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Review

Potassium: A vital regulator of plant responses and tolerance to abiotic stresses

Mirza Hasanuzzaman[1], M.H.M. Borhannuddin Bhuyan[2,3], Kamrun Nahar[4], Md. Shahadat Hossain[2], Jubayer Al Mahmud[5], Md. Shahadat Hossen[1], Abdul Awal Chowdhury Masud[1], Moumita[1], Masayuki Fujita[2,*]

[1] Department of Agronomy, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka-1207, Bangladesh; mhzsauag@yahoo.com [M.H.]; shahadat.hossen32@yahoo.com [M.S.H.]; chy.masud3844@gmail.com [A.A.C.M.]; moumita1ly@gmail.com [M.]

[2] Laboratory of Plant Stress Responses, Faculty of Agriculture, Kagawa University, Miki-cho, Kagawa 761-0795, Japan; shahadatsau24@gmail.com [M.S.H]; fujita@ag.kagawa-u.ac.jp [M.F.]

[3] Bangladesh Agricultural Research Institute, Joydebpur, Gazipur, Bangladesh; razon_sau@yahoo.com

[4] Department of Agricultural Botany, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka-1207, Bangladesh; knahar84@yahoo.com

[5] Department of Agroforestry and Environmental Science, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka-1207, Bangladesh; jamahmud_bd@yahoo.com

* Correspondence: fujita@ag.kagawa-u.ac.jp; Tel.: +81-87-891-3033

Abstract: Among the plant nutrients potassium (K) is one of the vital elements required for plant growth and physiology. Potassium is not only a constituent of plant structure but also plays regulatory function in several biochemical processes related to protein synthesis, carbohydrate metabolism, enzyme activation. There are several physiological processes like stomatal regulation and photosynthesis are dependent on K. In the recent decades K was found to provide abiotic stress tolerance. Under salt stress, K helps in maintaining ion homeostasis and regulation of osmotic balance. Under drought stress condition K regulates the stomatal opening and makes the plants adaptive to water deficit. Many reports provided the notion that K enhances the antioxidant defense in plants and therefore, protects the plants from oxidative stress under various environmental adversities. Also, it provides some cellular signaling alone or in association with other signaling molecules and phytohormones. Although a considerable progress in understanding K-induced abiotic stress tolerance in plants has been achieved the exact molecular mechanisms of such protections are still under research. In this review, we summarized the recent literature on the biological functions of K, its uptake, and translocation and its role in plant abiotic stress tolerance.

Keywords: Abiotic stress; Antioxidant defense; Enzyme regulations; Oxidative stress; Plant nutrients; Reactive oxygen species; Soil fertility

1. Introduction

Most of the cultivable crops experience one or more abiotic stress(es) of any form throughout the growth stages. So, resilience from abiotic stress is a great challenge to increase the food production by 70% to feed the increasing population by the year 2050 [1]. Abiotic stress hampers plant productivity by altering the growth pattern, physiological responses [2,3]. Combination of different stresses has become more common affecting the standing crop plant. The occurrence of drought and high temperature is the most common [4]. In arid and semi-arid regions salinity and high temperature stresses are imposed at a time. High light and high temperature stress, drought and salinity, or high temperature, drought and salinity together are privileged nowadays. Due to the complex nature of stress plants become upset, and the research with plant stress tolerance is ever changing and updating with the new form of stresses. These complex stresses cause changes in

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cropping pattern, crop cultural practices, extinction of plant species. Since the starting of agriculture, a range of cultural practices is being developed after continuous trial and error process. Among the cultural practices use of fertilizers and organic amendments are the oldest methods for improving plant productivity. Role of potassium (K) in plant developmental process is well known. Up-gradation of K status decreases the reactive oxygen species (ROS) generation in plants. Potassium reduces the activity of NAD(P)H oxidases and retains photosynthetic electron transport activity which helps to reduce ROS. Potassium deficiency can decrease photosynthetic CO_2 fixation and transport and utilization of assimilates [5]. Membrane and chlorophyll (chl) degradation have been privileged in K-deficient plants. Regulation of K is associated with the activity of enzymes involved in detoxification of ROS [6]. Potassium triggers in activating the ATP synthase enzyme. Plasma membrane-bound H-ATPase is influenced by K content [7]. K-deficient plants have been reported to be light-sensitive showing chlorotic and necrotic symptoms. K was reported to decrease different stress effects in plants such as drought, chilling, and high light intensity [6]. Potassium-induced combined high temperature and drought tolerance were reported by [8]. The role of K as nutrient has been recognized for long. But the arrays of its biological function in physiological processes of plants are still disengaging to realize. This is a comprehensive review articulating the biological function of K in plants and its role in plant adaptation to abiotic stresses.

2. Biological functions of potassium in plants

From seed germination to seed production plants require various macronutrients and micronutrients. Potassium is one of the most important macronutrients along with nitrogen (N) and phosphorous (P). Potassium is required for various biochemical and physiological processes, and these are responsible for plant growth and development. Potassium is related to protein synthesis, carbohydrate metabolism, enzyme activation. As well as it helps in cation-anion balance, osmoregulation, water movement, energy transfer and so on. Potassium also plays a mitigating role in various abiotic stresses like drought, salinity, metal toxicity, high temperature or chilling temperature, etc. When plants are in K deficiency, it shows stunted growth, yellowing leaf margins. Poor root system, lodging, yield reduction, are the common phenomenon of K deficiency. Lack of K fertilizer, increases the susceptibility of various disease and pest infestation and makes vulnerable damage in various stress condition.

3. Potassium uptake, transport, and assimilation in plants

To facilitate K uptake from outer environment and transport to different cellular compartments, many proteins are present in the cell, mainly in the membrane. These proteins are often called transporter, and channels. Based affinity towards K^+, K^+ transport components can be classified as high-affinity components (transporters) which are active at a low concentration of external K^+ and low-affinity components (channels) which are active at a higher concentration usually above 0.3 mM external K^+ [9]. Advancement in molecular approaches and tools lead to the identification of some low affinities and high-affinity transporters in different plant species including *Hordeum vulgare*, *Oryza sativa* and *Capsicum annuum* [10]. A yeast mutant lacking K uptake ability could grow only when the mutant transformed with a cDNA from barley. This study leads to the identification of high-affinity K^+ transporter HvHAK1 having homology to *Escherichia coli* and *Schwanniomyces occidentalis* HAK1 K^+ transporter [11]. To support low-affinity transport mechanism, inward rectifying K^+ channel, HKT has been proposed [10]. An *Arabidopsis* mutant lacking *HKT1* gene (screened from T-DNA insertion line) was able to grow at one mM KCl solution without growth reduction. However, at 100 µM KCl, the mutant showed significant growth reduction, indicating *HKT1* channel involvement in K^+ uptake from low K^+ solution [12]. In *Arabidopsis*, 75 genes encode the proteins that facilitate K^+ uptake and transport. These genes can be roughly categorized into seven categories viz. shaker-type K^+ channels (9 genes), two-pore K^+ channels (6 genes), putative K^+/H^+ antiporters (6 genes), KUP/HAK/KT transporters (13 genes), HKT transporters (1 gene), cyclic-nucleotide gate channels (20 genes), glutamate receptors [13]. Shaker-type K^+ channels further classified into three groups. These are an inward-rectifying channel, which facilitates K^+ uptake and is activated upon hyperpolarization; outward-rectifying channels, which mediate K^+ efflux and are activated upon membrane depolarization; and weakly-rectifying channels which can function in both K^+ influx and K^+ efflux, and are activated by membrane hyperpolarization [9]. Channels and transporters encoded by different genes are different regarding structure and function [9].

In root, K^+ uptake from the media is mainly mediated by two proteins, AKT1 and HAK5 as these two proteins are expressed in roots. Loss of function mutant *hak5* or *akt1*was able to survive at 100 µM KCl solution but the double mutant at *hak5 akt1* failed to survive at the same concentration, indicating AKT1 and HAK5 are high-affinity transporters that mediate sufficient K^+ uptake required for plant growth [14]. For long-distance transport, K^+ transport from root cortex to xylem mediated by outward-rectifying channels (Figure 1). Experimental evidence showed that a mutant lacking SKOR channel reduces the K^+ content in shoot by 50% and reduced K^+ content in xylem sap. Stomatal closure or opening depends on K^+ concentration in the guard cell, where inward channel KAT1 and KAT2 mediate K^+ uptake in the cell and outward rectifying K^+ channel, GORK channel mediates K^+ release to close stomata [15]. In case of K^+, voltage-dependent K^+ channel (TPK1TPK2, TPK3, and TPK5) and vacuolar Na^+, K^+/H^+ antiporters, such as, NHX1 and NHX2 are present in the tonoplast to facilitate K^+ influx and efflux in the vacuole [16,17,18].

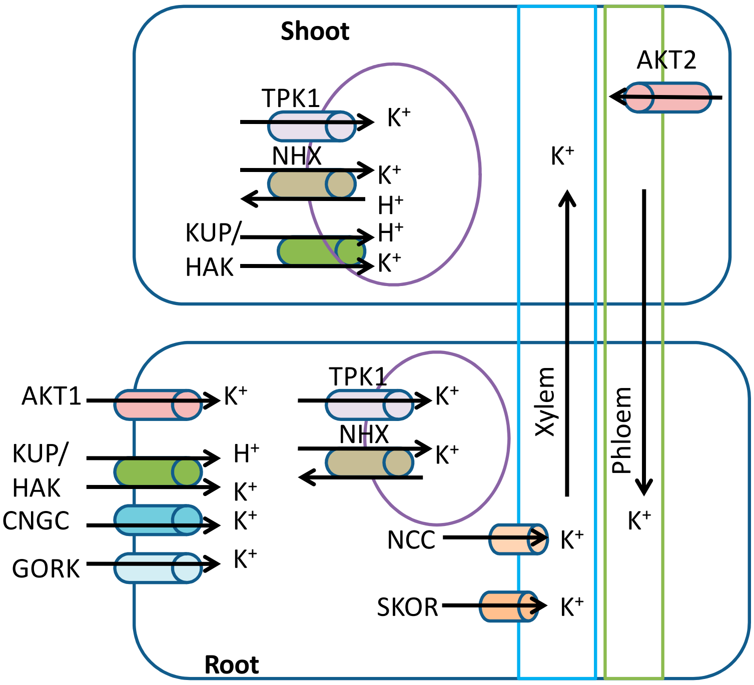

Fig. 1. Potassium uptake and transport in plants (Modified from Ahmad and Maathuis [19]). AKT, *Arabidopsis* (Shaker-type) K^+ channel: CNGC: cyclic nucleotide-gated channel; GORK: guard cell outward rectifying K^+ channel; HAK/KUP: high affinity K^+ transporters; KAT: Arabidopsis (Shaker type) K^+ channel; NCC: non selective cation channels; NHX: Na^+ proton exchanger; SKOR: stelar outward rectifying K^+ channel; TPK: tonoplast two-pore K^+ channel

4. Potassium and plant responses

Potassium plays significant regulatory roles in numerous plant physiological processes viz. seed germination and emergence, stomatal regulation, phloem transport, cation-anion balance, protein synthesis, photosynthesis, energy transfer, osmoregulation, enzyme activation, nutrient balance and stress resistance [20].

4.1. Seed germination and emergence

Potassium helps in seed germination by initiating rapid imbibitions of water and facilitates other physiological processes [21]. Potassium salts have been well studied as a good catalyst in improving seed germination and emergence rate. The most common form of K salt that used in seed priming is potassium nitrate (KNO_3), potassium chloride (KCl) and dipotassium hydrogenphosphate (K_2HPO_4) [22,23]. Using KNO_3 as a priming agent, good germination rate was obtained in cotton genotypes ([24]. Osmopriming with KNO_3 in rice suggested that KNO_3 performed best with maximum germination percentage, germinating rate, as well as other morphological attributes [25]. Therefore, in the light of above experimental findings, it can be concluded that K has a promising regulatory role in seed germination and emergence.

4.2 Growth

Among the essential plant nutrients, K is an indispensable mineral constituent, intrinsically acts a key role in the process of plant growth and development [26]. Maintenance of K level and its ratio with other essential plant nutrients especially with sodium (Na) in plant growing medium or in cellular level is very crucial for normal function as well as the growth of the plant [27]. Moreover, excess or deficient K in the growing medium hampers the overall growth of the plant. So, management of K fertilizer is advantageous for improving plant growth [28]. Hussain et al. [29] applied different levels of K (0, 30, 60, 90,120 kg ha^{-1}) and found maximum plant height at 90 kg ha^{-1} and minimum at 0 kg ha^{-1}. Zelelew et al. [30] experimented *S. tuberosum* growth with five K doses (0, 75, 150, 225 and 300 kg K_2O ha^{-1}) and found that plant height, aerial stem number and leaf number per plant were enhanced in increasing K levels from 0 to 150 kg. Gerardeaux et al. [31] observed that K deficiency in the vegetative phase of *Gossypium hirsutum* reduced plant dry matter production, leaf area and internodes size, which leads to a reduction of plant growth. Tang et al. [26] cultivated three *Ipomoea batatas* cultivars in K deficient soil and found a lack of K notably cut off total biomass productivity and root yield. Nodulation is a very common phenomenon for legume crop, which is closely related to plant growth itself. Level of K and its ratio with N and P determine the success of nodulation process [32].

4.3 Stomatal regulation

Proper stomatal regulation (opening and closing) is a must for uninterrupted production of energy through photosynthesis process, plant cooling, water, and nutrient transport. In the presence of K ion, stomatal guard cell gets swelled by absorbing water followed by stomatal opening and permitting gaseous movement in between plants and environment. In case of water deficit condition, K is pumped out from the guard cell letting the pores closed tightly. Thus, K controls the evapotranspiration of water through pores in a water deficit soil environment condition and protects the plant from water stress [33]. The stomata get lithergic in case of insufficient supply of K, which results in delayed stomatal closure even unfinished closure of the pores. Also, the osmotic gradient produced due to the accumulation of K in root helps to draw water in the root cells. Therefore, the reduced K supply in the plant results in decreased water uptake and faces water stress in case if the supply of water drastically reduced.

Taiz and Zeiger [34] described the stomatal activity in details that, three major events are happened, while light radiate into the plant cell and stimulate stomatal opening: proton pump ATPase, solute uptake, and organic solute synthesis. Electrochemical potential generated by the proton pump ATPase helps in uptaking K and associate anions like Cl^- malate. While solute and sucrose amount increases in guard cell vacuole, it eventually decreases in osmotic potential. Later on, the turgor pressure gets increased with increasing amount of water uptake results in stomatal opening. On the contrary, the stomatal closure operation is largely maintained by ABA activity. Calcium uptake is stimulated by ABA, which blocks the K channel and paves the way of anion (Cl^-) entry into the cell apoplast. Increased concentration of Ca in intercellular level reduces proton pump

ATPase that accelerated in cell membrane depolarization followed by deporting cytoplasmic K^+ to the cell apoplast. Therefore, the stomata close due to reduced turgor pressure.

4.4 Water uptake

Potassium is engaged in nearly all the physiological processes of the plant, where the presence of water is a must. These include stomatal regulation, translocation of photoassimilate, enzyme activation, and leaf heliotropic movements. Also, K helps in water transportation and mineral compounds translocation in the entire plant through the xylem vessels. In case if the K supply alters from optimum level, the translocation of mineral compounds like nitrates (NO_3^-), phosphates (PO_4^{3-}), calcium (Ca^{2+}), magnesium (Mg^{2+}) and amino acids is reduced in uptake [35].

4.5 Photosynthesis

Stomatal regulation during photosynthesis is a vital event that governs the continual photosynthesis operation is significantly moderated by the amount of K retained in the plant [20]. Potassium deficiency results in reduced stomatal conductance increased mesophyll resistance and lowered ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activity in plants that eventually decreased the total photosynthesis rate [36]. The rate of photosynthesis in plants is increased with the higher utilization and export of photoassimilates. Evidence showed that the sucrose level in leaf increased in several-folds when the plants supplied with sufficient level of K [36]. Also, both photosynthetic CO_2 fixation and utilization of photoassimilates reduced due to K deficiency accelerated ROS production in a plant that ultimately hastens rapid photooxidative damage [6].

Potassium commences the photosynthesis process by activating the ATPase enzyme thus generates ATP in plant cell. Shingles and McCarty [37] suggested that ATPase performance is best while K content in plant is in optimum level. Potassium controls the photosynthesis by sunlight interception. Furthermore, K modulates the photosynthesis rate by adjusting leaf area per unit. Combination of this two events triggers the photo assimilation pool in plant that retains continuous plant growth. Leaf surface area and sunlight interception both reduced drastically when K is below the requirement of plant [38]. The most significant function that K plays in regulating the stomatal aperture is balancing between CO_2 entry and H_2O vapor removal from intercellular spaces. However, the amount of CO_2 entry into the intercellular spaces represents the amount of photosynthates production in leaf.

4.6 Nutrient balance

In K deficit condition, protein formation is hampered although the abundance of N supply, therefore NO_3^-, amino acids, and amides accumulate in the cell [39]. Potassium activates nitrate reductase (NR), a starch synthetase and these two enzymes make a balance by producing protein and carbohydrate respectively. Therefore, the shortage of K leads to breakdown of these processes and plant suffers although other nutrients are available. Potassium has a role in xylem and phloem transport system. Consequently, Ca^{2+}, Mg^{2+}, NO_3^- and PO_4^{3-}, as well as plant hormones and enzymes, cannot be translocated, and source-sink relationship disrupted [40]. Whereas, exogenous application K at different growth stages decreases uptake of harmful nutrients, enhanced tolerance to abiotic stress and boosting yield and yield contributing characters [41].

Another vital micronutrient Fe also has a synergistic relationship with K [42]. In case of Mo/K deficiency reduces Fe uptake which leads to sterility of female flower parts at reproductive phase, while Mo application increases nodulation in roots, further seed yield in lentil [43].

4.7 Reproductive development

Potassium plays roles in flowering, pollen germination as well as in seed development. Fan et al. [44] found that externally applied K helps to increase the pollen germination rate also K increases

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the tube growth in *Arabidopsis.* Choudhury et al. [45] described that sucrose, boric acid, and different salts have a role in pollen germination, among them KNO_3^- also plays an important role in pollen germination and development. Makhdum et al. [46] described that in some cases, yield depends on the reproductive-vegetative ratio (RVR). If RVR is lower, it means vegetative growth is higher than the reproductive growth, and in this case, the yield is reduced. Amanullah et al. [28] reported that phenological development like flowering or physiological maturity delayed due to lower application of K. Sadiq and Jan [47] observed that split application of K delayed flowering and physiological maturity even after split application of 60 kg ha^{-1} K application but in case of 90 kg ha^{-1} K application as a basal dose, days to tasseling, silking and physiological maturity was increased. Asif et al. [48] showed that phenological development in maize increased with the application of 90 kg ha^{-1} K application and showed a positive relationship with number of split application of K. Full dose of K helps to increase the flowering, number of grains and early physiological maturity. In *T. aestivum*, K has an important role in grain filling stage. Application of K in a proper way significantly increased the photosynthesis during the grain filling stage, and obviously, it has a positive role to increase the grain number [49]. The higher amount of K helps to transfer of food material to develop grains, thus decrease the amount of sterile grain. In *O. sativa*, when K was applied at 100 kg ha^{-1}, grain sterility was lower compared to no K application. At 100 kg K ha^{-1}, grain sterility was 22.60% whereas without K it was 30.33% [50].

4.8 Yield

Potassium plays a role in biosynthesis, conversion, and allocation of metabolites that ultimately increase the yield. Many research works strongly supported the opinion that K is directly or indirectly responsible for higher yield of crops (Table 1). Islam and Muttaleb [50] experimented with rice with various doses of K fertilizer. They reported that K helps to increase the N uptake as well as N use efficiency that also helps in increasing the yield of rice. As a result, rice yield increased to 6.86 t ha^{-1} $year^{-1}$ with optimum doses of K, whereas without K the yield was 5.19 t ha^{-1} $year^{-1}$. Cheema et al. [51] 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 *Brassica napus*. Uddin et al. [52] found that along with these attributes 1000 grain weight, grain yield also increased with the use of K. Also, when other nutrients are in optimum condition, K played an important role to increase the yield of NERICA 1 rice. Though other nutrients are available, without K yield increase is not so much significant. Duan et al. [53] showed that yield of wheat increased by about 0 to 17.6% when they applied NPK fertilizer compared to only NP, and in case of rice yield increased by about 1.7 to 9.8 % after using NPK fertilizer to only NP. Raza et al. [54] showed that K increased the spike length, a number of spikelets per spike, no. of grains and grain yield of wheat under drought condition. K increased spike length by 21.8%, no. of spikelets/ spike increased by up to 23.27%, no. of grains/spike increased by 39.24% and ultimately yield was increased by 30.77% than without K application. Waraich et al. [55] reported that 2% KNO_3 application increased the plant branches, plant height, and no. of balls/plant in *Gossypium hirsutum* but in case of ball weight, 1.5% foliar application is better. According to Colpan et al. [56], K plays a vital role to increase the yield and yield components in *Lycopersicon esculentum*. They applied various doses of K viz. 0, 40, 80, 120, and 160 kg K_2O ha^{-1} and found the highest yield (195.7 t ha^{-1}) with 120 kg K_2O ha^{-1}. Fruit size, diameters of fruits, no. of fruits/plants, fruit weight all the yield contributing factors increased with the application of K. Khan et al. [57] experimented to show the effect of K on *O. sativa* and *T. aestivum*. They noticed that K increases the yield and yield contributing characters in both crops. In case of *T. aestivum*, yield was about 13% higher, while in *O. sativa* it was about 50% higher with the application of 60 kg ha^{-1} K compared to control.

4.9 Crop quality

Potassium is responsible not only for the higher production but also for the improved quality of harvest. Thus K ensures high valued crops and benefits to growers. Sometimes, K is called the "quality element" for better crop production and it is supported by many scientists. Yang et al. [58] showed that the protein percentage in *Z. mays* grain was higher where a balance N-P-K fertilizer was applied. But where only N-P fertilizer was applied protein percentage as well as grain quality was reduced. But in case of *T. aestivum*, when manure is applied with N-P-K the protein percentage was higher than the normal fertilization. In *T. aestivum* as well as in most of the cereal crops K helps in increasing better milling and baking qualities, more efficient use of nutrients, increase disease resistance and so on. In *G. hirsutum*, the important quality control parameters are fiber length, strength, uniformity, micronaire, color and so on. There are many research strongly support that, fiber quality depends on optimum K. When K supplies are not enough, osmotic potential of the fiber became more negative. Thus turgor pressure of the fiber decreased and primary fiber cell wall cannot be elongated ultimately results in shorter fibers [59]. Ginning out turn, fiber uniformity, length and strength increased when KNO_3 applied at 2% as a foliar spray [55]. According to Ashfaq et al. [60], K deficiency reduces the cotton yield and quality. Mehrandish et al. [61] showed that total soluble solids, soluble sugar content, refineable sugar, purity percentage of root juice of *Beta vulgaris* increased with the K application. Economakis and Daskalaki [62] explained, K increased dry matter, total soluble solids, firmness and vitamin C in tomato in both normal and saline condition.

Table 1: Effect of potassium on different crops to increase yield

Name of crops	K doses	Yield improvement	References
O. sativa	60 kg K_2O ha^{-1}.	Grain yield: 50%	[57]
O. sativa	40 kg K_2O ha^{-1}.	Grain yield: 35%	[63]
O. sativa	80 kg K_2O ha^{-1}.	Grain yield: 78.47%	[64]
O. sativa	93.96-112.03 kg K_2O ha^{-1}	Grain yield: 32.17%	[50]
T. aestivum	108.42 kg K_2O ha^{-1}	Grain yield: 10.66%	[65]
O. sativa	60 kg K_2O ha^{-1}.	Grain yield: 13%	[57]
O. sativa	40 kg K_2O ha^{-1}.	Grain yield: 21%	[63]
O. sativa	80 kg K_2O ha^{-1}	Grain yield: 41.16%	[66]
Lens culinaris	42.16 kg K_2O ha^{-1}	Grain yield: 34.16%	[67]
C. annuum	200 kg K_2O fed^{-1}	Pod/fruit yield: 22.20%	[68]
G. hirsutum	112 kg K_2O ha^{-1}	Lint yield: 10.18%	[69]
G. hirsutum	150 kg K_2O ha^{-1}	Lint yield: 13.79%	[70]
G. hirsutum	180.70 kg K_2O ha^{-1}	Lint yield: 5.7%	[71]
S tuberosum	225 kg K_2O ha^{-1}	Tuber weight: 13.34%	[72]
S. tuberosum	225 kg K_2O ha^{-1}	Tuber yield: 78.11%	[73]
S. tuberosum	150 kg K_2O ha^{-1}	Tuber yield: 22.41%	[74]
Z. mays	150 kg K_2O ha^{-1}	Grain yield: 36.33%	[75]
Z. mays	48.19 kg K_2O ha^{-1}	Grain yield: 33.12%	[76]
Jatropha curcas	60 kg K_2O ha^{-1}	Oil yield: 17.30%	[77]
Strawberry	66% K_2O foliar spray	Weight of primary fruits: 6.2%	[78]
Strawberry	66% K_2O foliar spray	Weight of secondary fruits: 6.95%	[78]
C. arietinum	40kg K_2O/fad	Grain yield: 34.50%	[79]
P. guajava	75 g K_2O/plant/ year.	Fruit yield: 35.65%	[80]
Carthamus tinctorius	3 g K_2O/pot	Oil yield: 86.84%	[81]
Arachis hypogaea	75 kg K_2O/plant/ year	Seed yield: 44.2%	[82]
Saccharum officinarum	722.82 kg K_2O ha^{-1}	Sugar yield: 30.17%	[83]
Beta vulgaris	72 kg K_2O /fed	Root yield: 24.83%	[84]
V. radiata	37.5 kg K_2O ha^{-1}	Seed yield: 28.29%	[85]

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Name of crops	K doses	Yield improvement	References
L. esculentum	120 kg K_2O ha^{-1}	Seed yield: 30.9%	[56]

5. Potassium-induced abiotic stress tolerance

In the previous headings, we described the role of K in various growth and physiological parameters of plants under normal condition. Many plant studies also showed that K functions as a vital protector against abiotic stresses. It is mainly due to its role in maintaining ion homeostasis, cellular integrity and enzymatic activities (Table 2, 3 & 4). In the following sections, we will describe the role of K in conferring tolerance against major abiotic stresses.

5.1 Drought

In addition to growth and productivity, K plays a role in cell turgor maintenance, osmotic adjustment [6] and aquaporin functioning [27] under drought condition. Therefore, a close relationship between K nutritional status and plant drought resistance has been demonstrated (Table 2).

Sufficient supply of K can improve the plant dry matter than a lower concentration of K^+ in soil under drought condition [86]. Increasing root growth through applying K improves the root surface under drought condition, which ultimately enhances the water uptake in plant cells [87].

It was observed that exogenous application of K not only improved the plant dry matter content and leaf area but also stimulated the water uptake when plants faced drought [88,89]. During drought condition, excess ROS production in plants may exaggerate cellular lipid peroxidation leads an increase of cellular membrane permeability which is evidenced by increases of electronic leakage (EL) and MDA content [90,91]. Soleimanzadeh et al. [92] carried out an experiment with *Helianthus annuus* and reported that adequate supply of K^+ significantly decreased MDA content under water shortage condition.

Kanai et al. [93] showed a relationship between aquaporin activities and K^+-channel/transporter, where K deficiency remarkably changed the K^+-channel activity resulted alteration of root hydraulic conductance and signal transduction with the consequent changes in aquaporin activity. Thus, reduction of root hydraulic conductance and water supply for transpiration was suppressed in time of K deficiency. According to Guo et al. [94], there is a positive correlation between water uptake and K^+ absorption in *Phaseolus vulgaris*. Potassium mediated the xylem hydraulic conductance and maintained cell turgor, stomatal movement and sufficient gas exchange as part of drought adaptation [95].

Table 2. Beneficial effect of exogenous application of potassium under Drought stress

Species and cultivars	Drought dose and duration	K doses	Protective effects	References
Z. mays	Withholding water 31d after planting	300 kg K ha^{-1}	• Cell membrane stability increased • Decreased leaf water potential	[96]
Hibiscus rosa-sinensis	Water deficit, 21d	10 mM K_2SO_4	• Enhanced root dry matter • Increased root:shoot ratio	[86]
H. annuus	Withholding irrigation at the end of growing period	100 kg K ha^{-1}	• Improved shoot dry matter • Decreased MDA content • Improved enzyme activity (SOD, CAT,	[92]

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Species and cultivars	Drought dose and duration	K doses	Protective effects	References
			GPX)	
Camellia sinensis	Field capacity, 5 d	2% muriate of potash	• Increased Pro contents • Improved water use efficiency • Enhanced root starch reserved	[97]
T. aestivum	15% PEG	10 mM K_2O	• Improved chl *a*, chl *b*, and car • Increased Pro content	[98]
T. aestivum	20% PEG, 7d	7.5 mM K_2CO_3	• Significantly increased shoot K^+ • Decreased electrolyte leakage and MDA	[99]
Z. mays	65 ± 5% water holding capacity of soil	0.42 g K kg^{-1} soil	• Strengthen the accumulation of K^+ and • Osmotic nitrides in plants • Increased endogenous glycine betaine	[100]
H. vulgare	50% soil water content	10 mM K_2CO_3	• Decreased MDA content • Enhanced K^+ content in plant • Decreased soluble carbohydrate	[101]
O. sativa	Withholding irrigation 30d after transplanting, 10d lasted	120 kg K ha^{-1}	• Increased shoot dry mass • Improved osmolytes synthesis	[89]
G. hirsutum	At flowering stage withholding water for 8d followed by 75±5% soil relative water content	300 kg K ha^{-1}	• Improved osmotic adjustment • Increased nitrogen metabolism • Enhanced free amino acid, sugars content	[102]

It has been reported that K increased the production of organic osmolytes, especially in Pro under drought condition [89]. When plant exposed to drought stress, Pro accumulation plays a highly protective role in plants which involve in osmotic adjustment [103]. In several studies, it was reported that under normal and drought stress conditions, Pro has been increased through K application in *O. sativa* [104], *B. napus* [105] and *T. aestivum* [98]. Zhang et al. [100] observed in their study that exogenous application of K increases the Pro content in *Z. mays* cultivars under drought condition. At the same time, Ali et al. **[**106**]** reported that under drought stress K application increase the shoot Pro content in *B. napus* in a dose-dependent manner. Similarly, Zahoor et al. **[**102**]** found that K application generates the Pro content during drought stress in *G. hirsutum*.

Therefore, proper supplementation of K^+ improves the osmotic adjustment and upgrades plant's withstand ability against drought stress. Figure 2 illustrates the involvement of K in plants tolerance under drought stress

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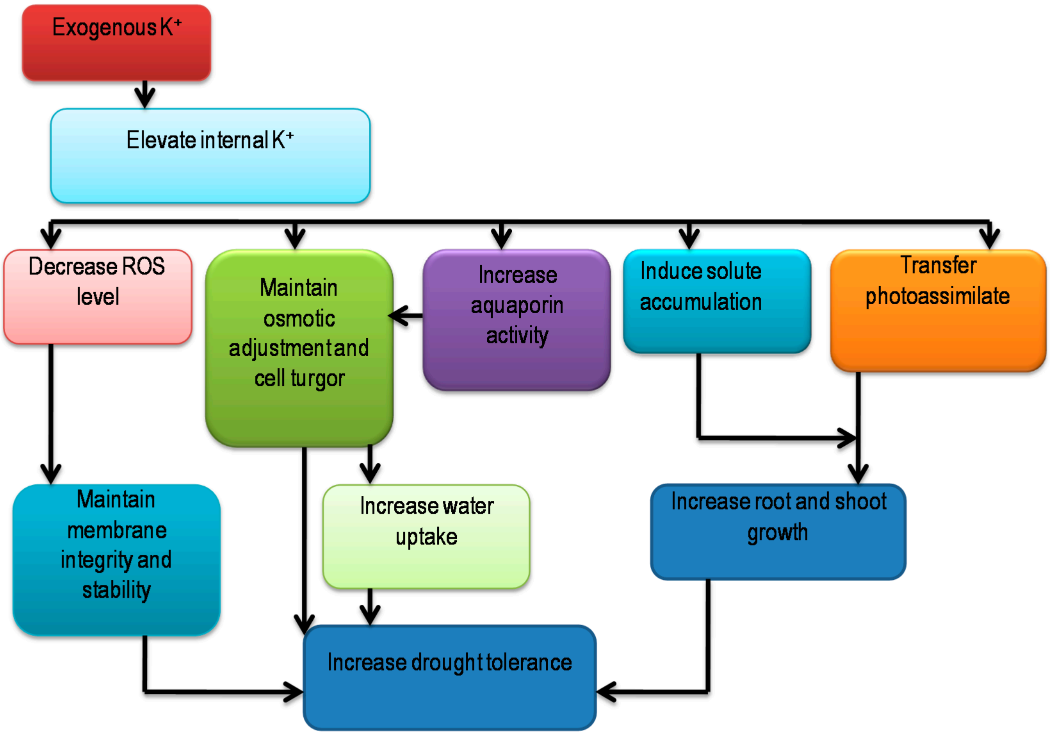

Fig. 2 Role of potassium under drought stress (Modified from Wang et al. [27])

5.2 Salinity

Potassium is an important macro-nutrient, which plays essential roles related to osmotic adjustment, maintaining turgor, regulation of membrane potential, cytoplasmatic homeostasis, protein synthesis, and enzyme activation under salt stress (Table 3) [107].

During salinity stress, osmotic effects and ion toxicity inhibited the plant root growth, which decreases nutrient uptake and translocation, especially K [27]. Sodium ion (Na^+) competes with K^+ for major binding sites as key metabolic processes in cytoplasm, including both low-affinity (non-selective cation channels, NSCC) and high-affinity (KUP and high-affinity K^+ transporter, HKT) transporters that disturbs plant metabolism [20,27]. Under salinity, furthermore, salinity induces membrane depolarization and decrease membrane integrity, which results K^+ leakage through depolarization-activated outward-rectifying (KOR) K^+ channels [108]. It is crucial for plant growth and salt tolerance to keep cellular K^+ content above a certain threshold and maintain high Na^+/K^+ ratio. Thus, higher application of K, increases K^+ content in plant cells and reduces Na^+ concentration, which increase the K^+/Na^+ ratio. HTK (high-affinity K^+ transporter) mediate Na^+-specific transport or Na^+-K^+ co-transport, which has a vital role in tolerance to Na^+ [109,110].

Table 3. Beneficial effect of exogenous application of potassium under salinity stress

Plant species	Salinity (NaCl) doses	K doses	Protective effects	References
T. aestivum	100 mM	10 mM KCl	• Increased shoot and root length • Increased K^+/Na^+ ratio	[111]
Olea europaea	100 mM	100 mM K_2SO_4	• Reduced K^+ uptake • Increased K^+ in leaves • Improved osmotic potential	[112]
B. campestris	80 mM	40 mg kg^{-1} soil	• Improved photosynthetic traits • Increased activity of antioxidant enzyme and the	[113]

Plant species	Salinity (NaCl) doses	K doses	Protective effects	References
			ascorbate and glutathione content • Decreased the ion accumulation and oxidative stress traits in the leaves	
Z. mays	70 mM	9 mM KCl	• Increased CAT activity, • Improved photosynthetic capacity, • Increased accumulation of K^+ in the leaves	[114]
H. vulgare	150 mM	10mM KNO_3	• Decreased Na^+/K^+ ratio • Improved shoot and root height • Increased proline content	[101]
L. esculentum	150 mM	2.39 mEq L^{-1} KH_2PO_4	• Increased root and shoot weight • Improved photosynthetic pigment	[115]
A. hypogaea	2 & 4 dS m^{-1}	30 kg K ha^{-1}	• Reduced uptake of Na^+ from soil and lesser accumulation in leaf tissue • Increased plant biomass	[116]
S. lycopersicum	75 mM	9 mM KNO_3	• Minimized oxidative stress and increased photosynthesis • Decreased the antioxidant activities (SOD, CAT, GSH) • Increased leaf K^+ levels and K^+/Na^+ ratio • Improved membrane stability index	[117]
B. vulgaris	7.6 dS m^{-1}	200 kg K_2O ha^{-1}	• Improved shoot and root dry matter • Increased sucrose and sugar contents	[118]

Taffouo et al. [119] found that K^+ content was decreased from the root and shoots due to reduced uptake and translocation of K^+ from root to shoot while increasing NaCl concentration in *V. subterranea*. But exogenous K^+ can positively correlate with plant root and shoot growth during salinity stress and K^+ deficient stage. Saida et al. [115] observed in their experiment that application of 2.39 mEq L^{-1} KH_2PO_4 against 150 mM NaCl increased shoot and root fresh and dry weights of *L. esculentum* under salt stress. Fayez et al. [101] experimented with *H. vulgare* crop and found that under 150 mM NaCl stress shoot fresh weight and height decreased, but after treating with K improved shoots fresh weight and height of barley crop. Simillarly, Amjad et al. [117] found in a study that application of 9 mM K improved the root and shoot dry weight under 75 mM NaCl stress in *S. lycopersicum*. Merwad [118] reported that higher salinity negatively affects tomato root, shoot, leaf and water use efficiency, recorded exogenous K^+ can have a positive effect on most of the *B. vulgaris* cultivars under salt stress.

In previous section (5.1 Drought), it has been shown that exogenous application of K can improve the organic osmolytes synthesis, especially Pro. Shabala and Lew [120] observed that the quickness of cell recovery in osmotic stress was regulated by higher accumulation of K^+, Cl^- and Na^+

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in epidermal root cells of *Arabidopsis*. Thus, higher Na^+ concentrations are toxic for cell metabolism; that's why it is essential to maintain cytosolic K^+ contents at a constant level for plant metabolic process [121, 122]. A constant cytosolic K^+ concentration is attributed to the consumption of vacuolar K during K^+-deficient situation [27]. Fayez et al. [101] observed that salinity increased Na^+/K^+ ratio in *H. vulgare*, which significantly decreased after application of K^+ and increased K^+/Na^+. As well, Chakraborty et al. [116] suggested that external K^+ application can have reduced the Na^+ uptake by adjusting the tissue ionic balance in *A. hypogaea*.

5.3 Extreme temperature

When temperature is more than 35-40^{0}C, plants suffer from extreme temperature stress. Almost all the plants suffer from this stress. Extreme temperature disrupted the various biochemical reactions and metabolism which are highly related with the temperature [3]. Nutrient management is one of the best options for extreme temperature stress tolerance and among all the nutrients K plays a significant role to cope up with the temperature stress. Potassium helps to activate the various physiological and metabolic processes and increases the tissue water potentiality which helps in extreme temperature stress tolerance. During high temperature stress plants accumulate various types of osmolytes to overcome the damages caused by the stress. K may works as an osmolytes and helps to maintain stomatal conductance to avoid the damages [123]. In K deficient plant, not only photosynthetic electron transport pathway but also NADPH oxidizing enzyme reaction produces ROS [5]. In this case K helps plant by protein synthesis, stimulate various enzymatic reaction, carbohydrate production and by increasing water use efficiency. In heat stress condition, foliar spray of potassium orthophosphate (KH_2PO_4) helps to increase the heat tolerance of wheat by preventing leaf damages [124]. When a significant amount of K lost from the chloroplast the photosynthesis is reduced. In this situation, K application helps to tolerate the heat stress, by increasing the photosynthetic ability in wheat. Foliar application of K also helps to increase the translocation and accumulation of photosynthates as well as the dry matter. These are related to stress resistance that ultimately helps the plant to increase the yield [125].

When plant faces chilling or freezing stress K regulated mechanisms like photosynthesis, and carbon assimilation, metabolism, and phloem activity are down-regulated. Inhibition of these processes produced ROS and caused oxidative damage within the cell as light energy cannot be utilized [126]. But sufficient K supply can be reduced these damages to the chilling or freezing stressed plants [6]. Seed treatment with KCl in cold sensitive maize variety showed better ROS defense and ultimately greater tolerance [21]. Plants facing freezing stress were evidenced to lose apoplastic water due to freezing, which causes dehydration; and sufficient K supply adjusts the osmotic potential and decreases freezing-induced dehydration [27]. Several field trails reports on various crops also point out the similar phenomena–sufficient K supply can eliminate the frost damage [127].

5.4 Toxic metals/metalloids

Toxic metal/metalloids contamination in soil is drastically increasing day by day owing to fast industrialization, which generates the tremendous trouble to world agriculture [128]. The most obvious reaction of plants under metal/metalloids toxicity is inhibition of other essential nutrient uptake and alteration in almost all the physiological processes including disturbance in stomatal action, alterations in membrane functions, inhibition of photosynthesis, upsetting the activities of several key enzymes, generation of excess ROS, reduction of water potential etc. [129,130]. Continuous reduction of plant growth and development ultimately leads to yield loss as well as food insecurity. Hence, toxic metal remediation from soil or increasing plant tolerance or resistance against stress is a very urgent task for plant scientists. Since K plays a crucial role in activation of several enzymes, synthesis of protein, photosynthetic activity, osmoregulation, movement of stomata, transfer of energy, phloem transport, cation-anion balance and stress resistance [27], so it is

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using as plant protector against most of the abiotic stress including metal/metalloids toxicity (Table 4).

Use of K against Cd toxicity confirmed its positive effect by ameliorating Cd-induced oxidative damages in *Vicia faba* [131]. In this study, 6 mM K was used in combination with 200 µM Cd for inspecting the role of it. Cd stress reduced the growth parameters (shoot and root length), decreased chl content, alter enzyme activity and increased MDA content of plants. On the contrary, the addition of K in Cd-treated plant increased the activity of catalase (CAT) and superoxide dismutase (SOD); decreased MDA content; increased chl content as well as the growth of the plant. Song et al. [132] experimented with the peach plant by using elevated exogenous K (10 mM) against Zn toxicity (2 mM). They observed that Zn damages plant by altering physiological process and nutritional balance. On the other hand, K mitigated Zn toxicity by improving photosynthesis, antioxidant defense systems, and plant K nutritional status. Potassium also upregulated the genes concerned with K acquisition, transport, and homeostasis. Zaheer et al. [133] experimented by cultivating gladiolus in Cd-contaminated growing media (50 mg kg^{-1}) and supplemented with K and silicon (Si). They found considerably increased in hydrogen peroxide (H_2O_2) and MDA content. In contrast supplementation of K with Si in Cd-stressed plant decreased the content of H_2O_2 and MDA by upregulating the activity of antioxidant enzymes which helps to improve plant condition through increasing root and shoot length, number of leaves, dry matter, and chl content. The application of K along with Si also improved production of protein and Pro in the Cd-treated plant. Furthermore, they improved the uptake of essential mineral constituent including Ca, Mg, Mn, and S. Interestingly Liu et al. [134] demonstrated that K deficiency increased the activity of different enzymes of rice seedlings which protects them from Cd toxicity.

Table 4: Exogenous potassium-induced heavy metal stress tolerance in plants

Plant species	Metal doses	K doses	Protective effects of K	References
V. faba	200 µM Cd, 7 d	6 mM K, 7 d	• Increased shoot and root length • Increased chl content • Increased proline content • Increased activity of SOD and CAT • Decreased MDA content	[131]
Prunus persica	2 mM $ZnCl_2$, 10 d	10 mM KCl, 10 d	• Improved photosynthesis • Activated antioxidant defense systems • Improved plant K nutritional status	[132]
Gladiolus grandiflora	50 mg kg^{-1} $CdSO_4.8H_2O$, 60 d	200 mg L^{-1} K along with 200 mg L^{-1} Si, 60 d	• Reduced content of MDA and H_2O_2 • Increased root and shoot length • Increased shoot and root dry weight • Increased chl content • Upregulated enzyme activity	[133]

5.5 Hight light

Several examples illustrated the combined effect of high light intensity and abiotic stress, which caused rapid leaf chlorosis resulted from impaired photosynthesis and photooxidative damages [135,136]. With the severity of stress, photosynthetic ability, RuBisCO activity, quantum yield and electron transport disrupted in tomato [137]. When plants face insufficient K supply leaf chlorosis increased at high light [6]. This severity increases due to enhanced activity of ascorbate peroxidase (APX) and glutathione peroxidase (GPX), and lower activity of RuBisCO [36,6]. But, leaves under

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partial shade exhibit lower chl destruction. Also, utilization of photoassimilates also reduced within the plants under insufficient K supply [138], and transport of sucrose via the phloem decreased [139]. Thus, K is required in a great quantity to utilize the absorbed high light, CO_2 fixation, and source-sink relation. Hence, plants receiving high light intensity may have greater K demand.

5.6 Waterlogging

Among the abiotic stress waterlogging is an important barrier for crop production and affected at least 10% of the global agricultural land. When the root zone is waterlogged plants face a severe shortage of oxygen supply (hypoxia or anoxia), which in terms disrupt the respiration process in roots resulted in energy shortage to the cells. The key mechanism is avoiding K^+ loss, at the time of hypoxia or anoxia, which gives resistance to plants in waterlogging condition [140; 141].

Several researchers have reported the effect of exogenous K application for ameliorating the adverse effects due to waterlogging. Increased plant height, photosynthetic capacity, chl content was reported in cotton due to K supplementation under waterlogging condition. They also found greater nutrient uptake by the plant as a result of higher K^+ applied to soil or foliage [142]. Application of K a higher dose improves non-structural carbohydrates (NSC) contents, photosynthetic pigments content and higher antioxidative activity as well as lower lipid peroxidation in submerged rice [143].

6. Role of potassium in the detoxification of reactive oxygen species

Various abiotic stresses cause overproduction of ROS such as singlet oxygen ($^1O_2$), superoxide ($O_2^{\bullet-}$), H_2O_2 and hydroxyl radical ($OH^\bullet$) [125], alkoxy radical ($RO^\bullet$), peroxy radical ($ROO^\bullet$) and organic hydroperoxide (ROOH) [144,145]. Inside plant cells low concentrations of ROS acts as a signaling molecule to protect the plants from stresses, while higher concentrations of ROS enhance the lipid peroxidation, oxidation of proteins, inhibition of enzyme activities, activation of the programmed cell death (PCD) pathway and ultimately leading to cell death [146]. During photosynthetic electron transport and membrane-bound NADPH (nicotinamide adenine dinucleotide phosphate) oxidase, increased the formation of ROS in plant cells under stress, which induces K deficiency. Hence, it was suggested that exogenous use of K^+ could decrease the ROS formation by maintaining the plant photosynthetic electron transport and diminishing the action of NADPH oxidase ([6]; Table 1; Figure 3).

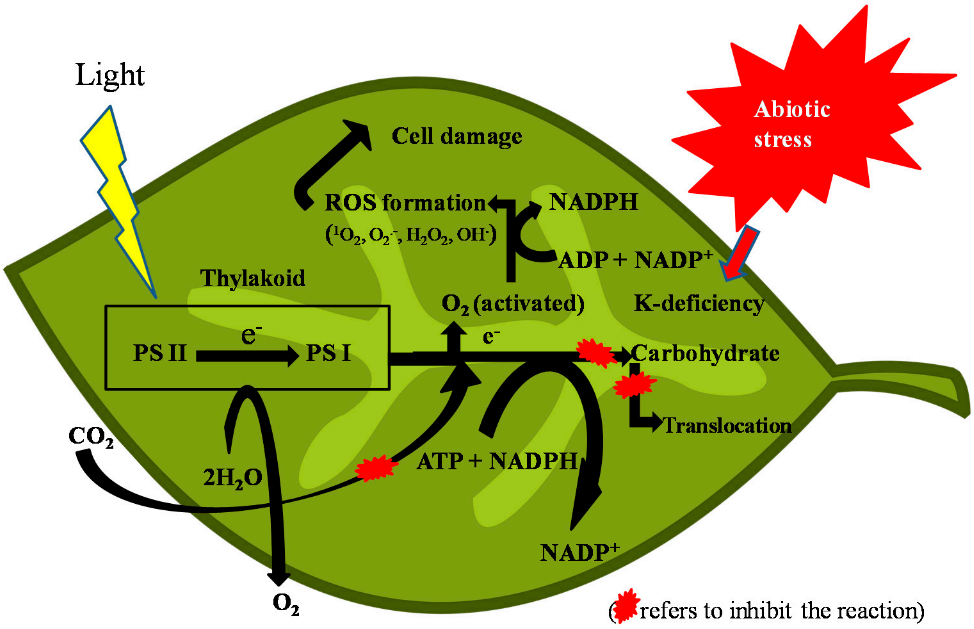

Fig. 3 Schematic representation of ROS formation in a leaf under stress (Modified from Cakmak [6]).

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While plants exposed to environmental stresses like the drought that enhance the requirement of K^+ and furthermore, increase the oxidative damage to cells by inducing the formation of ROS especially during photosynthesis [27]. At the time of drought stress, CO_2 fixation limited in plants which impacts on stomata regulation, transfer of light into chemical energy and translocation of photosynthates from source to sink ([147,148]; Figure 3). Due to impairment of photosynthetic CO_2 fixation, plant molecular O_2 is activated and increased ROS production within the plant cell [6,27], which causes degradation of photosynthetic pigment and cellular membranes. Sangakkara et al. [149] found a positive role of K^+ by reducing ROS formation and increasing the net photosynthesis rate under water stress condition on *V. radiata* and cowpea *V. unguiculata*. Walp. Egilla et al. [88] observed in a study that adequate K^+ availability to *H. rosa-sinensis* under drought stress reduced the inhibition of photosynthesis through mitigating ROS formation. Likewise, Milford and Johnston [150] suggested that K^+ plays a vital role in stomata opening and closing, transpiration and photosynthesis of plant cells. As well as Raza et al. [54] experimented with *T. aestivum* under drought condition and found that application of 1.5% K^+ decreased the ROS formation and improved the transpiration and photosynthesis rate. Thus, it was suggested that an adequate supply of K under drought condition improved the photosynthetic CO_2 fixation, export of photosynthates from source to sink organs and preventing the photosynthetic electron transport to O_2. As a result, the formation of ROS reduced [6, 27].

During saline condition, low K increased the toxicity of Na^+ in plant tissue. Thus, K^+/Na^+ ratio decreased and led to the ROS formation, which effects on stomatal closure, inhibition of the plant photosynthesis activity and increase the oxidative damage [151]. Higher production of ROS due to severe salinity leads to cellular membrane damage. As a result of K^+ leak from the plant cell due to activation of K efflux channels, this leads to programmed cell death [152]. External use of K in a saline growing medium involved in improving salt tolerance through reduced ROS formation in *T. aestivum* [153], *Z. mays* [154] and *O. sativa* [155]. Application of K enhanced the antioxidant enzyme activities such as SOD, CAT, and peroxidase (POD) on *Zingiber officinale* [156], which reduced the ROS formation in plant cells. Zheng et al. [157] suggested that application of suitable KNO_3 detoxified the ROS through increased SOD, CAT and POD enzyme activities in *T. aestivum* under salt stress. Jan et al. [158] reported that SOD, CAT and APX enzyme activities enhanced, while applying K under salt stress thus, detoxified the ROS.

Table 5. Exogenous application of potassium detoxified the ROS formation under stress conditions

Plant species	Levels of stresses	K doses	Protective effects	References
V. radiata	Drought (25% and 50% field capacity)	3 mM K	• Reduced ROS production • Enhanced the rate of net photosynthesis	[149]
L. esculentus	60 mM NaCl	5 mM KH_2PO_4	• Improved chl content • Decreased ROS production • Increased dry matter • Increased water used efficiency	[159]
H. rosa-sinensis	Water deficit after 54 days of transplanting	10 mM K_2SO_4	• Increased rate of net photosynthesis, transpiration, and stomatal conductance • Improved leaf water content and leaf water relations by decreasing the $\Psi\pi$	[88]
T. aestivum	100 mM NaCl	16 mM	• Increased SOD, CAT and POD activity	[157]

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Plant species	Levels of stresses	K doses	Protective effects	References
		KNO_3	• Reduced the formation of ROS	
O. sativa	200 mM NaCl	11.8 mM KNO_3	• Decreased ROS production • Improved photosynthetic performance	[154]
T. aestivum	Water deficit at milking stage	1.5% K	• Reduced ROS production • Improved transpiration and photosynthesis	[54]
Z. mays	70 mM NaCl	9 mM KCl	• Increased CAT activity • Improved photosynthetic capacity • Increased accumulation of K^+ in the leaves	[114]
S. lycopersicum	150 mM NaCl	9 mM KNO_3	• Minimized oxidative stress and increased photosynthesis • Decreased the antioxidant enzymes' activities (SOD and CAT) • Increased leaf K^+ levels and K^+/Na^+ ratio • Improved membrane stability index	[117]
T. aestivum	500 mg kg^{-1} NaCl	50 mg kg^{-1} KNO_3	• Increased SOD, CAT, APX activity • Improved photosynthetic capacity • Reduced ROS formation	[158]

NADPH-oxidizing enzymes reduce one electron O_2 to $O_2^{\cdot-}$ by using NADPH as an electron donor ([6]; Figure 3). Moreover, NADPH oxidase activity substantially enhanced under K deficiency, increasing NADPH-dependant $O_2^{\cdot-}$ production. Cakmak [6] found that K deficiency increased the NADPH oxidase activity in the cytosol of bean (*P. vulgaris*) root, with a corresponding increase in the NADPH-dependant $O_2^{\cdot-}$ generation, but exogenous K decreased NADPH oxidase activity. Most likely, K deficiency is the main reason for the increase of NADPH oxidase through generations of ABA. Peuke et al. [160] experimented *Ricunus communis* and found that K deficiency increased the biosynthesis of ABA in roots and increased the translocation of ABA from root to shoot. Moreover, ABA has likewise been appeared to be effective in increasing the accumulation of H_2O_2 and $O_2^{\cdot-}$ in plant roots [161], which ultimately increase the ROS formation but this is needed to clear in future studies [27]. It is clear that an improvement of K maintains the photosynthetic electron transport and inhibiting the NADPH oxidase activities, which reduce the ROS formation in plants.

7. Interaction of potassium with other biomolecules

Potassium plays an important role in growth, development, yield as well as metabolism of the plant, at the same time it has some interactive regulatory function with other biomolecules. Therefore, K deficiency leads to dysfunction of numerous physiological and biochemical processes, for example, water balance, enzyme activity, and charge balance, as well tolerance to biotic and abiotic stress [162]. Potassium is also essential for the function and performance of many plant enzymes—at least 60 enzymes require K^+ as a cofactor for activation [163]. These enzymes regulate the vital metabolic mechanisms in arable plants [164,20]. For increasing substrate attraction, K bound with the specific binding site of inactive enzymes and resulted in their activation, those involved in various metabolic and physiological mechanisms. Several types of research suggested that the activity of NR, RuBisCO, starch synthase, sucrose phosphate synthase, β-amylase, invertase, phosphofructokinase, and pyruvate kinase greatly depends on the K sufficiency of plants [165,166] Among the biomolecules carbohydrate had greater interactive relation with K. When plants get enough K, they synthesize large biomolecules, for example, cellulose, starch, protein, etc. As a result, the number of small molecules like free sugars, amino acids, organic acids and amides content reduced in the cell, while the concentration of phenols increased that aid in plant resistance [167] and increased the response of plants to abiotic stress [168]. Carbohydrates, mostly hexose content decreased in leaves due to sufficient K supply which was transported to another plant organ due to better phloem activity. On the other hand, K deficiency resulted in decreased activity of pyruvate kinase and/or increased invertase activity that reduces the concentration of starch in leaf because of inhibition of starch synthase [36].

Potassium has an optimistic relationship with plant hormone synthesis also [169]. When K concentration in the cell is low jasmonic acid (JA) and auxin biosynthesis are upregulated [170], but ethylene synthesis increased to two-fold in *Arabidopsis* when suffering from K-starvation [171]. and other biological function, decreased in roots and xylem sap, leading to sucrose accumulation, whereas cytokinin concentration in leaf and xylem sap decreased, when plants get sufficient amount of K [172,162]. Ethylene—another important plant hormone, mediated root morphology and stimulate ROS biosynthesis to tolerate low K condition in *Arabidopsis* [173]. Exogenous application of K and NAA can interact significantly to increase in growth and yield of *V. radiata* [174]. A similar result was also obtained by applying K and GA_3 on rice [175], K and SA on olive tree at salinity [176]. Increased levels of JA, hydroxy-12-oxo-octadecadienoic acids (HODs) and 12-oxo-phytodienoic acid (OPDA) were obtained under K-starved condition along with up-regulation of the 13-LOX pathway indicates the transcript levels of several biosynthetic enzymes with K interaction [177]. These phenomena are the indication of hormonal balance due to K interaction.

Polyamines have a role in wide range of environmental stresses, involved in various physiological processes. Their concentration in cellular level increased at K deficit condition in *Avena sativa* [178]. When plant faces any stress, they accumulate polyamines at a higher concentration. Polyamines have significant interaction with K in cellular level and regulate plasma membrane K^+ channel of guard cell for modulating stomatal regulation [179]. They also reported that spermidine, spermine, cadaverine, and putrescine powerfully block the opening and closer of stomata, which provided a link among stress, stomatal regulation, and polyamines level.

8. Potassium-induced abiotic stress signaling

In the dynamic environment, K^+ content in the soil may not be remaining same over the growing period of a crop. Interestingly, plant root can sense the fluctuation in K availability. Sensing the K deficiency by plant root, series of events take place in the plant at the molecular level to cope up with this condition. From signal perceiving to adaptive responses, some signaling components are involved (Fig. 4). For example, Ca^{2+} signaling, ROS, microRNA, membrane potential and phytohormone are the signaling components **[**9,180**]**. Under K^+ deficient condition, CIPK23 (a protein kinase) activates the K transporter AKT1 by phosphorylation. Calcium sensors, CBL1 and CBL2 regulate the activation of CIPK23 **[**181**]**. Later on, low K^+-induced two distinct Ca signal read by CBL1/9 was observed in *A. thaliana* [182]. Then CBL1/9 regulates the AKT1 by activating CBL1/9-CIPK23 complexes [182]. Overexpression of type III peroxidase, *RCI3* increased the production of ROS as well as HAK5 expression. However, mutant lacking this gene reduced both ROS production and HAK5 expression, indicating a relationship between ROS and low K^+ response [183]. Potassium channel like NSCC and GORK are very sensitive to ROS. Under the saline condition, ROS-mediated activation of NSCC and GORK is the main reason for K^+ pool reduction in the cytosol ([13,184]. Prolonged K^+ deficiency in the cytosol activates different endonucleases and protease which in turn cause cell death [13]. Phytohormones such as ethylene, auxin, cytokinin and JA are also involved in low K+-induced signaling process. Under K+ deficient condition, *HAK5* transcription is regulated by the upstream signaling molecule ethylene and ROS ([185]. However, cytokinin content decreases under low K+ stress to regulate *HAK5* by inducing ROS [185]. A K+ transporter in rice has found to be regulated by JA ([186]. Involvement of microRNAs in nutrient homeostasis in plants has been reported in many studies. For example, using gene chip overexpression of *OsmiR399* increased the nutrient content in the plant including K+. Under nutrient starvation, *OsmiR399* expression increases [187]. Taken together, different complex pathways are interlinked to sustain crop growth and productivity. Elucidation of a complex pathway that induced by K+ signaling allow us to engineer the pathway in a way to ensure optimum K+ level in the plant.

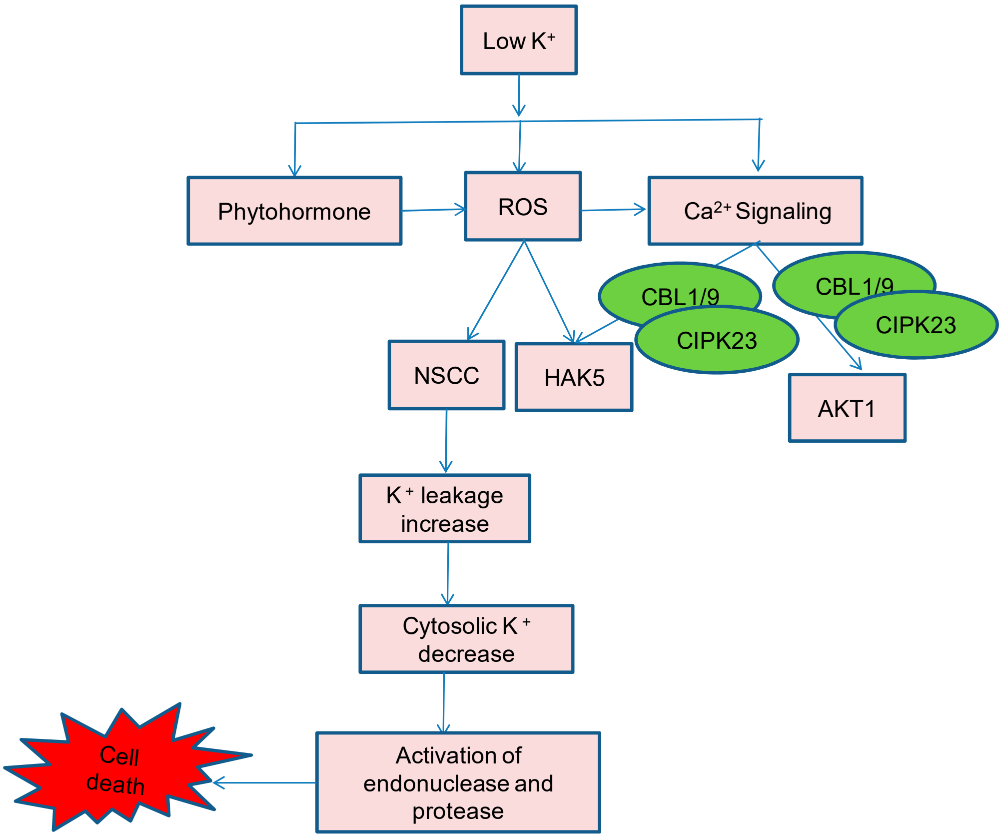

Fig. 4 K-induced signaling in the plant. ROS: Reactive oxygen species; NSCC: Non-selective cation channel; HAK5 and AKT1: K+ transporter, CBL1/9: calcineurin B-like proteins, CIPK23: A protein kinase.

10. Conclusion

Potassium is very important for plant survival under both normal and stress condition. It is not only a part of the chemical structure but also plays vital regulatory function in biochemical and physiological processes that contribute to plant growth and development. Proper use of K with other nutrients helps to attain sustainable productivity and quality of crops and ensure nutritional food security for animal and human being. As a sessile organism, plant is continuously disturbed by a range of abiotic and biotic stresses. Among the abiotic stresses, drought, salinity, toxic metal, high temperature, chilling, high light intensity, waterlogging, etc. confirmed their deleterious functions in crop plants. Important physiological activities including photosynthesis are greatly hampered under most of the abiotic stresses, which lead to increase toxic ROS in a plant cell. But adequate K supply to the plants during stress condition can lessen the production of ROS and improve the plant condition. Potassium also works in plant signaling system which helps to defend some stresses by activating antioxidant defense system. This review assesses K involvement in normal plant growth and in increasing tolerance/resistance against different stress conditions. This review would help to design K-based future research work for the betterment of modern agriculture.

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