK9 which negatively regulates its activity during the K^+ deficiency (Singh et al. 2018). According to the reports of the Yadav et al. (2018), CIPK9 forms a complex with CBL2/CBL3 at the tonoplast that helps in the activation of an unknown K^+ transporter which is located in the tonoplast. This unknown transporter helps in the uptake of K^+ ions from vacuole to the cytoplasm.

Reactive oxygen species in similar manner as Ca^{2+} is also a regulator for K^+ uptake under deficit condition (Buet et al. 2019). A rare cold-inducible gene 3 (RCI3) is involved in the production of ROS in response to K^+ deficiency. ROS produced helps in the enhancement of Ca^{2+} levels by activating Ca^{2+}-permeable channels (Demidchik 2018). Also, ROS helps in the regulation of a high-affinity K^+ transporter gene (AtHAK5) expression that helps in the uptake of K^+ into the cytoplasm of the cell (Kim et al. 2012). The whole mechanism involved in the K^+ homeostasis is shown in Fig. 6.2.

The effect of K^+ deficiency can also be seen on the movement of guard cells and the opening and closing of the stomata. K^+ deficiency again causes the hyperpolarization of plasma membrane through the H^+-ATPases which are activated during the deficiency of K^+. This hyperpolarization regulates the K^+ uptake and leads to opening of stomata (Jezek and Blatt 2017). In contrast, guard cell outward rectifier K^+ (GORK) activation leads to depolarization of plasma membrane and is thus responsible for closing of stomata (Lebaudy et al. 2010). Similar to K^+, ROS also regulates the opening and closing of stomata (Singh et al. 2017). It has been reported by Drerup et al. (2013) that CIPk26 targets the NADPH oxidase on the plasma membrane that regulates the production of ROS and thus the production of ROS elevates the level of Ca^{2+}. Elevation in the level of Ca^{2+} activates GORK, CIPK11 activates SLAC1 and CIPK23 activates AKT1, and thus these transporters regulate the uptake of K^+ ions (Saito and Uozumi 2019).

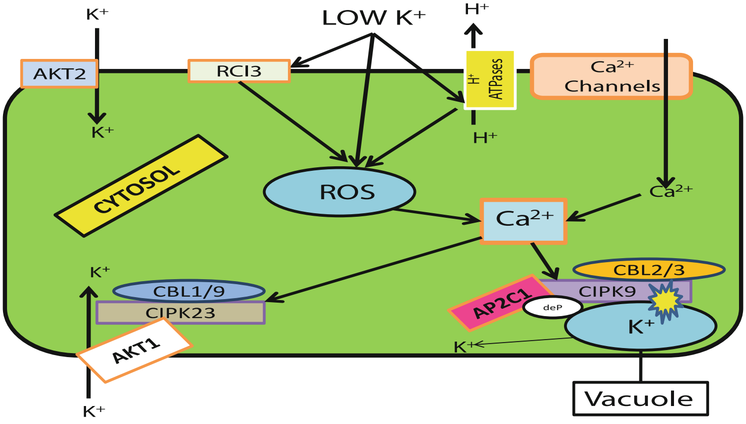

Fig. 6.2 Representation of mechanism involved in the homeostasis of potassium (K^+) in root cells of the plants at low K^+ concentration in soils

6.6 Potassium (K^+)-Induced Abiotic Stress Resistance in Plants

Several reports have suggested the prospective role of K^+ ions in providing abiotic stress tolerance to the plants through the regulation of enzymatic activities and membrane/osmotic potential maintaining cellular integrity/turgidity via ion homeostasis, cytoplasmic homeostasis and aquaporin function (Wang et al. 2013; Hasanuzzaman et al. 2018; Nieves-Cordones et al. 2019; Pandey and Mahiwal 2020; Sanyal et al. 2020; Zamani et al. 2020). In plants under abiotic stress, the highly conserved PP2C has a major function in stress signalling through regulation of K^+ channels via dephosphorylation (Sanyal et al. 2020). Therefore, K^+-induced stress tolerance is achieved through a complex network of phosphorylation-dephosphorylation which is regulated by calcium (Ca^{2+}) ion and K^+ ion signalling. The role of K^+ ions in plant stress tolerance under various kinds of abiotic stresses has been discussed in this section.

6.6.1 K^+ Regulation Under Drought Stress

In the arid or semi-arid areas, the plant growth and development has been observed to be limited by the less water leading to low soil water availability for water uptake by the roots of the plants (Nieves-Cordones et al. 2019). The plants affected by drought stress have been reported to produce more reactive oxygen species (ROS), and due to unbalance between ROS production and scavenging, the cell death is induced which results in loss of crop yield (Wang et al. 2013). Due to low availability of water in drought conditions, the root growth is limited which reduces diffusion of K^+ ions by the roots and thereby leads to the limitation of acquisition of K^+ ions by the roots of plants (Wang et al. 2013; Hasanuzzaman et al. 2018). Hence, K^+ ion concentration is reduced in drought-affected plants which directly affects the K^+ channels, membrane and cellular stability and integrity and activation of endonucleases and proteases which ensues cell death. Zahoor et al. (2017) emphasized on the drought stress protective role of K^+ in *Gossypium hirsutum* L. under drought stress. The cotton cultivars under drought stress revealed decrease in water potential of leaves, stomatal conductance, lowered rate and activity/yield of photosynthesis, enhanced rate of non-photochemical quenching as well as increased lipid peroxidation. Further application of K^+ ions reversed these symptoms in cotton cultivars under drought stress.

The seedlings of *Apocynum venetum* (a xerophytic plant) were subjected to different concentrations of K^+ ions, −0.2 MPa osmotic stress along with NaCl (salinity) to investigate the synergistic effects of both Na^+ and K^+ ions under drought stress (Cui et al. 2019). NaCl treatment was observed to stimulate Na^+ accumulation, regulation of osmotic adjustments and improvement of relative water content, promotion of photosynthetic activity and thereby enhanced growth of plants under osmotic stress. Hence, this study revealed the synergistic relationship between Na^+ and K^+ ions in regulating osmotic potential, water status and photosynthetic activity under drought stress. In another study by Zamani et al. (2020), effect of K^+ fertilization in combination with six drought conditions was studied in sunflower grown in the two fields under drought conditions to analyse the interaction between field/location and drought stress. Under drought stress, the concentrations of various stress markers like oleic acid, linoleic acid and proline were increased in sunflower. Application of 300 kg/ha K fertilizer resulted in improved seed components, biochemical qualities/quantities and better crop physiological mechanisms in drought-stressed sunflower.

In tobacco, effect of exogenous treatments of K^+ was studied under drought stress and K^+ deficiency (Bahrami-Rad and Hajiboland 2017). The improvement in relative water content, water use efficiency, leaf turgor, the leaf water potential, stomatal function, enhanced carbohydrate synthesis and accumulation of organic osmolytes and proline resulted in alleviation of photosynthesis and transpiration efficiencies in tobacco plants under drought conditions. The K^+ foliage application in drought-affected wheat stimulated the grain weight and grain filling through the promotion of both activity of wheat grain and sink capacity (Lv et al. 2017). K^+ foliage application also regulated the contents of zeatin, Z riboside and ABA, rate of ethylene evolution, activities of antioxidant enzymes (superoxide dismutase, peroxidase, catalase), malondialdehyde and the value of soil-plant analysis development and promoted senescence in drought-affected wheat plants.

The mesophyll K^+ has been observed to be maintained by the regulation of plasma membrane H^+-ATPase and various associated physiological responses in drought-affected tea plants (Zhang et al. 2018a). Another study by Zhu et al. (2019) revealed the impact of K^+ treatment on physiological and metabolic processes in rapeseed subjected to 7% PEG6000-induced drought. The production of 51 metabolites had been observed to be stimulated by K^+ application. For example, the levels of amino acids, amines, carbohydrates and their conjugates and organic

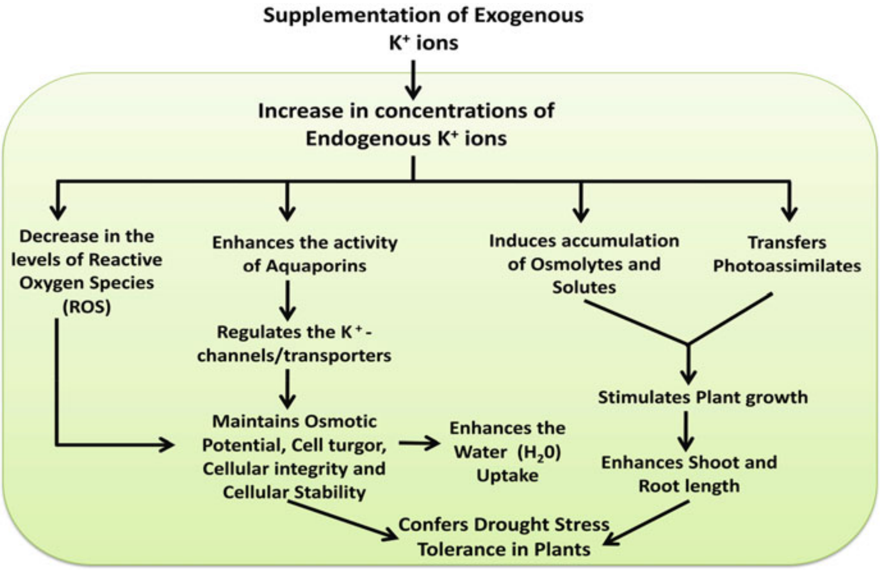

Fig. 6.3 Role of exogenous K$^+$ ions in drought stress tolerance in plants. (Modified after Hasanuzzaman et al. 2018)

acids of tricarboxylic acid cycle (such as α-ketoglutaric acid, L-malic acid, succinic acid, oxaloacetic acid) were regulated by the treatments of K$^+$ in drought-affected rapeseed. Moreover, K$^+$ had been observed to stimulate osmotic adjustments, balance of electric charge, antioxidant capacity and higher biomass which was directly associated with uptake and retention of K$^+$ during leading to rapeseed drought tolerance. Oddo and co-workers (2020) reported that availability of K$^+$ enhances potential productivity, degree of isohydry and stem hydraulic conductance in Sicilian grapevine cultivars exposed to mild drought stress. The recent investigations have revealed that exogenous K$^+$ treatment induces drought stress tolerance in various crop plants through uptake of K$^+$, stimulation of H$^+$-ATPase pumping activity and regulation of Ca^{2+} efflux mechanism (Fig. 6.3; Feng et al. 2016; Hasanuzzaman et al. 2018; Oddo et al. 2020).

6.6.2 K$^+$ Regulation Under Salinity Stress

Various anthropogenic activities, rapid use of agrochemicals and fertilizers and industrialization had resulted in land degradation and soil salinization (Chen et al. 2017). Due to increased concentrations of salt in soils, the uptake of water and nutrients by the root hairs of plants has been affected which leads to decline in growth and yield of plants grown in saline soils. This has also affected the water status and plant symbiosis with beneficial micro-organisms such as arbuscular mycorrhizal fungi under salt stress. In woody legume, *Robinia pseudoacacia*

L. (black locust) under salt stress, mycorrhizal colonization upregulated the expression of aquaporin genes, chloroplast genes in leaves and genes associated with K^+/Na^+ homeostasis in roots (encoding membrane transport proteins). Zhang and co-workers (2018b) reported that Na^+/K^+ balance (ionic homeostasis) and transport regulatory responses have been affected in weedy and cultivated rice exposed to salinity stress. During salt stress, contents of Na^+ and Ca^{2+} were enhanced, whereas the concentrations of K^+ and Mg^{2+} were decreased. The regulation of H^+-ATPases, H^+-PPases, antiporter SOS1 (SALT OVERLY SENSITIVE 1), HKTs (high-affinity potassium transporters) and NHXs (Na^+/H^+ antiporters) and ion (Na^+ and K^+) homeostasis have been well documented in various plants under salinity stress (Almeida et al. 2017).

In rice, *qSE3* gene encoding K^+ transporter gene, *OsHAK21*, was isolated, and it was observed that salt stress upregulated the expression of *qSE3* gene resulting in increased uptake of K^+ and Na^+ by germinating rice seeds under salinity stress (He et al. 2019). It was also associated with the increased biosynthesis and activation of ABA signalling responses and decline in levels of H_2O_2 in rice exposed to salinity stress. Liu et al. (2019) reported that in salt-stressed rice, differential salinity tolerance had been observed due to retention of K^+ ions in the root zones. This differential tolerance to salinity stress was due to activation of H^+-ATPase pump at transcriptional/functional level, decline in K^+ efflux channels' sensitivity for ROS and upregulation of stress-responsive genes (*OsGORK* and *OsAKT1*) in tolerant cultivars in response to salt stress.

Hydrogen sulphide (H_2S) has been reported to mitigate salt stress through the balancing of Na^+/K^+ homeostasis and regulating of oxidative defence system in cucumber (Jiang et al. 2019). Exogenous H_2S enhanced the level of endogenous H_2S, regulated the activities of key enzymes {D/L-cysteine desulfhydrase, β-cyanoalanine synthase, O-acetyl-L-serine(thiol)lyase and maintained the homeostasis of Na^+ and K^+. The ion homeostasis was balanced through stimulation of expression of associated genes (*PM* H^+*-ATPase*, *SOS1*, *SKOR*). Another study recommended the application of zinc (Zn) and K fertilizer for cotton seedlings exposed to salinity stress (Hatam et al. 2020). The differential salt tolerance has been observed to be induced through regulation of enzymes of Na^+ and K^+ transport system in two Egyptian maize (*Zea mays* L.) hybrids (Rizk et al. 2020). It has been observed that expression of *ZmHKT1;5* gene encoding for Na^+ exclusion *ZmHKT2* gene encoding for K^+ exclusion was regulated in salt-stressed maize. Besides this, the expression of *ZmNHX1* gene encoding for vacuolar Na^+ sequestration was also regulated during salinity stress in maize hybrid.

In a recent investigation by Yan and co-workers (2020), melatonin enhanced content of nitric oxide which had further improved the ion (K^+ and Na^+) homeostasis in salt-stressed rice seedlings. The pretreatment with melatonin resulted in decrease in relative electrolyte leakage; increase in fresh weight and dry weight, polyamines and arginine; improvement of K^+/Na^+ homeostasis; and enhanced activity of nitric oxide synthase in salt-stressed rice. It also improved the activity of H^+ pumps in plasma/vacuole membrane and the influx of K^+ during salinity stress.

6.6.3 K^+ Regulation Under Temperature Stress

Potassium acts as an important protector in the plants due to its vital role in maintaining the ion homeostasis, cellular integrity and enzymatic activity during the stress condition. Among various abiotic stresses, K^+ is also known to play a protective role in plants under temperature stress (both high and low temperature conditions). Plants face temperature stress when it exceeds the optimum range for the plants. During high temperature condition disruption in different biochemical reactions and plant metabolism is observed (Hasanuzzaman et al. 2013b). K^+ helps in avoiding the damage to cells by the regulation of the stomatal conductance by acting as an osmolyte (Azedo-Silva et al. 2004). Potassium also helps in activating different processes in plants as photosynthesis, respiration, water-potential enhancement, nutrient homeostasis, synthesis of protein and carbohydrates and increase in water use efficiency. It has been observed by Dias and Lidon (2010) that due to foliar spray of K^+ on wheat, heat tolerance was enhanced by increasing the photosynthetic efficiency of the wheat plant.

Low temperature causes destruction in the photosynthetic processes of plants and also reduction in the enzymatic processes. This reduction in the enzymatic activity leads to increase in the accumulation of ROS (Suzuki and Mittler 2006). It was observed by Devi et al. (2012) that due to K^+ application (exogenously), there is reduction in the accumulation of ROS produced under cold stress. It has also been reported by Wang et al. (2013) that various metabolic processes which are regulated with the help of K^+ (photosynthesis, carbon assimilation, metabolism and phloem activity) are downregulated under chilling stress. Chilling also causes loss of apoplastic water and dehydration. When K^+ is supplied exogenously, it helps in reducing the dehydration by the adjustment of osmotic potential and thus preventing plants from the risk of freezing.

6.6.4 Potassium Regulation Under Waterlogging Conditions

Plants being sessile are affected by different types of biotic and abiotic stressors. Among abiotic stresses, waterlogging poses hurdles in the crop productivity. The major consequences of waterlogging faced by plants are physiological drought and reduction in stomatal conductivity, which affects the delivery of nutrient components to the shoots. So, during initial stages of waterlogging, K^+ concentration increases in the xylem sap (Polacik and Maricle 2013). Furthermore, during the initial period of submergence or waterlogging, hypoxic conditions occur that result in the arrest of root growth, but the shoot growth persists normally. This further leads to reallocation of K^+ to the shoot, but due to loss of absorption capability of root, plants suffer from K^+ deficiency. Moreover, another factor involved in lowering the levels of K^+ during waterlogging is change in the redox potential of soil, because of elemental soil toxicity (Shabala 2011). On the onset of submergence, the levels of elements like Mn and Fe show an abrupt increase to a toxic level (Marschner 1955; Zeng et al. 2013). Iron, being a transition element, is redox active and upon the availability of hydrogen peroxide can lead to the production of reactive oxygen species like hydroxyl radical. These radicals have direct influence on K^+ channels and thus result in enhanced leakage of K^+ from cytosol.

To overcome this difficult situation, exogenous supplementation of K^+ to plants could alleviate the detrimental effects of submergence (Wang et al. 2013). In addition to this, application of K^+ results in improvement in photosynthetic pigments, antioxidative activity and lower lipid peroxidation in rice plant surviving under waterlogged conditions (Dwivedi et al. 2017). Supplementation of K^+ helps in maintaining water status under water stress conditions by maintaining the pace of physiological pathways and thus enhancing the yield of plants like rice, wheat, barley, corn, oil-seed rape and cotton to survive the adverse conditions of waterlogging (Rawat et al. 2016; Dwivedi et al. 2017).

6.7 Potassium Regulation by Phytohormones Under Abiotic Stress

6.7.1 Plant Growth Regulators (PGRs) and Associated K^+ Regulation Under Abiotic Stress Conditions

Phytohormones perceive the environmental cues and act accordingly to counter these abiotic environmental challenges. Phytohormones like ABA, ET, IAA and JA are well known to have regulatory correlations with K^+ under harsh environmental conditions.

6.7.1.1 Ethylene (ET)

Abiotic stresses disrupt the homeostasis of the K ions which ultimately hampered the photosynthetic efficiency of the plants. Ethylene, the first gaseous plant hormone, plays a key role in maintaining the homeostasis of the Na^+/K^+ ions. Jung et al. 2009 in his study elucidated the importance of ethylene in low K concentration in *Arabidopsis thaliana*. Salinity stress in soil hampered the plant growth by increasing Na^+ ions and decreasing K^+ ions. High level of Na^+ triggered the ethylene-dependent tolerance pathway. Lack of ETHYLENE OVERPRODUCER1 (ETO1) functioning promotes the increase of K ions in the tissue with enhanced HIGH-AFFINITY K^+ transporter5 gene (Jiang et al. 2013). In *Arabidopsis*, ZFP5 (Zinc finger protein 5), a transcription factor and a key regulator of root hair elongation, interacts with ethylene via EIN2 to combat the deficiency of P and K (Huang et al. 2020). Also, under low K^+ concentrations, ethylene triggers the production of ROS molecules as well as induces the transcriptional regulation of *AtHAK5* genes (Kim et al. 2012; Wang et al. 2020).

6.7.1.2 Abscisic Acid

Abscisic acid is considered as an important plant hormone in regulation of dehydration response, plant growth and development. It helps in regulating the mechanism of ion transport in guard cells and coordinating signal transduction in plants during stress conditions (Agarwal and Jha 2010; Huang et al. 2017). Stomatal opening and closing is controlled by the K^+ channels and regulated by ABA. Kim et al. (2010) documented the effective role of ABA under drought conditions by altering the ion transportation in guard cells. Decreased K^+ efflux has been observed in the presence of ABA in non-stomatal tissues which may be due to the cytoplasmic acidification by the hormone. In *Arabidopsis*, open stomatal 1 kinase, an ABA-activated protein kinase, arbitrates the stomatal closure (Mustilli et al. 2002; Konopka-Postupolska and Dobrowolska 2020). Intake of K^+ ions generates the osmotic pressure in the guard cells which further triggered the stomatal opening. Slow anion channel-associated 1 (SLAC1) is also called as an S-type channel that releases anions and K^+ which further depolarized the membrane (Sah et al. 2016). The decreased turgor pressure and volume in guard cell lead to closure of stomata (Watkins et al. 2017).

6.7.1.3 Jasmonic Acid (JA)

Jasmonic acid is among the member of molecules which is known to be produced in response of various environmental stresses. JA is found to increase when the level of K^+ drops from its optimal level (Armengaud et al. 2009; Hasanuzzaman et al. 2018). The transcript level of lipoxygenase, a key enzyme in JA biosynthetic pathway, is found to increase in respond to K starvation. Troufflard et al. (2010) reported 1.8-fold increases in shoot and 3-fold increase in *Arabidopsis thaliana* under K^+ starvation condition. The level of JA drops when K levels elevate to its normal. Evans (2003) reported the possible regulation of K^+ channel via JA and polyamines and suggested the role in redistribution of K^+ among different cellular compartments.

6.7.1.4 Auxin (IAA)

Auxins are considered as one of the most imperative growth stimulators and regulators of phototrophic and gravitropic response in plants. Among the initial responses to auxins is a hasty augment in the H^+-pumping bustle, involving the incorporation of vesicles, comprised of H^+-ATPase in the plasma membrane (Shabala and Pottosin 2014). As a consequence to this elevation in H^+-pumping activity, the external acidity and membrane hyperpolarization stimulate the K ion uptake induced by auxin-regulated stomatal movement (Shabala and Pottosin 2014). It was affirmed by Christian et al. (2006) that coleoptile growth in *Zea mays* plants was significantly augmented by auxin application and a similar dependency was also suggested on external K^+ levels in case of protoplast swelling. Along with directly stimulating K^+ influx by hyperpolarization, there was a simultaneous rectification of K^+ movement by auxin supplementation and is relatively elevated, and the elevation is attributed to integration of novel synthesis of K^+ channels inside the plasma membrane (Thiel and Weise 1999). Another observation by Philippar et al. (1999) revealed enhancement in K^+ ion influx stimulated by auxin in a dose-reliant manner. In addition to this, *ZMK1* gene expression is elevated in response to external augmentation in acidification (Bauer et al. 2000). Gene expression of imperative genes concerned with auxin biosynthesis is reversibly upregulated in response to K ion deficiency and further affirms the participation of auxin in K^+ deficiency

(Armengaud et al. 2004). The low K^+ concentration-stimulated alterations are highly species specific, for example, in *Oryza sativa* plants a plethora of auxin-induced genes were upregulated, and in *Arabidopsis thaliana* plants were mainly dependent upon jasmonate-reliant enzyme activation (Ma et al. 2012). Another researcher, Vicente-Agullo et al. (2004), also suggested that transportation and redistribution of auxin in plant system are directly dependent upon various transporters of K^+. They further suggested that transport of auxins via shoots to roots, root hair formation, retaliation to K^+ deficiency and gravitropic behaviour of plants are directly related to K^+ transporter expression, which are localized in the root tips, e.g. TRH1, and members of the KT/KUP/HAK family (Vicente-Agullo et al. 2004). Another major facilitator superfamily member, i.e. ZIFL1, was observed to be indirectly related to regulation of influx and transport of auxin through the plasma membrane (Remy et al. 2013).

Specifically the auxin-reliant genes modulate the levels of proteins which further influence the transcriptional repressors of a wide array of responses in plants in relation to stress (Shani et al. 2017). K has been widely documented to have synergistic association with plant growth regulator biosynthesis also (Ashley et al. 2006). In case the concentration of K^+ is low in a cell, certain phytohormones, viz. auxins and JA synthesis, are augmented (Armengaud et al. 2009), whereas of others such as ethylene biosynthesis is enhanced by two-folds in *Arabidopsis thaliana* plants exposed to K-deficient conditions (Shin and Schachtman 2004). Eventually these circumstances result in lowered root and shoot xylem sap levels subsequently leading to elevation in sugar levels. Similarly, growth and development of the root systems and growth of root hairs are all dependent on auxin biosynthesis (Teale et al. 2005). A positive crosstalk between auxin signalling cascade and K^+ movement exists involving TRH1/AtKUP4 K^+ transporter which also acts as auxin efflux facilitator and has been recognized as one of the regulatory components of root hair development and its gravitropism (Vicente-Agullo et al. 2004).

More recently it has been suggested that the *trh1* mutation leads to mispositioning of the PIN1 (PIN FORMED 1), an auxin efflux carrier (Rigas et al. 2013), resulting in disrupted auxin transport, i.e. acropetally along the shoot meristem and basipetally towards the root hair zone and eventually resulting in altered gravitropism of the roots and their growth. Moreover, it was further revealed that K^+ deprivation might also result in alteration of auxin transport by influencing the activity of TRH1 in turn resulting in decline in gravitropism, so that the roots can explore new soils (Rigas et al. 2013). K^+ transporter mutant trh1 (tiny root hair1) has also been affirmed to show a comparably strong root hair phenotype (Daras et al. 2015). An earlier study by Rigas et al. (2001) demonstrated that TRH1 had a significant role in regulating high-affinity K^+ influx in *Saccharomyces cerevisiae* cells, although the trh1 root hair morphology was suggested to be insensitive to K^+ uptake (Desbrosses et al. 2003). Plant cells can be rescued from such a situation by exogenous supplementation of auxin (Vicente-Agullo et al. 2004). All the above observation indicated that TRH1 has an imperative role in maintaining optimal levels of auxin in the root apex so as to sustain proper root hair growth and development (Rigas et al. 2013). In the root system, the K^+ efflux carrier is located in the plasmalemma in a polarized fashion. It coexists with PIN1 on the base of the cell in the stellar region in the elongation zone, whereas it is localized in cortex or rhizodermis in case of meristematic zone. As suggested earlier, TRH1 therefore might contribute towards both basipetal and acropetal transportations of auxins within the root tips (Rigas et al. 2013). This action aids in regulation of varied environmental cues, root hair growth and development and auxin signal transduction (Daras et al. 2015).

6.8 Crosstalk Between Different PGRs and Potassium (K^+) Under Different Abiotic Stressors

In plants, K^+ deprivation stimulates a wide array of responses at different levels in plants, viz. molecular, biochemical, physiological and phenotypical. The activation of various signalling networks such as ROS and several phytohormone cascades including auxins, ethylene, ABA and JA as well as Ca ion and phosphatidic acid are also activated (Hafsi et al. 2014). Plant growth regulators, viz. auxins, ethylenes, JA and cytokinins, are extensively involved in signal transduction in plants exposed to K-deprived conditions. Under K deprivation, HAK5 transcription is modulated by other signalling components such as ethylene and ROS which are present upstream (Schachtman 2015). On the other hand, the levels of cytokinins are lowered under K-deprived conditions in order to modulate HAK5 by stimulating ROS generation (Schachtman 2015). Auxins as well as cytokinins are the most imperative phytohormones involved in promoting growth and development and contribute towards upregulation of cell division, growth, formation of organs, vascular differentiation, phototropism and gravitropism (Chérel et al. 2014). An explicit interplay exists between auxin and ethylene (Lewis et al. 2011) and also among ROS and Ca^{2+} concentrations (Mazars et al. 2010). One of the earliest responses to water-deficit conditions is stomatal closure (Schroeder et al. 2001). This response is modulated by an intricate network of signalling cascades, in which ABA, JA, ethylenes, auxins and cytokinins have an implacable role (Huang et al. 2008). Usually the JA and ABA are considered as the affirmative stimulators of closing of stomata, whereas cytokinins and auxins are believed to be augmenting stomatal opening (Huang et al. 2008). During stomatal opening, the H^+-ATPase pump regulates the outward movement of H^+ from the guard cells of stomata. This H^+-ATPase is a member of a multiple gene family of P-type ATPases, whose 11 genes have been identified in guard cells of *Arabidopsis thaliana* plants (Ueno et al. 2005). The blue light and auxins act as a positive modulator of H^+-ATPase activity, although ABA and Ca^{2+} behave as negative influencers. The efflux of H^+ from the plasma membrane eventually results in influx of K^+ via simultaneous activation of K^+ channels including KAT1 and KAT2, i.e. potassium channel in *Arabidopsis thaliana* 1 and potassium channel in *Arabidopsis thaliana* 2, respectively, and AKT1, i.e. *Arabidopsis thaliana* K^+ transporter 1 (Szyroki et al. 2001).

6.9 Conclusion and Future Prospects

Plants are facing a consistent challenge under the changing environmental conditions. Among them, abiotic factors like drought, salinity, waterlogging and temperature are the main contributors in damaging the plants' physiological, metabolic and other regulatory processes. Under stress conditions, K^+ undergoes vital regulatory processes in minimizing the deleterious effects of these stress factors which further maintains the growth and developmental processes in plants. They also safeguard the photosynthetic machinery and neutralize the stress-mediated toxic ROS molecules inside the plant cells. On the other hand, phytohormones are well known to access these environmental cues. These phytohormones along with the K^+ ions synergistically act against these stressor molecules by activating antioxidant defence systems and other regulatory pathways in plants. Thus, it is concluded that K^+ deficiency leads to multiple challenges in plants and compromises the yield and performance. Also, there is an immediate need to understand the molecular aspects and crosstalk mechanisms between the K^+ ions and phytohormones under stress conditions.

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7

Role of Potassium in Drought Adaptation: Insights into Physiological and Biochemical Characteristics of Plants

Saima Liaqat, Shreya Chhabra, Peer Saffeullah, Noushina Iqbal, and Tariq O. Siddiqi

Abstract

Drought is one of the most expanding stresses limiting agricultural productivity worldwide. It most prominently affects the germination and yield of plants by damaging photosynthetic apparatus, reducing photosynthesis, and decreasing nutrient uptake. The plant growth is severely affected under water scarcity in limited potassium (K) supply. Water scarcity in plants causes increased cell permeability that leads to the outflow of ions especially K^+. The outflow of ions increases cell cytoplasmic water potential resulting in further decreased water absorbance capability of plants. The resulting K^+ starvation also disrupts plant metabolism as K^+ finds its direct role in osmotic adjustment, stomatal regulation, and activation of enzymes. Drought stress causes the physiological disorder by decrease in internal K^+ that leads to the decreased enzymatic activities of some K^+-dependent enzymes. K optimizes many physiological and biochemical processes that ultimately lead to increase in growth and yield of plant. In this chapter, we discuss the effects of drought on plant growth and various physiological parameters, the role of K in maintaining the various aspects of plant metabolism, and how K is responsible for mitigating the adverse effects of drought on plants by altering various physiological and biochemical mechanisms.

Keywords

Drought · Enzymatic activities · Potassium · Potassium outflow · Potassium starvation

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7.1 Introduction

Potassium (K) is the main element required for plant growth and productivity (Gupta et al. 2015). Excessive K outflow caused by the increased cell membrane permeability results in the limited plant growth. Normally, in K-repletion plants, K outflux is in balance with the K influx, but the potential of unidirectional K^+ influx and net K^+ uptake is impaired by stress conditions (salinity, drought, etc.), while internal K^+ concentration is maintained in the stressful situations by both K^+ influx and cell K^+ conservation (Assaha et al. 2017). It is an abundant cation in plants with cytoplasmic concentration ranging between 100 and 200 mM while apoplastic concentration ranging between 10 and 200 mM and can even reach up to 500 mM (Wang et al. 2013). Potassium being an essential nutrient affects biochemical and physiological processes like enzyme activation, osmoregulation, photosynthesis, stomatal operation, protein synthesis, phloem transport, and ionic balance in a plant, thereby influencing growth and metabolism. It is essential to functioning of multiple enzymes regulating various metabolic patterns and thus leading to change in metabolic concentrations (Canarini et al. 2019). The high molecular weight compounds such as starch, cellulose, and proteins get increased in K-sufficient plants leading to decreased low molecular weight compounds like soluble sugars, amides, and amino acids in the plant cells (Wang et al. 2013). It also enhances the survival of plants in various biotic and abiotic stresses and thus promoting stress resistance (Assaha et al. 2017).

Crop plants grown under open fields frequently pass through various abiotic stresses in their lifetime. Abiotic factors are associated to constrained agriculture production by reducing the quality and quantity of crops. Drought stress is one of the major abiotic stresses which limits crop performance and also becomes a threat for crop productivity, disturbing food supply and livelihood of individuals (Fathi and Tari 2016; FAO 2018).In plants, drought stress is characterized by stomatal closure which is one of the initial response, reduced turgor pressure and leaf water potential, and diminished cell growth and enlargement (Farooq et al. 2009; Hussain et al. 2018a, b). It also decreases the plant growth by influencing several biochemical and physiological functions such as ion uptake and their translocation, nutrient metabolism, respiration, photosynthesis, chlorophyll synthesis, and carbohydrate metabolism (Jaleel et al. 2008; Li et al. 2011; Hussain et al. 2018a, b).The effects of drought stress are given in Fig. 7.1. As photosynthetic carbon metabolism is downregulated, in turn, it results in production of excess excitation energy and generation of reactive oxygen species (ROS) which prompt damages to photosystem (Hajiboland 2014; Bahrami-Rad and Hajiboland 2017). Drought decreases both uptake of nutrients by roots as well as transport to the shoot due to the restricted transpiration rate and lessened membrane permeability and active transport. Furthermore, reduction in soil moisture leads to decline of diffusion rate of mineral nutrients available in soil to the absorbing root surface. Table 7.1 summarizes the effects of drought stress on different plant species.

The arid and semiarid regions are frequently exposed to limited soil water availability leading to reduced plant growth. Therefore, the drought-exposed plants

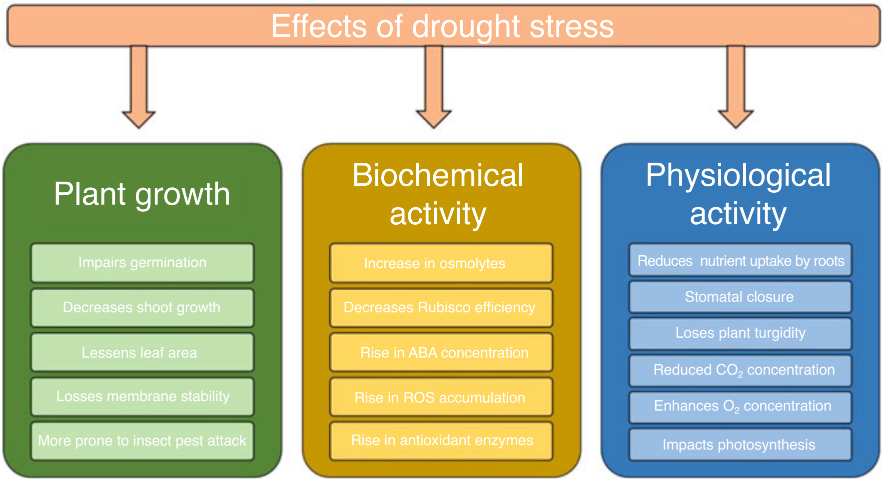

Fig. 7.1 Effects of drought stress on plant growth, biochemical, and physiological activities

lead to the increased production of ROS that further leads to increased cell permeability caused by elevated lipid peroxidation resulting in leaf damage (Wei et al. 2013). The increased cell membrane permeability causes excessive K^+ outflow resulting in increased cytoplasmic water potential and hence decreased water absorption therefore limiting plant growth (Boo and Jung 1999). The potassium uptake in plants is mainly due to the process of diffusion from higher concentration in soil to lower concentration in roots (Canarini et al. 2019). Thus, the potassium uptake process is highly dependent on the root development stages, and hence, the small and compromised roots limit the ability of plants to access potassium from soil. Also, the root growth and rates of K^+ diffusion into the roots is restricted, thus limiting K acquisition and further reducing the resistance of plant to drought stress (Sustr et al. 2019). There has been a close relationship between drought resistance and K nutritional status, and hence, maintaining the adequate K in a plant is critical for drought resistance. Furthermore, physiological mechanisms and water-use efficiency in drought stress modulated by K is not well understood. The ability of K to influence the osmoregulation in plants under stress conditions makes it a critical element for stress resistance. Several studies have explored the role of K in physiological and molecular mechanisms for drought resistance in a plant. In this chapter, we explore the different studies carried upon the role of K in mitigating the drought stress involving various physiological and biochemical characteristics.

Table 7.1 Effects of drought stress on various plant species

Plant name	Drought stage	Effects	Reference
Wheat (*Triticum aestivum*)	Tillering and jointing stages	Shortened the anthesis days and grain-filling duration Reduced dry matter Decreased grain yield traits such as number of spike per pot, grains per spike, and grain yield per pot	Abid et al. (2018)
Maize (*Zea mays*)	Five days after pollination stage	Reduced kernel size Affect carbohydrate metabolism and cell differentiation Growth retardation	Wang et al. (2019a)
Barley (*Hordeum vulgare*)	Starting of anthesis stage	Affects barley growth and grain quality Reduction in biomass accumulation and grain weight	Alghabari and Ihsan. (2018)
Cowpea (*Vigna unguiculata*)	Watering and flowering stage	Reduced growth parameters Decrease chlorophyll content	Biriah et al. (2016)
Rice (*Oryza sativa*)	Flowering stage	Reduced growth yield Poor grain quality Increase in chalky kernel and chalkiness	Yang et al. (2019)
Tomato (*Solanum lycopersicum*)	Vegetative stage	Decreased photosynthetic rate	Liang et al. (2019)
Sorghum (*Sorghum bicolor*)	Pollination stage	Affects pollination Decreased yield	Sarshad et al. (2021)
Sunflower (*Helianthus annus*)	Germinating and vegetative stage	Negatively affects seed germination and plant water relation Yellowing and falling of leaves Reduction in plant biomass	Hussain et al. (2018a, b)
Mung bean (*Vigna radiata*)	Six weeks after planting	Affects root system and shoot biomass production Reduced yield	Ranawake et al. (2011)
Soybean (*Glycine max*)	Seedling stage and seed-filling stage	Inhibited plant height and leaf area Reduced the chlorophyll content and relative water content	Dong et al. (2019)
Lentils (*Lens culinaris*)	Flowering and seed filling stage	Decrease in pod weight per plant, seed yield, and pod number per plant Reduction in yield	Rahimi et al. (2016)
Pea (*Pisum sativum*)	Flowering and pod filling	Reduction in yield Decrease in texture quality of peas	Sorensen et al. (2003)
Chickpea (*Cicer arietinum*)	Vegetative and flowering stage	Decrease in transpiration and stomatal conductance Proline content increases Reduction in chlorophyll a, chlorophyll b, and total chlorophyll content	Mafakheri et al. (2010)

7.2 Role of Potassium in Improvement of Plant Growth Under Drought Stress

Root growth is less affected than the aerial parts in drought stress, and thus, the root: shoot ratio is increased in water deficit conditions. The root elongation was reported to increase in maize along with the shoot elongation upon potassium application in drought stress (Aslam et al. 2013). In wheat, the drought stress was found to reduce the dry weight of roots and an insignificant decrease in the number of roots (Ashraf et al. 1998). Growth in seedlings got decreased by 32% in wheat under water scarcity, but the root growth and root:shoot increased. Also, roots grow fine and more fibrous in dried conditions than in favorable moisture conditions. The reduction in the water supply from roots to coleoptiles in drought stress results in the reduction of coleoptiles growth (El-Monayeri et al. 1984). The drought stress enhances the root mass on account of the reduction in shoot mass of the plant. A study on two cultivars of rapeseed, drought tolerant (YY57) and drought sensitive (CY36), indicated that low potassium (LK) conditions caused a more dramatic reduction in biomass and lower enzymatic activities than the normal potassium (NK) conditions in both the cultivars. Also, the LK caused a decrease by 29.1% in potassium concentration than the NK leading to metabolic disorder (Zhu et al. 2019). Another study on *E. urophylla* × *camaldulensis* clone under water deficit stress increased the biomass accumulation in shoot in the K-nourished conditions (Santos et al. 2020). The study on two barley cultivars (cv. Sahin-91 and cv. Milford) treated with two levels of K supply (0.04 and 0.8 mM K) along with polyethylene glycol 6000 (PEG) induced drought stress for 9 days, reporting a severe reduction in biomass of about 48% in low K status along with the osmotic stressed conditions. The osmotic stress also leads to the decreased leaf area expansion (Tavakol et al. 2018). The role of drought stress on germination index, growth index, fresh weight, and dry weight of shoot and root using polyethylene glycol (PEG) 6000 has been well documented.

7.3 Role of Potassium in Improvement of Photosynthetic Attributes Under Drought Stress

Drought stress leads to the closure of stomata resulting in decreased photosynthesis and chloroplast dehydration. Also, the adequate nutritional status of the plant helps in mitigation of the adverse of drought stress. It is widely known that water deficiency causes the degradation of photosynthetic pigments, and K application of higher concentrations is known to protect the cell membranes and chlorophyll pigments under water scarcity (Ahmad et al. 2018). Also, enhancement in K nutritional status in soil leads to the improvement of water relations in a plant. It has been reported that the K deficiency leads to reduction in leaf area and photosynthetic attributes. And a number of studies have been conducted on the role of K in improving the chlorophyll content, ultrastructure of chloroplast, and photosynthetic efficiency in controlled and drought conditions (Zhao, et al. 2001).

Stomatal closure is one of the initial responses to water deficit condition that in turn depresses photosynthesis as well as the plant's ability for dry matter production (Farooq et al. 2009). However, drought-induced decrease in photosynthetic activity is also linked to non-stomatal mechanisms, i.e., decline of enzyme activities (Chaves et al. 2009; Bahrami-Rad and Hajiboland 2017). Photosynthetic carbon metabolism downregulation leads to production of excess excitation energy and generation of ROS that brings damage to photosystems (Hajiboland 2014).

Carbon dioxide enters the leaf cells through the stomatal apertures. Their opening is facilitated by the stomatal guard cells, which constitute the first actively controlled resistance to the CO_2 movement into leaves. Potassium is the main inorganic osmolyte responsible for driving the fluctuations in guard cell turgor required for stomatal movement. Dynamic modification of stomatal aperture needs large amounts of K^+ to be quickly exchanged among apoplast, cytosol, and vacuoles of guard cells (Andrés et al. 2014). Because of osmotic role of potassium in guard cell regulation, it can be concluded that stomatal conductance is generally reported to drop under K-deficient conditions (Jákli et al. 2017). Though K is involved in the stomatal guard cells osmoregulation, deviations in stomatal conductance do not bound photosynthesis predominantly, even in situations when total leaf K concentrations are lower than the critical level required for photosynthesis. Potassium deficiency does not hinder stomatal functioning and the photosynthetic water-use efficiency (Trankner et al. 2018). Major effects of potassium deficiency associated with a decrease of the photosynthetic ability or CO_2 assimilation are (1) reduced protein synthesis, and thus Rubisco amount, and (2) anatomical modifications in leaf structure decreasing mesophyll conductance and therefore chloroplastic CO_2 concentration and (3) ultrastructure of chloroplast. Potassium also directly influences the phloem loading of sucrose and results in an accumulation of sucrose in source tissues, causing further downregulation of Rubisco activity (Trankner et al. 2018). Zahoor et al. (2017) reported that K application reduced the drop in Rubisco activity, photosynthesis, and biomass accumulation and partitioning in cotton plants. That is why potassium has a strong influence on carbon assimilation and allocation.

Potassium nitrate is also reported to increase the salt tolerance in cotton by improving its leaf area index, fiber quality, and yield (Pervez et al. 2006). A study in *Gossypium hirsutum* L. by Zahoor et al. (2017) reported an increase in photosynthesis and Rubisco activity. The effects of K application were linear with the increasing K rates, and the low K-sensitive cultivar, Siza 3, responded more than low K-tolerant cultivar, Simian 3, to an increasing rate of application of K under drought stress. K application also regulated the translocation of photosynthates and photo assimilation and also has the ability to reduce the negative impacts of drought in cotton (Zahoor et al. 2017). A desert plant, *Apocynum venetum*, with high K uptake and utilization efficiency was studied by Cui et al. (2019) under drought conditions. They concluded that accumulation of K^+ in *A. venetum* is vital to survive under osmotic stress. The supply of moderate NaCl (25 mM) under osmotic stress also leads to the enhancement of hydration and leaf photosynthesis in *A. venetum*. However, in presence or absence of NaCl, leaf K^+ concentration was significantly increased as compared to the control conditions, regardless of the K supply. It was also reported that K^+ contributed to the leaf osmotic potential by getting consistently increased to 37%, therefore suggesting K^+ as the major contributor to osmotic adjustment in *A. venetum*.

7.4 Role of Potassium in Cell Expansion and Membrane Stability Under Drought Stress

It is always valuable to effort for improving crop tolerance to stress. Promising results can be seen in inadequate soil moisture by inducing larger absorption surfaces, deeper rooting, and greater retention water in plant tissues. One way of achieving deeper rooting is by placing K fertilizer deep in soil along with other mineral nutrients, like N and P, both of which have root signalling roles (Kirkby et al. 2009). It has been found that the total dry mass of various crop plants can improve by using adequate amounts of K when compared with lower K concentrations (Wang et al. 2013). These findings might be ascribable to K which regulates stomatal movement and in turn enhances photosynthesis rate and plants ability for dry matter production. Moreover, K is an essential phytonutrient for the photo assimilates translocation in the root growth. Lindhauer (1985) in his study reported that sufficient K nutrition increased the leaf area and total dry mass of the plant and, furthermore, also enhanced the water retention capacity in plant tissues under drought conditions.

Maintenance of membrane stability and integrity is crucial for plant drought tolerance as the cell membrane stability under drought stress often significantly declined. Gruber et al. (2013) observed the inhibition of root elongation under low K conditions, which is allied with reduced cell expansion and turgor, and the loss of cell division activity in the primary root apical meristem region. Later on, Bahrami-Rad and Hajiboland (2017) in their work noticed that K application helps in restoration of root growth in both drought-stressed and well-watered plants. That is why a sufficient K supply is necessary to improve drought resistance by maintaining cell membrane stability and increasing root elongation.

7.5 Role of Potassium in Improvement of Water-Use Efficiency and Water Uptake Under Drought Stress

Drought stress causes the stomatal closure to prevent the loss of internal moisture. The turgor pressure regulation during stomatal movements in guard cells is substantially controlled by K nutrition (Shabala 2003). K^+ gets released from guard cells and enters into apoplast of leaf during stomatal closure; therefore, during water deficit conditions, it is difficult to keep stomata open in plants. It is also reported that the inhibition of photosynthesis by closure of stomata is caused by the K-deficiency (Bednarz et al. 1998; Kanai et al. 2007). On the contrary, some investigations also reported K-availability had no significant effect on stomatal conductance and photosynthetic rate (Hassan et al. 2017). However, K deficiency results in opening of stomata causing decreased photosynthetic rate and also the increased transpiration leading to rapid loss of water. These dissimilarities are however ascribed to type of plant species, experimental conditions, and setup. A study by Oddo et al. 2014 in laurel plants (*Laurus nobilis* L.) indicated that a short-term potassium supply (25 mM KCl) in water-stressed conditions lead to no significant changes in the leaf water potential (ψ_L), plant transpiration, or hydraulic conductivity. They concluded that short-term potassium fertilization did not result in any recovery of the plants from drought stress. Potassium-dependent stomatal closure was observed in sunflower and olive plants by Benlloch-González et al. (2008). They also reported that stomatal closure occurs by ethylene synthesis in low K status. K starvation increases the ethylene production by increasing gene transcription. Increased ethylene production leads to reduction in abscisic acid (ABA) and hence prevents stomatal closing (Benlloch-González et al. 2010). The K content upregulated in leaves and stems of *E. urophylla* × *camaldulensis* resulting in the improvement of chlorophyll *a* fluorescence, instantaneous water-use efficiency (WUE_I), gas exchange, and leaf water potential (Ψ_w) than *E. urophylla* clone. Also, *E. urophylla* experienced decreased K content in leaves and stem under water deficit conditions and reduced dry mass accumulation (Santos et al. 2020). K deficiency in drought stress leads the decreased performance of stomata and hence further loss of water, but the drought stress is known to increase the WUE by closure of stomata during water deficit. Hence, K^+ availability is essential for the plants resistance in drought stress and also to maintain WUE and crop growth under water deficit conditions. Relative water content (RWC) in the drought stress gets significantly decreased, and K application is highly correlated with RWC. K application at 120 mg kg^{-1} of soil in pots improved the RWC by 8.7% and 19.9% in mustard and sorghum under drought-stressed conditions. K application at 75 kg ha^{-1} in groundnut increased RWC by 17.7% under water-stressed conditions indicating a positive role of K in maintaining the turgor and facilitating the growth of plants under water stress (Umar 2006). The potassium application under drought stress also resulted in increase of leaf water potential, osmotic potential, and turgor potential in maize (Aslam et al. 2013). Table 7.2 summarizes the effects of potassium fertilization on different plant species under drought stress.

Water channels also known as aquaporins are intrinsic proteins present in plasma as well as intercellular membranes of plant cells. Aquaporins facilitate the highly regulated passive transport of water and the gaseous molecules like CO_2 and O_2 across the membranes and also show varying specificity for different substrates (Singh et al. 2020; Khan et al. 2020). They regulate hydraulic conductivity of membranes and osmotic potential and make alteration in water permeability of plants, thus playing a critical function in plant-water relation. Mirzaei et al. (2012) have identified 138 proteins which were specially accumulated to extreme drought response, 87 proteins which were induced specially to mild drought response, and 96 proteins which were specially localized in the abundant-watered controls in the root proteome of rice leaves. These identified proteins comprised nine aquaporins which were induced in drought stress response but slowly reduced upon rewatering. Regulation of aquaporin gene expression can help plants to maintain their water

Table 7.2 Effect of K application (its different sources and concentrations) on different plant species under drought stress

Plant species	Source of potassium and concentration used	Effects	References
Hibiscus rosa-sinensis	0 mM, 2.5 mM, and 10.0 mM K_2SO_4	Improved leaf water content (LWC) and leaf water relations by decreasing leaf osmotic potential (Ψπ) and sustained rates of net photosynthesis (PN), transpiration (E), and stomatal conductance (gs)	Egilla et al. (2005)
Helianthus annuus L.	0, 150 and 300 kg ha^{-1} K_2SO_4	Increased proline, oleic, and linoleic acid concentrations	Zamani et al. (2020)
Gossypium hirsutum L.	0 and 0.48 g potash kg^{-1} soil	Increased potassium accumulation, root morphology, and soil microbes	Wang et al. (2019b)
Zea mays L.	50 and 75 kg ha^{-1} KCl	Increased yield traits and water productivity; alleviated drought susceptibility	Ul-Allah et al. (2020)
Beta vulgaris	10, 20, 40, and 80 mg $kg^{-1}K_3PO_4$	Increased relative water content and MDA content; reduction of membrane damage and especially to the reduction of nonenzymatic antioxidants	Aksu and Altay (2020)
Helianthus annuus L.	1% K solution	Increased biological yield, head diameter, plant height, 1000 achene weight, achene yield, relative water content, and plant K contents	Raza et al. (2018)
Nicotiana rustica L.	3 mM and 6 mM KCl	Improved shoot growth, photosynthesis, and transpiration activities	Bahrami-Rad and Hajiboland (2017)
Triticum aestivum L.	30 mmol L^{-1} KCl	Increased zeatin (Z), Z riboside (ZR), abscisic acid (ABA), malondialdehyde (MDA), and ethylene (ETH); decreased superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) activities as well as the soil-plant analyses development (SPAD) value	Lv et al. (2017)
Canola cultivars	100 kg $ha^{-1}K_2SO_4$	Increased seed yield, stomatal resistance, oil yield, oil content, oleic acid, linoleic acid, linolenic acid, erucic acid, and glucosinolate content	Farahani et al. (2019)
Helianthus annuus L.	0, 5, 10, 15, 20, and 25 g L^{-1} K_2SO_4	Enhanced leaf gas exchange characteristics, proline, soluble proteins, free amino acids, and antioxidant defense system	Shehzad et al. (2020)
Solanum lycopersicum	0.1, 1 and 10 mM K_2SO_4	Increased shoot growth, fruit setting, and yield	De Luca et al. (2021)
Cicer arietinum L.	0.5, 1.0, and 1.5% K_2SO_4	Increased plant height, pods per plant, 1000-grain weight, grain yield, and biological yield	Mahmood et al. (2017)

balance under drought stress conditions (Lian et al. 2004; Galmes et al. 2007; Wang et al. 2013). During water deficit circumstances, roots adjusted their water and ion uptake capabilities by modifying K channel and plasma membrane intrinsic proteins at the transcriptional level to deal with the water deficiency (Smart et al. 2001; Cuéllar et al. 2010).

7.6 Potassium Involvement in Improvement of Osmolytes Under Drought Stress

In the stressed conditions, the osmotic change along with the formation of compatible solutes is vital to protect the membrane structures and enzymes leading to crop protection. The accumulation of compatible solutes also works as the scavenger of ROS. These organic solutes maintain the potential integrity of cells and prevent the cellular dehydration and also prevent degradation of macromolecules. These compounds which include amino acids (like proline), sugars, glycerol, sugar alcohols, and some low weight molecules (like glycine betaine) accumulate in large concentrations and function as osmoprotectants to maintain the integrity of protein in response to stress (Yancey 1994). In drought stress, the accumulation of compatible solutes is an important function for the water regulation (Fallon and Phillips 1989). Among the compatible solutes, sugars are the most important osmolytes playing role in the osmotic adjustment. The total soluble sugar and polyols accumulation in a plant is a characteristic feature under stress (Mohammadkhani and Heidari 2008). Polyols are also involved in the transcription of genes of NR genes and thus regulation of NR activity (Wolkers et al. 1998). In *Ziziphus mauritiana* under water deficit conditions, the accumulation of sugars has played a significant role in osmotic adjustment (Clifford et al. 1998). Moreover, potassium also improves the transport of sugars from leaves to the fruit under drought-stressed conditions (Aslam et al. 2013). In drought stress, the accumulation of sugars is mainly due to the decomposition of starch due to the increased amylase activity (Vaezi 2005). Wheat subjected to two different water regimes indicated the maximum increase in total soluble sugar of 49 mg g^{-1} of dry weight in limited water supply (Qayyum et al. 2011). Although the most promising tool in drought stress is the increase in the activities of antioxidant enzymes, e.g., SOD, APX, POD, CAT, the accumulation of total soluble sugar can also be taken into consideration (Li et al. 2009). In cotton cultivars, drought stress lead to an increase in sucrose content but decreased starch content while the K application sustained the high concentrations of sucrose under drought stress through increased activities of sucrose phosphate synthase (SPS) and sucrose synthase (SuSy) and decreased activities of soluble acid invertase (SAI) (Zahoor et al. 2017). Another important osmolyte, proline (low molecular mass compound) accumulates in the cytosol to improve the tolerance of plants under drought stress. It functions in osmotic adjustment and also stabilizes subcellular structures (membranes and proteins) from the damage caused by the drought stress. It also works as a protein, a compatible hydrotrope that helps plants to mitigate the stress by reducing free radicals and protecting cellular oxidation and reduction potential. It also acts as an important indicator of the environmental stress. Proline increase in the drought stress has been observed in rice (Mostajeran and Rahimi-Eichi 2009), wheat (Simova-Stoilova et al. 2008), sunflower (Cechin et al. 2008), *Vigna radiata* (Hooda et al. 1997), and alfalfa plants (Irigoyen et al. 1992). However, the physiological importance of stress-induced proline accumulation is still being investigated as there have been contrasting reports obtained by the researchers regarding the role of proline in stress tolerance mechanisms.

7.7 Potassium Controls ROS Production and Improvement of Antioxidant System Under Drought Stress

Drought stress leads to the disruption of photosynthetic efficiencies resulting in imbalance between antioxidant defense and production of ROS and hence significantly increasing the accumulation of ROS (Sharma and Zheng 2019). Imbalance among generation and detoxification of ROS signifies metabolic state which is mentioned as oxidative stress (Baier et al. 2005; Hussain et al. 2018a, b). Although ROS is produced under both optimum and stressful conditions in plant cells, the levels of ROS is generally tremendously high under stressed environments (Alscher et al. 2002, Khan et al. 2013). Various ROS such as singlet oxygen ($^1O_2$), hydroxyl radicals (OH^-), hydrogen peroxide (H_2O_2), and superoxide radicals (O^{2-}) are majorly produced in plants under stressful conditions. Chloroplasts are the chief ROS-producing organelles in plants (Asada 2000). Excess ROS accumulation results in RNA and DNA damage, protein oxidation, and lipid peroxidation in membrane and may lead to apoptosis (Apel and Hirt 2004).

ROS play a vital role in regulation of photosynthesis and in intercellular signalling to control plant growth and development. The concentration of ROS in cellular compartments defines its functions, e.g., a low concentration of ROS is responsible for triggering several stress defensive responses, and very high levels of ROS leads to oxidative damage resulting in cellular membrane degradation and cell death (Wang et al. 2013). K deficiency further enhances the production of ROS. It also leads to the considerable reduction in fixation of CO_2 by photosynthesis, reducing conversion to chemical energy and translocation of photosynthates from source to sink (Zhao et al. 2001; Wang and Wu 2013). The impairment of photosynthetic fixation of CO_2 by drought stress leads to the activation of molecular O_2 resulting in production of ROS. The appropriate availability of K nutrition prevents the damage caused by the consequence of water stress. Similarly, the photosynthetic efficiency of plants was improved under the adequate availability of K in drought stress. Also, K is known to decrease the production of ROS by increasing the photosynthetic fixation of CO_2 and increasing translocation of photosynthates from source to sink (Zhao et al. 2001). Another major contributor to the production of ROS is nicotinamide adenine dinucleotide phosphate (NADPH)-dependent oxidase activation under stress conditions. NADPH-oxidizing enzymes use NADPH as an electron donor to reduce one electron of O_2 to $O_2^{\cdot -}$ (Hassan et al. 2017). The activity of NADPH oxidase increases under K deficiency resulting in corresponding increase of

$O_2^{\cdot -}$ production by NADPH. The increment of NADPH oxidase is probably to the increased accumulation of ABA under K-deficiency conditions. ABA is also known to substantially increase the accumulation of H_2O_2 and $O_2^{\cdot -}$ in maize seedlings (Jiang and Zhang 2001). This study is further supported by Cakmak (2005) suggesting the improved K supply in water deficit conditions decreases the NADPH oxidase activity and maintains the electron transport chain leading to inhibition of accumulation of ROS. It therefore suggests that the K is important for the decreased ROS accumulation under drought stress conditions.

Oxidative stress often leads to cellular damage and can ultimately result in cell death. Therefore, plants have evolved a stimulating antioxidant defense system that functions to preserve levels of ROS under control in order to prevent or lessen the ROS-induced damage, allowing only the positive roles of ROS to continue. Usually, one or more antioxidants are available in cell in every organelle which acts on a particular ROS to detoxify it (Ahmad et al. 2010; Ahanger et al. 2017). Antioxidant defense systems comprised of both enzymatic and nonenzymatic components. Various studies revealed the result of K fertilization on the certain plant antioxidants concentration such as carotenoids (Kaur et al. 2018), phenolic compounds (Tavallali et al. 2018), tocopherols (Caretto et al. 2008), and ascorbic acid (Kaur et al. 2018). Potassium enhances growth-strengthening antioxidant system and also controls the oxidative stress-induced membrane lipids peroxidation (Ahanger and Agarwal 2017). Zhu et al. (2019) in his study reported that normal concentration of potassium in rapeseed tends to increase enzymatic activity of various antioxidants such as catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD) which gets lower with low concentration of potassium. Sonntag et al. (2019) found that antioxidant concentrations are affected with K fertilization, but additional abiotic factors may lessen or even converse those effects in natural cultivation environment in tomato.

Drought stress disturbs the balance of production of ROS and antioxidant defense system and leads to overproduction of ROS. The production of ROS triggers the antioxidant responses in the plant. Among the antioxidant enzymes, peroxidase (POD) reduces H_2O_2 to H_2O using a number of reductants to reduce the effect of stress in plant cells. A study by Liu et al. (2012) reported an increase in activity of POD in apple subjected to drought stress. They also reported an increase in POD activity of about 141.97% in root stocks of drought-tolerant *Malus prunifolia* and only 84.19% in drought-sensitive *Malus hupehensis*. Similar increase in POD activity was reported in bean cultivars under drought stress by Türkan et al. (2005). Another enzyme of the antioxidant system, CAT, was observed in wheat plants wherein its activity was increased mostly in subtle genotypes exposed to drought stress (Stoilova et al. 2010). However, Sharma and Dubey (2005) reported a decrease in CAT activity in rice seedlings exposed to water deficit conditions. Also, in *Glycyrrhiza uralensis* saplings, the combination of salinity and drought stress leads to the decreased CAT activity (Pan et al. 2006). In plants under drought stress, ascorbate peroxidase (APX) plays an important role in minimizing the stress (Selote and Khanna-Chopra 2004). As reported by Yang et al. (2008) in dragon spruce (*Picea asperata* Mast) and by Zlatev et al. (2006) in *P. vulgaris,* the activity of APX was enhanced due to the nonavailability of water. An important finding about the APX activity under drought stress was the increase in APX activity under mild drought stress, but as the plant wilts, it gradually gets decreased (Sharma and Dubey 2005). Another study in wheat at post-anthesis grain-filling stage during drought stress decreased SOD, CAT, and POD activities upon potassium foliar application (KFA) (Lv et al. 2017).

7.8 Potassium Improves Ionic Balance and Yield Components Under Drought Stress

During drought stress, the maintenance of proper water status in a plant is essential for the plant's survival. The prime mechanism adopted by the plants to maintain the turgor potential and water balance is the osmotic adjustment under drought stress (Blum 2017). Osmotic adjustment in leaf is primarily related to the tolerance of plants to drought stress. K^+ plays a major role as the primary osmoticum in water deficit conditions. The proper availability of K increases the solute accumulation and also reduces the osmotic potential leading to improved cell turgor in the water deficit conditions (Tuna et al. 2010). Lastly, the adequate availability of K favors osmotic adjustment and also helps in maintaining relative water content and cell turgor and hence improves the resistance of plants against drought stress. Drought stress also hampers the K uptake into plant roots due to poor diffusion rates causing decreased K levels in plants (Umar 2006). The ionome studies in rapeseed under drought stress revealed that K contents in leaves of the low potassium (LK) plants decreased by 29.1% than the normal potassium (NK) levels. However, K content in YY57 was significantly higher than that of CY36 (Zhu et al. 2019). They further analyzed the decrease in Fe and an increased-level Na, Ca, and Mg at LK treatment in drought stress. In rice under drought stress, the potassium fertilization leads to the increased uptake of N, P, K, Ca, Fe, and Mg (Zain et al. 2014). Potassium enhances the transpiration rates in the plants and increases water and nutrient uptake through xylem. This facilitation of nutrient or ionic uptake by potassium leads to the decrease of water stress effects in plants.

Plants need relatively large quantities of macroelements to carry out many cellular functions. Potassium is one of the macroelements, ranking third in the list of significance and necessity to the plants. It is required for the standard growth and development of plants including cotton (Dong et al. 2010; Oosterhuis et al. 2013; Tung et al. 2019). The demand for global K fertilizer is projected to rise further because of the targeted upsurge in global agricultural production (Dhillon et al. 2019). Plants generally absorb the beneficial elements from the soil solution mainly in the form of ions, and potassium is accessible to plants as K^+ (Ahanger et al. 2017).

Among the various abiotic stresses, drought stress has appeared as a critical production constraint in plants, mainly in arid and semiarid areas (Zhang and Hu 2018; Jin et al. 2019). The severity of drought stress is not only influenced by the intensity and duration but also depends on the growth phase at which plants are affected, i.e., germinating, vegetative, or flowering stage, all of which shows distinct responses, but finally, all lead to yield loss (Ge et al. 2012; Daryanto et al. 2016; Ul-Allah et al. 2020). Under drought stress, restricted photo assimilates synthesis as well as their poor partitioning in cotton plants is a foremost constraint to final yield production (Zahoor et al. 2017). So applications of potassium fertilizer have been established to fulfill the potassium demand during the growing period of cotton, which could increase the potassium utilization efficiency and decrease both time and labor cost (Yang et al. 2017; Chen et al. 2020). Several studies have revealed that applying controlled dose of potassium fertilizer enhances the fiber quality and postpones leaf senescence, and also, it greatly increases the cotton yield as well as fertilizer use efficiency (Yang et al. 2016; Tian et al. 2017). Ul-Allah (2020) in his study found that the performance of maize hybrids was increased manifold by potassium application and was maximum under potassium application at 75 kg ha^{-1}. Thus, maize farmers in arid areas where water deficit conditions are prominent may get higher productions by applying potassium at 75 kg ha^{-1} (Ul-Allah et al. 2020). Though potassium application enhanced yield traits and water productivity in both normal as well as water deficit conditions, still the effect was more pronounced under water deficit conditions than normal conditions.

7.9 Conclusion

Drought is a severe threat for crop production worldwide which affects many biological traits of plants and eventually causes heavy yield losses. Potassium is the macroelement necessary for optimum growth of plants nearly in all cropping systems. An adequate K status improves cell membrane stability, leaf area, root growth, and total dry mass of plants living under drought conditions. Potassium also increased water uptake as well as water conservation by enhancing the osmolyte content, ion accumulation, and antioxidant system. Maintaining a sufficient K nutritional status is essential for plant osmotic regulation and for alleviating the deleterious effects of drought-induced ROS. Therefore, supplementation of K is vital under environmental constrains in future of crop production.

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Role of Potassium in Heavy Metal Stress

8

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Abstract

Inside plant system, potassium (K^+) elements play an essential role required for plant growth and development by involving in many physiological (e.g., stomatal regulation and photosynthesis) and biochemical process (e.g., protein synthesis, carbohydrate metabolism, and antioxidant enzymatic activity). K^+ homeostasis, transportation, and acquisition play a very essential role in plant survival. Mainly under higher toxic heavy metal stress, K^+ loss from plant cells is very dramatic, also termed as K^+ efflux or electrolytic leakage that is responsible for PCD (Program cell death) through enhancing proteases and endonucleases enzymatic activity. However, in moderate stress conditions, K^+ efflux plays an indispensable role by stimulating catabolic processes that further help in saving "metabolic" energy for adaptation, repair, and restoration of plant's natural health. Many experimental evidences show that K^+ application reduces malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) content; enhanced protein, proline synthesis, and secondary metabolites like phenols and flavonoids synthesis; as well

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as improved antioxidant enzymes activity. Furthermore, many investigatory reports had shown that K^+ status increased through exogenous application causes the reduction in the activity of nicotinamide adenine dinucleotide phosphate (NADPH) oxidases that finally help in retaining the photosynthetic electron transport activity, which further helps in the reduction of reactive oxygen species (ROS) generation in plants. It plays a valuable role in minimizing the various kind of stress toxicity, boosting immunity, transportation, and signaling process which is finally responsible for plant's survival.

8.1 Introduction

In the period of extreme industrialization, metal consumption is increasing in manufacturing units (Awa and Hadibarata 2020). Heavy metals are one of the abiotic stress factors that affect plant's growth, yield, and human health by paving an easy entry into the food chain (Berni et al. 2019). The most promising side effects of metal toxicity includes turmoil in physiological processes, disturbance in stomatal mechanism, reduction in photosynthesis, formation of ROS, etc. (Chibuike and Obiora 2014).

Potassium has a great importance in all the living beings like bacteria, animal, as well as plants. Among these organisms, potassium content is most abundantly found in plants. Potassium plays essentially important roles as a nutrient as well as a major intracellular ion in plants. Potassium's mobile nature in plant system plays important role in affecting stomatal movements, phloem transport, photosynthetic activity, and stress resistance. There were many findings that clearly validate potassium's role as a protector against heavy metal stress. Ahmad et al. (2016) stated that application of potassium relieves negative impact of Cd by enhancing the levels of antioxidant enzymes and improving biosynthesis of photosynthetic pigments and lowers hydrogen peroxide levels. Potassium also plays a role in detoxifying ROS formation under stress as stated by Hasanuzzaman et al. (2018).

8.2 Heavy Metal Stress in Plants

Due to anthropogenic activities, mainly in the twentieth century, heavy metal pollution has emerged as one of the major threats to agricultural crops. The metals like Zn, Ni, Cu, V, Co, Cr etc., when exceed their permissible limits cause toxicity in plants (Schutzendubel and Polle 2002). Fifty-three of the 90 naturally occurring elements are heavy metals, but not all of them are of biological importance. Recently, the contents of these heavy metals have strongly increased up to dangerous levels due to natural as well as anthropogenic activities like volcanic eruption, mining, smelting operation, leather tanning, textile, electroplating, and excessive use of pesticides in agriculture. Heavy metals being persistent in nature get accumulated in soils and plants. Heavy metal toxicity to plants varies according to specificity of metal, plant species, metal concentration, types of chemical form, soil composition, and pH (Ghori et al. 2019).

Some heavy metals are essential micronutrients for plants, but their elevated concentration can lead to toxicity symptoms like chlorosis, necrosis, stunted plant growth, disintegration of cell organelles, photosynthetic impairing and finally plant death (Panda et al. 2003; Sharma and Agarwal 2005). In addition to inducing morphological abnormalities in plants, heavy metals also caused alteration in biochemical parameters that resulted in oxidative damage due to the excessive production of reactive oxygen species (ROS) such as hydroxyl radical ($OH^{\cdot}$), superoxide radical ($O_2^{\cdot -}$), alkoxyl radical ($RO^{\cdot}$), and hydrogen peroxide (H_2O_2). In plants, ROS are continuously produced predominantly in chloroplast, mitochondria, and peroxisomes. Production and removal of ROS have been balanced. However, the production and scavenging of ROS might be disturbed by number of biotic and abiotic factors including heavy metal stress (Apel and Hirt 2004). These ROS had the capacity to initiate lipid peroxidation and degrade proteins, lipids, and nucleic acids and may lead to cell death by enhancing the expression of the ROS-dependent and cell death-related genes. Other factors like MAPK-driven phosphorylation cascades and posttranscriptional modifications such as protein oxidation and nitrosylation might be involved in ROS-dependent cell death (Breusegem and Dat 2006).

In plants, these ROS are removed by enzymatic and nonenzymatic antioxidative defense system. Nonenzymatic antioxidative system includes the ascorbate, reduced glutathione (GSH), tocopherol, flavonoids, alkaloids, and carotenoids. Ascorbate and α-tocopherol are extremely effective antioxidants as they are relatively poor electron donors and effectively scavenge $OH^{\cdot}$ $O_2^{\cdot -}$ and singlet oxygen (Arora et al. 2002). Enzymatic antioxidative system consists of various antioxidative enzymes like superoxide dismutase (SOD), guaiacol peroxidase (POD), ascorbate peroxidase (APOX), catalase (CAT), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR). SOD act as first line of defense against ROS, dismutating $O_2^{\cdot -}$ to H_2O_2. Subsequently, CAT, APOX, and POD detoxify the H_2O_2 to H_2O. APOX and GR also reduced H_2O_2 to water through the ascorbate-glutathione cycle. APOX detoxify the H_2O_2 to H_2O by using ascorbate as reducing agent which oxidized into monodehydroascorbate. Later on, it can be regenerated into ascorbate with the help of MDHAR/DHAR using NADPH as reducing power. The extent of oxidative stress in a cell is determined by the amount of ROS. Consequently, the role of antioxidative enzymes becomes very important to combat the oxidative stress generated by heavy metal stress and to boost the resistance capacity of plants (Noctor and Foyer 1998; Arora et al. 2002; Ghori et al. 2019) (Fig. 8.1).

Heavy metals have also been shown to disrupt the flux of cations such as Ca^{2+} and K^+, alter membrane stability and permeability, and initiate the different stress response cascades including imbalance production of ROS and tissue degradation (Rodrigo-Moreno et al. 2013). In response to heavy metals in the soil, plants may adopt a variety of mechanisms to prevent toxicity that include avoidance and tolerance (homeostasis) (Malachowska-Jutsz and Gnida 2015). The plants which

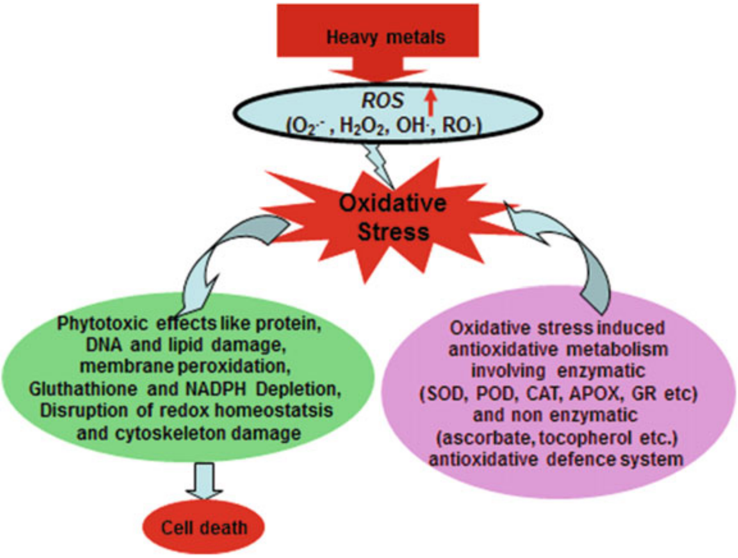

Fig. 8.1 Heavy metals-induced oxidative stress and related cellular damage in plants

are able to adopt these strategies are able to maintain osmotic balance, membrane integrity, and growth rate and regulate level of ROS. The roots of plants are the first point of exposure to soilborne abiotic stresses. So the flux rates of potassium and hydrogen ions have become very important in determining health of heavy metals-stressed plants (Redwan et al. 2016). Heavy metal stress affects the level of K^+ ions which are otherwise required for normal functioning of plant cells. Rate of efflux of K+ ions is proportionate to decrease in plant biomass and photosynthetic parameters. In *Cannabis sativa*, *Medicago sativa, Populus deltoides* × *nigra,* and *Salix matsudana,* it was reported that heavy metals like Ni, Zn, and Cu enhanced the efflux rate of root K^+ ions, thereby reducing the biomass of plants (Palm et al. 2017).

Interrelationship between heavy metals and K^+ ions further established by a report of Wu et al. (2020). K^+ ions help to mitigate heavy metal (Cd) toxicity in *Arabidopsis thaliana* by alleviating Cd-induced chlorosis in leaves, altering the binding capacity of cell wall and by increasing the expression of Cd detoxification-related genes.

8.3 Heavy Metal Stress Amelioration: Role of Potassium

8.3.1 Potassium Role in Soil as Fertilizers

Although K is the seventh most copious element in the lithosphere comprising about 2.6% of the earth's crust, its concentration fluctuates broadly somewhere in the range of 0.04 and 3.0% (Bertsch and Thomas 1985; Yadav and Sidhu 2016). The total soil

K is generally classified into four forms: water soluble (soil solution), exchangeable K, non-exchangeable or fixed, and structural or mineral K, depending upon its availability to the plants and other microorganisms. Out of these forms, only water-soluble and exchangeable K forms that merely constitute about 0.1–0.2% and 1–2%, respectively, of total soil potassium are readily available for plant and microbe uptake (Zörb et al. 2014). The amount of water-soluble fraction also referred to as soil solution K is not only little in soils but also is significantly unpredictable making it difficult to gauge (Sparks, 1987). Moreover, frequent leaching caused by runoff can further lower the water-soluble fractions (Sardans and Peñuelas 2015). Typically, concentration of K in soil solution varies between 0.1 and 6 mM (Ashley et al. 2006), whereas exchangeable K ions are adsorbed onto clay minerals and organic matter from where they can be easily desorbed or adsorbed again (Sparks 1987). On the other hand, fixed K is trapped in the interlayers, gaps, and wedge zones of minerals like vermiculites, micas, and intergrade clay minerals. Fixed K comprises of around 1–10% of total K, and it releases K when the concentration of plant readily available K decreases due to processes such as plant uptake, leaching, and elevated microbial activity. Lastly, the structural K that represents the bulk (i.e., around 90–98%) of the total soil potassium is very slowly available, but it ensures long-term K supply along with the fixed form (Zörb et al. 2014). This form exists as minerals, for instance, feldspars and micas (Römheld and Kirkby 2010). The release of K into the soil is relatively more readily from K feldspars minerals than from micas as K is strongly held by electrostatic forces in them (Zörb et al. 2014). Several factors, such as parent minerals, degree of mineral weathering, soil organic matter, topography, plant-soil interactions, soil microbial activities, and nutrient balance, strongly influence adsorption and desorption of K in the soil. Thus, a complex dynamic equilibrium exists among these different fractions that regulate the amount of plant available K (Zörb et al. 2014; Blanchet et al. 2017; Fig. 8.2).

Even though K is abundant in the lithosphere, vast areas of arable soils across the world are potassium deficient (Blanchet et al. 2017). Soils having low K statuses such as acid sandy, saline, or waterlogged soils could exhibit a comparatively high tendency of K depletion in less duration if K removal is not replenished by external K fertilization (Römheld and Kirkby 2010). However, responses to mineral K fertilization could be below expectation or even insignificant because of its tendency to be fixed to non-exchangeable form. Particularly, presence of minerals such as vermiculites and illite in the silt and sand fractions can play a significant role in soil K fixation (Portela et al. 2019). Nevertheless, K fixation is poor in soils where kaolinite, unweathered micas, and chlorite minerals predominate. In other words, positively charged K^+ can get easily entrapped in between the layers of illite where they are detained by negative charged ions on these layers, while K cannot enter the layers of kaolinite as they are tightly compacted (Yadav and Sidhu 2016).

Several studies have revealed that exchangeable K and non-exchangeable K contents are exhausting worldwide. For instance, a recent study conducted on Uruguay agricultural soils showed that long-term intensive agricultural practices coupled with inadequate K fertilization have lowered exchangeable K at the rate of

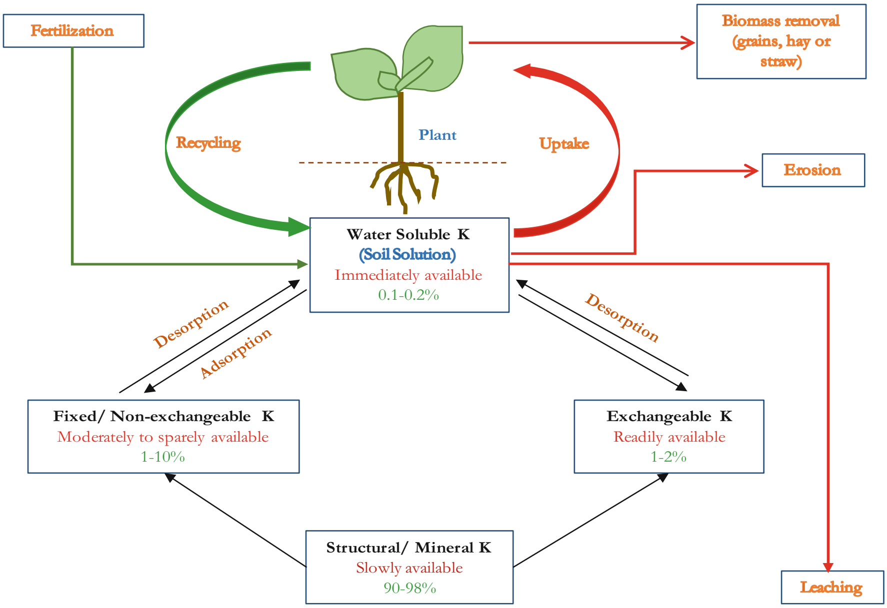

Fig. 8.2 Dynamics of K in soil. (Modified after Öborn et al. 2005; Römheld and Kirkby 2010)

0.04 mmol kg^{-1} $year^{-1}$ (Beretta-Blanco et al. 2019). Such practices can also induce changes in the composition of 2:1 clay minerals in soils that act as K reservoir for plant nutrition. Das and others (2019) reported that repeated indifference of Indian farmers toward K fertilizers has led to lessening of illite content with the corresponding increment in interstratified minerals in the intensively cultivated red soils of eastern India. Besides the issue of limited K fertilizer addition that disrupts the soil K balance, the soils also tend to get K deficient due to leaching, erosion, and/or biomass removal (Dhillon et al. 2019). Thus, understanding the whole process of K liberation from soil minerals become very essential for making the potassium ion available to plants so that plant can able to combat stress condition effectively.

8.3.2 Uptake, Transport, and Assimilation of Potassium in Plants

The uptake of K in plants mainly occurs in the cationic form (K^+). Other than this, different sources of K within soils may occur. For instance, in the form of fertilizers, they are mainly comprised of potassium chloride (KCl), potassium sulfate (K_2SO_4), KNO_3, and K_2CO_3 respectively (Snapp et al. 2005). Among them, muriate of potash is of higher demand and most commonly utilized in the agricultural practices for usually all types of crops (Kafkafi et al. 2001). And other categories of K fertilizers are used only in case of crops that show sensitivity toward chloride salts, amid of being expensive. To exemplify, KCl leads to leaf burning disease on tobacco due to excessive Cl uptake (Ishizaki and Akiya 1978).

Potassium availability seems to be very scarce; therefore, during such circumstances, the soil microflora assists K solubilization and make available the soluble form of K via acidification, ion exchange mechanism, and chelation process, respectively (Masood and Bano 2016). Being used as macronutrient, K is supplied in the basal doses within soils; however, in few cases, they might be exogenously applied as foliar spray (Sarkar and Malik 2001). It is quite a fact that foliar supply proves as an effective strategy even under water-logging conditions, yet their efficacy is dependent on their absorption ability and penetrating capacity. Henceforth, it could only serve as a partial compensation under limited root uptake conditions. Alongside, the efficiency of foliar application also lies in the presence of larger leaf surface area (Ashraf et al. 2011).

Adding to the abovementioned factors, the potential of plants for K^+ uptake is also one of the factors that controls K solubility, release from soil nutrients, as well as externally applied fertilizers. The uptake and translocation of K^+ in plants is usually observed by transporter families comprising of plethora of proteins. K^+ uptake from outside environment and its transport toward various cellular compartments and locations are induced by wide array of proteins residing specifically within the membrane. These proteins are comprised of transporter and channel proteins. According to their function and ability toward K^+ transport and translocation, they are divided into different categories. To elucidate, higher-affinity transporters are quite active at lower exogenous K^+ concentration, and lower-affinity transporters are activated at elevated levels of K^+ in the range of usually more than 0.5 mM (Wang and Wu 2013). With the intensified research and advancement in the molecular tools, the recognition for different lower- and higher-affinity transporters have been conducted in many different plant species such as *Hordeum vulgare, Oryza sativa,* and *Capsicum annuum,* respectively (Nieves-Cordones et al. 2014). Sidewise, there are different transporter families with different structure and mechanism of action, like TPK (tandem-pore)/TP (two-pore) channel proteins, shaker-like voltage-dependent carrier protein families (KT/HAK/KUP), cation proton antiporters (CPA), HKT uniporters/symporters, etc. (Rainer 2012; Nieves-Cordones et al. 2014; Sze and Chanroj 2018). A study reported that yeast mutant deficient of K^+ uptake can effectively grow after the mutant was transformed with barley cDNA, leading to the discovery of HvHAK1 transporter (high affinity), homologous to HAK1 K^+ transporter protein of different microbial strains (Santa-María et al. 1997). For the hold of lower-affinity transporters mechanism as internal K^+ channel, higher-affinity K^+ transporters were revealed (Nieves-Cordones et al. 2014). Experimental evidence reported that *Arabidopsis* mutant devoid of *HKT1* gene was observed to grow on KCl solution effectively, but with enhanced concentration of KCl, a significant retardation in growth was observed, depicting the role of KHT1 in K^+ uptake and translocation (Hirsch et al. 1998).

Apart from this, there are various other transport proteins like shaker-type protein channels, K^+/H^+ antiporters, glutamate receptors, and cyclic-nucleotide gate channel proteins (Anschütz et al. 2014). The shaker-type proteins are subdivided into further categories, namely, internal rectifying channels involved in K^+ uptake after activated through hyperpolarization and outer rectifying channels involved in K^+ efflux and are activated after membrane depolarization. Another category is of weak rectifying channels mediating both K^+ efflux and influx after activated by hyperpolarization of membranes (Wang and Wu 2013). The channel proteins encoded by specific genes vary in structure and function. Generally, in case of roots, K^+ uptake is assisted by two different type of proteins, AKT1 and HAK5, as revealed by the studies conducted in *Arabidopsis thaliana* and *Oryza sativa* (Yang et al. 2014). The deficient mutants, *hak5* and *akt1,* survived in KCl, but double mutants, *hak5* and *akt1,* were unable to survive such conditions, depicting the role of AKT1 and HAK5 (high-affinity transporters) for K^+ uptake in plants (Pyo et al. 2010). In case of *Oryza sativa,* AKT1 primarily enhanced K^+ uptake through regulatory action of three main proteins: CBL-associated protein kinase 23 (*CIPK23*), calcineurin B-like protein 1 (*OsCBL1*), and calcineurin B-like protein 1 (*OsCBL1*), respectively (Li et al. 2014). Moreover, when long-distance K^+ translocation from roots toward vascular tissues occurred, outer rectifying channels played a critical role. Also, the researchers showed that mutant deficient of outer rectifying K^+ channels lowers the K^+ levels in shoots as well as xylem sap. Furthermore, the stomatal functioning is co-linked K^+ levels in guard cells, where KAT1 and KAT2 induce K^+ movement into the cells, while outer rectifying K^+ channels and guard cell channels induce K^+ movement in nearby stomatal cells (Hosy et al. 2003). Apart from this, voltage-regulated channel proteins, TPL5, TPK2, TPK1, and vacuolar Na^+, K^+/H^+ antiporters, NHX1 and NHX2, located in the tonoplast region mediate K^+ efflux/influx within vacuole (Barragán et al. 2012) (Fig. 8.3).

8.4 Role of Potassium in Mitigating Stress Conditions

Nitrogen, phosphorus, and potassium (NPK) are essential nutrients for the enhanced productivity of crops. Among these nutrients, potassium is vital inorganic cation present in vacuole and cytosol in the cell and plays imperative role in various physiological, biochemical, and metabolic developments (Hafeez et al. 2018). It is involved in photosynthesis and distant transport of sugars, metabolites, and other minerals within the plant. It is the most important osmotic molecule present in plants cells, and therefore, its adequate concentration is important for regulating cell elongation and stomatal movement. It enables the diffusion of atmospheric CO_2 into chloroplasts (Tränkner et al. 2018). It is essential for the process involved for the growth of plants. It enhances yield and quality of crops. In potassium-deficient plants, sugars get accumulated and are not converted to starch (Prajapati and Modi 2012; Hafsi et al. 2014). Deficiency of potassium in plants affects their development and yield by negatively affecting various physiological and metabolic processes like cell expansion, maintaining turgor pressure, ionic and water homeostasis, photosynthesis, assimilation, and transport of solutes (Römheld and Kirkby 2010). Reduction in biomass, net photosynthetic rate, stomatal conductance, and transpiration are observed in potassium-deficient plants (Zahoor et al. 2017). Reduction in growth

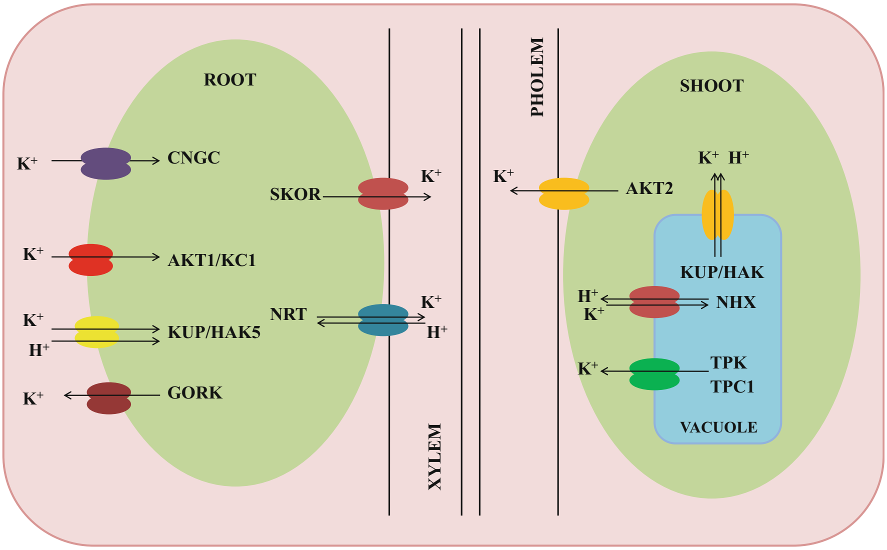

Fig. 8.3 Diagrammatic presentation of potassium uptake, transport, and accumulation within plants. *CNGC* cyclic nucleotide-gated channel; *AKT* shaker-type K^+ channel; *KUP/HAK5* high affinity K^+ transporters; *GORK* guard cell rectifying K^+ channels; *SKOR* Stellar outer rectifying K^+ channels; *NRT* nitrate transporter; *TPK/TPC1*, tonoplast two-pore K^+ channel proteins; *NHX* Na^+ proton exchanger

attributes, biomass, and yield was observed in potassium-deficient (0.5 mM K) soybean plants, but inhibition of photosynthetic processes along with decreased growth traits was seen under potassium-scarce (0.2 mM K) soybean plants (Singh and Reddy 2017). Exogenous application of potassium improved the photosynthetic pigments, reduced oxidative damage, and increased the growth parameters of *Triticum aestivum* grown under salt stress (Jan et al. 2017).

Potassium in the cell also plays important role in stomatal regulation during photosynthesis. Decreased stomatal conductance due to potassium deficiency enhanced the mesophyll resistance and causes the inhibition of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activity, resulting in the reduction in the net photosynthesis rate (Zhao et al. 2001). Adequate amount of potassium triggers the stomatal guard cells to absorb water resulting in stomatal opening which allows the exchange of gases among plants and the environment. During water scarcity, potassium is pumped out from the guard cell and pores close tightly preventing transpiration of water through pores, and it guards the plant from water stress. Scarcity of potassium disturbs stomatal regulation, resulting in late and incomplete stomatal closure (Cochrane and Cochrane 2009). It is observed that exogenous application of potassium improved transpiration and photosynthesis in *Nicotiana rustica* L. under drought and potassium-deficient conditions (Bahrami-Rad and Hajiboland 2017).

Maintaining the suitable concentration of potassium and its ratio with other macronutrients in growth medium is critical for the proper functioning and growth of the plant. Raised or low concentration of potassium in the medium generally impedes the growth of the plant (Wang et al. 2013). Appropriate ratio of potassium to nitrogen is critical for photosynthesis and better crop yield. It is suggested that potassium: nitrogen (1:1) is the most apposite ratio for the cotton production. Application of potassium in this ratio enhanced lint and seed cotton produce, photosynthetic attributes, and chlorophyll fluorescence (Hafeez et al. 2018).

Potassium reduces the production of ROS by suppressing the activity of nicotinamide adenine dinucleotide phosphate (NADPH) oxidases and keeps the activity of electron transport. Potassium-deficient plants show retarded growth and yellowing of leaves (Hasanuzzaman et al. 2018). It was reported that supplementation of potassium upregulated enzymatic and nonenzymatic defense of *Triticum aestivum* L. under water and salinity stress. It also improved growth parameters and enhanced the production of osmolytes like sugars, proline, and amino acids, enabling the plant to withstand water stress (Ahanger and Agarwal 2017).

8.5 Role of Potassium in Amelioration of Heavy Metal Stress and Detoxification of ROS Species

Heavy metal stress leads to produce surplus of ROS (hydroxyl radicals, OH; singlet oxygen, $^1O_2$; superoxide, $O_2^{\cdot -}$; organic hydroperoxides, ROOH; peroxy radicals, ROO, etc.). At low level, the reactive species act as a signal molecule, whereas elevated ROS level inhibits the activity of antioxidative defense system (SOD, POD, APOX, GPOX, etc.), increases the oxidation of lipids, and stimulates the PCD (programmed cell death) resulting in cell death (Sharma et al. 2012; Hasanuzzaman et al. 2012). At low concentration of potassium oxidation reactions and electron transport mechanism resulting in enhancing the production of ROS. Therefore, application of exogenous potassium suppresses the activity of NADPH oxidase and regulates the photosynthetic reactions (Hasanuzzaman et al. 2018). Some report showed the K^+ outflow from the roots of the plant, whereas Wang et al. (2017), Eker and Uysal (2013), Shamsi et al. (2010), and Liu et al. (2012) studies show that exogenous K^+ enhances the POD, SOD, and CAT antioxidant enzymes activity which leads to mitigate the cadmium stress. Zahedifar et al. (2016) also showed the same heavy metal mitigation process in *Ocimum basilicum.* Furthermore, there is alleviation of Cd stress under different form of potassium (KH_2PO_4, KCl, or $KHCO_3$) (Ahmad et al. 2016; Wang et al. 2017; Yang and Juang 2015). Other researchers (Siddiqui et al. 2012; Ahmad et al. 2016) also reported the synergetic suppression of potassium and calcium that boosts up the expression of special organic molecules and defensive enzymatic system against Cd toxicity. Medium concentration of potassium (0.5 mM K^+) enhances the photosynthetic pigments and antioxidative defense mechanism, decreases the MDA content, and makes the tobacco plant Cd tolerant (Wang et al. 2017). Recently, Wu et al. (2020) demonstrated that at 3 mM K^+ concentration upregulates the endogenous level of NO that induces the binding of Cd with hemicellulose and thus restricted its movement in roots of the plant. Molecular mechanism of potassium alleviation of heavy metal stress is still unknown and required the need for further investigation (Table 8.1).

8.6 Stress Signaling Induced by Potassium in Plants Under Heavy Metal Stress

Wang et al. (2013) stated potassium as valuable nutrient engaged in improving plant resistance to abiotic and biotic stress agencies. Potassium deficiency leads to chlorosis, curling of leaf tips, and diminished root growth (Srivastava et al. 2020). One of the first reactions in plants is hyperpolarization of the root cell membrane potential. K^+ deficiency is also associated with rise in cytosolic Ca^{2+} levels, which interacts with CBL-CIPK complexes (Pandey et al. 2014). CBL (calcineurin B-like proteins) further interact with CIPKs (CBL-interacting protein kinases) (Zhou et al. 2015). In Arabidopsis, CIPK23 is reported to phosphorylate a voltage-gated high-affinity K^+ channel, AKT1 (Arabidopsis K^+ transporter 1). Li et al. (2006) described that phosphorylation of AKT1 boost K^+ uptake activity. Furthermore, it was suggested that K^+ uptake is regulated by reversible phosphorylation/dephosphorylation of AKT1 (Sánchez-Barona et al. 2013). Apart from Ca^{2+}, ROS raises in K^+-deficient conditions (Buet et al. 2019). RCI3 (Rare Cold Inducible gene 3, a type III peroxidase) is involved in ROS production in response to K^+ deficiency. ROS adds to raise levels of Ca^{2+} by activating Ca^{2+} permeable channels (Demidchik, 2018). ROS upregulates expression of AtHAK5 (a high-affinity K^+ transporter gene) (Kim et al. 2012). Likewise, García et al. (2015) adds to existing knowledge by reporting increased ethylene and jasmonic acid production under K+-deficient conditions. To overcome the problem of potassium deficiency, plants have developed adaptive mechanism to maintain potassium cellular levels. Various channels and transporters are located in various parts of plant as in roots, leaves, and shoots. Table 8.2 enlists various channels and transporters involved in this process.

Potassium deficiency in plants leads to various defensive stress signalling. In plants, first symptom of K^+ deficiency is indicated by elevated expression of jasmonic acid signalling (Armengaud et al. 2004). Next symptom includes activation of root hair defective 2 (RHD2), an NADPH oxidase, which activates ROS-dependent signalling (Foreman et al. 2003). The next indication is raised production of ethylene in K-starved plants (Shin and Schachtman 2004). Potassium in soil is sensed majorly by roots; hence, they serve as sensing organs for the cation. Potassium uptake is regulated by external concentration of the cation in soil (Fig. 8.4). K^+ concentration above 0.0003 M in soil activates low-affinity K^+ uptake

Table 8.1 Various reports showing heavy metal stress amelioration by potassium

S. no.	Plant species	Heavy metal (concentration used)	Potassium concentration	Plant responses after giving potassium	References
1.	*Camellia oleifera*	26,963.69 mg kg^{-1} Mn	$\geq$200 mg kg^{-1}	Decreases the pH of the soil and stimulates the inflation of Mn in *C. oleifera*; enhances the phytoremediation of Mn by activating the enzymatic and nonenzymatic antioxidants (CAT, SOD, POD, PC, -SH, etc.)	Yu et al. (2020)
2.	*Arabidopsis thaliana*	50 Mm Cd	3 mM	Application of potassium ameliorates the Cd toxicity by enhancing the accumulation of NO lead to modify the ability of Cd binding with cell wall of Arabidopsis	Wu et al. (2020)
3.	*Tanzania guinea grass*	0.0, 0.5, 1.0, and 1.5 mmol L^{-1} Cd	0.4, 6.0, and 11.6 mmol L^{-1}	K^+ at 6.0 and 11.6 mmol L^{-1} concentration mitigates the Cd phytoextraction	de Anicésio and Monteiro (2019)
4.	*Ocimum basilicum* L.	40 mg kg^{-1} Cd	100 mg kg^{-1} 200 mg kg^{-1} KCl, K_2SO_4, K nano-chelate	Different K^+ sources affect the mobility of Cd in roots and shoots; furthermore, K-nano-chelates restrict the uptake and immobilization of Cd in roots and shoots; KCl considered efficient to stimulate the Cd phytoremediation	Zahedifar et al. (2019)
5.	*Lablab purpureus*	5000 μg kg^{-1} Ni 2000 μg kg^{-1} Pb 15,000 μg kg^{-1} Cr 3000 μg kg^{-1} Cd 600 μg kg^{-1} As	80 and 160 kg ha^{-1}	Higher application of potassium triggers the photosynthetic rate and increases immobilization of heavy metals in plant	Ruthrof et al. (2018)
6.	*Gladiolus grandiflora*	50 mg kg^{-1} $CdSO_4.8H_2O$	200 mg L^{-1}	Regulates the uptake of micronutrients and enhance the production of SOD, POD, and CAT; downregulates the production of MDA and H_2O_2	Zaheer et al. (2018)
7.	*Nicotiana tabacum L.*	5 μM $CdCl_2$	0.5 mM	0.5 mM K^+ alleviates the Cd toxicity by reducing the oxidative damage and enhancing the photosynthetic rate result in inducing the Cd resistance in tobacco plant	Wang et al. (2017)
8.	*Gladiolus grandiflora*	50 or100 mg kg^{-1} Cd	60 mg kg^{-1}	Reduces the level of proline and boosting the activities of antioxidants enzymes	Yasin et al. (2018)

9.	*Carpobrotus aequilaterus*	2000 mg kg^{-1}	30–60 kg ha^{-1}	Addition of potassium salt in *C. aequilaterus* enhances the phytostabilization of Cu that leads to crippling of the metal in roots of the plant	Tapia et al. (2017)
10.	*Prunus persica*	2 mM $ZnCl_2$	10 mM	K^+ supply upsurges the activity of ROS scavenging, downregulates the production of proline, and also increases the chlorophyll synthesis	Song et al. (2015)
11.	*Vicia faba*	200 µM Cd	6 mM	Elevates the synthesis of photosynthetic pigment and triggers the activation of antioxidant defense system	Siddiqui et al. (2012)

Table 8.2 Various channels and transporters involved in potassium signaling under stress conditions

S. no.	Location	Channel/transporter	References
1.	Root	Cyclic nucleotide-gated channels (CNGC)	Jha et al. (2016)
2.	Root	Arabidopsis (shaker-type) K^+ channel (AKT1)	Rubio et al. (2008)
3.	Root	High-affinity K^+ transporters (HAK5)	Qi et al. (2008)
4.	Root	Guard cell outward-rectifying K^+ channel (GORK)	Hosy et al. (2003)
5.	Root	Na^+/H^+ exchangers (NHXs)	Barragán et al. (2012)
6.	Root	Nonselective cation channels (NSCC)	Tyerman (2002)
7.	Root	Stellar outward-rectifying K^+ channels (SKOR)	Johansson et al. (2006)
8.	Shoot	Vacuolar transport systems such as TPK, NHX, and KUP/HAK	Pandey and Mahiwal (2020a, b)
9.	Leaves	Potassium channel in *Arabidopsis thaliana* (KAT1, KAT2)	Pilot et al. (2001)
10.	Leaves	One guard cell outward rectifier K^+ channel, GORK	Pandey and Mahiwal (2020a, b)

mechanism, whereas concentration lower than 0.0002 M activates high-affinity K^+ uptake mechanism (Wang and Wu 2013).

8.7 Conclusions and Future Perspective

Intercellular abundance of potassium ion in plants cells indicates its massive important role in plant growth and development especially in agriculturally important crops as well as in stress tolerance. Heavy metal stress exerts deleterious effects in plants. It disturbs various physiological activities in plants by increasing the production of ROS. Adequate supply of K individually or along with others nutrients mitigates the oxidative stress in plants under the exposure of heavy metal. However, major challenge faced by plants is to use limited pool of available potassium present in soil. There is a need to develop new area of research for the extraction of limited potassium from soil and make it easily available to plant in order to prevent the potassium deficiency in plants. Genetic modification of plant by Srivastava et al. (2020) and Pandey and Mahiwal (2020a, b) stated that together with known stress signals Ca^+ and ROS, K might be responsible for providing signals for adaptive responses which further help in mitigating stress from plants.

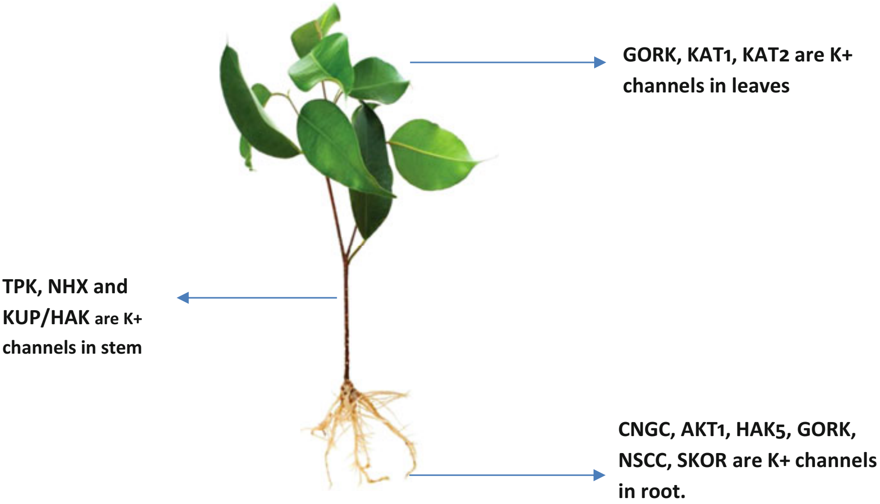

Fig. 8.4 K^+ channels located in different regions of plant parts

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Salt Stress Alleviation Strategies to Maintain Potassium Homeostasis in Plants

9

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Abstract

Soil salinity is one of the most influential stresses limiting agricultural production. Saline soil is characterized by an excess concentration of chloride, sulfate, and carbonate salt of sodium, calcium, magnesium, and potassium in the root zone, making the plants difficult to extract water and nutrients from the soil causing plant injury. Salinity affects the physiological and biochemical characteristics of plants reducing plant's photosynthetic potential and growth. There are various strategies to tolerate salt stress, and among them, accumulation of osmolytes, antioxidants, and salt-tolerant plant growth-promoting rhizobacter (ST-PGPR) are involved. Here, we have tried to analyze the different strategies involved in salt tolerance and how they maintain potassium homeostasis in plants.

Keywords

Antioxidants · Osmolytes · Potassium · Salinity · ST-PGPR

9.1 Introduction

Soil salinity is one of the most influential stresses limiting agricultural production. Saline soil is characterized by an excess concentration of chloride, sulfate, and carbonate salt of sodium, calcium, magnesium, potassium in the root zone, making the plants difficult to extract water and nutrients from the soil and causing plant injury. Soil with an electrical conductivity (EC) of the saturation extract of more than 4 dS m^{-1} in the root zone at 25 °C with 15% of exchangeable sodium is considered to be saline under salinity stress (Shrivastava and Kumar 2015). Salinity inhibits

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plant growth by exerting low water potentials, ion toxicity, and ion imbalance. Plants record low yields because of adverse effects of salinity by experiencing reduction in relative water content, total dry weight, plant height, and number of leaves per plant. Plant's response to salt stress is physiologically and genetically complex because salt tolerance is controlled by multiple genes and involves various biochemical and physiological mechanisms (Flowers 2004). Around 20% (45 million ha) of irrigated land, producing one-third of the world's food, is salt affected. The total area of salt-affected soils across the globe is 932 m ha, of which 351 m ha is saline and 581 m ha is sodic (CSSRI n.d.). India has total salt-affected area of 6.74 m ha out of which 3.79 m ha is sodic and 2.95 m ha is saline soils. Gujarat (2.22 m ha) and Uttar Pradesh (1.37 m ha) has maximum area under salt-affected soils. United Nations' Food and Agriculture Organization (FAO and ITPS 2015) in its report "The status of the world's soil resources" has identified nine major threats to soil functions, and soil salinization is one of them. The delta regions of India, Myanmar, and Bangladesh which majorly contribute in world rice production are facing serious threats to food security due to salinization of coastal soil (Szabo et al. 2016). Salt-affected soils can be classified as solonchak and solonetz. Solonchaks are characterized by the accumulation of high-soluble salts, whereas solonetz are commonly known as alkaline soils and sodic soils and contain a large proportion of adsorbed Na and in some cases also Mg ion, covering an area of 260 and 135 million hectares, respectively (USS-WGWRB 2015). Salt accretion in the root zone causes development of osmotic stress and disturbs cell ion homeostasis by inhibition in the uptake of essential elements like K^+, Ca^{2+}, and NO_3^- and the accumulation of Na^+ and Cl^- ions (He et al. 2008). Salinity adversely affects relative water content (RWC), transpiration, protein, carbohydrate, and starch content, but diffusive resistance increased significantly in the wheat genotypes at tillering and ear emergence stage (Singh et al. 2013). The harmful effects of salinity on plant growth are low-water potential of the root medium which triggers water deficit within the plant, toxic effects primarily of Na^+ and Cl^- ions, and nutritional imbalance created by decreased nutrient uptake and transport to the shoot (Hasegawa et al. 2000). In majority of saline areas, low precipitation is inadequate for leaching these salts below root zone levels, and these excessive soluble salts in the root zone inhibit plant roots from withdrawing water from neighboring soil, reducing the plant-available water. There are also specific ion toxicities and damage caused by the accumulation of sodium, chloride, and boron in the tissue of transpiring leaves (Singh and Flowers 2010). Accrual of these ions first hinders photosynthesis and protein synthesis, inactivate enzymes, and injure chloroplasts and other organelles. These effects increase with age of leaf and are more critical in older leaves as they have been transpiring for the longest period and accrue more ions. The Na^+ and Cl^- are most influencing ions of saline soils which affect the cell membrane by interaction, competition, and selectable ion penetration and disorder on the absorption of macro- and microelements. In groundnut, the salinity stress decreased seedling emergence, radical elongation, plant height, and dry matter weight when saline level is beyond 2.60 mS/cm, while high heritability and genetic advance values in

Table 9.1 Country-wise crop-specific genotypes showing salinity tolerance

Saline-tolerant genotypes	Country reported	Crop	References
Ex-Dakar and RRB 12	Nigeria	Groundnut	Mensah et al. (2006)
KRL 19 and NW 1012	India	Wheat	Roy and Srivastava (2001)
Zhongmu-1	China	Alfalfa	Sandhu et al. (2017)
Orthadian, Chovvarian, Kuttusan, and Kuthiru	India	Rice	Joseph and Mohanan (2013)
CIM-473 and CIM-446	Pakistan	Cotton	Anjum et al. (2005)
Pusa Vishal	India	Mung bean	Sehrawat et al. (2015)

characters such as 100 seed weight, pods/plant, and seeds/pod was more, indicating that these are controlled by additive genes (Mensah et al. 2006) (Table 9.1).

9.2 Effect of Salt Stress on Physiological and Biochemical Attributes

The influence of salt stress occurs in two phases. The first phase is governed by the osmotic effect due to high salt concentration in root zones, whereas the second phase is governed by toxic effects due to high salt accumulation in leaf tissues (Munns 2005). The high root zone salt concentration causes higher osmotic pressure in soil solution than in plant cells, reducing the ability of plants to uptake water and essential minerals like potassium and calcium (Munns et al. 2006). In severe salt stress, the soil solution becomes hyperosmotic, causing the root cells to lose water, which results in severe wilting or plant senescence. Osmotic stress initially reduces leaf growth and eventually causes a reduction in shoot development and reproductive growth, primarily due to the water deficit in plant tissues. Salt stress induces decreased photosynthetic rate due to osmotic stress-induced partial stomatal closure (Munns and Tester 2008). Carbohydrates are synthesized through photosynthesis, and photosynthetic rates are generally lower in plants exposed to salinity (Ashraf and Harris 2004; Parida and Das 2005).

High salt stress increases the concentrations of sodium, total sulfur, chloride, magnesium, and phosphorus and decreases the concentrations of potassium and calcium in the shoots (Cornacchione and Suarez 2015). The maintenance of the K^+ /Na^+ ratio is necessary through Na^+ exclusion from the root epidermis, but NaCl-induced K^+ efflux from the root causes the deficiency of macronutrients (nitrogen and potassium), reducing plant production and productivity. Generally, the cultivated plants are sensitive to salt stress where sodium chloride causes a diminution in carbohydrates that are required for cell growth. Ion exclusion, ion sequestration, osmotic regulation, and membrane transport system adjustment to saline environments are the main strategies conferring salt tolerance in plants (Arzani 2008).

Salinity alters photosynthetic pigments (i.e., chlorophyll content); reduces membrane stability, relative water content, and growth rates; and increases lipid peroxidation, proline, and hydrogen peroxide (H_2O_2) contents in the leaf tissue (Chaparzadeh and Mehrnejad 2013). Increased level of proline content is associated with improved salt tolerance (Campanelli et al. 2013). Effective osmoregulation in salt-tolerant cultivars is associated with increased levels of sucrose and pinitol in leaves and a high accumulation of starch in roots (Bertrand et al. 2015). The pinitol accumulation is a characteristic of halophytic plants growing in a saline environment.

The biochemical composition of plant tissues under salt tolerance can help plant scientists to quantify the compounds and image their structures with minimal sample modifications in synchrotron-based approaches (Vijayan et al. 2015). The synchrotron is a powerful facility that accelerates charged particles, namely, electrons in a large ringlike trajectory at relativistic (near-light) speed, and generates light ranging from infrared to soft and hard X-rays at high intensities. Thus, synchrotron techniques have been employed to study heat-tolerant field pea (*Pisum sativum* L.) genotypes (Lahlali et al. 2015), drought tolerance traits in spring wheat (*Triticum aestivum* L.) (Willick et al. 2017), and *Fusarium* head blight tolerance in wheat (Lahlali et al. 2015). Synchrotron beamlines are also applied to study the accumulation and distribution of organic compounds and salt ions in leaf, stem, and root tissues of alfalfa cultivars with different salt tolerances (Bhattarai et al. 2019) and ion localization in plant tissues for salt tolerance.

9.3 The Oxidative Stress and Antioxidant Response During Salt Stress

Salinity induces oxidative stress in plants at the subcellular level. Salt stress increases the accumulation of superoxide radicals ($O_2^{\cdot}$) and hydrogen peroxide (H_2O_2) in cell compartments including chloroplast and mitochondria (Acosta-Motos et al. 2017), causing lipid peroxidation and protein oxidation. Increase in peroxidase (POX) in salt-tolerant cultivars (Ashrafi et al. 2015) suggests that the analysis of antioxidant enzymes could be useful in understanding the salt tolerance of plants. During seed germination and seedling growth, increased salt stress also increases the activities of superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase activity (APX), and the increase is higher in salt-tolerant cultivars (Wang and Han 2009). Under salt stress, the unsaturated fatty acids of plant membranes are decomposed to malondialdehyde (MDA), and the rate of lipid peroxidation in terms of MDA can be used as a biochemical indicator to evaluate salt-tolerant cultivars (Jain et al. 2010). The salt tolerance of alfalfa is also improved by melatonin application, which acts as an antioxidant in scavenging H_2O_2 and enhances antioxidant enzymes' activities (Cen et al. 2020).

9.4 Effect of Salt Stress on Ion Uptake

About 98% of the ions in soil solutions are excluded from the root in most plants under salt stress, while the rest are transported to shoot tissues. To prevent tissue ion toxicity, the plants adopt several ion exclusion mechanisms which include the minimal uptake of particular toxic ions by the root and maximization of ion efflux to the soil, restricting excessive ion loading into the xylem, increasing the ion retrieval from xylem to other tissues like the root and stem, and increasing the ion transport from shoot to root through the phloem (Tilbrook and Roy 2014). Tissue tolerance to salinity stress is genotype specific. Tolerance to high concentrations of sodium and chloride ions in leaves is achieved by the intercellular partitioning of ions, thus avoiding their accumulation in the photosynthetic organelles (Munns and Tester 2008). Salt-tolerant species can sequester ions in the cell vacuoles in leaves, and the comparison of leaf injury scores under high salt stress can be used as a morphological marker for identifying salt-tolerant genotypes in early phases.

9.5 Role of Potassium and Impact of Its Starvation in Plants

Potassium is the most abundant inorganic cation in plants, comprising up to 10% of a plant's dry weight (Leigh and Jones 1984). Its role in plants include enzyme activation, stabilization of protein synthesis, neutralization of negative charges on proteins, and maintenance of cytoplasmic pH homeostasis and osmotic changes. Like stomatal movement, light-driven and seismonastic movements of organs, or phloem transport, charge-balancing counter-flux essential for sustaining the movement of other ions, H^+-ATPases, relies on overall H^+/K^+ exchange, and transport of sugars, amino acids, and nitrate is accompanied by K^+ fluxes (Marschner 1995).

Potassium can be reallocated between different compartments and tissues under fluctuating external potassium conditions due to its high mobility. Plants therefore grow well over a wide range of external potassium supply (approx. 10 μM to10 mM). Various physiological responses of potassium deficiency include reduced cell extension, reduced photosynthesis, and impaired regulation of transpiration and can easily be linked to known functions of potassium, but in many cases, it is difficult to determine which K^+-dependent process is the most crucial in creating deficiency symptoms. For example, reduced photosynthesis can be linked to both the impossibility of establishing a H^+ gradient and direct inhibition of several K^+-dependent photosynthetic enzymes. Decreased phloem transport in K^+-starved plants impacts on sugar content of tubers and other storage organs. Disturbance of sugar metabolism and allocation may also be the reason for increased susceptibility to fungal attack and frost damage of K^+-deficient crops (Laegreid et al. 1999).

9.6 Potassium in Homeostasis

Potassium in enzyme activation and protein biosynthesis relies on stable high potassium concentrations in the cytoplasm and other metabolically active compartment. K^+ homeostasis is not necessarily effective in all cell types. In barley epidermal leaf cells, cytoplasmic K^+ levels as low as 15 mM were measured (Cuin et al. 2003). These cells were still alive but had probably very low metabolic activity. Indeed, low epidermal K^+ concentrations reflect selective tissue allocation of K^+ within leaves, which allows the plant to protect metabolically active mesophyll cells against potassium deficiency. Volkov et al. (2004) found that in *Thellungiella halophila*, under low-salt conditions, the K^+ content of epidermal cells was greater than the one of mesophyll cells, whereas in high-salt conditions, the opposite was observed. This resulted in relatively high K^+/Na^+ ratios in the mesophyll, an essential prerequisite for maintenance of enzyme activity under salt stress. Both cellular and tissue potassium homeostasis rely on the presence of K^+ transport systems in different subcellular membranes and in different cell types and that these systems must have different affinities and modes of function, depending on prevailing electrochemical potentials and direction of transport.

Sodium toxicity is accompanied with potassium deficiency since Na^+ and K^+ resemble each other in ion radius and share basic physicochemical properties. Because of this similarity, one of the main reasons for Na^+ toxicity lies in the fact that Na^+ interferes with vital K^+-dependent processes, i.e., Na^+ can displace K^+ from enzyme-binding sites (Wyn Jones and Pollard 1983). K^+/Na^+ ratio in the cytoplasm is critical for stress tolerance rather than the absolute Na^+ concentration (Maathuis and Amtmann 1999). Indeed, elevated K^+ (and Ca^{2+}) in the soil solution alleviates salt stress.

9.7 Driving Forces for K^+ and Na^+ Movement Across Membranes

The driving force for ion movement across a membrane has two components: a chemical component, i.e., the concentration difference between the two compartments separated by the membrane, and an electrical component, i.e., the difference between the electrical potentials in the two compartments. The prevailing negative potential of the cytoplasm generally facilitates passive uptake of cations such as K^+ and Na^+. The exact amount of the potential difference between the cytoplasm and its neighboring compartments determines the concentration at which passive influx of a cation has to be replaced by an active (energy-requiring) uptake system. According to the Nernst equation, a plasma membrane potential of -180 mV (a common value in plants) allows passive cation accumulation by a factor of approximately 1000. Assuming a cytoplasmic K^+ concentration of 100 mM, this means that K^+ uptake from the external medium does not require energy as long as the external K^+ concentration is higher than 100 μM. Similar considerations apply to the uptake of Na^+ from the external medium. The potential difference between the vacuole and the cytoplasm is much smaller (around 25 mV), and therefore, the driving force for accumulation or release of K^+ or Na^+ into/from the vacuole follows more or less the concentration differences for the two ions between the compartments. K^+ and Na^+ follow both symplastic and apoplastic routes. The apoplast represents the cell wall continuum, while the symplast is formed by the cellular cytoplasm linked through plasmodesmata. Apoplastic journey ends at the endodermis where secondary thickening of the cell wall (the Casparian strip) restricts further apoplastic ion movement. Although the endodermis represents the final barrier for apoplastic movement, it appears that much of the apoplast/symplast transfer of K^+ already takes place in epidermal and cortical cells as these cell types have to satisfy their own K^+ requirements (Amtmann et al. 2018).

9.8 Role of Plasma Membrane During Salinity

The crucial role of the plasma membrane (PM) in overcoming various stresses is based on the maintenance of the PM integrity under environmental threats that have been reported (Maejima et al. 2014). Maintaining the PM stability is crucial for proper cell and plant performance under salt stress (Anbu and Sivasankaramoorthy 2014). The pivotal role of the PM stability maintenance in salinity tolerance is supported by the finding that NaCl-induced K^+ efflux is a result of the PM disintegrity and not due to ion channel mediation in rice (Coskun et al. 2013). The PM composition is an important factor in salt tolerance because PM lipids and proteins of tolerant plants are protected from oxidative attack, through enhancing antioxidant systems, a mechanism that minimizes lipid and protein oxidation and retaining the PM integrity (Mansour 2013). Damage to the PM has been found to be associated with changes in membrane physical structure and/or chemical properties and thus increased salt sensitivity in response to salinity (Huang et al. 2006). It is interesting to note that heat shock proteins are stress-responsive proteins produced under various stresses and have been shown to protect the PM components (Wang et al. 2004). Cell membrane stability has been similarly indicated as a measure of salt tolerance in canola (Ashraf and Ali 2008). Several studies believe that the PM might be a primary site of salt injury and salt tolerance (Flowers and Flowers, 2005; Mansour 2014). The PM lipid composition in regulating the activity of PM-associated transport systems greatly affects ion homeostasis and in turn tolerance to high salinity (Mansour 2014). Further evidence supporting the involvement of the PM lipids in salt tolerance is that expression of genes coding for major membrane lipid biosynthetic enzymes and fatty acid desaturases demonstrates a possible relationship between the variations in membrane lipid composition and tolerance to salinity stress (Zhai et al. 2012). Salinity stress, like other stresses, is perceived at the PM, which then triggers intracellular-signaling cascades that modulate gene expression and consequently responses leading to salt stress tolerance. Evidence indicates that saline environments change the lipid composition/content of the PM, which proposed to contribute to salinity adaptation (Bargmann et al. 2009; Zamani et al. 2010). High salinity results also in changing the PM transport systems, PM general proteins, as well as its fluidity and permeability (Ghaffari et al. 2014), which have great impact on plant differential responses to salinity. PM lipid composition greatly affects ion homeostasis and in turn tolerance to high salinity (Mansour 2014). PM components have a pivotal role in cellular signal transduction under different stresses (Ruelland et al. 2015). Many studies showed qualitative and quantitative differences in the PM proteins of plant species/genotypes contrasting in salt sensitivity under saline conditions (Zamani et al. 2010; Kosová et al. 2013). Salt-tolerant plants are able to maintain adaptive biosynthetic activities at high salinity (Mansour 2013). Among salt-responsive PM proteins, protective proteins, transport proteins, and sensory proteins have overexpression of the genes encoding, and these proteins contribute to enhancing tolerance to high salinity (Wang et al. 2014). PM integrity depends on its lipid composition, and published reports therefore indicate that total lipid composition of the PM is important for salt resistance of plants (Russell et al. 1995; Mansour 2013). Impaired PM total lipids in salt-sensitive plants may result from the salt-induced lipid peroxidation and degradation. Salinity-induced decrease in the PM lipid content may also be interpreted as caused by a reduction in lipid biosynthesis via reducing expression of lipid biosynthetic enzymes. Guimaraes et al. (2011) report that membrane total lipids decreased in leaves of cowpea under salt treatment was associated with increased lipid peroxidation, membrane damage, and salt sensitivity. The lipid contents in both roots and shoots decreased dramatically in the salt-sensitive rice (Huynh et al. 2012) and sensitive maize cultivars (Chaffai et al. 2005). Kerkeb et al. (2001) found that the PM isolated from tomato calli tolerant to 100 mM NaCl exhibited higher phospholipids content relative to sensitive one (Table 9.2).

9.9 Salt Stress Alleviation by Application of Micronutrient Zn

Impaired water and ionic balance and deficiency of nitrogen, phosphorus, and zinc are some of the yield-limiting factors under salinity. Zinc is a component of proteins and acts as a structural, functional, or regulatory cofactor of a number of enzymes and plays a significant role in plant metabolism. Generally, the presence of excess salt decreases photosynthesis, total carbohydrate, fatty acid, and protein, where zinc has the tendency to offset the negative effects of salinity on plant growth (Rani et al. 2019). Zinc fertilizer alleviates the adverse effects on physiological and biochemical parameters in wheat genotypes in the saline soil environment (Sarkar et al. 2007). Harris et al. (2008) reported an increase in wheat germination, emergence, and seedling growth by increasing the application of Zn. Aktas et al. (2006) reported that under the highest salt treatment, increase in the zinc application from 2 to 10 mg kg^{-1} soil decreased the shoot concentration of Na$^+$ and elevated the K$^+$ concentration. As a result, K/Na ratios of the plant were highest under the highest Zn application conditions. By affecting structural integrity and controlling the

Table 9.2 Effect of K application on physiological, biochemical, growth and yield parameters in crops subjected to salinity stress

Crop	K application	Parameters improved	References
Wheat	2 mmol L^{-1} potassium nitrate foliar spray at wheat booting stage	Improved plant weight, 100-seed weight, seed yield, ear length, and photosynthesis rate	Ahmad (2014)
Sunflower	1% K (KOH)	Increase in leaf K content and yield	Akram et al. (2007)
Cucumber	1 mM KH_2PO_4 and 2 mM K_2SO_4	Improved yield, plant growth, water use, and membrane permeability	Kaya et al. (2001)
Pearl millet	Application of 200 kg/ha K_2SO_4	Improved carbohydrate content, biological yield, and leaf K content	Heidari and Jamshid (2010)
Tomato	Application of 6.6 mM K/kg to soil and foliar spray of 9.9 mM K	Improved total soluble solids, titratable acidity, pH, dry matter %, and yield	Amjad et al. (2014)
Strawberry	Application of 1000 ppm potassium silicate	Higher MSI as well as lower MDA and H_2O_2 and significant increase in activity of peroxidase (POD) and superoxide dismutase (SOD) enzymes	Yaghubi et al. (2016)
Mustard	Application of 40 mg K/kg soil	Improve plant growth, photosynthetic traits, activity of antioxidant enzymes, the ascorbate and glutathione, and reduced ion accumulation in the leaves	Umar et al. (2011)
Peanut	Application of 30 kg K_2O ha^{-1}	Improved K accumulation and osmotic adjustment	Chakraborty et al. (2016)
Barley	Application of 10 mM KNO_3	Low MDA contents and decreased Na^+/K^+ ratio in leaves	Fayez and Bazaid (2014)
Soybean	Application of 2.5 mM potassium persulfate	Improved antioxidant activities, polyphenol, flavonoid, carotenoid, and chlorophyll contents	Adhikari et al. (2020)

permeability of root cell membranes, Zn nutrition plays a protective role in reducing the excess uptake of the Na^+ by root in the saline conditions.

9.10 Salt-Tolerant Plant Growth-Promoting Rhizobacteria (ST-PGPR) for Enhancing Crop Productivity of Saline Soils

The conventional methods of reclamation of saline soil involve scraping, flushing, leaching, or adding an amendment (e.g., gypsum, $CaCl_2$, etc.) that have proved excellent options because of cost-effectiveness but adversely affect the agroecosystems (Keren 2005; Ayyam et al. 2019). Developing sustainable methods which increase the productivity of saline soil without harming the environment are necessary, and several genotypes have been developed. Salt-tolerant microbes survive in osmotic and ionic stress, and genera of salt-tolerant plant growth-promoting rhizobacteria (PGPR) isolated from extreme alkaline, saline, and sodic soils can help in alleviation of salt stress on plants. Salt-tolerant PGPR (ST-PGPR) can be used for the reclamations of saline agroecosystems. ST-PGPR adaptive responses toward salt stress are related to the ability to produce osmoprotectants, compatible solutes, and specialized transporters. ST-PGPR are now being used as bioinoculants for enhancing crop yields, protection from phytopathogens, and improving soil health.

The high salt concentration adversely affects soil respiration, residue decomposition, nitrification, denitrification, soil biodiversity, and microbial activity (Schirawski and Perlin 2018). The loss of crop productivity and high salinity is also noticed where fertilizer input is too high in soil (Rütting et al. 2018) as high-salt index fertilizers impose osmotic effect causing difficulty in extraction of water for plant growth (Herger et al. 2015). Morton et al. (2019) also highlighted that despite vigorous efforts from the research community, only few salt-tolerant genes have been identified, having real applications in improving productivity of saline soils. Upadhyay et al. (2009) explored the genetic diversity of ST-PGPR isolated from the wheat rhizosphere, and most of the isolates belong to the genus Bacillus and tolerate up to 8% NaCl. The salt-tolerant bacteria isolated from paddy rhizosphere in Taoyuan, China, was reported by Zhang et al. (2018), where out of 305 bacterial strains, 162 were tested for salt tolerance up to 150 g/l NaCl concentration. ST-PGPR strain *Bacillus licheniformis* SA03 isolated from Chrysanthemum plants grown in saline-alkaline soil of China conferred increased salt tolerance in Chrysanthemum (Zhou et al. 2017). From tsunami-affected regions in Andaman and Nicobar Islands of India, 121 bacterial strains were isolated, majority are *Bacillus* spp., and rest were *Alcaligenes faecalis, Microbacterium resistance*, *Enterobacter* sp., and *Lysinibacillus* sp. of which 23 showed salt-tolerance up to 10% NaCl with PGP (plant growth promotion) characteristics including production of indole acetic acid (IAA), siderophore, extracellular enzymes, and phosphate solubilization (Amaresan et al. 2016). *Bacillus safensis* VK from the desert of Gujrat, India, showed salt tolerance up to 14% NaCl and pH ranging from 4 to 8 (Kothari et al. 2013). Further study of this *B. safensis* strain deciphered that its genome harbors several genes associated with PGP traits and those functioning in conditions of high salt, drought, and heavy metals. ST-PGPR *Enterobacter* sp. UPMR18 with ability to produce 1-aminocyclopropane- 1-carboxylic acid (ACC) deaminase showed improvement in crop productivity through induction of reactive oxygen species (ROS) scavenging enzymes including superoxide dismutase (SOD), ascorbate peroxidase (APX), and catalase (CAT) and upregulating to ROS pathway genes (Habib et al. 2016).

9.11 Mechanisms of PGPR-Mediated Salt Stress Tolerance

The ST-PGPR produce various type of phytohormones, such as auxins, gibberellins, cytokinins, synthesize ACC deaminase enzyme, produce secondary compounds such as exopolysaccharides and osmolytes (proline, trehalose, and glycine betaines), regulate plant defense system, and activate plant's antioxidative enzymes under salt stress (Hashem et al. 2016). The IAA (indole acetic acid) produced by a ST-PGPR *Leclercia adecarboxylata* MO1 have its linkages with sugar synthesis, organic acid production, and chlorophyll fluorescence improvement (Fv/Fm) in tomato (Kang et al. 2019). Patel and Saraf (2017) reported that bacterial strains *Pseudomonas stutzeri*, *Stenotrophomonas maltophilia,* and *P. putida* isolated from the Coleus rhizosphere produced indole acetic acid (IAA), gibberellic acid, and cytokinin under saline conditions.

Ali (2014) also reported that ACC-deaminase activity in halotolerant bacterial genera of *Arthrobacter, Bacillus, Brevibacterium, Gracilibacillus, Virgibacillus, Salinicoccus, Pseudomonas,* and *Exiguobacterium* isolated from the rhizosphere and phytoplane of *Suaeda fruticosa* (L.) Forssk stimulated growth of maize in saline conditions. In nodulation process, ACC deaminase plays an essential role to enhance persistence of infection thread which is negatively affected by ethylene level and thus help in nodule formation in saline conditions (Nascimento et al. 2016). While exposing to salt stress, salt-tolerant bacteria may temporarily increase their cytoplasmic content of K^+, but the accumulation of osmolytes is more sustained stress response to prevent water loss (Bremer and Kramer 2019). Kushwaha et al. (2019) studied osmoprotection in *Halomonas* sp. SBS 10 and found that at low NaCl, betaine accumulation suppresses the de novo synthesis of ectoine, whereas at a high NaCl concentration, the ectoine concentration increases abruptly as compared to the betaine and hence concluded that ectoine accumulation is transcriptionally upregulated by the salinity stress. Role of trehalose as an osmoprotectant under salt stress is also well documented, and a large number of ST-PGPR have been discovered having gene for trehalose biosynthetic pathways (Orozco-Mosqueda et al. 2019; Shim et al. 2019). Under adverse conditions, copious number of EPS (exopolysaccharide) is formed, the composition and amount of which vary with ST-PGPR strains (Khan and Bano 2019). EPS work as physical barrier around roots and support plant growth in high salinity stress (Vaishnav et al. 2016). The salt-tolerant EPS producing *B. subtilis* subsp. *inaquosorum* and *Marinobacter lipolyticus* SM19 reduced adverse effects of salinity and drought stresses in wheat (Atouei et al. 2019). Chu et al. (2019) showed possible role of EPS producing salt-tolerant *Pseudomonas* PS01 strain in regulation of genes related to stress tolerance in *Arabidopsis thaliana* and found upregulation of LOX2 gene which encodes a lipoxygenase, an essential component of the jasmonic acid (JA) synthesis pathway. The JA is a positive regulator and accumulates rapidly in plants (under salt stress), and bacterial EPS provide additional benefits to survive under salt stress. Inoculation of plants with ST-PGPR decreases the negative effects of oxidative stress by producing antioxidative enzymes (Islam et al. 2016). ST-PGPR, such as *Enterobacter cloacae*, *Pseudomonas pseudoalcaligenes,* and *Bacillus* sp., increased level of ascorbate peroxidase (APX) and catalase (CAT) in Jatropha leaves in response to salt stress and also stimulated the roots and increased biomass; N, P, and K uptake; and chlorophyll content in the vegetative parts of the plant (Patel and Saraf 2013).

ST-PGPR *B. subtilis* enhanced wheat yield by around 18% in salt-affected soil at EC 5.2 dSm^{-1} (Upadhyay and Singh 2015). Ansari et al. (2019) reported that a high salt concentration tolerating and biofilm-forming *Brevibacterium pumilus* FAB3 strain enhanced wheat yield by 9.8% at 250 mM kg^{-1} NaCl. Misra et al. (2017) revealed that among all, *Bacillus* sp. with ACC deaminase activity were most dominant in amelioration of salt stress and enhancing biomass of rice. Salt-tolerant species of *Pseudomonas* improve the health of groundnut (Saravanakumar and Samiyappan 2007), common beans (Egamberdieva 2011), fava beans (Metwali et al. 2015), and chickpea (Jatan et al. 2019). Application of ST-PGPR *B. firmus* SW5 on soybean grown under salt stress showed its beneficial effect on nutrient uptake, chlorophyll synthesis, osmolyte levels, gas exchange parameters, total phenolic, flavonoid contents, and antioxidant enzyme activities in comparison to control (El-Esawi et al. 2018). The ACC deaminase containing rhizobacterium *Variovorax paradoxus* 5C-2 increased total biomass of pea by 25 and 54% under salinity level of 70 and 130 mM NaCl, respectively (Wang et al. 2016). *B. japonicum* USDA 110 and *P. putida* TSAU1 were reported with salt tolerance activity and abilities to work synergistically with each other to enhance growth and productivity of soybean in high salinity (Egamberdieva et al. 2017). In a study, fluorescent Pseudomonas improved root and shoot length of sunflower under saline conditions (Tewari and Arora 2016). Van Oosten et al. (2018) reported that inoculation of tomato plants with *A. chroococcum* 76A under both moderate (50 mM NaCl) and severe (100 mM NaCl) salt stresses increased growth parameters, i.e., shoot dry weight, fresh fruit weight, and fruit number per plant. Ge and Zhang (2019) showed that under salt stress (3% NaCl), *Rhodopseudomonas palustris* G5 increased shoot height, root length, fresh weight, dry weight, total chlorophyll content, and soluble sugar content of cucumber seedlings. Recently, Tahir et al. (2019) conferred that consortium of salt-tolerant *Bacillus* strains enhanced potato tuber yield by the production of auxin and antioxidant enzymes and regulating uptake of Na^+, K^+, and Ca^{+2} in normal and salt-affected soils.

9.12 Conclusion

Salinity stress elicits two-phase response in plants with the first phase governing osmotic stress while the second phase governs ionic imbalance. High salt stress increases the concentrations of sodium, total sulfur, chloride, magnesium, and phosphorus and decreases the concentrations of potassium and calcium in the shoots. Sodium toxicity is accompanied with potassium deficiency since Na^+ and K^+ resemble each other in ion radius and share basic physicochemical properties. Because of this similarity, one of the main reasons for Na^+ toxicity lies in the fact that Na^+ interferes with vital K^+-dependent processes, i.e., Na^+ can displace K^+ from enzyme-binding sites. K^+/Na^+ ratio in the cytoplasm is critical for stress tolerance rather than the absolute Na^+ concentration.

A number of strategies are adopted to overcome the adverse impact of salt stress in plants which exhibit ion exclusion mechanisms with minimal uptake of toxic ions by the root and maximization of ion efflux to the soil, restricting excessive ion loading into the xylem, increasing the ion retrieval from xylem to root and stem, and increasing the ion transport from shoot to root through the phloem. Exogenous application of K, Ca, and Zn fertilizers play vital roles in maintaining ion homeostasis in the cytosol. Salt-tolerant microbes surviving in osmotic and ionic stress and genera of salt-tolerant plant growth-promoting rhizobacteria (ST-PGPR) isolated from extreme alkaline, saline, and sodic soils help alleviate salt stress on plants. The ST-PGPR produce as auxins, gibberellins, cytokinins synthesize ACC deaminase enzyme, produce compounds exopolysaccharides and osmolytes (proline, trehalose, and glycine betaines), regulate plant defense system, and activate plant's antioxidative enzymes under salt stress. ST-PGPR are now being used as bioinoculants for enhancing crop yields, protection from phytopathogens, and improving soil health.

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Potassium Ion Homeostasis, Signaling, and Changes in Transcriptomes and Metabolomes Enduring Salinity Stress

10

Amrit Lal Singh, Sushmita Singh, Kirti Rani, and Kiran Reddy

Abstract

Salinity stress is one of the most devastating abiotic stresses affecting plant's growth performance and yield. It disturbs the homeostasis of ions leading to osmotic stress, ion toxicity, nutrients imbalance, and decreased photosynthesis. Potassium is an important nutrient that helps to reduce salt severity by restricting the uptake of Na^+ through the Na^+/K^+ antiporters that helps to extrude Na^+ either from the root cell or distribute it within tissues. The K transporters, like the High-Affinity K^+ Transporters 1 (HKT 1), are another mechanism by which Na^+ is extruded from the shoot. The present chapter discusses the transcriptomics and metabolomics changes under salinity stress that occurs through K regulation. The pathways by which salt uptake is restricted during ionic stress, osmotic stress, and ROS accumulation are intricately entwined to target the restoration of K^+ homeostasis in the cytosol required for the stability of cellular membranes, protein structures, and function and thereby essentially contributing to the survival of plants during salt stress.

Keywords

Antiporters · Potassium · Salinity · Transporters

10.1 Introduction

Soil salinity has emerged as one of the most devastating abiotic stresses across the world as it imposes a number of adverse impacts on plant growth and development by causing osmotic stress, ion toxicity, nutritional imbalance, reduced stomatal

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conductance, and lower photosynthetic efficiency which subsequently results in severe yield reduction. The salt tolerance capabilities of plants categorize them into halophytes which have both ion exclusion and compartmentalization under higher salinity and glycophytes which can exclude the salts well at the soil-plant interface only.

Soil, due to climate change and irrational human behavior, is more affected by secondary salinity (Munns and Tester 2008). Globally about 10% of the land area (950 million ha) is affected by soil salinization, and the climate change is exacerbating this issue (Su et al. 2019). Soil salinization is a big global issue for crops causing yield losses to agricultural production. The salt stress is associated with ion toxicity, osmotic stress, Na^+ accumulation, and inhibition of photosynthesis (Zhu 2002; Parida and Jha 2013; Feng et al. 2014). The Na^+ accumulation in plants is often associated with a decrease in quantity of K^+ (Shabala and Cuin 2008). The K^+/Na^+ ratio is therefore considered an important parameter for the assessment of plant salt tolerance (Shabala and Cuin 2008). Further, salinity stress decreases peanut germination and seedling growth of peanut (Singh and Prasad 2009; Salwa et al. 2010). External potassium is needed to maintain K^+ homeostasis and enhance crop growth under salt stress (Abbasi et al. 2015; Chakraborty et al. 2016).

Osmotic stress, a rapid response to increased soil osmotic pressure, and ionic response occurring after sodium ion (Na^+) gets accumulated in the photosynthetic tissues are the two major plant responses to salinity (Munns and Tester 2008). The quick response during osmotic stress generated just after salt stress exposure manifests in the form of reduced stomatal conductance which is triggered by a signaling cascade from root to shoot. This forms a vital move to preserve more water during stress by subsequent reduction in transpiration rate and net photosynthesis. The reduction in photosynthesis is attributed to a decreased chlorophyll content and a distortion in their ultrastructure (Zhang et al. 2014). The ionic tolerance is generated at the level of root which is triggered in response to increased Na^+ influx into the root. Na^+ is known to competitively inhibit the availability and absorption of potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}), causing the nutritional imbalance of these vital cations (Rodriguez-Navarro 2000). Such imbalance deviates the source-sink coordination, thereby reducing the overall yield and nutritional quality of the edible plant parts.

10.2 Ionic Imbalance: A Consequence of Disturbed K^+ Homeostasis

The K^+ is a rate-limiting factor for crop yield and quality (Zorb et al. 2014), in addition to its vital metabolic roles in protein synthesis, turgor maintenance, stomatal movements, energy transfer, phloem loading, and membrane stability, mediating plant responses during both abiotic and biotic stresses, thereby imparting stress-alleviating attributes. The level of tolerance to salinity in a plant is determined on the basis of its ability to maintain higher cellular K^+ levels which is generally expressed in terms of Na^+/K^+ ratio (Singh et al. 2016). Increased Na^+ level has a number of consequences for K^+ uptake in the plant especially in glycophytes. Higher salt levels cause specific ion toxicities of Na^+, Cl^-, or SO_4^{2-}, decreasing the uptake of nutrients like P, K^+, and Ca^{2+} (Zhu 2001). Rise in Na^+ level in the soil solution inhibits the K^+ availability to the roots by competing for the uptake sites at plasma membrane, thereby lowering the K uptake in plants. The disrupted translocation of K^+ from root to shoot impairs stomatal movements and turgor maintenance of leaves, adversely affecting the growth processes. The older leaves, not being able to dilute the salts accumulating to toxic levels, die, and this reduces the overall photosynthetic capacity of the source since the leaf size as well as numbers get reduced during salt stress. The reduced K^+ uptake causes a decline in net photosynthetic rate due to reduced stomatal conductance and chlorophyll degradation (Tavakkoli et al. 2011).

10.3 Mechanisms Regulating Na^+ and K^+ Fluxes

10.3.1 Signaling Pathways for Ionic Stress

The cytosol maintains about 100 mM K^+ and 10 mM Na^+ optimal for enzymatic activities under nonsaline conditions. Elevated Na^+ concentration competes for transport proteins sites which regulate high-affinity K^+ uptake. Furthermore, higher Na^+ levels reduce the Ca^{2+} activity in the apoplast by displacing Ca^{2+} from sites on the cell wall. This increases the influx of Na^+ through nonselective cation channels (NSCC) and constitutively allows the influx of monovalent cations restricting the Ca^{2+} entry in the cytosol which would otherwise cause efflux of Na^+ across the plasma membrane during salt stress.

To maintain the cellular homeostasis in plant cells, it is crucial to perceive salt stress and generate the signaling across the plant system. A putative sensor or receptor in plants for higher Na^+ concentration is not well known, and it is still not clear how Na^+ is sensed by the plants (Zhu 2016; Yang and Guo 2018a, b). However, the discovery of salt overly sensitive (SOS) pathway describes the ionic stress signaling during salt stress (Zhu 2002). The key components of SOS pathway include SOS1, SOS2, and SOS3 which through intricated network of regulations cause Na^+ extrusion to maintain ionic homeostasis in the cytosol. Salt stress perception generates a spike of Ca^{2+} in the cytosol of root cells which invoke the SOS signal transduction pathway to detoxify the effect of elevated salt accumulation (Chinnusamy et al. 2005).

SOS3, a myristoylated Ca^{2+} binding protein, primarily perceives the triggered Ca^{2+} level in response to elevated extracellular or intracellular Na^+ entry in the cytosol (Ji et al. 2013). The SOS3 are mainly expressed in roots, and SCaBP8/CBL10 P which are SOS3-like Ca^{2+}-binding protein are expressed in shoots (Zhu 2016). These upon binding with Ca^{2+} activates a serine/threonine protein kinase SOS2 belonging to SnRK3, sucrose non-fermenting-1-related protein kinase family (Quan et al. 2007). Under nonsaline conditions, the proteins 14-3-3 and GIGANTEA (GI) inhibit the kinase activity of SOS 2 (Zhou et al. 2014). During salinity stress, both 14-3-3 and GI proteins get targeted for degradation through 26S proteasomal activity which subsequently releases the SOS2 kinase activity (Tan et al. 2016). SOS3-SOS2 complex recruit SOS2 to the plasma membrane causing downstream activation of SOS1 which is a Na^+/H^+ antiporter, and this subsequently extrudes the excessive Na^+ from the cytosol through plasma membrane (Quintero et al. 2011). Thus, the SOS pathway responding to salt stress generated Ca^{2+} signal which is perceived by SOS3 which then interacts with and activates SOS2 forming SOS3-SOS2 complex. This activated complex then phosphorylates and activates SOS1 responsible for excluding out the Na^+ ions out of the cytosol through its Na^+/H^+ antiporter activity.

The excess Na^+ causing K^+ deficiency causes phosphorylation and activation of AKT1 potassium channel mediated by CBL1/CBL9-CIPK23 to enhance selective uptake of K^+ for maintaining K^+/Na^+ ratio in plant cells (Ma et al. 2017).

10.3.2 Signaling Pathways for Osmotic Stress

Salinity stress imposes two phase effects, i.e., ionic and osmotic effects, both of which are mostly temporally distinct with osmotic stress as the immediate effect while ionic effect taking place at a comparatively later stage. The plants encounter these effects through different signaling pathways which would ensure optimum K^+/Na^+ ratio in the cytosol required to maintain the overall enzymatic reactions responsible for growth and development of the plant. It is essential for plants to reestablish osmotic equilibrium either by accumulating inorganic ions to balance the osmolarity or through de novo synthesis of organic, compatible osmolytes which mostly enlists proline, glycine betaine, polyols, and polyamines as the primary osmo-protectants (Mansour and Ali 2017). These compatible osmolytes help in alleviation of osmotic stress by lowering down the osmotic potential of the cell which is crucial to maintain cell turgor, providing stability to protein structure and cellular organization (Munns 2002). A number of proteins become participatory in sensing of osmotic stress in plants. The hyperosmotic stress results in accumulation of phosphatidic acid derived from phospholipase D (PLD) which in turn activates the MAPK signaling cascade (Gasulla et al. 2016). ABA-dependent signaling pathway is another alternative mediating osmotic stress signaling by activating SnRK2.2/3/6/7/8 (Zhu 2016). An important aspect of osmotic stress tolerance in plants is regulating leaf starch degradation which is ABA dependent. ABA-dependent SnRK2 activates ABA-responsive element-binding protein (AREB) which activates the promoters of BAM1/AMY3 resulting in starch degradation into sugar and sugar derivatives (Thalmann et al. 2016).

In response to hyperosmolarity, OSCA1, a putative sensor for hyperosmotic situation, forms a Ca^{2+}-permeable channel. MSL8 (MscS-like 8) is another ion channel in the PM of *Arabidopsis* pollen, regulating pollen hydration and germination during hyperosmotic shock (Hamilton et al. 2015).

10.4 Plant Mechanisms for Regulating K Uptake During Salinity Stress

Plants employ a number of mechanisms to retain the K^+ homeostasis and overcome the salinity-induced ion toxicity through restricted salt uptake in plants from the soil, controlled long-distance transport of salt, compartmentalization of salts in specific tissues, and salt extrusion from the plants. All of these mechanisms prioritize the maintenance of optimum Na^+/K^+ ratio in the cytosol.

The strategy which a plant employs to alleviate salinity stress varies with species, length of exposure to salt stress, salt concentration, edaphic factors, and the other abiotic and biotic stress factors. However, all the plant processes involved to reduce the adverse impacts of salinity have broadly been classified into three major categories (Munns and Tester 2008). Osmotic stress tolerance is the first perception occurring at the level of roots when the soil solution contains higher Na^+ levels. This involves long-distance signals reducing shoot growth by decreasing stomatal conductance and synthesizing compatible osmolytes for conserving water for the essential processes and completion of life cycle. The Na^+ exclusion prevents its accumulation to the toxic levels in leaves by selectively excluding the Na^+ from the roots. Tissue tolerance requires compartmentalization of toxic ions like Na^+ and Cl^- to specific tissues, thereby essentially maintaining the cytosolic processes.

The glycophytes ensure their survival during salt stress by employing a number of tolerance strategies including ion homeostasis, osmotic adjustment, and ROS scavenging systems (Flowers and Colmer 2008).

10.5 Ion Homeostasis

The onset of salt stress causes a considerable decline in the membrane potential across the plasma membrane (PM) of root cells leading to membrane depolarization. This depolarized state facilitates the passive entry of Na^+ into the cells since the Na^+ concentration is elevated in the soil solution. On the contrary, the extrusion of excess Na^+ from the cytosol requires ATP-dependent energy-driven process (Maathuis 2014). NSCCs nonselectively transports Na^+ across the PM of root cells. Once they enter the root cells, Na^+ gets transported to shoots through bulk flow via xylem vessels. The transpiration pull further drives continuous movement of water across the plant (Nobel 2009), and subsequent accumulation of Na^+ ions occurs to the toxic levels in leaves. Thus, to maintain ionic homeostasis, it is essential for plants to minimize salt-induced K^+ efflux and Na^+ influx.

Higher plants mostly rely on H^+- ATPases and H^+- pyrophosphatases to drive Na^+ across the membranes (Conde et al. 2011) by creating proton motive force. The Na^+/ H^+ antiporters including SOS1 located on PM (Ji et al. 2013) and NHX1 on tonoplast (Fukuda et al. 2011) mediate the exclusion of Na^+ to the soil and compartmentalization in the vacuole, respectively. Furthermore, the high-affinity potassium transporters (HKTs) like HKT1 control the long-distance transport of Na^+ by mediating the reabsorption of Na^+ from xylem sap into the root cells, thereby preventing large accumulation of Na^+ in the transpiration stream (James et al. 2006).

Salt stress generates a rapid elevation in cytosolic Ca^{2+} levels which is decoded by Ca^{2+} sensors including calmodulin (CaM), calcineurin B-like proteins (CBLs), and CBL-interacting protein kinases (CIPKs). These Ca^{2+} in turn trigger multiple signal transduction pathways regulating ion channels, enzymatic activities, and gene transcription all of which collectively contribute to restoring ion homeostasis in the cytosol (Adams and Shin 2014).

10.6 Osmotic Adjustment

Maintenance of cell turgidity at lower osmotic potential is crucial to maintain K^+-dependent biochemical processes in the cytosol, and the hyperosmolarity caused by salt stress may result in disruption of essential cellular activities. The plants thus respond through various physiological and biochemical adaptations to maintain cellular pH, redox balance, and protein structure. Osmotic adjustment is one such vital mechanism that help the plants to maintain tissue hydration during hyperosmotic stress generated in response to salt accumulation in the soil. This is accomplished by accumulation of compatible osmolytes which maintain the cell turgidity by maintaining an osmotic gradient across the cell by lowering down the osmotic potential of the cell without affecting the biochemical environment for the cellular processes.

The most common osmolyte accumulating in salt-stressed plants is proline which is an amino acid contributing to osmotic adjustment, redox potential balance, and stabilizing the cellular structures including membranes and proteins. Proline has been widely reported to induce the expression of salt stress-responsive genes which also possess proline-responsive elements in their promoters (Chinnusamy et al. 2005). The signaling mechanisms regulating proline biosynthesis may be ABA dependent or ABA independent (Zhu 2002). Proline provides osmo-protection to plants growing under salt stress, thereby enhancing growth (Yancey 1994). Exogenous application of proline at lower concentration ameliorates salinity and causes reduction in lipid peroxidative damage in groundnut (Hayat et al. 2012) and enhanced uptake of essential nutrients including K^+, Ca^{2+}, P, and N in *Zea mays* (Ali et al. 2008).

Glycine betaine (GB), a quaternary ammonium compound, is abundant in chloroplasts where it protects thylakoid membrane and stabilizes quaternary protein structures like PSII during salinity stress (Genard et al. 1991). Exogenous application of GB has been ameliorative to salt stress in many crops including rice (Lutts 2000) and tomato (Makela et al. 1998) where it enhances K^+ accumulation in shoots which is attributed to GB-induced vacuole productions in root cells which accumulate more Na^+, thereby reducing its transportation to the shoot (Ashraf and Foolad 2007). GB pretreatment upregulates a number of genes including lipoxygenase, calmodulin, protein kinase, and receptor protein kinase which mediate the signal transduction pathways during salt stress (John 2002). Thus, GB contributes to salt stress alleviation in plants through signal transduction and ion homeostasis (Yilmaz 2004).

The polyols, the sugar alcohols comprising of inositol, sorbitol, and mannitol, mediate osmotic balance by facilitating Na^+ sequestration in vacuoles and protect cellular structures by interacting with protein complexes during stress (Kanayama et al. 2006). There occurs a higher accumulation of mannitol is response to salt stress (Mitoi et al. 2009), and this acts by quenching hydroxyl radicals generated during fenton reaction (Gill and Tuteja 2010a). Transgenic potato plants having mannitol-1-phosphate dehydrogenase (*mtlD*) showed better tolerance to salt stress owing to greater mannitol production (Askari and Pepoyan, 2012). In transgenic peanut plants with enhanced mannitol synthesis (*mtlD* activity), a higher level of tolerance to salt stress was observed (Bhauso et al. 2014).

Polyamines are another group of small aliphatic amines which are increased to a higher endogenous level upon exposure of plants to any type of abiotic stress (Gill and Tuteja 2010b), with the most abundant types including putrescine (Put, 1, 4-diaminobutane), spermidine (Spd, N-3-aminopropyl-1, 4-diaminobutane), and spermine (Spm, bis (N-3-aminopropyl)-1,4-diaminobutane). The putative role of polyamines in imparting salt stress tolerance is attributed to their effects on ion transport (Pandolfi et al. 2010; Bose et al. 2011) wherein they interact with phospholipids of the PM, thereby enhancing their membrane stability (Saha et al. 2015). The Spm may block inward rectifying K^+ channels (KIRC) and nonselective cation channels (NSCCs) which would limit Na^+ influx and K^+ efflux, thereby directly influencing the ion transport during salt stress (Shabala et al. 2007; Zhao et al. 2007). During salt stress, polyamines accumulate to a larger level and make the tonoplast cation conductance more K^+ selective which leads to enhanced Na^+ sequestration in the vacuoles, thereby improving the K^+/Na^+ homeostasis in the cytosol (Zepeda-Jazo et al. 2008).

10.7 ROS Detoxification

Plants generate reactive oxygen species (ROS) comprising of superoxide ($O_2^{\cdot-}$), hydroxyl radicals ($OH^{\cdot}$), singlet oxygen ($^1O_2$), and hydrogen peroxide (H_2O_2) (Das and Roychoudhury 2014), as a part of normal metabolic reactions, but the level of ROS generation abruptly increases during stress. Excessive ROS generation during salinity stress is manifested in the form of enhanced lipid peroxidation of the membranes, reduced membrane stability, enzymatic inactivation, and loss of protein structure and function which ultimately leads to programmed cell death (PCD) (Mishra et al. 2011). Stomatal closure during salt stress causes unavailability of carbon dioxide for Calvin cycle causing depletion of oxidized $NADP^+$ pool subsequently transferring the electrons to O_2 generating $O_2^{\cdot-}$ (Mehler 1951). Thus, exposure of chloroplasts to excessive excitation energy ultimately generates ROS. The major sites of ROS generation and the corresponding processes therein are photosynthesis in chloroplasts, respiration in mitochondria, photorespiration in peroxisomes, and NADH oxidation at plasma membrane (Hossain and Dietz 2016).

A tight regulation of generation and quenching of ROS requires detoxification signaling which includes enzymatic and nonenzymatic systems to mitigate ROS stress. The enzymatic detoxification system includes a number of ROS scavenging enzymes, namely, superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), and guaiacol peroxidase (GPX) (Wang et al. 2017). The first line of defense against ROS damage starts with SOD which converts $O_2^{\cdot -}$ to H_2O_2; H_2O_2 is further taken up by APX, CAT, and GPX to generate H_2O (Ismail et al. 2014). The nonenzymatic detoxification also becomes a function upon exposure to stress, and the scavengers are enlisted as ascorbic acid, carotenoids, flavonoids, tocopherol, phenolics, and GSH (Abdallah et al. 2016). DHAR, MDHAR, and GR mediate the generation of ascorbic acid from dehydroascorbate (DHA), monodehydroascorbate (MDHA), and oxidized glutathione (GSSG) (Fig. 10.1).

10.8 Expression/Activation of Saline-Tolerant Genes and Changes in Transcriptome and Metabolomes

Salt tolerance in plant is very complex and governed by genetic factors. The receptors of plant cell membrane sense extracellular salt stress stimuli, and these external signals are translated into intracellular signals through the formation of second messengers such as calcium (Ca), ROS, and inositol phosphates (IPs). Later on, these messengers activate transcription factors (TFs) or protein kinases (PKs), causing differential expression of multiple stress-responsive genes, the translated products of which directly or indirectly confer tolerance (Huang et al. 2012). The TF families, WRKY, AP2/ERF, MYB, ZIP, NAC, and HSF, are known to be involved in the response to salt stress (Bera et al. 2013; Hu et al. 2008; Tian et al. 2015). In maize, TFs are differentially activated in response to salt stress, and exogenous glycine betaine-induced salinity mainly belongs to the MYB, MYB-related, AP2-EREBP, bHLH, and NAC families (Chen et al. 2020). The Na^+ efflux and Na^+ localization signaling pathways that are regulated by Ca-activated 14-3-3 proteins are the complex network of genes triggered in response to salt stress (Yang and Guo 2018a, b; Yang et al. 2019). The mitogen-activated protein kinases (MAPKs) and SOS (salt overly sensitive) participate in Na^+ efflux and Na^+ localization signaling pathways to maintain ion equilibrium in response to stress (Yang and Guo 2018a, b). The PKs RLKs (OsRLCK253 (receptor-like cytoplasmic kinase 253), RPK1 (receptor-like protein kinase 1) (Giri et al. 2011), SRLK (S-receptor-like kinase) (de Lorenzo et al. 2009), MAPKs (mitogen-activated protein kinases such as *AtMKKK4/6, ZmMKK1, GhMKK3, ZmMPK4, ZmMPK6/7* and *SIMPK3/7))* participate in response to salt stress (Moustafa et al. 2008; Yu et al. 2015). In addition, CBLs (calcineurin B-like proteins), CIPKs (CBL-interacting protein kinases (CIPKs), and CPKs (Ca-dependent protein kinases) also play a key role in response to salinity by sensing external signals and activating signal transduction pathways via phosphorylation of downstream genes (Zhu, 2002). The CBLs are Ca^{2+} sensors and regulate a group of Ser/Thr protein kinases (CIPKs), and

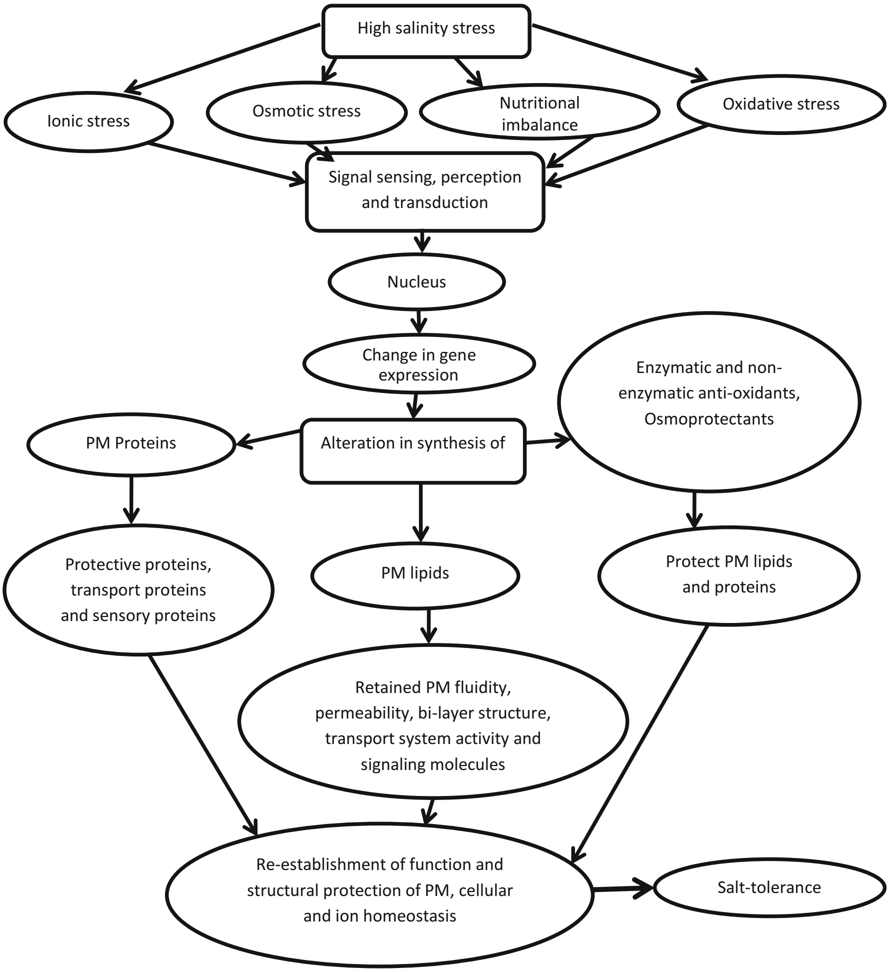

Fig. 10.1 Salt-induced signaling cascade mediating salt tolerance

CIPK-CBL complexes play an essential role in response to salt (Guo et al. 2001; Liu et al. 2015a, b). *CBL1* (*SCABP5*) acts as a positive regulator of salt stress responses (Cheong et al. 2003), and *CBL10* (*SCABP8*) interacts with the *CIPK24* to protect *Arabidopsis* shoots from salt stress (Quan et al. 2007). In addition, *CIPK21, CIPK25,* and *CIPK31* have also been reported to regulate plant response to salinity (Pandey et al. 2015; Meena et al. 2015). *ZmCPK12* and *OsCPK21* have been reported to confer tolerance to salt stress (Asano et al. 2011; Wang and Song 2013).

A specific gene *SKC1*, regulating the homeostasis of K^+/Na^+ and *OsMAPK33*, a gene in the MAPK signal pathway, allows rice plants to cope with salt stress by maintaining cell osmotic balance (Ren et al. 2005; Lee et al. 2011). Li et al. (2011) through the transcriptional expression profile of the roots of *Medicago truncatula* seedlings found a new transcription factor (TF) gene *MtCBF4* to play role under salt stress. In maize, a metal ion-binding protein gene (*LOC100281997*), KUP family potassium transporter gene (potassium transporter 21-like, *LOC103643618*), and a phosphate transporter protein gene *(LOC100502494*) were reported to maintain ion balance under salt stress (Chen et al. 2020). Protein phosphatase 2C gene increases the salt tolerance of *Arabidopsis thaliana* through positive regulation in abscisic acid (ABA) pathway (Liu et al. 2012).

The SOS signaling pathway is the most widely studied pathway in salt tolerance in plants (Yang et al. 2009) which involves five major components: calcineurin B-like protein (SCaBP5/8)/CBL-interacting serine/threonine-protein kinase (SOS2) complex, the CBL-interacting serine/threonine-protein kinase (PKS5)/14-3-3 protein complex, SOS1 (a plasma membrane Na^+/H^+ antiporter), AHX (a vacuolar Na^+/H^+ exchanger), and ATPase (Yang and Guo 2018a, b).

The genes encoding osmoregulation, carbohydrate metabolism, and redox regulation-related proteins, those encode PRPs, HSPs (heat shock proteins), LEA (late embryogenesis abundant) proteins, chaperone proteins, and LTSRs (low-temperature and salt-responsive proteins), are differentially expressed in response to salt stress. Delta1-pyrroline-5-carboxylase synthase (P5CS), a key enzyme involved in proline synthesis, is induced by salt stress (Huang et al., 2012). *LEA* proteins improve the resistance of plants to abiotic stress, and *HVA1, OsLEA3,* and *LEA14* have been shown to confer tolerance to salt stress (Battaglia and Covarrubias 2013; Jia et al. 2014).

A large number of secondary metabolites playing their role in the adaptability of plants to stressful environments are accumulated in plant (Ahmed et al. 2015; Wu et al. 2016). In *Arabidopsis,* expression of cytochrome P450 enhanced the salt tolerance, involved in xenobiotic metabolism and steroid biosynthesis (Mao et al. 2013). Accumulation of dihydroxy B-ring flavonoids improves the salt tolerance in soybean (*Glycine max*) (Pi et al. 2018). In maize, expression of P450 family 2 subtype gene (Ent-cassadiene C2-murhydroxylase-like, *LOC103626064*) one cyanidin 3-O-rutinoside 5-O-glucosyltransferase gene, *LOC103630119)* improves salt tolerance (Chen et al. 2020).

The synthesis of antioxidant enzyme such as peroxidase to minimize oxidative damage is another mechanism to adapt to salt stress-induced accumulation of ROS. In maize, peroxidase-related genes peroxidase 2 *(LOC103633480*), L-ascorbate peroxidase 1 *(LOC103634427*), peroxidase 67 *(LOC100285577*), peroxidase-1 (*LOC103633557*), APx1-cytosolic ascorbate peroxidase (*LOC100283822),* and peroxidase 2-like *(LOC103633483*) are reported to be upregulated under salt stress (Chen et al. 2020). Glutathione S-transferases (GSTs) provide resistance to oxidative toxicity and inhibit cell death under stress. GST gene improves salt tolerance in transgenic *A. thaliana* plants (Qi et al. 2010). GST 9 (*LOC542629*) regulates in maize line under salt stress (Chen et al. 2020).

Potato is a salt-sensitive crop, but some salt-tolerant tetraploid potato germplasm resources do exist. A few salt-responsive genes have been identified in potato, such as zinc finger protein gene (*StZFP1)* (Tian et al. 2010), ethylene-responsive TFs (*StERF1, StERF3,* and *StERF6)* (Bouaziz et al. 2015*),* dehydration-responsive element-binding protein genes (*StDREB1, StDREB2, StDREB3,* and *StDREB4)* (Bouaziz et al. 2015), *StNAC024, StNAC067,* and *StNAC108* (Singh et al. 2013). The RNA seq analysis under NaCl salt stress, the tolerant cultivar, Longshu No. 5, revealed genes in categories of TFs, PKs, stress-induced proteins, antioxidation proteins, ion transport proteins, and Ca signaling-related proteins to be involved in tolerance (Li et al. 2020).

The transcriptome analysis in sesame revealed differentially expressed salt-responsive genes related to metabolism of amino acid (alanine, aspartate, and glutamate) and carbohydrate (galactose), biosynthesis of secondary metabolites (carotenoids), glycolysis/gluconeogenesis, glyoxylate and dicarboxylate metabolism, porphyrin and chlorophyll metabolism, plant hormone signal transduction, and oxidation-reduction processes. Metabolome profiling under salt stress showed accumulation of metabolites in salt-tolerant genotypes, due to enhanced amino acid metabolism and sucrose and raffinose family oligosaccharides metabolism (Zhang et al. 2019).

Sugar beet *(Beta vulgaris* L.) is highly adaptable to salinity, and the transcriptome analysis under salt stress showed that a large number of differentially expressed genes (DEGs) were enriched in various metabolic pathways, and most of these genes were involved in carbon metabolism and amino acid (AA) biosynthesis. The metabolomic analysis revealed that sucrose metabolism (decreased sucrose content) and the activity of the tricarboxylic acid (TCA) cycle increased (decreased content of organic acids such as L-malic acid and 2-oxoglutaric acid) in response to salt stress. The AAs, betaine, melatonin, and (S)-2-aminobutyric acid increased, expression of the gene encoding xanthine dehydrogenase (XDH) was upregulated, and the expression of the gene encoding allantoinase (ALN) was downregulated, resulting in a large accumulation of allantoin (Liu et al. 2020).

Peanut is considered as a moderately salt-sensitive species (Singh et al. 2008). However, few peanut genes have been reported to function in response to salt stress. Drought-induced peanut gene *AhNAC2* overexpressed in transgenic *Arabidopsis* exhibited enhanced tolerance to drought and salinity stress (Liu et al. 2011). Overexpression of peanut allene oxide cyclase *(AhAOC*) in rice conferred tolerance against salinity (Liu et al. 2015a, b).

The salt tolerance genes enhancing tolerance to salinity in transgenic plants are *AlSAP* (A20/AN1 zinc-finger gene) (Ben Saad et al. 2010), *BADH* (betaine aldehyde dehydrogenase gene) (Kumar et al. 2004), *CCD1* (a gene-encoding calcium-binding protein with a C-terminal centrin-like domain) (Jing et al. 2016), *PtVP1.1* (H^+-pyrophosphatase gene) (Yang et al. 2015), *mtlD* (a gene for mannitol biosynthesis) (Abebe et al. 2003), *NHX* (a Na^+/H^+ antiporter gene) (Qiao et al. 2007), *P5CS* ($delta^1$-pyrroline-5-carboxylate synthetase gene) (Hmida-Sayari et al. 2005), *SOS1* (*Salt Overly Sensitive* pathway gene) (Feki et al. 2014), and *OsbZIP23* (basic leucine zipper transcription factor gene) (Xiang et al. 2008).

10.9 Mutation in Ion Transporter Amino Acid Sequence Improves Salinity Tolerance

The salinity tolerance in plants is determined by the transport of ions via plasma membranes. Under salinity, there is need to decrease Na^+ net influx and increase K+ uptake to modify mineral nutrition via root cells. Plants use various Na^+ transporters to deal potential harmful effects of Na^+. These are antiporters of Na^+/H^+ that extrude Na^+ from root cells and/or distribute Na^+ within tissues (Quintero et al. 2011) and HKT1 (HIGH-AFFINITY K^+ TRANSPORTER1)-type transporters (Rubio et al. 1995) that reduce accumulation of Na^+ in the shoots by retrieving Na^+ from the xylem (Davenport et al. 2007; Munns et al. 2012).

The first *HKT* gene in plants, *TaHKT2;1, a* Na^+-K^+ cotransporter, was reported in bread wheat *Triticum aestivum* (Rubio et al. 1995). These Na^+ transporters plant HKTs are divided into two subclasses based on amino acids sequence and ion selectivity (Mäser et al. 2002). Subclass-1 (HKT1) contain a Ser residue at the first pore-loop domain and transport Na^+, whereas subclass-2 (HKT2) contain a Gly residue at the first pore-loop domain and are permeable to both ions (Horie et al. 2001). In japonica rice cultivar, seven functional *OsHKT* genes have been identified (Garciadeblás et al. 2003). Of these, four genes *OsHKT1;1, OsHKT1;3*, *OsHKT1;4* and *OsHKT1;5* were grouped in the *HKT1* subclass, and products showed Na^+ selectivity.

The *Arabidopsis* contains a single-copy *AtHKT1* gene (Uozumi et al. 2000); *Thellungiella salsuginea* (Ts) has three copies of *HKT1*-type genes *TsHKT1*;*1, TsHKT1*;*2, and TsHKT1*;*3* in a tandem array (Wu et al. 2012); and another halophytic *Schrenkiella parvula* contains two *HKT1* genes *TpHKT1*;*1* and *TpHKT1*;*2* (Dassanayake et al. 2011). The three HKT1 genes in *T. salsuginea* and two in *S. parvula* contain a Ser residue at the selectivity filter in the first pore-loop domain and were defined as class-1 transporters although *TsHKT1*;*2* is more selective to K^+ (Platten et al. 2006). Morever, *TsHKT1;2, TpHKT1;2* and Yeast *ScTRK1,* selective K^+ transporter, contain conserved Asp residues (Asp-207 and Asp-205, respectively) in their second pore-loop domains as well as in the adjacent transmembrane domain (Asp-238 and Asp-236, respectively); hence, Asp-207, and probably Asp-238, may impart differential selectivity to ions in subclass-1 HKT1 (Ali et al. 2012). However, *HKT1* in dicots has either Asn or Ser residues (Wang et al. 2014).

Serine in the first pore-loop domain appears to be an essential amino acid that favors Na^+ uptake by *HKT1* transporters and cation selectivity and thus can be altered by a single amino acid substitution. Further, substitution of Asn residue (N) in the second pore-loop domain by Asp (D) greatly reduces Na^+ uptake and increasing K^+ transport capacity of *AtHKT1;1* by two-2 to three3fold. Vice versa, replacing Asp in the protein sequence of *TsHKT1;2* by Asn increases Na^+ permeability and decreases the K^+ uptake. *TsHKT1;2* and *TpHKT1;2* have two conserved Asp (D), second pore-loop domain (D207/205) and adjacent transmembrane domain (D238/236). The D207 and D205 play an important role in determining the Na^+/K^+ transport in *TsHKT1;2* and *TpHKT1;2* respectively. In contrast, most other HKTs include either Asn (N) or less frequently Ser (S), instead of the D207/205. When Asp residues are present, the K^+ ion was confined to the pore region of the proteins because of a strong salt bridge interaction between the K^+ ion and oxygen atoms in Asp residues, thereby allowing K^+ permeation through the HKT transporter, whereas the weak binding of K^+ when Asn residue is present apparently enabled binding of Na^+ ions and successfully substitute K^+ ions. So Asp residue in the pore region is critical for K^+ selectivity in HKT1-type transporters and salt tolerance. So a point mutation in a pore-loop region could give rise to the rectifying property of HKT transporters; however, it depends also on other amino acids that are present in transporters protein sequence (Ali et al. 2016).

10.10 Conclusion

Salt tolerance in plants is a complex trait and governed by physiological, biochemical, and genetic factors. The cell membrane receptors perceive the extracellular salt stress stimuli, which get translated into intracellular signals through enhanced formation of second messengers such as calcium, ROS, and inositol phosphates. These messengers further activate transcription factors or protein kinases, causing differential expression of multiple stress-responsive genes, the translated products of which directly or indirectly confer tolerance. The salt tolerance genes enhancing tolerance to salinity in transgenic plants are *AlSAP* (A20/AN1 zinc-finger gene), *BADH* (betaine aldehyde dehydrogenase gene), *CCD1* (a gene encoding calcium-binding protein with a C-terminal centrin-like domain), *PtVP1.1* (H^+-pyrophosphatase gene), *mtlD* (a gene for mannitol biosynthesis), *NHX* (a Na^+/H^+ antiporter gene), *P5CS* (delta^1-pyrroline-5-carboxylate synthetase gene), *SOS1* (*salt overly sensitive* pathway gene), and *OsbZIP23* (basic leucine zipper transcription factor gene). The plants deal with potential harmful effects of Na^+ by employing antiporters Na^+/H^+ extruding Na^+ from root cells and/or distributing Na^+ within tissues and HKT1 (HIGH-AFFINITY K^+ TRANSPORTER1)-type transporters, which reduce accumulation of Na^+ in the shoots by retrieving Na^+ from the xylem.

The plants, thus, prioritize the maintenance of low Na^+/K^+ ratio in the cytosol through restricted salt uptake in plants from the soil, controlled long-distance transport of salt, its compartmentalization in specific tissues, and salt extrusion from the plants. The pathways undertaken during ionic stress, osmotic stress, and ROS accumulation are intricately entwined to target the restoration of K^+ homeostasis in the cytosol required for the stability of cellular membranes, protein structures, and function and thereby essentially contributing to the survival of plants during salt stress.

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Potassium: A Potent Modulator of Plant Responses Under Changing Environment

11

Radwan Khalil, Nesma Elsayed, Tanveer Alam Khan, and Mohammad Yusuf

Abstract

Potassium is an essential plant nutrient and required in large amounts for proper growth and reproduction of plants. Potassium is considered second only to nitrogen, when it comes to nutrients needed by plants, and is commonly considered as the "quality nutrient." However, its deficiency causes severe alteration in various physiological processes such as photosynthetic CO_2 fixation and impairment in utilization of photosynthates under abiotic stresses. On the other hand, exogenous application of potassium plays pivotal role in cell turgor maintenance, osmotic adjustments and regulates stomatal opening under various environmental cues. Many reports revealed that exogenous application of potassium boost antioxidant arsenal in plants under stressful conditions and showed significant role in mitigation of oxidative stress in plants. Additionally, many evidences showed that presence of potassium could greatly lower the reactive oxygen species (ROS) production by reducing activity of NAD(P)H oxidases and maintaining photosynthetic electron transport. In this chapter, we will shed light on the data related with the role of potassium-mediated regulatory functions against abiotic stresses, its possible molecular mechanisms for regulation of

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various physiological processes under changing environment, and its role in conferring tolerance against abiotic stresses. Lastly, we will discuss the cross talk of potassium with various phytohormones under stress and stress-free conditions.

Keywords

Abiotic stress · Antioxidant system · Plant · Potassium · Tolerance

11.1 Introduction

The world population is increasing quickly and may reach to 9.7 billion by the year 2050 (United Nations Department of Economic and Social Affairs 2019). This requires to increase the crop production for future generations. The crop production exposed to many biotic (e.g., pathogens, weeds, insects) and abiotic (e.g., salinity, drought, cold, waterlogging) factors that can decrease the quantity and quality of crop production. Increasing evidence suggested that mineral nutrients play main role in plant stress tolerance (Kafkafi 1990; Kant et al. 2002; Marschner 2012). One of these minerals, potassium (K), is one of the essential nutrients for plant growth. It is classified as a macronutrient, as nitrogen (N) and phosphorus (P). K plays essential role in plant growth and metabolism processes, and contributes greatly to the survival of plants under biotic and abiotic stresses. Plants deficient in potassium are less resistant to drought, more water, and high and low temperatures. Potassium affects quality factors such as size, shape, color, and vigor of the seed or grain and improves the fiber quality of cotton. The increase in crop yields by K application results in the increase in root growth, improved drought tolerance, and increase in the enzyme activities involved in growth and also enhances the protein content of plants and food formation through the photosynthesis process. In addition, it helps translocate sugars, maintains turgor, and reduces water loss and wilting. The application of K has been shown to enhance photosynthetic rate, as well as plant growth and crop yields, and water shortage resistance in different crops under water stress conditions (Yadav et al. 1999; Egilla et al. 2001).

Potassium is considered as a regulatory element for most of plant physiological process through seed germination, stomatal movement, cation-anion balance, nutrient balance, phloem transport, photosynthesis, energy transfer, protein synthesis, osmoregulation, and enzyme activation, in addition to tolerance to biotic and abiotic stresses (Marschner 2012; Tu et al. 2017). Recently, K has ameliorated role in abiotic stress tolerance. Under salinity stress, K was found to preserve ion homeostasis and to organize the osmotic balance. Under drought stress conditions, K regulates the opening of stomata and adapts plant to water shortage. Many reports support the notion that K increases antioxidant arsenal in plants and therefore protects them from oxidative stress under various environmental adversities.

Besides, this mineral provides some cellular signaling alone or in association with other signaling molecules and phytohormones (Mirza Hasanuzzaman et al. 2018).

Environmental stresses such as drought, salinity, temperatures, soil acidity, flooding, and pathogenic infections are increasing due to elevation in world population and intensive use of natural resources. These environmental stresses lead to a significant reduction in crop yields below its maximum potential. Bray et al. (2000) showed that the relative decrease in potential maximum crop yields (i.e., yields under ideal conditions) correlated with abiotic stress factors varies between 54% and 82%. Abiotic stresses such as water shortage, salinity, excess light, temperature, soil acidity, and inadequate mineral nutrient supply resulted in decreasing yield. Therefore, to increase crop production and preserve food security, the detrimental effects of environmental stresses should be minimized by (1) raising chemical and physical fertility as well as maintaining productivity of cultivated soils by adequate and balanced supply of mineral nutrients and (2) applying modern breeding techniques and biotechnological tools. Enhancing evidence suggests that mineral-nutrient status of plants plays a critical role in increasing plant resistance to environmental stress factors (Marschner 1995). Of the mineral nutrients, K plays a particular role in contributing to the survival of crop plants under environmental stress conditions. Potassium is essential for many physiological processes, such as photosynthesis, translocation of photosynthates into sink organs, maintenance of turgescence, activation of enzymes, and reducing excess uptake of ions such as Na and Fe in saline and flooded soils (Marschner 1995; Mengel and Kirkby 2001).

Potassium was found to have a geochemical origin as a consequence of weathering of mica and feldspar minerals. Zorb et al. (2014) reported that plants can use about 2% of the total K quantity because most of soil K is present as non-exchangeable K and in interlayer forms which are not available to plants. Soil K can be divided chemically into slowly available K (non-exchangeable K), unavailable K (mineral K), and readily available K (water-soluble and exchangeable K) (Iren and Amalu 2012). Potassium can be easily exchanged to plants and readily replaced with other cations at exchange sites in soils (Sparks 2000). Plants can take up K gradually in the long term, especially when exchangeable K content is low (Schneider 1997).

McLaren and Cameron (2005) showed that the mineral K refers to “structural” or “lattice” K of the primary soil minerals, such as feldspars and micas. These forms have various dynamic inter-relationship, whereby release and fixation may occur simultaneously. K-solubilizing bacteria (KSB) can increase availability of K from unavailable (insoluble/mineral) forms in soils, and thereby, they have important roles in crop establishment on K-limited soils. Etesami et al. (2017) reported that the significant role of K-solubilizing bacteria can result from soil acidification (decreasing pH), the release of chelating compounds, and also by releasing organic acids. The central vacuole of plant cells contains majority of K^+, where it acts as an osmoticum, and this pool may not be essential because other osmotica can replace for K^+ when it is in short supply (Leigh and Wyn Jones 1984). Instead, the main requirement for K+ seems to link its role as an activator of biochemical processes in the cytosol, especially protein synthesis (Leigh and Wyn Jones, 1984; Walker et al. 1998).

Recent advancements help in understanding the extent to which K^+ concentrations in plant cells are controlled (Walker et al. 1996). In parallel, the identification and characterization of both K^+ channels and active K^+ transporters result from the application of molecular biological approaches (Schachtman 2000; Rodriguez-Navarro 2000). The influence of K^+ on soil structural stability is obscure given that many studies detected destabilizing as well as stabilizing effects due to the presence of K^+. Markgraf and Horn (2006) revealed that an increase in soil stability results from higher K^+ rates, presumably due to decreased electrostatic repulsion. These results were similar to that obtained by Holthusen et al. (2010, 2012). Then again, K^+ is said to have a dispersive character and tends to hamper aggregation (Dexter and Chan 1991). Besides, K^+ may affect soil stability indirectly, e.g., by increasing plant growth and thereby increasing organic matter (OM) content that can either stabilize (Zhang and Hartge 1992) or destabilize soil structure (Blanco-Canqui et al. 2005). Another factor is the pH which relies on nutrient utilization by plants (equal to proton release) or the actual soil type, etc. Also, the type of clay mineral is assumed to depend on K^+ rate in soil (Tributh et al. 1987; Srinivasa Rao and Khera 1994). Laribi et al. (2005) showed that various clay minerals come along with a various structure and therefore soil stability. Thus, the mechanisms by which K^+ causes either an increase or a decrease in soil strength affect soil stability.

In this chapter, we will give you a basic understanding of K, including plants' K nutrition; the evidence for the regulation of K^+ concentration in plant cells, particularly in the cytosol and vacuole; how transport is controlled to achieve this; how it reacts in soils; its function in plants; its role in efficient crop production; and the roles of K in minimizing adverse effects of environmental stress conditions on crop production.

11.2 Signaling and Transport of Potassium

Potassium transferred from the soil to the roots through a combination of diffusion and mass flow. Low- and high-affinity systems have been identified to explain the uptake of K (Sardans and Penuelas 2015). K increases in the vacuole in large pool in plant cells, and the concentration of K in vacuoles depends on the K supply and the type of plant tissue (Leigh and Wyn Jones 1984; Walker et al. 1996). K absorption by the root cell and translocation from root to shoot is against the concentration gradient, a process conducted by plant K^+ transports components such as channels and K^+ transporters. Ward et al. (2009) reported that in many higher plant species, most of the genes encoding K transporters and channels have been cloned and identified. Thesis transporters and channels vary in their energetic coupling, affinity, and selectivity for K^+ and shape the complex K^+ transport system in plant cells.

Potassium ions could be recycled and distributed between the cytoplasm and vacuole (K^+ pool). The voltage-independent K^+-selective channels were initially identified at the tonoplast of stomatal guard cells, and they are necessary for vacuolar

K^+ release during stomatal closure (Ward and Schroeder 1994). Also, K^+ transporters participate in intracellular K^+ distribution in plant cells. These systems create an electrical gradient from active release of protons due to the entrance of net-positive electric charge. Potassium can cause a marked deficiency in many plants when it declines below 10 g kg^{-1} dry weight. It is well known that K has vital functions in the field and vegetable crops such as cotton, sweet potato, alfalfa, and sugarcane. It affects water relations in plants under water shortage stress through increasing water uptake by controlling transpiration and stomatal moving. Absorption of K by plants is highly related to its level of available forms and fertilization. Potassium enhances stress tolerance, enzyme activation, and resistance of plants against diseases and insects. Moreover, it plays marked roles in many metabolic processes, including photosynthesis, turgor-driven movements, osmoregulation, protein biosynthesis, and the plasma membrane potential (Oosterhuis et al. 2013).

It has been reported that K has a geochemical origin as a consequence of weathering of mica and feldspar minerals. The plants used about 2% of the total potassium quantity because most of soil K is present as nonexchangeable K and in interlayer forms that are not available to plants (Zorb et al. 2014). Chemically, soil K can be divided into readily available K (water-soluble and exchangeable K), slowly available K (nonexchangeable K), and unavailable K (mineral K) (Iren and Amalu 2012). Exchangeable K is easily available to plants and can be readily replaced with other cations at exchange sites in soils (Sparks 2000). Slowly available K can be gradually taken up by plants in the long term, especially when exchangeable K content is low (Schneider 1997). The K element also refers to “structural” or “lattice” K of the primary soil minerals, such as feldspars and micas (McLaren and Cameron 2005). Potassium uptake efficiency is controlled by mechanisms depending on root morphology (El Dessougi et al. 2002), uptake capacity at the root surface (Ashley et al. 2006), and the capacity to mobilize nonexchangeable K by root exudates (Trehan et al. 2005). Potassium-use efficiency is driven by effective K translocation between organelles, cells, and organs (Rengel and Damon 2008) and the capability to use other osmolytes (e.g., soluble sugars, NO_3, or amino acids) or cations (e.g., Na^+, Ca^{2+}) to substitute K^+ (Pettigrew 2008). Jalali and Zarabi (2006) studied kinetics of K^+ release and wheat uptake in a greenhouse experiment in some calcareous soils. They observed that the rate of K^+ released to 0.01 M $CaCl_2$ was correlated with cumulative K^+ uptake. They concluded that a fraction of nonexchangeable K^+ was taken up by wheat. Several attempts have been proposed to characterize the capacity of total available K^+ by extracting a fraction of nonexchangeable K^+ (Richards and Bates 1988).

It is worthwhile to try to improve crop tolerance to stress in low-moisture soils by inducing deeper rooting, larger absorption surfaces, and greater water retention in plant tissues. Deeper rooting could be achieved by deep placement of K fertilizer that is associated with other mineral nutrients, such as P and N, which both have root signaling functions (Kirkby et al. 2009). Because plant roots are the sites of initial K^+ deficiency sensing, it is reasonable to expect their cells to contain sensors for K^+ deficiency signals. These K^+ sensors could plausibly be located at the PMs of epidermal cells or root hairs and have the capacity to sense changes in external K^+

concentration. Unfortunately, no K^+ sensor has yet been identified at the molecular level. At the early stage of plant responses to K^+ deficiency, plant cells may mobilize K^+ ions from the vacuole (K^+ pool) into the cytoplasm to compensate for the reduced K^+ uptake from the external medium (Walker et al. 1996). The K^+ in cytoplasm is therefore not significantly decreased in the short term. In the longer term, the K^+ gradually reduces, ultimately affecting physiological processes in plant cells. The activities of most enzymes in plant cells need K^+ ions as a cofactor. Thus, these K^+-activated enzymes may act as K^+ sensors in the cytoplasm. Among these enzymes, pyruvate kinase is considered the most likely candidate (Amtmann and Armengaud 2009; Armengaud et al. 2009). This kinase is highly sensitive to cytoplasmic K^+ (Ramirez-Silva et al. 2001), and its activity can be directly inhibited by low $[K^+]$ cyt in root cells after plants are subjected to long-term K^+ deficiency stress (Armengaud et al. 2009). Ca^{2+} sensors are involved in K^+ uptake in *Arabidopsis* roots, especially under K^+-deficient conditions (Li et al. 2006; Xu et al. 2006), which suggests that plant cells may require a specific Ca^{2+} signal for K^+ deficiency stress. The elevation of $[Ca^{2+}]$ cyt induced by low $[K^+]$ ext. has been reported in guard cells (Allen and Ort 2001), and recent experiments have shown that K^+ deficiency in the external medium could also induce $[Ca^{2+}]$ cyt elevation in Arabidopsis root cells, although this K^+ deficiency Ca^{2+} signal needs to be further characterized. The Ca^{2+} influx mediated by these channels may subsequently generate the specific Ca^{2+} signal for K^+ deficiency stress. Although these Ca^{2+} sensors have been shown to play a role in the regulation of K^+ nutrition, the mechanisms for how they respond to specific Ca^{2+} signals remain unclear.

Reactive oxygen species, as an important signal component, plays a crucial role in plant stress response, development, pathogen reaction, and many other physiological processes (Horie and Schroeder 2004). Nutrient deprivation—including deficiencies in K^+, nitrogen, phosphorus, and sulfur—could also induce ROS signals in plant root cells (Schachtman and Shin 2007; Shin et al. 2005; Shin and Schachtman 2004). Benlloch-González et al. (2010) explained that the low plant K status could inhibit water stress-induced stomatal closure via ethylene synthesis, and stomatal conductance could be significantly reduced in K^+-starved plants after the adding of an ethylene synthesis inhibitor (cobalt). Potassium starvation increases the transcription of genes involved in ethylene production and signaling and stimulates ethylene production (Shin and Schachtman 2004; Benlloch-González et al. 2010). Then the increased ethylene could inhibit the action of abscisic acid (ABA) on stomata and delay stomata closure (Tanaka et al. 2005, 2006).

Photosynthesis inhibition can further disturb the balance between ROS production and antioxidant defense (Reddy et al. 2004; Cruz de Carvalho 2008), resulting in ROS accumulation. The ROS have a dual action in biotic and abiotic stresses that depends on their cellular concentration (Dat et al. 2000). Low levels of ROS could be involved in the stress-signaling pathway by triggering stress defense/acclimation responses (Dat et al. 2000; Vranova et al. 2002). However, ROS became extremely injurious to cellular membranes and other cellular components when its concentrations reached the point of phytotoxicity, resulting in oxidative stress and, eventually, cell death (Dat et al. 2000; Mittler 2002).

11.3 Effect of Exogenous Potassium on Growth and Bio-productivity

From seed germination to seed production, plants require various macronutrients and micronutrients. Among the plant nutrients, potassium (K) is one of the vital elements required for various biochemical and physiological processes that are responsible for plant growth and development. Potassium is not only a constituent of the plant structure, but it also has a regulatory function in several biochemical processes related to protein synthesis, carbohydrate metabolism, and enzyme activation (Mirza Hasanuzzaman et al. 2018). When plants experience K deficiency, they exhibit stunted growth and yellowing in their leaf margins. Moreover, a poor root system, lodging, and yield reductions are common phenomena associated with K deficiency (Fig. 11.1).

Potassium assists in seed germination by initiating the rapid imbibition of water, and it also facilitates other physiological processes (Farooq et al. 2008). Potassium salts have been thoroughly studied as good catalysts for improving seed germination and the emergence rate. The most common forms of K salts used in seed priming are potassium nitrate (KNO_3), potassium chloride (KCl), and dipotassium hydrogen phosphate (K_2HPO_4) (Copeland and McDonald 2001; Mohammadi 2009). Potassium as a macronutrient plays important role in plant growth and development (Fig. 11.1). Potassium has a role in cell expansion, maintains the turgor pressure of plants, assists in osmoregulation of cell, helps in opening and closing of stomata, and activates more than 60 enzymes (Hawkesford et al. 2012). Maintaining the K level and its ratio with other essential plant nutrients (especially with sodium, Na) in plant growth medium or at the cellular level is crucial for normal function as well as the growth of the plant (Wang et al. 2013). Gerardeaux et al. (2010) observed that the K deficiency in the vegetative phase of cotton (*Gossypium hirsutum* L.) reduced the

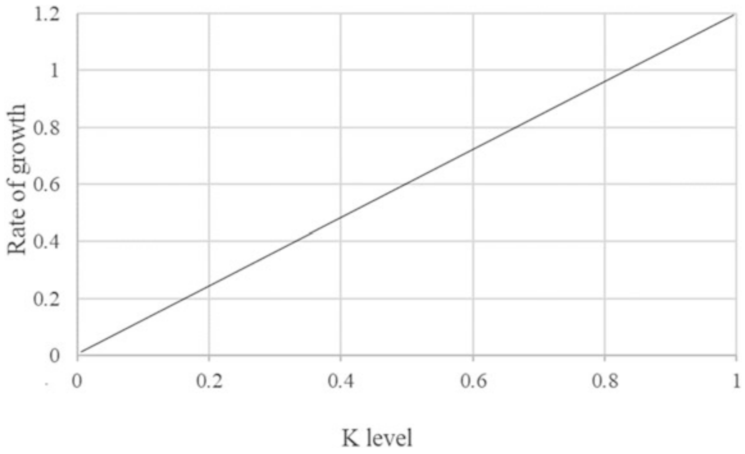

Fig. 11.1 Relation between rate of growth and K level

plant dry matter production, leaf area, and internode size, which leads to a reduction in plant growth.

Soil fertilization is the most common method for supply of essential nutrients to plants. However, higher plants can also absorb mineral nutrients when applied as foliar spray in appropriate concentrations (Eichert and Fernández 2012). Foliar fertilization facilitates the rapid absorption of mineral elements; it can be performed throughout the growing season particularly during peak periods of nutrients demand without interaction with soil components, precipitation, adsorption onto soil surfaces, or risk of loss by erosion (Fernández and Brown 2013). Potassium plays an imperative role in the photosynthesis process and the subsequent carbohydrate translocation and metabolism, which eventually increases the crop yield and improves the grain quality (Pettigrew 2008; Lu et al. 2016). Both the leaf number and the leaf size are reduced while the plant is deficient in K. The leaf number and size reduction later hasten the diminished photosynthetic rate per unit leaf area and thus account for an overall reduction in the amount of photosynthetic assimilates available for growth (Pettigrew 2008). Furthermore, K controls photosynthesis through sunlight interception. The leaf surface area and sunlight interception were both reduced dramatically when the K was below the level required by the plant (Bednarz et al. 1998). The photosynthesis rate in plants increased with the higher utilization and export of photoassimilates. Evidence showed that the sucrose level in the leaves was increased by several folds when the plants were supplied with a sufficient level of K (Zhao et al. 2001). Potassium plays an essential role in activating the ATP synthase enzyme, thus assisting in the photosynthesis process. Shingles and McCarty (1994) suggested that the ATPase performance is best when the K content in the plant is at an optimum level.

Potassium plays roles in flowering and pollen germination as well as in seed development. Fan et al. (2001) found that externally applied K helps to increase the pollen germination rate, and K also increases tube growth in *Arabidopsis*. Makhdum et al. (2007) described that in some cases, the yield depends on the reproductive-vegetative ratio (RVR). If the RVR is lower, then the vegetative growth is higher than the reproductive growth, and in this case, the yield is reduced. Sadiq and Jan (2001) observed that a split application of K delayed flowering and physiological maturity even after a split application of a 60 kg ha^{-1} K application, but when using the 90 kg ha^{-1} K application as a basal dose, the numbers of days to tasseling, silking, and physiological maturity were increased.

Potassium regulates the biosynthesis, conversion, and allocation of metabolites that ultimately increase the yield. Islam and Muttaleb (2016) reported that K helps to increase the N uptake as well as N use efficiency that helps in increasing the yield of rice. Cheema et al. (2012) found that K helps to increase the utilization of carbohydrates, and it increases the leaf area index, which helps to increase the dry matter accumulation and ultimately increase the yields in rapeseed (*Brassica napus* L.). Waraich et al. (2011) reported that 200 mM KNO_3 application increased the plant branches, plant height, and number of balls per plant in *G. Hirsutum*, but in case of ball weight, 150 mM foliar application is better. According to Colpan et al.

(2013), K plays a vital role to increase the yield and yield components in tomato (*Lycopersicon esculentum* L.).

Potassium is responsible not only for higher production but also for the improved quality of the harvest. Thus, K ensures high-value crops and benefits to growers. K is sometimes called the “quality element” for its association with better crop production, which is supported by many scientists. Yang et al. (2004) showed that the protein percentage in maize (*Zea mays* L.) grain was higher when a balanced N-P-K fertilizer was applied. However, when only N-P fertilizer was applied, the protein percentage as well as the grain quality was reduced. In G. *hirsutum*, the important quality control parameters are the fiber length, strength, uniformity, micronaire, color, and many others. Many reports strongly support the idea that the fiber quality depends on having optimum levels of K. When the K supplies are not sufficient, the osmotic potential of the fiber becomes more negative. According to Ashfaq et al. (2015), K deficiency reduces the cotton yield and quality. Mehrandish et al. (2012) showed that the total soluble solids, soluble sugar content, refinable sugar, and purity percentage of sugar beet (*Beta vulgaris* L.) root juice increased with K application. Economakis and Daskalaki (2003) explained that K increased the dry matter, total soluble solids, firmness, and vitamin C content in tomatoes under both normal and saline conditions. The seed yield was significantly enhanced by K application compared to the control treatment (Tian et al. 2017).

11.4 Effect of Exogenous Potassium on Photosynthesis and Plant Water Relations

Potassium greatly effects on the photosynthesis process and the subsequent carbohydrate translocation and metabolism that improve the grain quality and increase the crop yield (Pettigrew 2008; Lu et al. 2016). The deficiency in K leads to reduction in leaf number and leaf size of plant. This reduction later accelerates the diminished photosynthetic rate per unit leaf area and consequently accounts for a total reduction in the amount of photosynthetic assimilates available for growth (Pettigrew 2008). Moreover, K dominates photosynthesis through sunlight interception. Both the leaf surface area and sunlight interception were reduced dramatically when K was below the level required by the plant (Bednarz et al. 1998).

During photosynthesis, stomatal regulation governs the continual photosynthesis operation and is significantly moderated by the amount of K kept in the plant (Marschner 2012). Potassium lack resulting in reduced stomatal conductance raised the mesophyll resistance and minimized the ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activity in plants that ultimately lowered the overall photosynthesis rate (Zhao et al. 2001). The photosynthesis rate in plants increased with the higher utilization and export of photoassimilates. Evidence showed that elevated sucrose levels in the leaves confirm suppling plant with a sufficient level of K (Zhao et al. 2001). Potassium deficiency leads to reduction in photosynthetic CO_2 fixation and the utilization of photoassimilates, which accelerated the plant ROS production, eventually accelerating rapid photooxidative damage (Waraich et al. 2012).

Consequently, the most important function of K in regulating the stomatal aperture is in balancing CO_2 entry and H_2O vapor elimination from intercellular spaces. However, the amount of CO_2 entry into the intercellular spaces symbolizes the amount of photosynthate production in the leaf. Potassium has a significant role in activating the ATP synthase enzyme, assisting in the photosynthesis process. Shingles and McCarty (1994) proposed that the ATPase performance is best when the K content in the plant is at an optimum level. However, the molecular identification of the K^+ transporters implicated in photosynthetic regulation has increased the importance of K in plants. Recent studies have detected that the substantial roles of three K^+ efflux antiporters, AtKEA1/AtKEA2/AtKEA3, were involved in photosynthesis and primary chloroplast development in Arabidopsis. AtKEA1 and AtKEA2 are located at the inner envelope membrane of the chloroplasts, while AtKEA3 localizes to the thylakoid membrane (Kunz et al. 2014).

A significant damage in the chloroplast development and photosynthesis rate was observed in the AtKEA1, AtKEA 2, and AtKEA3 triple mutants, leading to the stunted growth of the mutant plants (Kunz et al. 2014; Dana et al. 2016). Regulation of chloroplast development results from AtKEA1 and AtKEA2, which show polar distribution in small and dividing plastids. AtKEA3 is an H/K antiporter that mediates H efflux from the thylakoid lumen to the stroma through H/K exchange and regulates the proton motive force (pmf) across the thylakoid membranes, and thus, it adjusts photosynthesis as well as photosynthetic acclimation in fluctuating light environments (Armbruster et al. 2014; Wang et al. 2017).

11.5 Effect of Exogenous Potassium on Plants Exposed to Water Stress

The main limitation for plant growth and crop production in arid and semiarid regions is soil water availability. Plants that are continuously exposed to water shortage can form ROS, which leads to leaf damage (Foyer et al. 2002; Oerke and Dehne 2004; Cakmak 2005) and, ultimately, decreases crop yield.

Water is required in several ways for the growth and development of agricultural crops. One function is to act as solvent and as transport medium for nutrients in soil and plant. In soil, dissolved substances move toward the root by mass flow and diffusion (Peiter 2014). While mass flow is important for the supply of plants with mineral such as calcium, magnesium, nitrate, and borate, diffusion plays the conclusive role in the case of potassium, phosphate, manganese, and copper (Schilling 2000). Therefore, water shortage may cause nutrient deficiency. On the other hand, water is required for many physiological processes within the plant. It functions as building material in photosynthesis, as medium for biochemical reactions and transport processes, and as swelling agent for enzymes, other proteins, and cells, and it is essential for the generation of turgor (Shao et al. 2009; Taiz and Zeiger 2010). In addition, water stabilizes the temperature of the plant because of its high thermal capacity and its latent heat at transpiration. Therefore, shortage of water induces various malfunctions in metabolism and eventually reduces dry matter

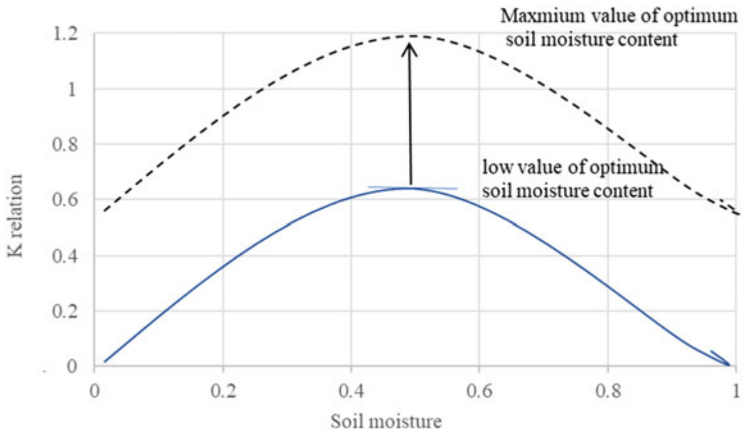

Fig. 11.2 Relationship between K and water

production and growth. Potassium has been frequently shown to relieve some of the negative effects of drought, which may be linked to its positive effects on soil-water relationships (Damm et al. 2013) and to its role as effector of most enzymes in the plant (Romheld and Kirkby 2010; Marschner 2012; White 2013; Zorb et al. 2014). For instance, the cation stabilizes the efficiency of CO_2 fixation due to its involvement in the activation of ribulose bisphosphate carboxylase/oxygenase (Oosterhuis et al. 2013). A further important interaction between potassium and water exists in the regulation of stomatal aperture (Zorb et al. 2014), which affects water use efficiency and also CO_2 assimilation (Brag 1972). Accordingly, it has been shown that a relatively high photosynthetic capacity can be maintained in leaves of highly K-supplied plants at low water potential (Gupta et al. 1989). Hence, the misallocation of electrons out of the photosynthetic flow is avoided, and the generation of reactive oxygen species (ROS) as superoxide radical ($O_2^{\cdot -}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($OH^{\cdot}$) is retarded. Potassium deficiency also aggravates NADPH oxidase-mediated ROS formation (Cakmak 2005). Because ROS species cause membrane damage and chlorophyll degradation, K may mitigate those effects of water shortage by the inhibition of their generation Fig. 11.2.

Besides their impact on primary substance production, K shortage as well as drought stress affect the translocation and portioning of the assimilates within the plant (Sangakkara et al. 2000; Hermans et al. 2006). This begins with the active phloem loading with sucrose (Deeken et al. 2002), which is favored by K (Gajdanowicz et al. 2011). In addition, K is relevant for the pressure gradient-driven transport within the phloem and for the storage of assimilates in sink tissues. Therefore, the interactions of K and water are very versatile, and a high K supply may be important for mitigating damages caused by drought stress (Grzebisz et al. 2013; Kerschberger and Preusker, 2014).

Potassium nutrition not only increased plant total dry mass and leaf area but also improved the water retention in plant tissues under drought stress (Lindhauer, 1985).

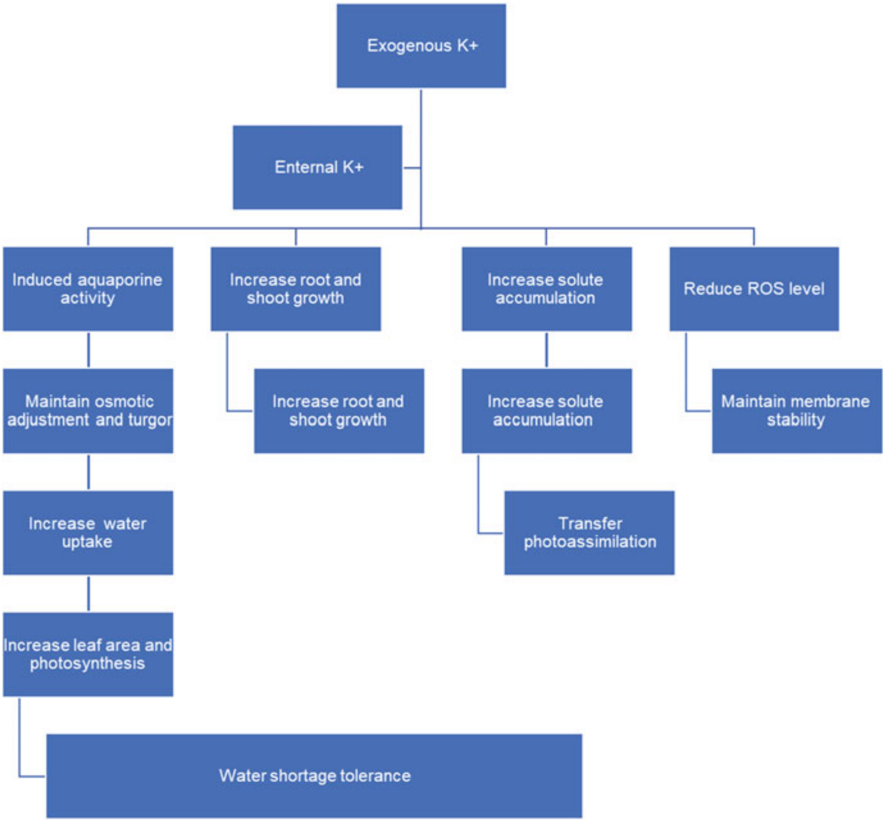

Fig. 11.3 Role of K^+ under water shortage stress

Increased evidence shows that the maintenance of membrane integrity and stability under drought stress is also essential for plant drought tolerance (Bajji et al. 2002). Cell membrane stability was significantly declined under drought stress (Wang and Huang 2004). In a study by Premachandra et al. (1991), maize plants with higher K applications showed greater adaptation to water stress. This improvement was mainly attributed to the role of K in improving cell membrane stability and osmotic adjustment ability. An adequate K supply is essential to enhancing drought resistance by increasing root elongation and maintaining cell membrane stability Fig. 11.3.

Aquaporins are channel proteins that are present in the plasma and intracellular membranes of plant cells. They play a crucial role in plant water relation by regulating the osmotic potential and hydraulic conductivity of membranes and make changes in plant water permeability (Maurel and Chrispeels 2001; Heinen et al. 2009). Under drought stress conditions, aquaporin gene expression can be regulated (Tyerman et al. 2002; Lian et al. 2004) to help plants maintain their water balance (Tyerman et al. 2002; Kaldenhoff et al. 2008). 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; Galmes et al. 2007; Cuéllar et al. 2010). Liu et al. (2006) observed that transcription expression levels of the PIPs and K^+ channel-encoding genes were induced by K^+ starvation and could be downregulated by a polyethylene glycol (PEG)-mediated water deficit in rice, which may result in a reduction in the membrane water permeability and then promote cellular water conservation during drought stress. Kanai et al. (2011) also observed close coupling between aquaporin activities and K-channel transporters. The initial response of K deficiency was perceived in the form of a change in K-channel activity, which altered root hydraulic conductance, and transduction of the follow-up signal resulted in a shift of aquaporin activity. They found that aquaporin activities might have been suppressed by K deficiency and result in a reduction of root hydraulic conductance and water supply to the growing stem for diameter expansion and the leaf for transpiration. Water channels and K^+ channel/transporters are functionally co-regulated as a part of plant osmoregulation to maintain appropriate cytosolic osmolarity and acclimate the plant to drought or other stresses (Liu et al. 2006).

The maintenance of a favorable water status is critical for the plant's survival under drought stress. Osmotic adjustment is a major trait that is associated with maintaining high cellular turgor potential and water retention in response to drought stress. Many studies have shown that osmotic adjustment of leaves is positively correlated with drought tolerance in various plant species (DaCosta and Huang 2006). As one of the most prominent inorganic osmotica in plants, K^+ plays a key role in formation of the osmotic adjustment ability, even under drought conditions (Marschner 2012). Cell turgor recovery in osmotically generated stress was regulated by increasing K^+, Cl^-, and Na^+ uptake by root cells, which was partly mediated by voltage-gated K^+ transporters at the cellular plasma membrane (Shabala and Lew 2002). Furthermore, sufficient K induces solute accumulation, thus lowering osmotic potential and helping to maintain plant cell turgor under osmotic stress (Fig. 11.3). Drought stress-induced ROS production can additionally be enhanced in K-deficient plants (Cakmak 2005). Under drought stress, photosynthetic CO_2 fixation in K-deficient plants is substantially limited by impairment in stomata regulation, conversion of light energy into chemical energy, and phloem export of photosynthates from source leaves into sink organs (Egilla et al. 2005). As the impairment in photosynthetic CO_2 fixation occurs, molecular O_2 is activated, leading to extensive generation of ROS (Cakmak 2000) and, thereby, oxidative degradation of chlorophyll and membranes. The maintenance of adequate K nutrition is critical for mitigating or preventing damage by drought stress and controlling the water balance (Abdel Wahab and Abd-Alla 1995). Egilla et al. (2005) suggested that increasing extra-chloroplastic K^+ concentrations in plant cells with an excess K+ supply could prevent photosynthesis inhibition under drought stress. An adaptive K requirement for drought-stressed plants could be related to the role of K in enhancing photosynthetic CO_2 fixation and transport of photosynthates into sink organs and inhibiting the transfer of photosynthetic electrons to O_2, thus reducing ROS production (Cakmak 2005).

11.6 Effect of Exogenous Potassium on Plants Exposed to Heavy Metal Stress

Toxic metal/metalloid pollution in soil is greatly growing with time because of rapid industrialization that has created major problems in global agriculture (Hasanuzzaman and Fujita 2012). Reaction of plants under metal/metalloid toxicity can be summarized as prevents utilization of other essential nutrients and alters almost all the physiological processes, including disturbances in stomatal action, alterations in membrane functions, and the inhibition of photosynthesis, affecting the activities of several key enzymes, the production of excess ROS, the lowering of the water potential, etc. (Chibuike and Obiora 2014; Emamverdian et al. 2015). The persistent decreasing in plant growth and development eventually leads to yield losses as well as food insecurity. Hence, remediating toxic metals in soils or increasing plant tolerance or resistance to stress is a very imperious task for plant scientists. Potassium is used as a plant protector against most abiotic stresses, including metal/metalloid toxicity, as it plays a critical role in the activation of several enzymes, synthesis of protein, photosynthetic activity, osmoregulation, movement of stomata, transfer of energy, phloem transport, cation-anion balance, and stress resistance (Wang et al. 2013). Song et al. (2015) experimented with peach plants using elevated exogenous K (10 mM) against Zn toxicity (2 mM). They observed that Zn damages the plant by altering the physiological process and nutritional balance. However, K mitigated the Zn toxicity by improving the photosynthesis, antioxidant defense systems, and plant K nutritional status. Potassium also upregulated the genes related to K acquisition, transport, and homeostasis.

11.7 Effect of Exogenous Potassium on Plants Grown Under Salinity Stress

Saline soils generally have higher concentrations of Na^+ than K^+ and Ca^{2+}. This may lead to passive accumulation of Na^+ in root and shoot (Bohra and Doerffling 1993). Elevated levels of Na^+ able to displace Ca^{2+} from root membranes alters their integrity and consequently affects the selectivity for K^+ utilization (Cramer et al. 1985, 1987). Xylem loading of K^+ is organized by K^+ uptake from external solution (Engels and Marschner 1992). This indicates that Na^+ salinity, beside reducing the K^+ uptake rate, also interferes to a greater extent in K^+ translocation from root to shoot that results in a lower K^+ shoot content and a higher K^+ root content. Botella et al. (1997) indicated that the inhibitory effect of salinity on K^+ translocation was stronger with low K^+ concentration in the nutrient solution, when compared at two levels of K^+ supply in maize seedlings, i.e., 0.1 and 1 mmol/L. Thereby, root dry weight was not affected by salinity but was significantly reduced by low level of K^+ in the nutrient solution. Similar responses have been found in spinach plants, which responded to an increasing K^+ concentration, reducing the differences in shoot growth between plants grown in low and high salinity (Chow et al. 1990). The effect of K^+ deficiency and/or Na^+ toxicity in the plants explains the salinity-induced inhibition of shoot growth at low level of K^+ in root. Any stress that is leading to K^+ leakage out of the cell will ultimately cause depression of cell growth. Growth was linearly connected with K^+ content in callus cells of citrus roots (Ben-Hayyim et al. 1987). Increasing levels of Na^+ in the external medium reduced K^+ in the cell. Salt-tolerant cells could hold the K^+ in the vacuole against leakage when Na^+ was increased in the external medium. Salt stress might result in limited transport of essential nutrients to the shoot (Termaat and Munus 1986). It was found that the net transport of K^+, Ca^{2+}, Mg^{2+}, and total nitrogen to the shoot was lower in NaCl-grown plants.

Salt tolerance has been partially related with the regulation of leaf Na^+ concentration (Taleisnik and Grunberg 1994) and to selectivity for K^+ over Na^+ (Cuartero et al. 1992). There are different pathways by which Na^+ is avoided from reaching to the leaves: by adjusting Na^+ influx at the plasmalemma of root cells (Jacoby and Hanson 1985), by eliminating Na^+ from the xylem stream, by sequestering Na^+ in parenchyma cells of roots and lower part of stem (Johanson and Cheesman 1983), and by retranslocating Na^+ from shoots to roots through phloem (Jacoby 1979). In suspension cells of *Brassica napus*, increased tolerance to NaCl arises by alteration of K^+ uptake system (Lefebvre 1989), and tobacco cell cultures show enhanced K^+ uptake capacity when adapted to NaCl (Watad et al. 1991). Schachtman et al. (1989) reported that salt-tolerant cultivars of wheat translocate less Na^+ from roots to shoots than salt-sensitive genotypes.

Plant species differ in their capacity to satisfy metabolic requirements for K^+, and higher K^+ fluxes and lower Na^+ fluxes in the presence of salinity are related to differences in salt tolerance (Cerda et al. 1995). Taleisnik and Grunberg (1994) showed that K^+/Na^+ selectivity ratio was higher in tomato cultivar "Edkawi" than in "Ace." The variance between the cultivars was due to greater replacement of K^+ contents by Na^+ in all the plant parts of cultivar Ace. This indicates that Edkawi has higher capacity to keep K^+ under salinity, a feature that may contribute to its salt tolerance. Chow et al. (1990) reported that photosynthetic capacity and quantum yield of oxygen evolution were sharply reduced under high salinity conditions with decreasing K^+ supply in spinach plants due to malfunctioning of photosystem II. The results showed that there was higher K^+ requirements for shoot growth under high salinity (250 mM NaCl) than low salinity (50 mM NaCl) conditions.

Reductions in plant and shoot biomass imposed by an increase in salinity and overcome Na^+ toxicity were ameliorated in case of increasing total salt content with addition of K^+ supply to roots. Marschner (1995) indicated that higher Na^+ accumulation in leaves may help in turgor maintenance but cannot replace adequate K^+ levels in leaves, as K^+ is specifically required for protein synthesis and enzymes activation. Thus, maintenance of adequate cytoplasmic levels of K^+ and K^+/Na^+ ratios in the cell is essential for normal functioning under saline conditions (Greenway and Munns 1980; Chow et al. 1990). Muhammed et al. (1987) and Benlloch et al. (1994) showed that K^+ addition to saline culture solution increases the plant dry weight and K^+ content with a corresponding reduction in Na^+ content in rice and bean plants. A competition with nitrate was suggested as a practical agricultural method to inhibit salt damage to tomato (Kafkafi et al. 1982) and avocado (Bar et al.

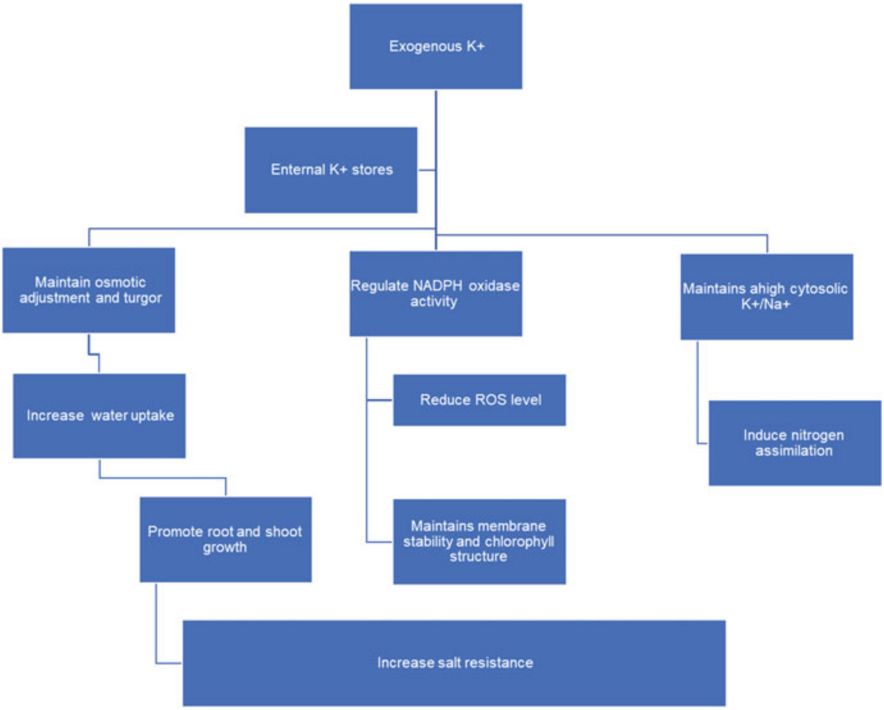

Fig. 11.4 Role of K^+ under salinity stress

1997) since Na + in most of the natural salinity cases is correlated with chloride. A general review on Cl behavior in plants is reported by Xu et al. (2000). Potassium is an essential macronutrient that plays important roles related to the osmotic adjustment, to maintaining turgor, and to regulating the membrane potential, cytoplasmic homeostasis, protein synthesis, and enzyme activation under salt stress (Almeida et al. 2017) (Fig. 11.4). Under salt stress, plant root growth is inhibited due to the osmotic effects and ion toxicity which reduce nutrient uptake and translocation, especially that of K^+ (Wang et al. 2013). The sodium (Na^+) and potassium ions (K^+) compete on the binding sites during key metabolic processes in the cytoplasm, with these binding sites including both low-affinity (nonselective cation channels, NSCC) and high-affinity (KUP and high-affinity K^+ transporter, HKT) transporters. This competition disturbs the plant metabolism (Wang et al. 2013; Marschner 2012). Salinity induces membrane depolarization and decreases the membrane integrity, which results in K^+ leakage through depolarization-activated outward-rectifying (KOR) K^+ channels (Shabala and Cuin 2008). Maintaining the cellular K content above a certain threshold and maintaining a low Na^+/K^+ ratio is crucial for plant growth and salt tolerance. Thus, higher applications of K increase the K^+ content in plant cells and reduce the Na^+ concentration, which increases the K^+/Na^+ ratio. The

HTK (high-affinity K^+ transporter) mediates Na^+-specific transport or Na^+– K^+ cotransport, which has vital roles in plant Na^+ tolerance (Su et al. 2015a, 2015b).

Taffouo et al. (2010) showed that the K^+ content was decreased in the roots and shoots due to the reduced uptake and translocation of K^+ from the roots to the shoots while increasing the NaCl concentration in *Vigna subterranea* (L.) Verdc. However, exogenous application of K can positively correlate with plant root and shoot growth during salt stress and the K-deficient stage. Saida et al. (2014) found that applying 2.39 mM KH_2PO_4 against 150 mM NaCl increased the root and shoot fresh and dry weights of *L. esculentum* under salinity stress. Fayez and Bazaid (2014) observed that application of K improved the shoot fresh weight and height of barley (*H. vulgare*) crop under 150 mM NaCl stress. Similarly, application of 9 mM K in *S. lycopersicum* improved the root and shoot dry weights treated with 75 mM NaCl stress (Amjad et al. 2016). The exogenous application of K mitigated the negative affect on tomato roots, shoots, leaves, and WUE of *B. vulgaris* cultivars under high salinity stress (Merwad 2016). Shabala and Lew (2002) reported that application of K ameliorates the organic osmolyte synthesis, especially that the higher accumulation of K^+, Cl^-, and Na^+ in the epidermal root cells of Arabidopsis regulates rapid rate of cell recovery under osmotic stress. Thus, it is necessary to maintain the cytosolic K^+ contents at a constant level for plant metabolic processes because higher Na^+ concentrations are toxic for cell metabolism (Flowers et al. 2015; Shabala et al. 2016). Wang et al. (2013) indicated that the consumption of vacuolar K^+ in K^+-deficient situations leads to a constant cytosolic K+ concentration. Fayez and Bazaid (2014) observed that application of K reduces the increased Na^+/K^+ ratio in *H. vulgare* that results from salinity and increases the K^+/Na^+. The external K applications could have reduced the Na^+ uptake through regulation of the tissue ionic balance in peanut (*Arachis hypogaea* L.) (Chakraborty et al. 2016).

11.8 Effect of Exogenous Potassium on Plants Grown Under Temperature Stress

Chilling effects in the range of 5 to 10 °C are commonly occurring in plants of warm climates. Beringer and Troldenier (1980) reported that a sudden change in membrane fluidity originates from the temperature decline, and this change is specific to each cell and dependent on the relative composition of the various phospholipids. The plant sensitivity to chilling is reduced by the balanced proportion of fatty acids. McKersice and Leshem (1994) showed that the higher ratio of unsaturated/saturated fatty acids in the cell membrane, the more tolerant is the tissue to low temperatures. Application of K results in an increase in phospholipids, membrane permeability, and improvement in biophysical and biochemical properties of cell, thus leading to maximum growth response and chilling resistance in tomato, eggplant, and pepper plants (Hakerlerker et al. 1997). Yermiyahu and Kafkafi (1990) studied the effect of increasing K^+ level on yield and chilling damage in the carnation cultivar standard grown on a sandy loam soil. It was observed that exposure to cold night events below 8 °C for 5–6 weeks followed by clear sunny days increased the percentage of stem brittle incidence. Increasing K^+ concentration in the irrigation water decreases the weekly loss of broken stems. The stem brittle was recorded around 31% when the K level in the fifth leaf was decreased below 4% and leads to heavy losses to the farmer. It was only 18% loss when the K^+ content in the plant 162 days after planting was greater than 4%. Stem brittle susceptibility was significantly reduced by supplying high levels of potassium to the irrigation water at the same level of total N concentration from the beginning of the growing season. As long as the temperature did not drop below 12 °C, the high doses of K^+ would have been regarded as "luxury" or waste. The economical saving to the farmer after only one-night event of low temperature is more than the entire price paid to the fertilizer in the whole season. The fact that the K^+ effect is detected only about 5 weeks after the cold events probably explains why such K^+ effects are not reported more frequently. The continuous supply of potassium at a much higher concentration in the soil solution than that regarded as "sufficient" for maximum yield might prove as an "insurance" against unexpected climatic events.

The susceptibility to such cold events is also dependent on the plant variety. K-stressed potato plants may be more susceptible to frost. Applying high rates of K^+ fertilization can effectively increase the frost resistance of some of the frost-sensitive genotypes (Roberts and Mc-Dole 1985). The effects of nitrogen and potassium on spikelet sterility induced by low temperature (15/15 °C: day/night, for two duration of 3 and 5 days) at reproductive stage of two rice cultivars were studied by Haque (1988). The spikelet sterility decreased with the increase of K^+ supply and increase of K/N ratio in the leaves of cultivars *Fujisaka-5* and *IR36*. However, the effect of K + in reducing the spikelet sterility was more conspicuous in cultivar *Fujisaka-5* than *IR36*. The changes in varietal response to chilling effects might be due to differences in the fatty acid composition of their root membranes. The root membrane composition has effects on the rates of ion and water transport in the root, carbohydrate content of the plant or translocation of nutrients, and metabolites in the plant (Marschner 1995). The effect of soil temperature around the crown node of wheat on growth and nutrient translocation was studied by Boatwright et al. (1976). Careful chilling of the crown zone only enabled them to demonstrate that the cold zone restricted translocation of 86Rb and, by inference, also of potassium to the top. It is the actual transport through the chilled zone that influenced the wheat yield. Since the roots and the top were exposed to optimal temperatures, it is probable that the changes in membrane fluidity could be the cause for low transport of ions through that barrier. The effects of the high K+ content of the cell in increasing frost tolerance have also been related to regulation of osmotic and water potential of the cell sap and reduction of electrolyte leakage caused by chilling temperature (Beringer and Troldenier 1980; Singer et al. 1996).

11.9 Conclusions

It has been documented that potassium application induces stress tolerance mechanism in the leaves that play a pivotal role for survival of plants under environmental field conditions. Comparison of exogenous application of potassium through leaves and roots revealed that under well-watered conditions, application of potassium through root showed more improvement of plants dry matter, leaf photosynthesis, antioxidants, and water relation parameters. Under stressful conditions, treatment of leaves with potassium excelled over root in the retrieving root biomass, leaf photosynthesis, and leaf water potentials. Maintaining an optimum potassium nutritional status is necessary for plant tolerance to various environmental cues. Balanced fertilization and efficient potassium usage in combination with other nutrients not only contribute to sustainable crop's growth, yield, and quality but also influence plant health and reduce the environmental risks. However, our understanding about the role of potassium in the entire plant stress response mechanisms is limited. In this chapter, various future needs and prospects for research about the role of potassium in agriculture include:

1. Investigating more details about the molecular mechanisms of K in plant stress resistance
2. Examining the role of K on plant resistance to biotic and abiotic stresses in differentiated cells, tissues, and organs and connecting the data relevantly
3. Identifying the common or specific response of K to distinct stress and the role of K on long-term plant responses under multiple stress conditions in field conditions
4. Understanding the relationship between K and other nutrients in relation to plant adaptation to stresses in different agroecological systems
5. Developing models for better K recommendations based on soil, plant, and environmental factors
6. Investigating more research on the importance of K on crop production, nutritional quality, and human and animal health

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An Overview of Potassium in Abiotic Stress: Emphasis on Potassium Transporters and Molecular Mechanism

12

Alessandra Francini, Stefania Toscano, Daniela Romano, and Antonio Ferrante

Abstract

Crop performance depends on their adaptability to agroecosystems and tolerance to a wide number of biotic and abiotic stresses. Potassium (K) is an essential mineral nutrient that directly or indirectly regulates plant growth and metabolism. It has been demonstrated that K contributes to enhance crop tolerance against abiotic and biotic stresses. It is important in plant nutrition and regulates many physiological and biochemical processes. Potassium deficiency reduces growth and development of plants, and under abiotic stress conditions, the damages become more severe. The use of fertilizers containing this macronutrient will increase with the higher demand of foods derived from the increase of worldwide population. Potassium plays a regulation role for different enzymes at transcriptional and posttranscriptional level. It is involved in the leaf transpiration, acting on the stomata opening. Therefore, potassium has a potential involvement in the drought and salinity stress tolerance. Potassium uptake is regulated by the high-affinity and low-affinity K^+ uptake systems in plants. At molecular level, it has been demonstrated that this system in different environmental condition has directly involved in the potassium use efficiency (KUE) of crops. Since potassium has involved in different mechanism of abiotic stresses tolerance, the molecular

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studies can provide important details as improve the crop performance acting on the potassium uptake and translocation in plants. At physiological and biochemical levels, the abiotic stresses can affect potassium utilization in plants. In particular, it is important to highlight the interaction of potassium with other cations and anions. The cellular homeostasis can improve crop survival or performance under stressful conditions. Transcriptional profiles data on crops under potassium deficit can reveal the role of this macronutrient in plants and the potential correlation with the main abiotic stresses. In this chapter, the role of potassium in plants under different abiotic stress conditions and the expression profiles of the genes for K^+ transporters will be reviewed.

Keywords

Abiotic stresses · Drought · High temperature · Flooding · Salinity · Transporters

12.1 Introduction: Role of Potassium in Plants

Potassium derives from the English word potash. The chemical symbol K derives from the medieval Latin word *kalium*, which derives from the Latin *quali*, which means alkali. Potassium (K) is a silvery white metal belonging to the alkali group of the periodic table. In water is a cation K as ionic form. The most application of K is as fertilizer in agriculture for the 95%. In the agricultural system, K is an important nutrient and represents 2–10% of the plant dry biomass. The amount of K absorbed from plants can be even higher than nitrogen. The availability in the soil depends on several factors, mainly from the cation exchange capacity, and it is low in sandy soil compared with clay or soil rich in organic matter. K^+ in plants plays important role at cell membrane polarization, development, stomatal opening, and tolerance to abiotic stress conditions. The cytosolic and chloroplast concentrations of K^+ range from 100 to 200 mM, while in the guard cells of stomata can reach 500 mM. The K plays a fundamental role in the biosynthesis and translocation of carbohydrates, in the regulation of tissue turgidity, and in transpiration, maintenance of water, and ionic homeostasis. It is also found at high concentrations in meristematic tissues, demonstrating a role of potassium in cell division activity. In deficiency condition, plants try to maintain a sufficient supply of K especially in young leaves, with growing tissues, while in old leaves, its concentration is maintained only if there are no problems of absorption and availability (Wang and Wu 2015). Plants have many HAK/KUP/KT K^+ transporters, which are not only involved in the K uptake and translocation but also in the osmotic potential regulation, salinity tolerance, root morphogenesis, plant growth, and development. The osmoregulation in crop takes place in the vacuole cells with the accumulation of osmolytes. The K^+ with other mineral elements such as Ca^{2+}, Na^+, and Cl^- are accumulated in the vacuole contributing to the osmoregulation (Fig. 12.1). The K^+ can be replaced by other cations such as Mg^{2+} and sugars as organic solutes. In particular conditions, the K^+ can have a primary role as osmolyte.

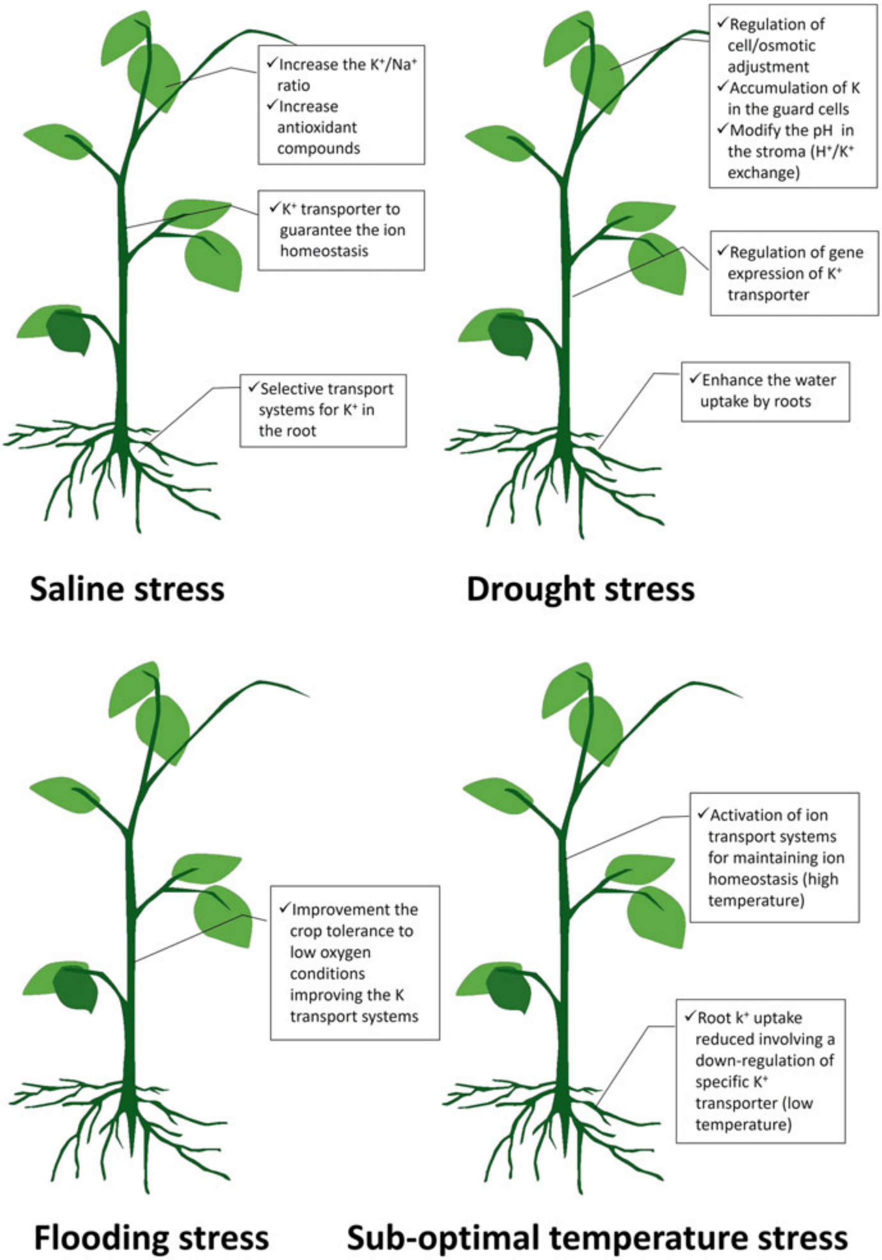

Fig. 12.1 Effect of K on crops under different abiotic stresses

12.2 Plant K Uptake Under Optimal and Limited K Conditions

The K^+ uptake as also for nitrogen occurs through two distinct systems characterized by different K^+ affinity with the nutrient. The high-affinity K^+ transport system (HAKTS) works via H^+/K^+ symport at low external K concentration below 0.2 mM and a low-affinity K^+ system (LAKTS) acting via ion channels at high concentration above 0.5 mM. The HAKTS is the predominant uptake system since in soil, the K^+ concentration usually ranges from 100 to 150 mM. These two K^+ transporters are also responsible for the remobilization of this mineral nutrient inside plants at the cellular and organ levels. The K transporters are clustered into five different families: shaker-like K channels, tandem-pore K^+ (TPK) channels, HAK/KUP/KT K^+ transporters, HKT transporters, and cation/proton antiporters (Santa-María et al. 2018; Srivastava et al. 2020). In *Arabidopsis thaliana* (L.) Heynh., as model plant, the K^+ transporter gene families have been reported and described. In the *A. thaliana,* 71 genes have been identified and involved in the K transport systems. HAK/KUP/KT transporters are localized to plasma membranes, vacuolar membranes, chloroplast thylakoid membranes, and other endomembrane as observed in barley (*Hordeum vulgare* L.), Arabidopsis (*A. thaliana*), rice (*Oryza sativa* L.), and maize (*Zea mays* L.) (Table 12.1).

In cotton, instead, 134 HAK/KUP/KT family genes have been identified. In the *Gossypium* genus and in the following species *G. arboretum* L.*,* *G. raimondii* Ulbr.*,* *G. hirsutum* L., and *G. barbadense* L., the expression of K^+ transporters have been recently studied (Yang et al. 2020). In this particular work, the distribution of K^+ transporters among species was also analyzed.

In the *Ipomoea batatas* (L.) Lam., HAK/KUP/KT family genes were identified and studied in order to verify the different organ expression and stress conditions. Gene expression analysis showed that *IbHAK2*, *IbHAK*3, *IbHAK*8, *IbHAK*10, *IbHAK*11, *IbHAK*18, *IbHAK*19, and *IbHAK*21 were induced and exposed to low K^+ conditions. Results were confirmed in both two cultivars used for the study (Jin et al. 2021).

In sugarcane (*Saccharum spontaneum* L.), 30 genes encoding for *HAK/KUP/KT* were found, and phylogenetic analysis showed that these genes could be clustered in four groups (I–IV). The organ expression data revealed that they were mainly expressed in the photosynthetic part and mature zone of the stem (Feng et al. 2020). The *SsHAK1* and *SsHAK21* were found to be upregulated in limited K^+ availability. The expression pattern during the day showed that Ss*HAK8* and *SsHAK9* were influenced by diurnal cycles (Feng et al. 2020). Analogous study was carried out in *Camellia sinensis* (L.) Kuntze and the phylogenetic analysis identified and classified the *HAK/KUP/KT* genes family. As observed for the *S. spontaneum* also in *C. sinensis,* the *CsHAKs* identified were grouped in four clusters (I–IV), containing 21 genes (Yang et al. 2020). Among the *CsHAKs,* the expression in low K availability, the *CsHAK7, CsHAK8, CsHAK11, CsHAK12, CsHAK18,* and *CsHAK20* were strongly induced in roots. These results suggest their role in K^+ uptake under limited soil availability.

Table 12.1 Potassium transporters identified in *Arabidopsis thaliana* model plant and available in NCBI database

Name/gene ID	Description	Location	Pseudonyms
HKT1 ID: 826623	High-affinity K^+ transporter 1	Chromosome 4, NC_003075.7	AT4G10310, ATHKT1, HKT1;1, T9A4.5, high-affinity K^+ transporter 1
KT1 ID: 817206	K^+ transporter 1	Chromosome 2, NC_003071.7	AT2G26650, AKT1, ATAKT1, F18A8.2, F18A8_2, K^+ transporter 1, potassium transporter
KUP3 ID: 821063	K^+ uptake transporter 3	Chromosome 3, NC_003074.8	AT3G02050, *Arabidopsis thaliana* potassium transporter 4, ATKT4, ATKUP3, F1C9.17, F1C9_17, K^+ uptake transporter 3, KUP3
KT5 ID: 829385	K^+ transporter 5	Chromosome 4, NC_003075.7	AT4G32500, AKT5, F8B4.200, F8B4_200, K^+ transporter 5
KUP7 ID: 830799	K^+ uptake permease 7	Chromosome 5, NC_003076.8	AT5G09400, K^+ uptake permease 7, T5E8.200, T5E8_200
KT2 ID: 818649	Potassium transporter 2	Chromosome 2, NC_003071.7	AT2G40540, ATKT2, ATKT2P, ATKUP2, KUP2, SHY3, T2P4.11, T2P4_11, TRK2, potassium transporter 2
KUP9 ID: 827740	K^+ uptake permease 9	Chromosome 4, NC_003075.7	AT4G19960, ATKUP9, F18F4.60, F18F4_60, HAK9, K^+ uptake permease 9, KT9
TRH1 ID: 828464	Potassium transporter family protein	Chromosome 4, NC_003075.7	AT4G23640, ATKT3, F9D16.110, F9D16_110, KUP4, TINY ROOT HAIR 1
KUP11 ID: 818071	K^+ uptake permease 11	Chromosome 2, NC_003071.7	AT2G35060, F19I3.29, F19I3_29, K^+ uptake permease 11
KEA3 ID: 825822	K^+ efflux antiporter 3	Chromosome 4, NC_003075.7	AT4G04850, ATKEA3, K^+ efflux antiporter 3, T4B21.3, T4B21_3
KEA2 ID: 825834	K^+ efflux antiporter 2	Chromosome 4, NC_003075.7	AT4G00630, ATKEA2, F6N23.15, F6N23_15, K^+ efflux antiporter 2
KUP5 ID: 829492	K^+ uptake permease 5	Chromosome 4, NC_003075.7	AT4G33530, K^+ uptake permease 5, T16L1.20, T16L1_20
KUP10 ID: 839997	K^+ uptake permease 10	Chromosome 1, NC_003070.9	AT1G31120, F28K20.5, F28K20_5, K^+ uptake permease 10
KEA1 ID: 837332	K^+ efflux antiporter 1	Chromosome 1, NC_003070.9	AT1G01790, ATKEA1, K^+ EFFLUX ANTIPORTER 1, K^+ efflux antiporter 1, T1N6.21, T1N6_21
GORK ID: 833728	Gated outwardly rectifying K^+ channel	Chromosome 5, NC_003076.8	AT5G37500, MPA22.4, MPA22_4, gated outwardly rectifying K^+ channel
KUP6 ID: 843366	K^+ uptake permease 6	Chromosome 1, NC_003070.9	AT1G70300, F17O7.17, F17O7_17, K^+ uptake permease 6
KEA5 ID: 835245	K^+ efflux antiporter 5	Chromosome 5, NC_003076.8	AT5G51710, ARABIDOPSIS THALIANA K^+ EFFLUX ANTIPORTER 5, ATKEA5, K^+ efflux antiporter 5, MIO24.16, MIO24_16

(continued)

Table 12.1 (continued)

Name/gene ID	Description	Location	Pseudonyms
AT1G60160 ID: 842311	Potassium transporter family protein	Chromosome 1, NC_003070.9	AT1G60160, T13D8.5, T13D8_5
AT5G14880 ID: 831340	Potassium transporter family protein	Chromosome 5, NC_003076.8	AT5G14880, KUP8, T9L3.180, T9L3_180, potassium uptake 8
KEA6 ID: 831053	K$^+$ efflux antiporter 6	Chromosome 5, NC_003076.8	AT5G11800, ARABIDOPSIS THALIANA K$^+$ EFFLUX ANTIPORTER 6, ATKEA6, K$^+$ efflux antiporter 6, T22P22.190, T22P22_190
KEA4 ID: 816479	K_+ efflux antiporter 4	Chromosome 2, NC_003071.7	AT2G19600, ATKEA4, F3P11.20, F3P11_20, K$^+$ efflux antiporter 4
KAT3 ID: 829400	Potassium channel protein	Chromosome 4, NC_003075.7	AT4G32650, A. thaliana low-K$^+$-tolerant 1, ARABIDOPSIS THALIANA K$^+$ RECTIFYING CHANNEL 1, ATKC1, AtLKT1, F4D11.150, F4D11_150, K$^+$ INWARD RECTIFYING CHANNEL PROTEIN, KC1, potassium channel in Arabidopsis thaliana 3

In wheat (*Triticum aestivum* L.), the K$^+$ limitation induced the fast expression of *TaHAK1*, *TaHAK7*, and *TaHAK18*, which were immediately induced after 1 h (Cheng et al. 2018).

Also, in tree plants such pear (*Pyrus bretschneideri* Rehder), the *KT/HAK/KUP* gene family was studied, and similar patterns of expression were observed. The *PbrHAK1* and *PbrHAK12/16* genes were upregulated in K$^+$ deficiency conditions (Wang et al. 2018). These studies demonstrated that plants overcome K$^+$ soil limitation by regulating different genes encoding for K$^+$ transporters, ensuring an adequate concentration for maintaining the physiological and biochemical processes. As observed in different studies, the induction of K$^+$ transporters can be the same in similar environmental conditions.

12.3 K Uptake Under Drought Stress

The K element is involved in the stomata opening regulation and directly affects cell turgor by modulating crop transpiration and maintaining the water balance. It is also involved in cell osmotic adjustment under drought conditions. Stomata opening is regulated by abscisic acid and the osmotic changes in the two guard cells forming the stomatal complex. The role of K in the guard cells osmotic regulation was demonstrated in the late 1960s (Fujino 1967; Fischer and Hsaio 1968). Among the ionic concentration in the guard cells, the K accumulation was correlated with the stomata opening. The changes of K concentration during the day are associated with stomata aperture, indicating the importance of this element in the ecophysiological response of plant to environment (Fig.12.1). The increase of K availability and uptake in plants was associated with a higher thermoregulation ability; this response could be an indirect positive effect of K in the regulation of water balance (Nieves-Cordones et al. 2019). Stomata opening and transpiration rate regulation ensure the water balance at leaf level to correspond the water uptake at roots level. The K has direct effect on photosynthesis activity under drought stress by regulating the pH in the stroma in a H^+/K^+ exchange through the chloroplast membrane. It has been observed that high K availability reduces the photosynthesis decline under water stress. These findings were also confirmed in woody shrubs such as *Hibiscus rosa-sinensis* L. that is exposed to water deprivation and different K^+ levels. Net photosynthesis, transpiration, stomata conductance, and the ratio between photosynthesis and transpiration are improved and retained under adequate levels of K. It has been observed that K is able to enhance the adaptation of plants under stress conditions (Nieves-Cordones et al. 2019).

At molecular level, there are several studies that showed the regulation of gene expression of K^+ transporters under water stress (Table 12.2). In the *Ipomoea batatas,* among the different *HAK/KUP/KT* genes, the most interesting was the *IbHAK8* that was upregulated by drought. The *IbHAK8* expression increased 15-fold in leaves after 6 h exposures to water deprivation (Jin et al. 2021).

In crop, such as sunflower (*Helianthus annuus* L.), the drought tolerance was increased by the application of 300 kg/ha K. This K supply under water stress condition enhanced yield and quality of seed components (Zamani et al. 2020).

In *Eucalyptus grandis* W. Hill, the K fertilization improved the maximum photosynthetic rate and increased water uptake by 30%–50% and photosynthetic water use efficiency (pWUE) by 300% compared to K-deficient trees. The positive effect of K supply could be associated to the better use efficiency of light and water. These results were also beneficial for the wood biomass production (Asensio et al. 2020).

In *Camellia sinensis* (L.) Kuntze, the drought conditions artificially stimulated by PEG6000 induced the expression of *CsHAKs* at different time points. Among the different *CsHAKs,* the *CsHAK7* and *CsHAK12* showed similar trend and reached maximum of expression at 48 h. On the contrary, the expression of *CsHAK5*, *CsHAK18,* and *CsHAK20* did not significantly change under water limitation. The *CsHAK17* expression was diversely regulated by stress showing a downregulation during 24 h of stress and an increase after 48 h (Yang et al. 2020). Analogous study performed on *Triticum aestivum* L. demonstrated that the expression of K^+ transporters under drought simulated with 20% PEG6000 was highly induced in *TaHAK2, TaHAK7, TaHAK16, TaHAK17*, and *TaHAK18* (Cheng et al. 2018).

In willow (*Salix alba* L.) plants under simulated stress with 15% PEG6000, six genes were influenced. *SpuHAK5, SpuHAK7*, and *SpuHAK21* were upregulated, while *SpuHAK3*, *SpuHAK4*, and *SpuHAK12* were downregulated (Liang et al. 2020).

Table 12.2 The effect of stress conditions on the expression of genes encoding for the K^+ transporters in different species

Plant species	K transporter	Effect of stress	References
Arabidopsis thaliana L.	*HAK5*	Downregulation in salinity	Nieves-Cordones et al. (2010), Santa-María et al. (2018)
Arabidopsis thaliana L.	*KUP/HAK2, HKT1, AKT2,3, KUP/HAK6, KUP/HAK11*	Salt stress 80 mM NaCl	Maathuis (2006)
Arabidopsis thaliana (L.) Heynh.	*HKT1*	Upregulation increase sensitivity to salinity	Khaleda et al. (2017)
Camellia sinensis (L.) Kuntze	*CsHAK7, CsHAK12, CsHAK17*	Upregulated under drought	Yang et al. (2020)
Gossypium sp. pl.	*GhPOT3, GhPOT4, GhPOT6, GhPOT11, and GhPOT7 12 h*	Upregulated by drought induced by 18% PEG6000	Yang et al. (2020)
Ipomoea batatas (L.) Lam.	*IbHAK8*	Upregulated after exposure to drought and salt stress	Jin et al. (2021)
Manihot esculenta Crantz	*MeKUP3*	Upregulated by 300 mM NaCl, osmostic stress, and cold	Ou et al. (2018)
Oryza sativa L.	*OsHAK1*	Regulated K uptake under salt conditions	Chen et al. (2015)
Oryza sativa L.	*OsHAK16*	Regulated K uptake under salt conditions	Feng et al. (2019)
Oryza sativa L.	*OsHAK21*	Upregulation under salinity and induce salt tolerance	Shen et al. (2015)
Pyrus bretschneideri Rehder	*PbrHAK1, PbrHAK12/16*	Upregulated under K^+ deficiency	Wang et al. (2018)
Saccharum spontaneum L.	*SsHAK1, SsHAK21*	Upregulated under K^+ limitation	Feng et al. (2020)
Salix alba L.	*SpuHAK5, SpuHAK7, SpuHAK21*	Upregulated by drought induced by 15% PEG6000	Liang et al. (2020)
Salix alba L.	*SpuHAK3, SpuHAK4, SpuHAK12*	Downregulated by drought induced by 15% PEG6000	Liang et al. (2020)
Salix alba L.	*SpuHAK10, SpuHAK11, SpuHAK18*	Upregulated by 150 mM NaCl	Liang et al. (2020)
Solanum lycopersicum L.	*AKT1, LKT1, SIHAK5, HAK26*	Downregulation of K^+ transporter under suboptimal conditions (5/10 °C)	Gao et al. (2020)
Triticum aestivum L.	*TaHAK2, TaHAK7, TaHAK16, TaHAK17, TaHAK18*	Under drought induced by 20% PEG6000	Cheng et al. (2018)

(continued)

Table 12.2 (continued)

Plant species	K transporter	Effect of stress	References
Triticum aestivum L.	*TaHAK1, TaHAK11, TaHAK17, TaHAK18, TaHAK23*	Downregulated by 200 mM NaCl	Cheng et al. (2018)
Triticum aestivum L.	*TaHAK7, TaHAK9, TaHAK16*	Upregulated by 200 mM NaCl	Cheng et al. (2018)

In cotton plants using PEG-induced stress, the K^+ transporters were *GhPOT6* and *GhPOT4* immediately after 6 h PEG and *GhPOT3, GhPOT11*, and *GhPOT7* 12 h PEG (Yang et al. 2020).

12.4 K Uptake Under Salinity Stress

Salt stress is a major abiotic stress in different agricultural systems. Salinity severely reduces crop growth and productivity, which correspond to high commercial losses. Salinity is an agricultural limiting factor that affects about 7% of total global land area, and the percentage has been increasing. In many geographical areas, the salinity stress is associated with the increase of Na^+ accumulation in tissue (Mariani and Ferrante 2017). The high Na^+ concentration in soil induces plants to activate selective transport systems with high selectivity for K^+ (Shabala and Cuin 2008). The vital physiological and biochemical processes can be preserved by accumulating the Na^+ into the vacuole (Srivastava et al. 2020). This avoids unbalance against the low extracellular osmotic potential provoked by salinity stress. Since in the cytosol the most important processes take place, the K^+/Na^+ ratio must be high, and tolerance salinity crops have higher ratio (Fig. 12.1). The salinity can be due to high salts in soils or irrigation water, and these situations can be found in different Mediterranean areas. Crops subjected to salinity stress undergo osmotic stress, leading to water stress, nutrients imbalance, oxidative stresses, and physiological disorders (Ashraf and Foolad 2007). The beneficial effects of K^+ have been studied in soybean (*Glycine max* (L.) Merr.) plants grown in salinity conditions. Foliar applications of 2% potassium sulfate or potassium chloride have been applied to maintain high concentration of K^+ in leaves. The potassium sulfate under stress conditions increased the antioxidant compounds compared to the potassium chloride (Adhikari et al. 2020). Analogous results were obtained in sunflower (*Helianthus annuus* L.) and safflower (*Carthamus tinctorius* L.) plants irrigated with saline water of 4.8 and 8.6 dS/m (EC) and foliar sprayed with potassium nitrate solution at 250 mg/L. The plant treated with nitrate potassium showed higher leaf area and fresh and dry weight per plant (Jabeen and Ahmad 2011). The mitigation of salt damage has been observed in one-year-old *Thymus vulgaris* L. exposed to salinity of 100 mM NaCl and foliar sprayed with 10 mM potassium chloride (Zrig et al. 2021). On the contrary, the K deficiency and salinity stress have synergistic negative effect on plants. This evidence has been reported for the salinity-tolerant *Sulla carnosa* (Desf.) B.H.Choi & H.Ohashi plants (Hafsi et al., 2021).

At molecular level, in model plant such as *Arabidopsis,* the gene *AtAKT1* is highly regulated under salt stress and with high-affinity K^+ transporter 5 (*HAK5*), and shaker-like K^+ outward rectifying channel (SKOR) guarantees the ion homeostasis (Horie et al. 2009). These genes have the same behavior in the sugar beet (*Beta vulgaris* L.) exposed to 300 mM NaCl (Li et al. 2021). The Na^+ absorbed in plants can move through the xylem and HIGH-AFFINITY POTASSIUM (K^+) TRANSPORTER (*HKT*) family members which demonstrated high affinity for the Na^+ in tissue. The *HKT1* in the root stele has been identified as the key regulator of the reabsorption of Na^+ from xylem vessels into xylem parenchyma cells with less translocation and accumulation of Na^+ into shoot. HKT transporters classified as class 1 can remove Na^+ excess from the xylem, keeping this element below the phytotoxic levels in the photosynthetic leaves (Schroeder et al. 2013).

However, the HAK family members are believed to play an important function plant salinity tolerance, but the biological mechanisms are still unclear. The gene expression of *OsHAK21* study under high-salinity treatment demonstrated a positive role of this gene in salt tolerance in rice (Shen et al. 2015).

The *HKT* transporters class 2 have sequester Na^+ and K^+ in the vacuole, avoiding negative effects on the cytoplasm biochemical processes.

In rice, *OsHAK1* is also found to be essential for plant growth under salinity stress-independent K^+ availability (low or high K^+ concentrations). Functional analysis of *OsHAK1* using mutants with loss of function of this gene showed stunted roots and shoot growth compared to wild type. On the contrary, plants overexpressing this gene showed high accumulation of K^+ demonstrating its role in K uptake (Chen et al. 2015). Another functional study focused on the salt tolerance and K^+ transporter demonstrated the importance of *OsHAK16* and its role. Knockout mutants were more sensitive to salinity, and overexpressing lines showed higher tolerance (Feng et al. 2019). The overexpression of *OsHAK16* enhanced the K^+ concentration in shoot rather than in roots.

In wheat (*Triticum aestivum* L.), the exposure of plants to 200 mM NaCl in a time course from 0 to 24 h different K^+ transporters was differently expressed. In particular, *TaHAK1, TaHAK11, TaHAK17, TaHAK18*, and *TaHAK23* genes were repressed, while *TaHAK7*, *TaHAK9*, and *TaHAK16* were upregulated (Cheng et al. 2018).

In tree plants (*Manihot esculenta* Crantz), transcriptional studies allowed the identification of several K^+ transporters, and the *MeKUP3* gene was upregulated and exposed to 300 mM NaCl (Ou et al. 2018).

These studies demonstrated that more than one gene encoding for K^+ transporter can contribute to the salt tolerance (Table 12.2). Their role is important in maintaining the equilibrium of ions in the cell, avoiding the accumulation in cytosol.

12.5 K Uptake Under Flooding

Waterlogging is a common stress that can occur during winter or during raining season in soil with poor drainage. The effect of flooding on plant induces a wide number of disorders related to soil physiochemical properties such as pH, redox potential, and oxygen availability. Prolonged flooding conditions induce oxygen deprivation, and plants must face against hypoxia or anoxia. The plants must adapt to different abiotic conditions and involve the activation of specific physiological and biochemical pathways. Under flooding, different crops can use different strategy. Plants can survive by the modification of their tissue morphology and the ability to uptake nutrients.

The uptake of mineral elements is affected by the soil conditions. Plants exposed to long period of flooding have altered nutrient uptake. The K^+ in leaves of the flooded plants is lower than unflooded. The lower K^+ concentration is related to K transport systems (Chen et al. 2005). Under flooding, the cytosolic K^+ concentration is transiently lowered. The cytosolic K^+ reduction is compensated by vacuolar supply. Exogenous applications such as foliar applications can improve the plant tolerance to flooding (Fig. 12.1). These results indicate a direct role of K in the improvement of crop tolerance to low oxygen conditions (Shabala and Pottosin 2014).

12.6 K Transport Under Suboptimal Temperature Conditions

The temperature has direct effect on the crop metabolism and can regulate the main physiological processes such as photosynthesis and respiration. The high temperatures usually increase transpiration for regulating leaf temperature and have effect on the nutrient uptake (Ferrante and Mariani, 2018). In plants stressed for high temperature, the K^+ can be used by the plants as osmoregulatory agent. Ion transport systems must be active in stress conditions and are essential for maintaining ion homeostasis for nutrition and ionic balance in cells. However, the heat stress decreased the influx rate of K^+ at root level when tomato plants were exposed for 6 days at 42 °C (Giri et al. 2017).

In low-temperature conditions, the K^+ uptake is usually reduced, and this involves a downregulation of specific K^+ transporters (Table 12.2). In tomato, the exposure of plants to 5/10 °C downregulated the following genes *AKT1* (*Solyc09g005220*.1), *LKT1* (*Solyc12g006850*.1), *SIHAK5* (*Solyc12g005670*.1), and *HAK26* (Solyc06g051830.1), and these results were confirmed in two different cultivars (Gao et al. 2020).

12.7 Conclusion

The role of K^+ transporters in plants has not completely explored, and the functional analysis of the key genes seems to have a major role in the plant adaptation under stress conditions. Most of studies have been performed in model plants. However, recent studies have been focused on agricultural crops. Transcriptomic data on different crop species can help in the elucidation of the role of the different K^+ transporters in different species and different stress conditions. Molecular characterization can help in the selection of new cultivars for the different field conditions. Furthermore, the genetic studies and analyses on the HAK/KUP/KT gene family can provide useful tools for driving the genetic improvement for crop with specific abiotic tolerance.

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Nitric Oxide Synthesis Affects Potassium and Nitrogen Homeostasis in Plants for Salt Tolerance

13

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Abstract

Agricultural production continues to be forced by a salt stress that can reduce crop yield quantity and quality. Nitric oxide (NO), a signaling molecule, plays multiple roles in plant growth and development and in response to salt stress. Nutrient management strategy is critical for salt stress alleviation in plants. NO is recognized as a main participant in response to changes in nutrient availability. In particular, potassium (K) and nitrogen (N) are important nutrient for plants, as both nutrient carry out most of the biochemical and physiological processes or vital functions in metabolism, growth, and stress adaptation in plants. The following chapter focuses on the synthesis of NO with emerging role of K and N nutrients under salt stress. The synthesis of NO and its effects on plant growth, morphology, and plant metabolism are discussed. The physiological and molecular mechanisms of K and N function with NO in plant salt stress resistance are reviewed. This study summarizes a vital role of NO synthesis in modulating the homeostasis of K and N and its nutrition in plants and highlights the future needs for research about the role of K and N with NO synthesis under salt stress in agriculture.

Keywords

Nitric oxide · Nitrogen · Potassium · Salt stress

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13.1 Introduction

The world population is increasing rapidly and will become from its existing number of approximately 7 billion to 9.4 billion by the year 2050 (FAO 2009; United States Census Bureau 2012). For an expanding world population, a substantial increase in crop production is required to meet the food demands of future generations while conserving ecological resources of our world. However, agricultural production continues to be repressed by abiotic factors such as drought, salinity, cold, frost, etc., that cause severe negative impact on the gross agronomy and reduce the quantity and quality of crop production (Wang et al. 2013). However, in abiotic stress, plant exposed to salt stress becomes a major concern in the world. Salt stress has impaired chlorophyll biosynthesis due to downregulation of gene expression and influenced growth, development, and yield of crops. The reduced photosynthesis affected by salt stress is attributed to decline in chlorophyll fluorescence, perturbation of thylakoid membrane fluidity, and consequent decline in CO_2 assimilation and protein trafficking to chloroplasts (Fatma et al. 2021). Photosynthetic inhibition in plants under salt stress results from the inhibition of the activation of Rubisco and the Calvin cycle reactions together with the decrease in stomatal conductance and intercellular CO_2 concentration (Fatma et al. 2016). It is, therefore, important to understand the mechanism of salt-induced physiological dysfunctions in crops of agricultural importance.

Plants have developed a wide range of mechanisms to resist a variety of stressed conditions. In particular, nitric oxide (NO), a crucial gaseous signaling molecule which has attracted much attention because of its diverse role in physiological responses in plants, ranges from germination and senescence to photosynthesis and cellular redox balance (Nabi et al. 2019; Jahan et al. 2020). Nitric oxide plays an important role in resistance to salt stress by its antioxidant properties and also by inducing the activity of ROS-scavenging enzymes to alleviate oxidative stress (Fatma et al. 2016). The study of Lopez-Carrion et al. (2008) showed the relationship between NO and the induction of proline in response to salt stress and suggested that NO could mitigate the damage associated with salt stress. Moreover, several studies also suggested that the coordination between NO and nutritional signaling plays an important role in salt tolerance (Jahan et al. 2020; Fatma et al. 2021).

Among the mineral nutrients, potassium (K) and nitrogen (N) are well-characterized nutrients in plant defense mechanisms and plays a critical role in plant growth and metabolism, and it contributes greatly to the survival of plants that are under various biotic and abiotic stresses. An essential nutrient, K is the most abundant cation in plants and plays essential roles in enzyme activation, protein synthesis, photosynthesis, osmoregulation, stomatal movement, energy transfer, phloem transport, cation-anion balance, and stress resistance (Marschner 2012). Similarly, N is also an essential macronutrient and is a constituent of many vital compounds of plants (Krapp 2015; Jahan et al. 2020). Recent reports have highlighted a role of NO in N assimilation and N uptake in plants and have suggested that NO is a vital signaling molecule of the nitrate-sensing pathway (Balotf et al. 2018), and it shows connection between N assimilation and NO synthesis.

There are several publications individually on the K and N under abiotic stress (Abbasi et al. 2015; Iqbal et al. 2015; Jahan et al. 2020) and NO, as important plant growth regulator under salt stress (Fatma et al. 2016; Sehar et al. 2019). However, the information on the role and underlying mechanism of K and N nutrients with NO in plants under salt exposure is scanty. Here, we summarize some of the old and current information regarding the role of NO synthesis in some of the responses to K and N nutrients under salt stress. The available chapter clearly established that NO biosynthesis and perception largely affect the homeostasis of K and N, as a mineral nutrient with a strong influence on plant growth and development. An abundant understanding of the interaction between NO and nutrients, K and N under salt stress will provide new strategies for improving crop potency and development under changing environment. In this chapter, the effect of NO pathway on K and N homeostasis under salt stress and plant responses is reviewed and discussed. The information supporting a role for NO synthesis in the homeostasis of K and N nutrient responses under salt stress is critically analyzed.

13.2 Basic Biochemistry of Nitric Oxide

Nitric oxide is a small-sized highly diffusible gas and a ubiquitous bioactive molecule. Nitric oxide acts a versatile signal molecule in plants since it possesses unique chemistry. Nitric oxide is a diatomic inorganic gaseous molecule and is comprised of an atom each of N and O compose NO, where seven electrons from N and eight electrons from O are involved to form an uncharged molecule ($N\equiv O$). Therefore, NO functions through interactions with cellular targets via either redox or additive chemistry. Moreover, depending on its concentration and the site of production, NO varyingly influences major physiological and molecular processes in plants, wherein its both positive and negative effects may be perceptible (Rather et al. 2020). Nitric oxide transmits its bioactivity, and eventual physiological/biochemical and molecular changes occur in plants mainly as a result of its interaction with proteins, abscisic acid, auxins, osmolytes (such as proline and glycine betaine), and nonenzymatic antioxidants (such as reduced GSH). Nitric oxide modulates the activity of proteins through nitrosylation and probably tyrosine nitration. In fact, the protein tyrosine nitration and the production of nitrite ($ONOO^-$) occur as a result of the reaction of NO with ROS such as superoxide anions. Additionally, NO-accrued cysteine S-nitrosylation yields S-nitrosothiols (SNOs). NO-GSH reaction produces S-nitrosoglutathione (GSNO) that, in turn, can be transported to other cells/tissues (and help NO travel long distance) and be converted into oxidized glutathione (GSSG) and NH_3 by GSNO reductase (GSNOR) (reviewed by Rather et al. 2020). Interaction of NO with plant lipids such as nitro-fatty acids (NO_2-FA) (Sánchez-Calvo et al. 2013; Fazzari et al. 2014) and mitogen-activated protein kinase (MAPK) (Ye et al. 2013) results in cell signaling processes and the modulation of plant stress responses. On the other, NO interaction with abscisic acid and auxins results in inhibition of the programmed cell death along with the reduction of detrimental stress factor (Nabi et al. 2019; Sharma et al. 2020). Nitric oxide can also act as a

Ca^{2+}-mobilizing messenger (Besson-Bard et al. 2008). Nitric oxide-mediated increased cellular levels of the major osmolytes (such as proline and glycine betaine) have also been reported in plants (Ahmad et al. 2016; Khan et al. 2020).

13.3 Biosynthesis of Nitric Oxide

The major sites of NO biosynthesis in plants are protoplasts, chloroplasts, mitochondria, and peroxisome. Nitric oxide can be synthesized in plants both by enzymatic as well as nonenzymatic systems. Enzymatic systems contributing NO synthesis in plants include nitrate reductase (NR), nitrite: NO reductase (NiNOR), and NOS-like enzymes. The major nonenzymatic mechanisms for NO generation include chemical reduction of NO_2^- at acidic pH, carotenoids in the presence of light, and at acidic pH in the presence of a reductant such as ascorbic acid (reviewed by Ferreira and Cataneo 2010). Further, enzymatic and nonenzymatic pathways for NO synthesis in plants have been classified as either oxidative or reductive pathways depending on the substrate involved (Fig. 13.1). To date, several pathways for NO biosynthesis have been discovered in plants. There are two pathways included in plant tissues: enzymatic and nonenzymatic pathways (Sánchez-Calvo et al. 2013; Rather et al. 2020).

A brief discussion on the major enzymatic and nonenzymatic pathways involved in NO synthesis is presented hereunder.

13.3.1 Enzymatic Pathways

The reductive pathways for NO synthesis depend on NO_2^- as a primary substrate and include NR, plasma membrane-associated nitrite:NO reductase (NiNOR), and other molybdoenzymes (such as xanthine oxidoreductase, XOR), and also mitochondrial and chloroplastic electron transport chains (Galatro et al. 2020).

13.3.1.1 Nitrate Reductase (NR)

Nitrate reductase (NR) is molybdoenzyme and is involved in catalysis of the first and rate-limiting step in nitrate assimilation, where nitrate (NO_3^-) is reduced to nitrite (NO_2^-) in the presence of NADPH. Notably, NR pathway is among the best-identified pathway for NO biosynthesis in plants. NO_2^- thus formed is reduced to NO via NR itself or electron transport chain in mitochondria. Nitrate reductase can undergo a regulatory switch from its preferential high-affinity substrate NO_3^- ($K_{m\ \mathrm{nitrate}} = <40\ \mu M$) to NO_2^- (low affinity; $K_{m\ \mathrm{nitrite}} = 100\ \mu M$) and producing NO (Mur et al. 2013). The generation of NO via NR has been reported to require both low oxygen concentration and cellular pH. Additionally, NR-mediated NO generation may also occur during closure of stomata, flowering, and formation of lateral roots and, most importantly, during abiotic stress responses (Moreau et al. 2010; Prochazkova et al. 2014).

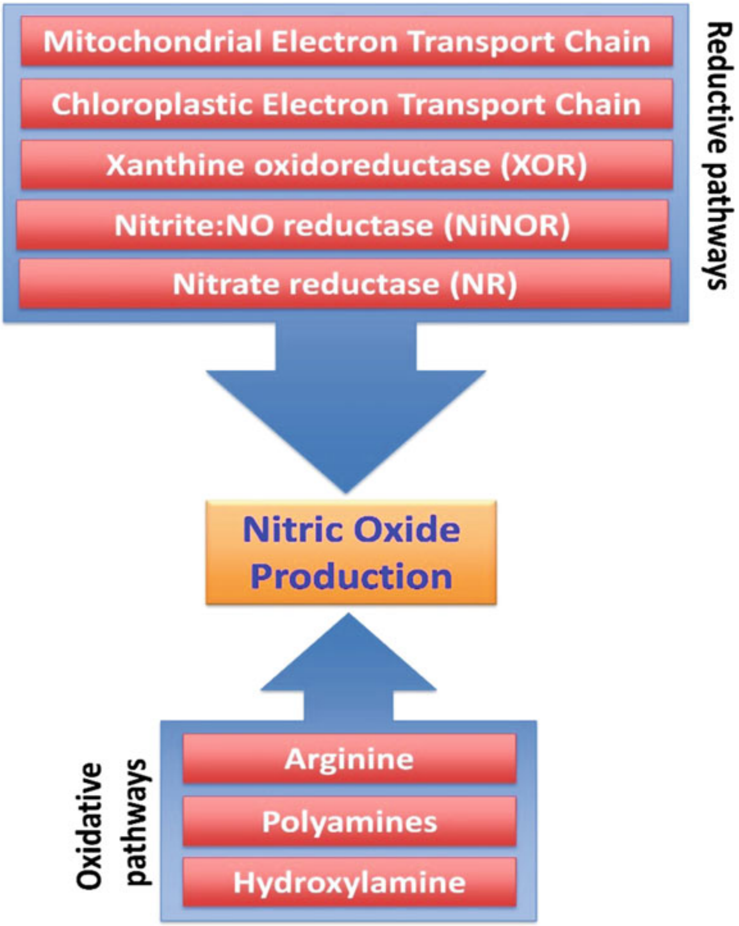

Fig. 13.1 Summary of major sources of nitric oxide biosynthesis in plants

13.3.1.2 Xanthine Oxidoreductase (XOR)

Xanthine oxidoreductase (XOR), a peroxisomally located and Mo-containing ubiquitous enzyme exists in two interconvertible forms, namely, xanthine oxidase (XO) and xanthine dehydrogenase (XDH). Xanthine oxidoreductase reduces NO_2^- to NO at the expense of NADH under anaerobic conditions (Corpas et al. 2008). In particular, XO can reduce organic and inorganic NO_3^- and NO_2^- and eventually release NO (Godber et al. 2000). On the other, Wang et al. (2010) noticed the involvement of XDH in NO synthesis in roots of *Lupinus albus* grown under phosphate (PO_4^-) deficiency.

13.3.1.3 Nitrite:NO Reductase (NiNOR)

NO-forming nitrite reductase (NOFNiR) is a dual system that also includes NR as a necessary partner. Ni:NOR does not require the Mo-center of NR; however, it depends on the NR electron transport chain from NADPH to heme for the production of NO. An in vitro study has indicated cytochrome c as an electron donor (Wilson et al. 2008). NR:NiNOR system can sense nitrate availability in the soil (Meyer and Stöhr 2002), whereas Ni-NOR-mediated NO production regulates root infection by mycorrhizal fungi (Moche et al. 2010).

13.3.1.4 Nitric Oxide Synthase (NOS)-Like Enzymes

Plants possess strategies for using the sources of N other than NO_3^- and NO_2^- in the production of NO. To this end, NOS-like enzymes act as an important arsenal in NO_3^--independent synthesis of NO. NOS-like enzymes deaminate L-arginine into L-citrulline and eventually NO in the presence of NADPH and O_2 (Rümer et al. 2009). NOS activity was measured in a number of plants including *Pisum sativum* (Corpas et al. 2006), *Glycine max* chloroplasts (Simontacchi et al. 2004), *Sorghum bicolor* seed embryonic axes (Jasid et al. 2006), and *Pisum sativum* and *Zea mays* tissues (Barroso et al. 1999; Ribeiro et al. 1999). Search for the presence of transcripts encoding NOS proteins in land plants (>1000 species) resulted in no typical NOS sequences (Jeandroz et al. 2016). Only a few algae species including the green alga *Ostreococcus tauri* was among photosynthetic organisms that contained NOS orthologs (Foresi et al. 2010; Jeandroz et al. 2016; Santolini et al. 2017). In *Glycine max* primary roots, NOS-like enzyme (and NR also) has been proposed to regulate the gravitropic root response (Hu et al. 2005).

13.3.1.5 Other Notable Enzymes

The enzymatic production of NO can also be mediated by a number of other enzymes including copper amine oxidase 1, polyamine oxidases, horseradish peroxidase, cytochrome P450, catalase and hemoglobin (reviewed by Prochazkova et al. 2014). To this end, del Río et al. (2004) reported the release of NO via cytochrome P450-catalyzed oxidation of N-hydroxy-arginine (NOHA) in the presence of NADPH and O_2.

13.3.2 Nonenzymatic Pathways

Various nonenzymatic pathways are associated with NO generation in plants (Prochazkova et al. 2014). The oxidative pathways do not require NO_2^- as a substrate and comprise NO production from arginine, polyamines (PAs), or hydroxylamine. In *Arabidopsis thaliana* seedlings, PAs induced rapid biosynthesis of NO (Tun et al. 2006). Employing fluorimetry and fluorescence microscopy (using the NO-binding fluorophores DAF-2 and dye diaminorhodamine 4 M (DAR-4 M), a fluorescent probe for NO), an exogenous application of PAs putrescine, spermidine, and spermine to *Arabidopsis* seedlings was reported to induce therein the production of NO. Ascorbate (AsA) can mediate the reduction of NO_2^- and produce NO (and also dehydroascorbic acid at acidic pH) (Bethke et al. 2004; del Río et al. 2004). Earlier, carotenoids-mediated reduction of NO_2 into NO was reported in *Spinacia oleracea* (Cooney et al. 1994).

13.4 Nitric Oxide Synthesis on Potassium and Nitrogen

13.4.1 Nitric Oxide Synthesis Affects Potassium Homeostasis in Plants

Potassium is a major nutrient and main inorganic cation in plant cells which interacts with negative charges on nucleic acids and proteins and maintains cytosolic pH homeostasis. Inside the cell, K acts as a cofactor activating specific enzymes and also work in maintaining the membrane potential (Maathuis 2009; Dreyer and Uozumi 2011). The maintenance of potassium ion (K^+) homeostasis enables plants to activate the metabolic pathway for setting the osmotic potential for plant growth and movement (Buet et al. 2019). The movement of K^+ nutrition within the cells and between plant organs includes several transporters (Véry et al. 2014; Santa-María et al. 2018; Buet et al. 2019). Accordingly, there are several ways in which K^+ nutrition interacts with NO like in root architecture, where NO generally exerts a specific effect on K^+ transport and works in the stomata. The indirect effects of NO on root elongation associated with defective K^+ nutrition are likely to occur, as observed in plants lacking K^+ channels (AKT1 activity), in which root length proved to be hypersensitive to the SNP as a NO donor (Xia et al. 2014). Besides, SNP stimulates K^+ efflux, while the cPTIO as NO scavenger reduces it, indicating that these K^+ currents are associated with NO signaling. High levels of NO increase the content of pyridoxal 5′-phosphate, an active form of vitamin B6, which in turn inhibits the activity of AKT1 and ultimately decreased the K^+ content in the plant cell (Xia et al. 2014). Similarly, Song et al. (2018) observed that *Nicotiana tabacum* cultivar with low K^+ susceptibility have decreased total root length, root volume, and number of first-order lateral roots under K^+ deficiency with increased levels of NO while tolerant cultivar did not show any effect. This study suggested that NO plays an important role in modulating the growth of first-order lateral roots as susceptible cultivar roots showed increased levels of NO after K^+ limitation. In support of this piece of evidence, the addition of cPTIO, L-NAME, or tungstate resulted in an increase in the first-order root length. Therefore, NO mediates K^+ homeostasis by the negative regulation of K^+ uptake via K^+ channels. The hormone NO regulate K^+ channel indirectly, in which case NO integrates with protein phosphorylation and intracellular Ca^{2+} release signals to inactivate the inward-rectifying K^+ channels and close stomata (Garcia-Mata et al. 2003; Sokolovski et al. 2005). The NO seems to play a role in water-stress signaling, and its situation within ABA-related signaling pathways and its relationship to ion transport that drives stomatal movement have remained unclear. However, Garcia-Mata et al. (2003) demonstrated that NO acts on inward-rectifying K^+ channels and anion channels by activating ryanodine-sensitive Ca^{2+} channels of intercellular Ca^{2+} stores to elevate $[Ca^{2+}]$ in *Vicia faba* guard cells. At these very low levels, NO had no influence on $I_{K,out}$, consistent with the Ca^{2+} insensitivity of these K^+ channels. However, NO could be expected to possess additional effects on stomatal behavior at higher concentrations. Oxidative stress in plants is known to suppress stomatal closure (Willmer and Fricker 1996) and, in some circumstances, can suppress $I_{K,out}$ (Kohler et al. 2003) and promote stomatal opening (Black and Black 1979). Indeed, NO can bond covalently with the SH residues of Cys to make S-nitrosothiols, and this easy reaction is the basis of the many regulatory cascades (Stamler et al. 2001; Ahern et al. 2002), including vascular homeostasis and endotoxic shock in animals (Liu et al. 2004). In subsequent experiments, a reversible decrease in $I_{K,out}$ with moderate elevation to sub-micromolar NO has been observed and has explored the effects of NO on the $I_{K,out}$ in vivo. The key observations were that a NO-mediated block of $I_{K,out}$ is suppressed by reducing reagents, especially British anti-Lewisite (BAL; 2,3-dimercapto-1-propanol), and is mimicked by the oxidizing reagent phenylarsine oxide that targets vicinal SH residues. These findings indicate that the $I_{K,out}$ can become locked down under nitrosative stress and led to propose that NO action on $I_{K\ out}$ is mediated by direct S-nitrosylation of Cys residues closely associated with the ion channel. In other words, NO inactivate the activity of outward-rectifying K^+ channel in *Vicia faba* guard cell through direct S-nitrosylation of cysteinyl residues, the not-yet identified channel, or its closely attached protein (Sokolovski and Blatt 2004). Additionally, Zhang et al. (2018) showed that NO-mediated alteration in K^+ homeostasis was known as a result of work with *Arabidopsis* roots subjected with excess iron. An exposure of toxic concentrations of iron to the root tips increased the levels of NO and leads to growth arrest, which was in part related to NO-induced alteration in K^+ homeostasis (Arnaud et al. 2006). These findings revealed a pivotal role of NO synthesis in modulating the homeostasis of K and its nutrition in plants.

13.4.2 Nitric Oxide Synthesis Affects Nitrogen Uptake and Homeostasis in Plants

Nitrogen is an essential macronutrient and component of many biological molecules like proteins and nucleotides. Chlorophyll molecules also have N which makes it critical for growth and development of plants (Wang et al. 2012; O'Brien et al. 2016). Several enzymes and intermediates are involved in N uptake and metabolism, including NR, NiR, glutamate synthase (GS), glutamate dehydrogenase (GDH), and glutamine synthetase (GOGAT) (Andrews et al. 2013; Zhang et al. 2020). The main sources of N for the plants are NO_3^- and NH_4^+ which are easily taken up by the plants. There are many reports that suggest a connection between the N assimilation and NO production in plants. It has been observed that not only the amount of N but its form of supply (NO_3^- or NH_4^+) also affects the NO production in plants (Caro and Puntarulo 1998; Jin et al. 2009; Sun et al. 2015; Zhu et al. 2016). For the production of NO, nitrite (NO_2^-) and arginine are the main substrates and are derived through the N assimilation pathway. Mainly, NO is produced by the reduction of nitrate to nitrite using NADH as major electron donor in the cytosol. However, plants may have optimized the use of NO_2^- as a main source for NO synthesis (Jeandroz et al. 2016; Santolini et al. 2017). Nitrate reductase is a key enzyme in N metabolism and synthesizes NO as a by-product of NO_2^- decomposition in a reaction catalyzed by NR (Klepper 1987). Besides NR, plants can generate NO under acidic conditions from HNO_2 in the presence of ascorbate or GSH

(Wendehenne et al. 2004). On the basis of root response and expression of NR and nsHbs which are involved in NO synthesis and scavenging, respectively, it was suggested that NO_3^- play role in NO production (Trevisan et al. 2011). The role of N (NO_3^- or NO_3^- / NH_4^+) has been confirmed in the root response through the involvement of NR and NO either using the in situ chemical detection of NO and application of tungstate (inhibit NO synthesis) or NO inhibitor [cPTIO; 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1- oxyl-3-oxide] in maize and rice (Manoli et al. 2014; Sun et al. 2015). Moreover, Sun et al. (2015) observed increase in NO content in lateral root and root tip region of Nanguang rice cultivar (with high-nitrate response) which grows under limited NO_3^- conditions, and this NO accumulation was mainly from an NIA2-dependent NR source. Similarly, *Zea mays* plants showed increase in 4-amino-5-methylamino-2′,7′-difluorofluorescein diacetate (DAF-FM DA) fluorescence (corresponding to NO detection) in the first minutes after NO_3^- treatment in the meristematic apex and transition zone. After study of the transcriptome and proteome, Trevisan et al. (2015) found that the transition zone was critical in detecting NO_3^- and also stated that NO_3^--mediated response was induced by NO. Recently, Nejamkin et al. (2020) observed that deficiency of N retards the growth (leaf area, protein content, and seed yield) of *Nicotiana tabacum* plants that showed lesser expression of NOS enzyme. In plants, NO is produced from NO_2 through photoconversion by carotenoids and reaction with NRs (Rockel et al. 2002) and with glycine decarboxylase (Chandok et al. 2003). In NR-deficient *Arabidopsis*, stomata fail to close in ABA (Desikan et al. 2002). Furthermore, NO scavengers suppress ABA action in closing stomata, and NO donors promote closure in the absence of ABA (Neill et al. 2002; Garcia-Mata and Lamattina 2002). In N metabolism, NR is a key enzyme and a source of NO, and its activity may be exaggerated by NO levels (Chamizo-Ampudia et al., 2017). In *Triticum aestivum* leaf, NR activity is negatively modulated by NO released from NO donor (SNP or GSNO); concurrently, nitrate content significantly increased, indicating that the substrate for NR activity was present in amounts enough to be not a limiting factor for NR activity (Rosales et al. 2011). Nevertheless, some in vitro and in vivo experiments have confirmed the generation of NO via NR with low oxygen concentration and cellular pH as two of the most important requirements for the activity of NR (Prochazkova et al. 2014; Sharma et al. 2020). The NO generation through NR has been reported in many plant species, such as *Helianthus annuus, Spinacia oleracea, Zea mays, Triticum aestivum, Malaxis monophyllos, and Aloe vera* (Xu and Zhao 2003).

13.5 Influence of Nitric Oxide Synthesis on Potassium and Nitrogen Homeostasis Under Salt Stress

Salt stress closely associated with nutrient deficiency especially for K and N nutrients due to competitive inhibition of ion transporters and decline of nutrient uptake in the plant roots. As a result, diverse signaling molecules must be integrated in order to accomplish K and N balance under salt stress at a whole plant or cellular level. Hence, the study can assume that NO as a versatile hormone has an important function in this process. The study focuses the role of NO synthesis and its signaling on K and N homeostasis under salt stress.

One of the major limiting elements of plant growth is K, and crops often suffer from low K^+. The availability of K^+ varies with environmental conditions, such as drought and soil density (Kuchenbuch et al. 1986; Liebersbach et al. 2004). Therefore, plants may frequently experience K^+ deficiency. Nitric oxide production is altered when plants are subjected to abiotic or biotic stresses (Lamattina et al. 2003; Leitner et al. 2009). High salt limits agriculture yield, induces a fast endogenous NO accumulation in plants (Bai et al. 2011; Wang et al. 2009), and triggers enhanced Na^+ influx and reduced K^+ absorption in the root (Zhu 2003). Both endogenously produced NO and exogenously applied NO have been proposed to enhance plant salt tolerance (Zhang et al. 2006; Zhao et al. 2007; Molassiotis et al. 2010; Chen et al. 2010) by attenuating high salt-induced increases in the Na^+ to K^+ ratio. Genetic analysis showed that K^+ nutrition, but not Na^+, plays critical role in plant salt tolerance (Zhu et al. 1998). In a study, Xia et al. (2014) found that NO reduces the activity of the K^+ channel (AKT1) in *Xenopus* oocytes and protoplasts under conditions of adequate K supply under salt stress. They suggested the possible roles of NO on K^+ uptake in response to low-K^+ condition rather than its roles on root growth by speculating that low-K^+ -induced NO accumulation would have a feedback modulation of K^+ uptake through downregulating several K^+ transporters. Zhang et al. (2007) reported that NO enhanced salt tolerance in *Populus euphratica* callus under salinity by increasing the K^+/Na^+ ratio, where H_2O_2 was involved in the increase of (PM) H^+-ATPase activity. Ruan et al. (2002) reported that NO stimulated proline accumulation under salt stress, owing to NO-induced increase in K^+ in *Triticum aestivum* seedling roots under salt stress conditions. Sung and Hong (2010) concluded that NO mediates K^+/Na^+ homeostasis and antioxidant defense in NaCl-stressed callus cells of two contrasting *Populus euphratica*. Accordingly, these studies suggest that K^+ homeostasis is important as a signal in growth and development of plants under salt stress conditions and function mainly as redirecting the energy from metabolic reactions to defense responses.

Nitrogen can be absorbed from the soil either in inorganic forms such as NO_3^- and NH_4^+ or in organic forms, mostly as free amino acids (Kiba et al. 2011), but NO_3^- is one of the commonest N forms available in plants in high pH soils and aerobic condition, which is often affected by salt stress (Masclaux-Daubresse et al. 2010; Li et al. 2019; Feng et al. 2020). Plants may have optimized the use of NO_2^- as a main source for NO (Jeandroz et al. 2016; Santolini et al. 2017). In addition, in NO regulation of NR activity, NO seems to modulate N uptake and distribution systems (Simon et al. 2013; Dong et al. 2015). Schinko et al. (2010) reported that nitrate assimilation involved in generating NO as a by-product. Nitrate reductase activity, as the first enzyme in the nitrate assimilation process (Iqbal et al. 2015; Khanna et al. 2021), has been shown to decrease in salt-stressed leaves of different plant species, including *Morus rubra* (Surabhi et al. 2008), *Helianthus annuus* and *Carthamus tinctorius* (Jabeen and Ahmad 2011), *Cucumis sativus* seedlings (Li et al. 2019), *Triticum aestivum* (Sehar et al. 2019; Khanna et al. 2021), as well as *Vigna* *radiata* (Hussain et al. 2020). However, the supplementation of N with NO nullified the toxicity of salt stress and increased the NR activity. In *Zea mays* roots, NO has been reported as a key signal in nitrate sensing (Trevisan et al. 2011; Manoli et al. 2014), and NO improve capacity of N uptake by regulating lateral root initiation and the rate of uptake of N (Sun et al. 2015), signifying that NO concerned in regulating N uptake in plant; nonetheless, the physiological and molecular mechanisms of NO on N assimilation under salt stress remain unclearly. Recently, Jahan et al. (2020) suggested that the application of NO plus split application of N and S more significantly promoted assimilation of N and S, through increased N- and S-use efficiency, photosynthesis, and growth in mustard plants under salt stress. Sehar et al. (2019) reported that decrease N content and NR activity under salt stress are restoration with the use of SNP. They also reported the positive role of NO on N assimilation. Moreover, the application of NO improved the assimilation of N- and S and antioxidant metabolism which confer tolerance against Cd stress in *Vigna radiata* (Hasan et al. 2020). In *Oryza sativa*, N uptake and accumulation is inhibited by salt stress, but those negative effects can be alleviated by NO. Furthermore, NO regulates the expression of genes related to N uptake and salt resistance in *Oryza sativa* plants (Huang et al. 2020).

The increase in NO levels after ABA perception in guard cells depends on the NR activity as it was confirmed by Chen et al. (2016) using the *nia1nia2 Arabidopsis* mutant, which lacks the two genes coding for NR. The double mutant showed reduced NO synthesis and lower leaf K content, and its stomata exhibited ABA insensitivity; however, they responded to exogenous NO addition. According to this, ABA-induced stomatal closure involves NO derived from NR activity which contributes to the inhibition of inward currents mediated by the KAT1 and AKT1 K channels through a Ca^{2+}-dependent mechanism in *Arabidopsis* guard cells (Chen et al. 2016). The study suggests that NO synthesis would be involved in the control of long-distance transport of K^+ and also understood in terms of the mutual interaction between K^+ and N nutrition. To conclude, the available reports suggest a main role for NO synthesis in modulating K^+ accumulation and N homeostasis in plants, which may be particularly relevant when plants are under salt stress conditions (Fig. 13.2). In view of the complexity of mineral nutrients homeostasis with signaling hormone in plants, a truly multidisciplinary program is the only mode to make progress in understanding the incorporation of ion transport in response to nutrient deficiency and salinity.

13.6 Conclusion

Plants are constantly exposed to salt stress that adversely affects their yield and growth. In order to acclimatize under salt stress, plants initiate their defense mechanism. The synthesis of NO and its signaling is one such defense response that may be activated in response to stress associated with the changes in K and N nutrients. Nitric oxide plays an important role under salt stress in plants, whether there is increase or decrease in the level of this hormone. It develops an adaptive mechanism

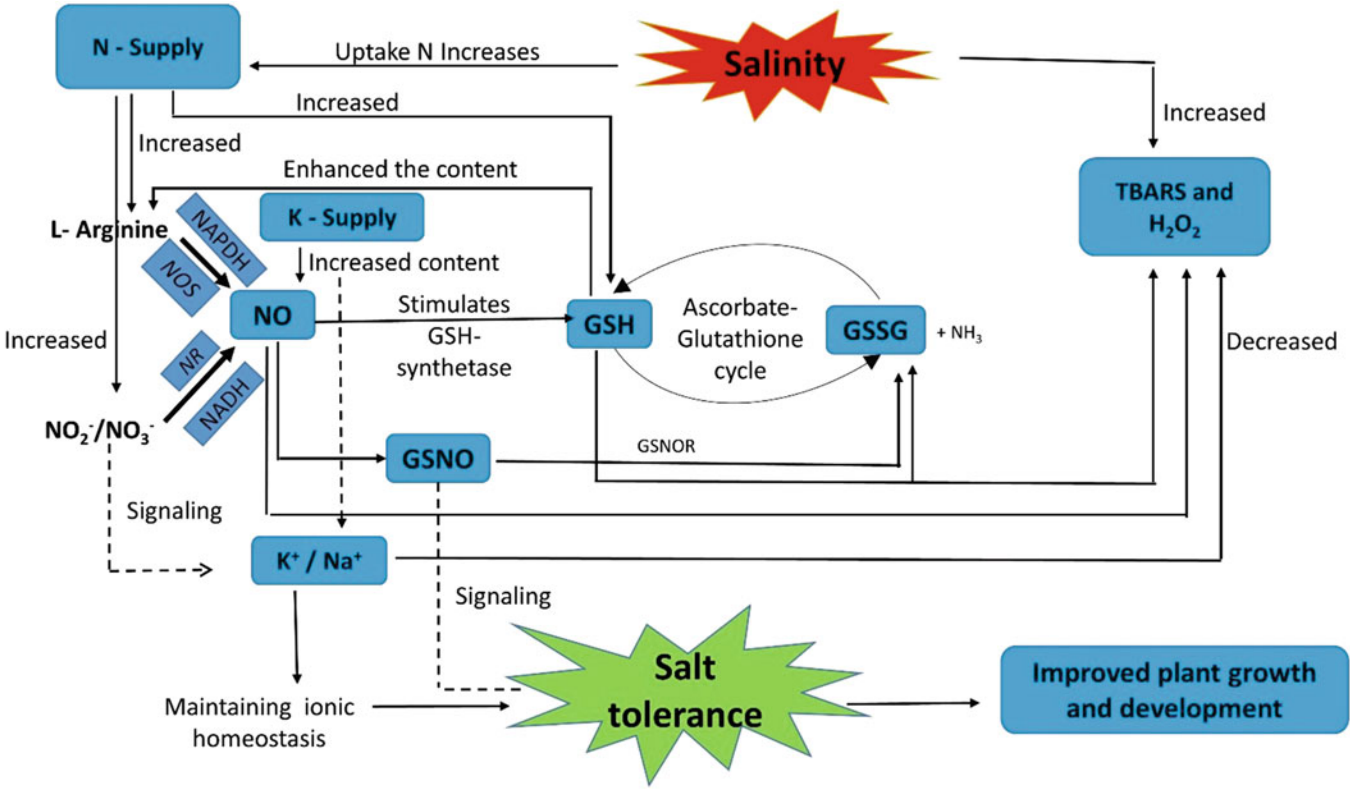

Fig. 13.2 Schematic representation of the major effect of nitric oxide and their involvement in potassium and nitrogen homeostasis in plants for salt tolerance. The figure shows that NO reacts with GSH and leads to the formation of GSNO in the presence of GSNOR enzyme. This metabolite can be converted to GSSG

and NH_3 in ascorbate-glutathione cycle and decreases the content of oxidative stress (H_2O_2; TBARS) for salt tolerance. Supply of K and N increases the content of NO and maintains the homeostasis of K and N. Additionally, supply of K helps in maintaining the K^+/Na^+ ratio through the increase in the accumulation/synthesis of NO. Arrow (---) indicates signaling between NO and GSH. *GSH* reduced glutathione, *GSNO* S-nitrosoglutathione, *GSNOR* S-nitrosoglutathione reductase, *GSSG* oxidized glutathione, H_2O_2 hydrogen peroxide, *K* potassium, K^+/Na^+ ratio of potassium ion to sodium ion, *N* nitrogen, *NADH* nicotinamide adenine dinucleotide hydride, *NADPH* nicotinamide adenine dinucleotide phosphate hydrogen, *NH3* ammonia, *NO* nitric oxide, NO_3^- nitrate, NO_2^- nitrite, *NOS* nitric oxide synthase, *NR* nitrate reductase, *TBARS* thiobarbituric acid reactive substances to tolerate salt stress in plants by modulating the homeostasis of K and N nutrition in plants, but whether they act dependently or independently on each other is debatable. The interaction between N availability and NO is well known, and relationship of N with K is also studied. However, the influence of K on NO and salt stress is still to be explored. The underlying mechanism between K and N with NO can be manipulated for adjusting plants to the changing environment for sustainable agricultural development. However, future studies are needed to deepen our knowledge about the role of NO in the modulation of the physiological and molecular mechanisms associated with other plant hormones and nutrients in order to improve crop growth under various stresses. Current understanding is carried out to build the databases of gene expression, proteomic changes, and metabolic pathways and is pointed in the right direction. Such a data pool is constantly reanalyzed and reinterpreted as we progress in our study.

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