



Review

Potassium: A Vital Regulator of Plant Responses and Tolerance to Abiotic Stresses

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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 the plant structure but it also has a regulatory function in several biochemical processes related to protein synthesis, carbohydrate metabolism, and enzyme activation. Several physiological processes depend on K, such as stomatal regulation and photosynthesis. In recent decades, K was found to provide abiotic stress tolerance. Under salt stress, K helps to maintain ion homeostasis and to regulate the osmotic balance. Under drought stress conditions, K regulates stomatal opening and helps plants adapt to water deficits. Many reports support the notion that K enhances antioxidant defense in plants and therefore protects them from oxidative stress under various environmental adversities. In addition, this element provides some cellular signaling alone or in association with other signaling molecules and phytohormones. Although considerable progress has been made in understanding K-induced abiotic stress tolerance in plants, the exact molecular mechanisms of these protections are still under investigation. In this review, we summarized the recent literature on the biological functions of K, its uptake, its 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 cultivable crops experience one or more abiotic stress(es) of some type throughout their growth stages. Thus, increasing plant resilience in response to abiotic stress is a great challenge in the effort to improve food production by 70% to feed the increasing population by the year 2050 [1]. Abiotic stress hampers plant productivity by altering plant growth patterns and physiological responses [2,3]. The combination of different stresses that affect crops has become more common; for example, the occurrence of drought and high temperature is the most common [4], while in arid and semi-arid regions, salinity and high temperature stresses are imposed at the same time. High light and high temperature stress, drought and salinity, or high temperature, occur simultaneously under current

conditions. Due to the complex nature of this stress, plants are more adversely affected, and hence, research on plant stress tolerance is constantly changing and being updated with the new forms of stresses [1,3]. These complex stresses cause changes in cropping patterns, crop cultural practices, and sometimes, the extinction of plant species. Since the beginning of agriculture, a range of cultural practices has been developed through continuous trial and error processes. Among the cultivation practices, the use of fertilizers and organic amendments are the oldest methods for improving plant productivity. However, as a chemical fertilizer, potassium (K) has been used on crop field since the nineteenth century [5].

The role of K in the plant developmental process is well known. The upregulation of the K status decreases reactive oxygen species (ROS) generation in plants. Potassium reduces the activity of nicotinamide adenine dinucleotide phosphate (NADPH) oxidases and retains the photosynthetic electron transport activity, which helps to reduce ROS. Potassium deficiencies can decrease the photosynthetic CO₂ fixation and the transport and utilization of assimilates [6]. Membrane and chlorophyll (chl) degradation are favored in K-deficient plants. The regulation of K is associated with the activity of the enzymes involved in ROS detoxification [5]. Potassium triggers the activation of the adenosine triphosphate (ATP) synthase enzyme. The plasma membrane-bound H⁺-ATPase is influenced by the K content [7]. Potassium-deficient plants have been reported to be light-sensitive, and thus they exhibit chlorotic and necrotic symptoms [5]. Potassium was reported to decrease different stress effects in plants such as drought, chilling, and high light intensity [6]. A combined high temperature and drought tolerance induced by potassium was reported [8]. The role of K as a nutrient has been recognized for a long time. However, its arrays of biological functions in plant physiological processes have still not been fully explored. In recent years, the correlation between phytohormones and K has been studied [9]; phytohormones interact with one another and other signaling molecules, which regulate biochemical processes and metabolism, exerting physiological responses in relation to almost all the features of plant growth and development and enhancing stress tolerance. Auxin-regulated genes regulate proteins that affect the transcriptional repressors of stress responses in plants [10]. Abscisic acid (ABA) influences the expression of genes that modulate complex stress-responsive regulatory networks [11]. The roles of other different hormones including cytokinin [12], ethylene and jasmonic acids (JA; [13]), gibberellic acid (GA; [14]), and salicylic acid (SA; [15]) have been documented for their ability to confer abiotic stress tolerance. However, the complex process that occurs in response to abiotic stress tolerance is still under investigation. This is a comprehensive review articulating the biological function of K in plants and its role in plant adaptations 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) [16]. Potassium is required for various biochemical and physiological processes that are responsible for plant growth and development. Potassium takes part in protein synthesis, carbohydrate metabolism, and enzyme activation [9]. It assists in the cation-anion balance, osmoregulation, water movement, energy transfer, and many other processes. Potassium also plays a mitigating role in various abiotic stresses such as drought, salinity, metal toxicity, high or chilling temperatures, etc. [9]. 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. A lack of K fertilizer increases plant susceptibility to various diseases and pest infestation and makes plants vulnerable to damage under various stress conditions [9].

3. Potassium Uptake, Transport, and Assimilation in Plants

The potassium reserve in soil is very high and accounts for nearly 2.1–2.3% of the earth's crust [17,18]. Therefore, soil K reserves are generally large [17]. Plants uptake K as cation (K^+) and many sources of K are available in soils or provided as fertilizers, including potassium chloride (KCl), potassium nitrate (KNO_3), potassium sulfate (K_2SO_4), and potassium carbonate (K_2CO_3). Among these forms, KCl, or muriate of potash, is the most inexpensive and most frequently used for agronomic crops, with some exceptions [19]. Other forms such as K_2SO_4 and KNO_3 are used for some crops that are sensitive to chloride (Cl^-), although they are expensive. For example, KCl causes leaf burn in tobacco due to its chloride ions [20]. However, the availability of K^+ from soil or fertilizers depends on the soil texture, soil moisture content, pH, and some other factors. Apart from the common and soluble forms of K compounds, some forms such as K silicate minerals are also available in some soils. The availability of these compounds is very low, and in these cases, some microbes (especially bacteria and fungi) assist in solubilizing K and converting it into soluble forms through acidification, chelation, and exchange reactions [21]. As a macronutrient, K is mostly applied as a basal dose to the soil. In some cases (e.g., sandy soil), K is applied as a foliar spray [22]. Foliar application is also very effective under waterlogged conditions [23]. However, the effectiveness of the foliar spray is dependent on the absorption capacity by and penetration into leaves; therefore, it can only partially compensate for insufficient uptake by the roots. Moreover, the efficacy of foliar application also requires a sufficient leaf area [24].

Apart from the factors detailed above, the capacity of plant species to take up K^+ is another factor that controls K release from the soil minerals or applied fertilizers. To facilitate K^+ uptake from the outer environment and transport it to different cellular compartments, many proteins are present in the cell, primarily in the membrane. These proteins are often called transporters and channels. Based on their affinity for 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 at more than 0.3 mM external K^+ [25]. Advances in molecular approaches and tools have led to the identification of some low-affinity and high-affinity transporters in different plant species including barley (*Hordeum vulgare* L.), rice (*Oryza sativa* L.), and capsicum (*Capsicum annuum* L.) [26]. A yeast mutant lacking the ability to take up K^+ could grow only when the mutant was transformed with cDNA from barley. This study led to the identification of the high-affinity K transporter HvHAK1, which is homologous to the *Escherichia coli* and *Schwanniomyces occidentalis* HAK1 K^+ transporter [27]. To support the low-affinity transport mechanism as an inward rectifying K^+ channel, a high-affinity potassium transporters (HKT) has been proposed [26]. An *Arabidopsis* mutant lacking the *HKT1* gene (which was screened from a T-DNA insertion line) was able to grow in a 1 mM KCl solution without experiencing growth reduction. However, at 100 μ M KCl, the mutant showed significant growth reduction, indicating *HKT1* channel involvement in K^+ uptake from the low K solution [28]. 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 (nine genes), two-pore K^+ channels (six genes), putative K^+/H^+ antiporters (six genes), KUP/HAK/KT transporters (13 genes), HKT transporters (one gene), cyclic-nucleotide gate channels (20 genes), and glutamate receptors [29]. The Shaker-type K^+ channels were further classified into three groups. These types 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 they are activated by membrane hyperpolarization [25]. The channels and transporters encoded by different genes are different with respect to structure and function [25].

In roots, the K^+ uptake from the media is primarily mediated by two proteins, AKT1 and HAK5, because these two proteins are expressed in the roots of *Arabidopsis* [30] and rice [31,32]. The loss of function mutants *hak5* or *akt1* were able to survive at 100 μ M KCl solution, but the double *hak5 akt1* mutant failed to survive at the same concentration, indicating that AKT1 and HAK5 are high-affinity

transporters that mediate sufficient K^+ uptake for plant growth [30]. In rice, Os-AKT1 mediated K^+ uptake as regulated by a complex of two proteins, calcineurin B-like protein1 (Os-CBL1) and CBL-interacting protein kinase23 (CIPK23) [31]. For long-distance transport, K^+ transport from the root cortex to the xylem was mediated by outward-rectifying channels (Figure 1). Experimental evidence showed that a mutant lacking the stellar outward rectifying K^+ channel (SKOR channel) reduces the K^+ content in the shoots by 50% and reduces the K^+ content in the xylem sap. Stomatal closure or opening depends on the K^+ concentration in the guard cell, where inward channel KAT1 and KAT2 mediate K^+ uptake into the cell and outward rectifying K^+ channel, and the guard cell's outward rectifying K^+ channel (GORK channel) mediates K^+ release to close the stomata [33]. In the 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 [34–36].

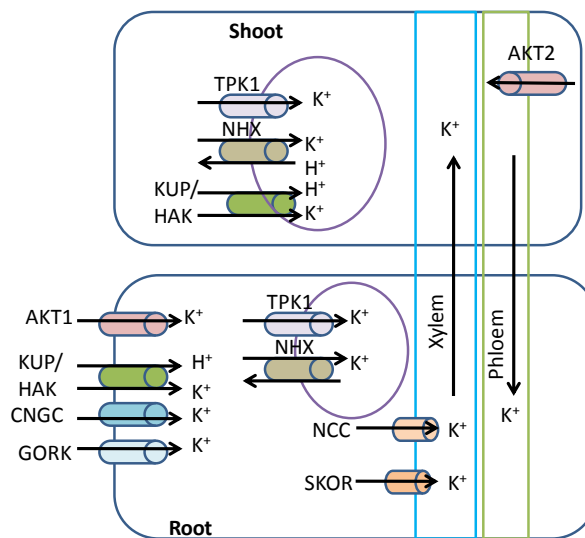


Figure 1. Potassium uptake and transport in plants (Modified from [37]). AKT: *Arabidopsis* (Shaker-type) K^+ channel; CNGC: cyclic nucleotide-gated channel; GORK: guard cell outward rectifying K^+ channel; HAK/KUP: high affinity K^+ transporters; KAT: *Arabidopsis* (Shaker type) K^+ channel; NCC: non selective cation channels; NHX: Na^+ proton exchanger; SKOR: stellar 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 [38].

4.1. Seed Germination and Emergence

Potassium assists in seed germination by initiating the rapid imbibition of water, and it also facilitates other physiological processes [39]. 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) [40,41]. By using KNO_3 as a priming agent, a good germination rate was obtained in cotton genotypes [42]. Osmopriming with KNO_3 in rice suggested that KNO_3 performed best for the maximum germination percentage and germination rate as well as other morphological attributes [43]. Therefore, in light of the 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 playing a key role in plant growth and development processes [44]. 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 [9]. Moreover, excess or deficient K in the growing medium hampers the overall growth of the plant. Thus, managing K fertilizer is advantageous for improving plant growth [45]. Hussain et al. [46] applied different levels of K (0, 30, 60, 90, and 120 kg sulfate of potash (SOP) ha⁻¹), and they found a maximum plant height at 90 kg SOP ha⁻¹ and a minimum at 0 kg ha⁻¹. Zelelew et al. [47] experimented on potato (*Solanum tuberosum* L.) growth with five K doses (0, 75, 150, 225, and 300 kg K₂O ha⁻¹) and found that the plant height, aerial stem number, and leaf number per plant increased with the increasing K levels from 0 kg to 150 kg ha⁻¹. Gerardeaux et al. [48] observed that the K deficiency in the vegetative phase of cotton (*Gossypium hirsutum* L.) reduced the plant dry matter production, leaf area, and internode size, which leads to a reduction in plant growth. Tang et al. [44] cultivated three sweet potato (*Ipomoea batatas* (L.) Lam.) cultivars in K-deficient soil, and they found a lack of K, notably a cut-off in the total biomass productivity and root yield. Nodulation is a very common phenomenon in legume crops, and it is closely related to plant growth itself. The level of K and its ratio to N and P determine the success of the nodulation process [49].

4.3. Stomatal Regulation

Proper stomatal regulation (opening and closing) is necessary for the uninterrupted production of energy during the photosynthesis process, plant cooling, and water and nutrient transport. In the presence of K⁺, stomatal guard cells are swollen by absorbing water followed by stomatal opening and the allowance of gaseous movement in between plants and the environment. Under water-deficit conditions, K⁺ is pumped out from the guard cell, allowing the pores to close tightly. Thus, K controls the evapotranspiration (ET) of water through pores under a water deficit in the soil environment, and it protects the plant from water stress [50]. Insufficient K supply adversely affects stomata functionality, resulting in delayed stomatal closure and even the unfinished closure of the pores. In addition to these effects, the osmotic gradient produced due to the accumulation of K in the roots helps to draw water into the root cells. Therefore, the reduced K supply in the plant results in decreased water uptake, and the plant faces water stress under drought conditions.

Taiz and Zeiger [51] described the stomatal activity in detail, indicating that the following three major events occur while light radiates into the plant cell and stimulates stomatal opening: the activation of the proton pump ATPase, solute uptake, and organic solute synthesis. The electrochemical potential generated by the proton pump ATPase helps to take up K and its associated anions such as Cl⁻ and malate. While the solute and sucrose amounts increase in the guard cell vacuole, they eventually decrease the osmotic potential. Later, the turgor pressure is increased with the increasing amount of water uptake, resulting in stomatal opening. By contrast, the stomatal closure operation is largely maintained by the ABA content. Calcium uptake is stimulated by ABA, which blocks the K⁺ channel and paves the way to anion (Cl⁻) entry into the cell apoplast. An increased concentration of Ca²⁺ at the intercellular level reduces the proton pump ATPase activity that accelerates cell membrane depolarization, followed by the deportation of cytoplasmic K⁺ to the cell apoplast [52]. 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 which require water. These processes include stomatal regulation, the translocation of photoassimilates, enzyme activation, and heliotropic leaf movements. In addition, K assists in water transportation and mineral compound translocation for the entire plant through the xylem. In cases in which the K supply is not at

its optimum level, the translocation of mineral compounds such as nitrates (NO_3^-), phosphates (PO_4^{3-}), calcium (Ca^{2+}), magnesium (Mg^{2+}), and amino acid uptake is reduced [53]. Optimal K fertilization helped plants to mitigate the effect of the water deficit through better water use efficiency (WUE), which was related to the lower leaf ET. Martineau et al. [54] reported the appearance of pronounced leaf rolling under a water deficit condition after K addition, which prevented water losses, and thus, they concluded that adding K to K-deficient soils can help maize to cope with drought and could be a new management option [54]. The hydraulic conductance of the xylem varies in response to changes in the solute content of the sap, and in particular to the K concentration. This phenomenon, which is known as the ionic effect, is improved in embolized stems, in which it can compensate for the cavitation-induced loss of hydraulic conductance. That report suggests that the potassium concentration in the xylem sap and the hydraulic conductance of well-irrigated laurel plants (*Laurus nobilis* L.) increased 24 h after KCl fertilization [55].

4.5. Photosynthesis

Potassium plays an imperative role in the photosynthesis process and the subsequent carbohydrate translocation and metabolism, which eventually increase the crop yield and improve the grain quality [56–58]. 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 [56]. 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 [59].

Stomatal regulation during photosynthesis is a vital event that governs the continual photosynthesis operation, and it is significantly moderated by the amount of K retained in the plant [38]. Potassium deficiency resulting in reduced stomatal conductance increased the mesophyll resistance and lowered the ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activity in plants, which eventually decreased the total photosynthesis rate [60]. 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 [60]. In addition, both the photosynthetic CO_2 fixation and the utilization of photoassimilates were reduced due to K deficiency, which accelerated the plant ROS production, ultimately hastening rapid photooxidative damage [6]. Thus, the most significant function K plays in regulating the stomatal aperture is in balancing 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 photosynthate production in the leaf. Potassium plays an essential role in activating the ATP synthase enzyme, thus assisting in the photosynthesis process. Shingles and McCarty [61] suggested 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 involved in photosynthetic regulation has increased the apparent importance of K in plants. Recent studies have revealed the important roles of three K^+ efflux antiporters, AtKEA1/2/3 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 [62]. Both the chloroplast development and photosynthesis rate were significantly damaged in the AtKEA, 2, 3 triple mutant, resulting in the stunted growth of the mutant plants [62,63]. AtKEA1 and AtKEA2 show polar distribution in small and dividing plastids, which regulate chloroplast development [64]. 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 consequently, it regulates photosynthesis as well as photosynthetic acclimation in fluctuating light environments [65,66].

4.6. Nutrient Balance

Under K-deficit condition, protein formation is hampered even when there is an abundant N supply; therefore, NO_3^- , amino acids, and amides accumulate in the cell [16]. Potassium activates nitrate reductase (NR), a starch synthetase, and these two enzymes create a balance by producing protein and carbohydrates, respectively. Therefore, K shortages lead to a breakdown in these processes and the plants suffer, even though other nutrients are available. As previously stated, K has a role in the 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 the source-sink relationship is interrupted [67]. The exogenous application of K at different growth stages decreases the uptake of harmful nutrients, enhancing tolerance to abiotic stress and boosting the yield and yield-related characteristics [68].

Iron (Fe) is another vital micronutrient that also has a synergistic relationship with K [69]. Under Mo/K deficiency, the Fe uptake is decreased, which leads to the sterility of female flower parts at the reproductive phase, while Mo application increases nodulation in the roots, leading to additional seed yields in lentils [70].

Potassium can also be toxic. During charge compensation, K is the dominant cation for counterbalancing immobile anions in the cytoplasm, chloroplasts, vacuoles, xylem and phloem. When plants take up excess K, organic acid anions will then accumulate to counterbalance the excess K^+ transported into the cytoplasm. Notably, with the K^+ counterbalance anion of NO_3^- at the time of nitrate metabolism and the reduction of excess NO_3^- in the leaves, the K concentration is increased. As a result, organic acids such as malate are synthesized in the leaf tissue to support the charge balance. Part of this K-malate is transported to the root cells for NO_3^- uptake [38].

4.7. Reproductive Development

Potassium plays roles in flowering and pollen germination as well as in seed development. Fan et al. [71] found that externally applied K helps to increase the pollen germination rate, and K also increases tube growth in *Arabidopsis*. Choudhury et al. [72] noted that sucrose, boric acid, and different salts have a role in pollen germination, and among the studied compounds, KNO_3 plays an important role in pollen germination and development. Makhdum et al. [73] 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. Amanullah et al. [45] reported that phenological development such as flowering or physiological maturity was delayed due to the lower application of K. Sadiq and Jan [74] 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. Asif et al. [75] showed that the phenological development of maize increased with the application of 90 kg ha^{-1} K, and they showed a positive relationship to the number of split K applications. A full dose of K helps to increase the flowering, the number of grains and early physiological maturity. In wheat (*Triticum aestivum* L.), K has an important role during the grain filling stage. Applying K in an appropriate way significantly increased photosynthesis during the grain filling stage, and it also has a positive role in increasing the grain number [76]. The higher amount of K helps to transfer food material to develop grains, thus decreasing the amount of sterile grain. In *O. sativa*, when the K was applied at 100 kg ha^{-1} , the grain sterility was lower compared to the treatment with no K application. At 100 kg K ha^{-1} , the grain sterility was 22.60%, whereas without K, it was 30.33% [77].

4.8. Yield

Potassium regulates the biosynthesis, conversion, and allocation of metabolites that ultimately increases the yield. Many research works strongly supported the notion that K is directly or indirectly responsible for higher yield of crops (Table 1). Islam and Muttaleb [77] experimented on rice with

various doses of K fertilizer. They reported that K helps to increase the N uptake as well as N use efficiency that help in increasing the yield of rice. As a result, rice yield increased to $6.86 \text{ t ha}^{-1} \text{ year}^{-1}$ with optimum doses of K, whereas without K the yield was $5.19 \text{ t ha}^{-1} \text{ year}^{-1}$. Cheema et al. [78] 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.). Uddin et al. [79] found that 1000 grain weight, grain yield increased by 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. [80] 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. [81] showed that K increased the spike length, number of spikelets per spike, number of grains and grain yield of wheat under drought condition. K increased spike length by 21.8%, number of spikelets spike⁻¹ increased by up to 23.27%, number of grains spike⁻¹ increased by 39.24% and ultimately yield was increased by 30.77% than without K application. Waraich et al. [82] reported that 200 mM KNO₃ application increased the plant branches, plant height, and number of balls plant⁻¹ in *G. hirsutum* but in case of ball weight, 150 mM foliar application is better. According to Colpan et al. [83], K plays a vital role to increase the yield and yield components in tomato (*Lycopersicon esculentum* L.). They applied various doses of K as for example 0, 40, 80, 120, and 160 kg K₂O ha⁻¹ and found the highest yield (195.7 t ha^{-1}) with 120 kg K₂O ha⁻¹. Fruit size, diameters of fruits, number of fruits plants⁻¹ and fruit weight increased with the application of K. Khan et al. [84] 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.

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

Name of Crops	K Doses	Yield Improvement	References
<i>Oryza sativa</i>	60 kg K ₂ O ha ⁻¹	Grain yield: 50%	[84]
<i>O. sativa</i>	40 kg K ₂ O ha ⁻¹	Grain yield: 35%	[85]
<i>O. sativa</i>	80 kg K ₂ O ha ⁻¹	Grain yield: 78.47%	[86]
<i>O. sativa</i>	93.96–112.03 kg K ₂ O ha ⁻¹	Grain yield: 32.17%	[77]
<i>Triticum aestivum</i>	108.42 kg K ₂ O ha ⁻¹	Grain yield: 10.66%	[87]
<i>O. sativa</i>	60 kg K ₂ O ha ⁻¹	Grain yield: 13%	[84]
<i>O. sativa</i>	40 kg K ₂ O ha ⁻¹	Grain yield: 21%	[85]
<i>O. sativa</i>	80 kg K ₂ O ha ⁻¹	Grain yield: 41.16%	[88]
<i>Lens culinaris</i>	42.16 kg K ₂ O ha ⁻¹	Grain yield: 34.16%	[89]
<i>Capsicum annuum</i>	476.19 kg K ₂ O ha ⁻¹	Pod/fruit yield: 22.20%	[90]
<i>Gossypium hirsutum</i>	112 kg K ₂ O ha ⁻¹	Lint yield: 10.18%	[56]
<i>G. hirsutum</i>	150 kg K ₂ O ha ⁻¹	Lint yield: 13.79%	[91]
<i>G. hirsutum</i>	180.70 kg K ₂ O ha ⁻¹	Lint yield: 5.7%	[92]
<i>Solanum tuberosum</i>	225 kg K ₂ O ha ⁻¹	Tuber weight: 13.34%	[93]
<i>S. tuberosum</i>	225 kg K ₂ O ha ⁻¹	Tuber yield: 78.11%	[94]
<i>S. tuberosum</i>	150 kg K ₂ O ha ⁻¹	Tuber yield: 22.41%	[95]
<i>Zea mays</i>	150 kg K ₂ O ha ⁻¹	Grain yield: 36.33%	[96]
<i>Z. mays</i>	48.19 kg K ₂ O ha ⁻¹	Grain yield: 33.12%	[97]
<i>Jatropha curcas</i>	60 kg K ₂ O ha ⁻¹	Oil yield: 17.30%	[98]
<i>Fragaria × ananassa</i>	64 kg K ₂ O ha ⁻¹	Weight of primary fruits: 6.2%	[99]
<i>Fragaria × ananassa</i>	64 kg K ₂ O ha ⁻¹	Weight of secondary fruits: 6.95%	[99]
<i>Cicer arietinum</i>	95.23 kg K ₂ O ha ⁻¹	Grain yield: 34.50%	[100]
<i>Carthamus tinctorius</i>	95.5 kg K ₂ O ha ⁻¹	Oil yield: 86.84%	[101]
<i>Arachis hypogaea</i>	90.35 kg K ₂ O ha ⁻¹	Seed yield: 44.2%	[102]
<i>Saccharum officinarum</i>	722.82 kg K ₂ O ha ⁻¹	Sugar yield: 30.17%	[103]
<i>Betavulgaris</i>	171.42 kg K ₂ O ha ⁻¹	Root yield: 24.83%	[104]
<i>Vigna radiata</i>	37.5 kg K ₂ O ha ⁻¹	Seed yield: 28.29%	[105]
<i>Lycopersicon esculentum</i>	120 kg K ₂ O ha ⁻¹	Seed yield: 30.9%	[83]

4.9. Crop Quality

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. [106] 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. Nevertheless, when manure was applied along with N–P–K to *T. aestivum*, the protein percentage was higher than it was under normal fertilization. In *T. aestivum*, as well as in most of the studied cereal crops, K helps to provide better milling and baking qualities, a more efficient use of nutrients, increased disease resistance and many other favorable traits. 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. Thus, the turgor pressure of the fiber decreased and the primary fiber cell wall cannot be elongated, ultimately resulting in shorter fibers [107]. The ginning out turn, fiber uniformity, length, and strength increased when KNO₃ was applied at 200 mM as a foliar spray [82]. According to Ashfaq et al. [108], K deficiency reduces the cotton yield and quality. Mehrandish et al. [109] showed that the total soluble solids, soluble sugar content, refineable sugar, and purity percentage of sugarbeet (*Beta vulgaris* L.) root juice increased with K application. Economakis and Daskalaki [110] explained that K increased the dry matter, total soluble solids, firmness, and vitamin C content in tomatoes under both normal and saline conditions.

5. Potassium-Induced Abiotic Stress Tolerance

In the previous sections, we described the role of K in the various growth and physiological parameters of plants under normal conditions. Many plant studies also showed that K functions as a vital protector against abiotic stresses. This function is primarily due to its role in maintaining ion homeostasis, cellular integrity and enzymatic activities (Tables 2–4). In the following sections, we will describe the role of K in conferring tolerance to 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 function [9] under drought conditions. A close relationship between the K nutritional status and plant drought resistance has been demonstrated (Table 2).

A sufficient supply of K can improve the plant dry matter better than a lower concentration of K can in soil under drought conditions [111]. Increasing root growth, by applying K, increases the root surface area under drought conditions, which ultimately enhances the water uptake by plant cells [112].

The exogenous application of K not only improved the plant dry matter content and leaf area but also stimulated water uptake when the plants faced drought [113,114]. Under drought conditions, excess ROS production in plants may exaggerate cellular lipid peroxidation, leading to an increase in the cellular membrane permeability, which is evidenced by increases in the electrolyte leakage (EL) and malondialdehyde (MDA) content [115,116]. Soleimanzadeh et al. [117] performed an experiment with sunflower (*Helianthus annuus* L.) and reported that an adequate supply of K significantly decreased the MDA content under water shortage conditions which clearly indicates the role of K in mitigating oxidative stress.

Kanai et al. [118] showed a relationship between the aquaporin activities and the K-channel/transporter, in which K deficiency markedly changed the K⁺-channel activity, resulting in an alteration 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. According to Guo et al. [119], there is a positive correlation between water uptake and K absorption in common bean (*Phaseolus vulgaris* L.). Potassium mediated the xylem hydraulic conductance and maintained cell turgor, stomatal movement, and sufficient gas exchange as part of the drought adaptation because these events help to maintain water balance in plants [120].

An adequate supply of K can reportedly increase the organic osmolyte production under drought conditions, especially Pro [114]. When plants are exposed to drought stress, Pro accumulation plays a highly protective role in plants, and it is involved in osmotic adjustments [121]. In several studies, it was reportedly increased through K application in *O. sativa* [122], *B. napus* [123], and *T. aestivum* under normal and drought stress conditions [124]. Zhang et al. [125] observed that exogenous K applications increase the Pro content in *Z. mays* cultivars under drought conditions. At the same time, Ali et al. [126] reported that under drought stress, K applications increase the shoot Pro content in *B. napus* in a dose-dependent manner. Similarly, Zahoor et al. [127] found that K application generates the Pro content in *G. hirsutum* during drought stress.

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

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

Species and Cultivars	Drought Dose and Duration	K Doses	Protective Effects	References
<i>Z. mays</i>	Withholding water 31 days (d) after planting	300 kg ha ⁻¹	<ul style="list-style-type: none"> Cell membrane stability increased Decreased leaf water potential 	[128]
<i>Hibiscus rosa-sinensis</i>	Water deficit, 21 days	10 mM	<ul style="list-style-type: none"> Enhanced root dry matter Increased root:shoot ratio 	[111]
<i>Helianthus annuus</i>	Withholding irrigation at the end of growing period	100 kg ha ⁻¹	<ul style="list-style-type: none"> Improved shoot dry matter 	[117]
<i>Camellia sinensis</i>	Field capacity, 5 days	2% KCl	<ul style="list-style-type: none"> Increased proline (Pro) contents Improved WUE Enhanced root starch reserved 	[129]
<i>T. aestivum</i>	15% PEG	10 mM K ₂ O	<ul style="list-style-type: none"> Improved Chlorophyll <i>a</i> (chl <i>a</i>), chlorophyll <i>b</i> (chl <i>b</i>) and carotenoid (Car) Increased Pro content 	[124]
<i>T. aestivum</i>	20% PEG, 7 days	7.5 mM K ₂ CO ₃	<ul style="list-style-type: none"> Significantly increased shoot K⁺ Decreased electrolyte leakage and MDA 	[130]
<i>Z. mays</i>	65 ± 5% water holding capacity of soil	0.42 g kg ⁻¹ soil	<ul style="list-style-type: none"> Strengthen the accumulation of K⁺ and osmotic nitrides in plants Increased endogenous glycine betaine 	[125]
<i>Hordeum vulgare</i>	50% soil water content	10 mM K ₂ CO ₃	<ul style="list-style-type: none"> Enhanced K⁺ content in plant Decreased soluble carbohydrate 	[131]
<i>O. sativa</i>	Withholding irrigation 30 days after transplanting, 10 days	120 kg ha ⁻¹	<ul style="list-style-type: none"> Increased shoot dry mass Improved osmolytes synthesis 	[114]
<i>G. hirsutum</i>	At flowering stage withholding water for 8 days followed by 75 ± 5% soil relative water content	300 kg ha ⁻¹	<ul style="list-style-type: none"> Improved osmotic adjustment Increased nitrogen metabolism Enhanced free amino acid, sugars content 	[127]

WUE: water use efficiency.

5.2. Salinity

Potassium is an important macronutrient that plays essential 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 (Table 3) [132]).

Under salinity stress, the osmotic effect and ion toxicity inhibited plant root growth, which decreases nutrient uptake and translocation, especially that of K^+ [9]. The sodium ion (Na^+) competes with K^+ for major binding sites during key metabolic processes in the cytoplasm, with these binding sites including both low-affinity (non-selective cation channels, NSCC) and high-affinity (KUP and high-affinity K^+ transporter, HKT) transporters; this competition disturbs the plant metabolism [9,38]. Salinity induces membrane depolarization and decreases the membrane integrity, which results in K^+ leakage through depolarization-activated outward-rectifying (KOR) K^+ channels [133]. 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 increase the K^+/Na^+ ratio. The HTK (high-affinity K^+ transporter) mediates Na^+ -specific transport or Na^+-K^+ co-transport, which have vital roles in plant Na^+ tolerance [134,135].

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

Plant Species	Salinity (NaCl) Doses	K Doses	Protective Effects	References
<i>T. aestivum</i>	100 mM	10 mM	<ul style="list-style-type: none"> • Increased shoot and root length • Increased K^+/Na^+ ratio 	[136]
<i>Olea europaea</i>	100 mM	100 mM	<ul style="list-style-type: none"> • Reduced K^+ uptake • Increased K^+ in leaves • Improved osmotic potential 	[137]
<i>Brassica campestris</i>	80 mM	0.54 mM	<ul style="list-style-type: none"> • Improved photosynthetic traits • Decreased the ion accumulation and oxidative stress traits in the leaves 	[138]
<i>Z. mays</i>	70 mM	9 mM	<ul style="list-style-type: none"> • Improved photosynthetic capacity • Increased accumulation of K^+ in the leaves 	[139]
<i>H. vulgare</i>	150 mM	10 mM	<ul style="list-style-type: none"> • Decreased Na^+/K^+ ratio • Improved shoot and root height • Increased Pro content 	[131]
<i>L. esculentum</i>	150 mM	2.39 mM	<ul style="list-style-type: none"> • Increased root and shoot weight • Improved photosynthetic pigment 	[140]
<i>A. hypogaea</i>	20 and 40 mM	30 kg ha ⁻¹	<ul style="list-style-type: none"> • Reduced uptake of Na^+ from soil and accumulation in leaf tissue • Increased plant biomass 	[141]
<i>S. lycopersicum</i>	75 mM	9 mM	<ul style="list-style-type: none"> • Increased photosynthesis • Increased leaf K^+ levels and K^+/Na^+ ratio • Improved membrane stability index 	[142]
<i>B. vulgaris</i>	76 mM	200 kg ha ⁻¹	<ul style="list-style-type: none"> • Improved shoot and root dry matter • Increased sucrose and sugar contents 	[143]

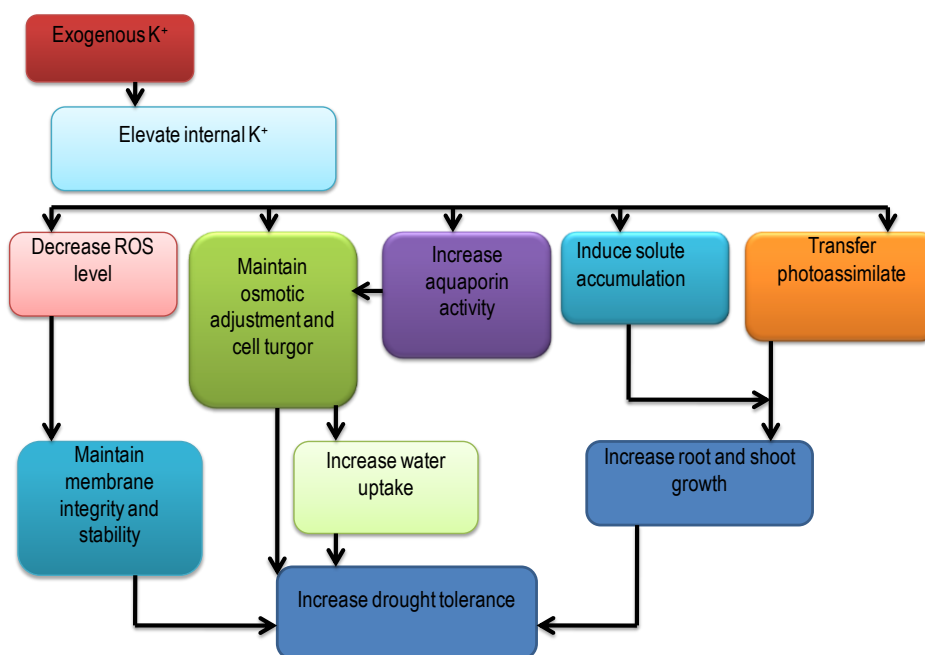


Figure 2. Role of potassium under drought stress (Modified from [9]).

Taffou et al. [144] found 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 K can positively correlate with plant root and shoot growth during salinity stress and the K deficient stage. Saida et al. [140] observed that applying 2.39 mM KH_2PO_4 against 150 mM NaCl increased the shoot and root fresh and dry weights of *L. esculentum* under salt stress. Fayez et al. [131] experimented with a *H. vulgare* crop and found that under 150 mM NaCl stress, the shoot fresh weight and height decreased, but treating with K improved the shoot fresh weight and height of a barley crop. Similarly, Amjad et al. [142] found that applying 9 mM K improved the root and shoot dry weights under 75 mM NaCl stress in *S. lycopersicum*. Merwad [143] reported that higher salinity negatively affected the tomato roots, shoots, leaves and WUE, and they recorded that exogenous K can have a positive effect on most of the *B. vulgaris* cultivars under salt stress.

In a previous section (Section 5.1), the exogenous application of K was shown to improve the organic osmolyte synthesis, especially that the rapid rate of cell recovery under osmotic stress was regulated by the higher accumulation of K^+ , Cl^- , and Na^+ in the epidermal root cells of *Arabidopsis* [145]. Thus, higher Na^+ concentrations are toxic for cell metabolism; that is why it is essential to maintain the cytosolic K^+ contents at a constant level for plant metabolic processes [146,147]. A constant cytosolic K^+ concentration is attributed to the consumption of vacuolar K^+ in K^+ -deficient situations [9]. Fayez et al. [131] observed that salinity increased the Na^+/K^+ ratio in *H. vulgare*, which significantly decreased after the application of K and increased the K^+/Na^+ . In addition, Chakraborty et al. [141] suggested that external K applications could have reduced the Na^+ uptake by adjusting the tissue ionic balance in peanut (*Arachis hypogaea* L.).

5.3. Extreme Temperature

When the temperature is greater than the optimum, plants suffer from high temperature stress. Extreme temperatures disrupted various biochemical reactions and the plant metabolism, which are highly related to 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 in coping with temperature stress. Potassium helps to activate the various physiological and metabolic processes

such as photosynthesis, respiration, and nutrient homeostasis, and it increases the tissue water potentiality, which assists in extreme temperature stress tolerance. Under high temperature stress, plants accumulate various types of osmolytes to overcome the damage caused by the stress. Potassium may work as an osmolyte, and it helps to maintain stomatal conductance to prevent damage [148]. In K deficient plants, not only photosynthetic electron transport pathways but also the NADPH oxidizing enzyme reaction produces ROS [5]. In this case, K helps plants by supporting protein synthesis, stimulating various enzymatic reactions, assisting in carbohydrate production and increasing the WUE. Under heat stress conditions, the foliar spraying of potassium orthophosphate (KH_2PO_4) helps to increase the heat tolerance of wheat by preventing leaf damage [149]. When a significant amount of K is lost from the chloroplast, the photosynthesis is reduced. In this situation, K application helps the plant to tolerate the heat stress by increasing the photosynthetic ability in wheat. Foliar applications of K also help to increase the translocation and accumulation of photosynthates as well as the dry matter. These factors are related to stress resistance and ultimately help to increase plant yields [150].

When plants face chilling or freezing stress, K-regulated mechanisms such as photosynthesis and carbon assimilation, metabolism, and phloem activity are down-regulated. Seed treatments involving KCl in a cold-sensitive maize variety led to better ROS defense and ultimately greater tolerance [39]. Plants facing freezing stress were found to lose apoplastic water due to freezing, which causes dehydration; and a sufficient K supply adjusts the osmotic potential and decreases freezing-induced dehydration [9]. Several field trials in various crops also show a similar phenomenon in which a sufficient K supply can eliminate frost damage [151].

5.4. Toxic Metals/Metalloids

Toxic metal/metalloid contamination in soil is dramatically increasing with time owing to rapid industrialization, which has generated tremendous problems in global agriculture [152]. The most obvious reaction of plants under metal/metalloid toxicity is the inhibited uptake of other essential nutrients and the alteration of 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 generation of excess ROS, the reduction of the water potential, etc. [153,154]. The continuous reduction in plant growth and development ultimately 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 urgent task for plant scientists. Because K plays a crucial role in the activation of several enzymes, the synthesis of protein, photosynthetic activity, osmoregulation, the movement of stomata, the transfer of energy, phloem transport, cation-anion balance, and stress resistance [9], this element is used as a plant protector against most abiotic stresses, including metal/metalloid toxicity (Table 4).

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

Plant Species	Metal Doses	K Doses	Protective Effects of K	References
<i>Vicia faba</i>	200 μM Cd, 7 days	6 mM K, 7 days	<ul style="list-style-type: none"> Increased shoot and root length Increased chl content Increased Pro content 	[155]
<i>Prunus persica</i>	2 mM ZnCl_2 , 10 days	10 mM KCl, 10 days	<ul style="list-style-type: none"> Improved photosynthesis Improved plant K nutritional status 	[156]
<i>Gladiolus grandiflora</i>	50 mg kg^{-1} $\text{CdSO}_4 \cdot 8\text{H}_2\text{O}$, 60 days	200 mg L^{-1} K along with 200 mg L^{-1} Si, 60 days	<ul style="list-style-type: none"> Increased root and shoot length Increased shoot and root dry weight Increased chl content 	[157]

The use of K against Cd toxicity confirmed the positive effect of this element by ameliorating Cd-induced oxidative damage in broad bean (*Vicia faba* L.; [155]). In this study, 6 mM K was used in combination with 200 μM Cd to inspect the role of the potassium. Cd stress reduced the growth

parameters (shoot and root lengths), decreased the chl content, altered the enzyme activity and increased the MDA content of the plants. Song et al. [156] 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.

5.5. High Light

Several examples illustrated the effect of high light intensity, which caused rapid leaf chlorosis resulted from impaired photosynthesis and photooxidative damages [158,159]. With the severity of stress, photosynthetic ability, RuBisCO activity, quantum yield, and electron transport disrupted in tomato [160]. When plants face insufficient K supply leaf chlorosis increased at high light [6]. This severity decreases the utilization of photoassimilates within the plants under insufficient K supply [161], and transport of sucrose via the phloem decreased [162]. Thus, K is required in a great quantity to utilize the absorbed high light for CO₂ fixation, and source-sink relation. Hence, plants receiving high light intensity may have greater K demand.

5.6. Waterlogging

Among the abiotic stresses 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 the plants in waterlogging condition [163,164].

Several researchers have reported the effect of exogenous K application for ameliorating the adverse effects due to waterlogging. Increased plant height, photosynthetic capacity, and chl content was reported in cotton due to K supplementation under waterlogging condition [23]. They also found greater nutrient uptake by the plants as a result of higher K application to soil or foliage [23]. Application of K at 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 [165].

6. Role of Potassium in the Detoxification of Reactive Oxygen Species

One of the common consequences of abiotic stress is the overproduction of ROS such as singlet oxygen (¹O₂), superoxides (O₂^{•-}), H₂O₂ and hydroxyl radicals (OH[•]) [166], alkoxy radicals (RO[•]), peroxy radicals (ROO[•]), and organic hydroperoxides (ROOH) [167,168]. Inside plant cells, low concentrations of ROS act as a signaling molecule to protect plants from stresses, while higher concentrations of ROS enhance the lipid peroxidation, oxidation of proteins, inhibition of enzyme activities, and activation of the programmed cell death (PCD) pathway, ultimately leading to cell death [169]. During photosynthetic electron transport and membrane-bound NADPH oxidase reactions, the formation of ROS in plant cells is increased due to K deficiency. Hence, it was suggested that the exogenous use of K could decrease ROS formation by maintaining the plant photosynthetic electron transport and diminishing the action of NADPH oxidase ([6]; Table 5; Figure 3).

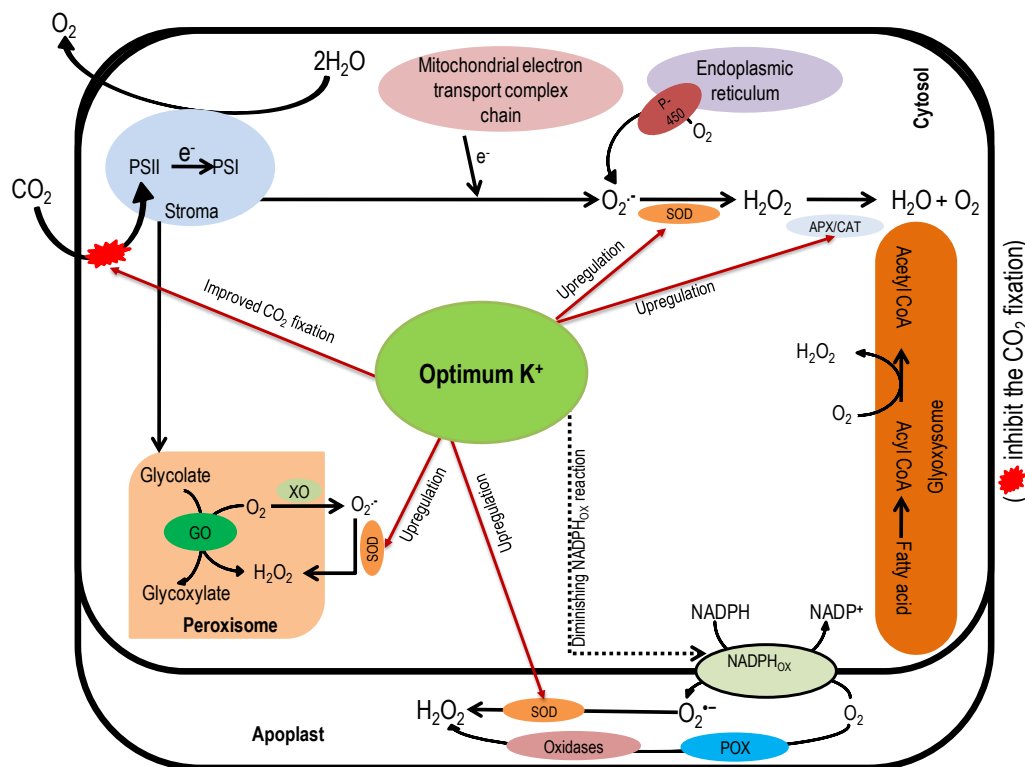


Figure 3. Schematic representation of the role of K to detoxify the reactive oxygen species (ROS) formation under stress (Modified from [166] with permission from Springer).

Plants that are exposed to environmental stresses such as drought show enhanced K requirements, and furthermore, they show increased oxidative damage to cells by inducing the formation of ROS, especially during photosynthesis [9]. At the time of drought stress, CO₂ fixation is limited in plants, and it impacts the stomata regulation, transfer of light into chemical energy and translocation of photosynthates from source to sink (Figure 3; [170,171]). Due to the impairment of photosynthetic CO₂ fixation, plant molecular O₂ is activated and ROS production is increased within the plant cell [6,9,172], which causes the degradation of the photosynthetic pigment and cellular membranes. Sangakkara et al. [173] found a positive role for K by reducing ROS formation and increasing the net photosynthesis rate under water-stressed conditions in mung bean (*V. radiata*) and the cowpea (*V. unguiculata*). Egilla et al. [113] observed that adequate K⁺ availability to China rose (*Hibiscus rosa-sinensis* L.) under drought stress reduced the inhibition of photosynthesis by mitigating ROS formation. Likewise, Milford and Johnston [174] suggested that K plays a vital role in stomatal opening and closing and in the transpiration and photosynthesis of plant cells. Raza et al. [81] experimented with *T. aestivum* under drought conditions and found that an application of 1.5% K decreased the ROS formation and improved the transpiration and photosynthesis rates. Thus, it was suggested that an adequate supply of K under drought conditions improved the photosynthetic CO₂ fixation and the export of photosynthates from source to sink organs and prevented photosynthetic electron transport to O₂. As a result, the formation of ROS was reduced [6,9].

Under saline conditions, low 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 increases oxidative damage [175]. The higher production of ROS due to severe salinity leads to cellular membrane damage. Programmed cell death occurs as a result of K⁺ leaks from the plant cells due to the activation of K⁺ efflux channels [176]. The external use of K in a saline growing medium was involved in improving salt tolerance through reduced ROS formation in *T. aestivum* [177], *Z. mays* [178], and *O. sativa* [179]. The application of K enhanced the antioxidant

enzyme activities such as those of superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) in zinger (*Zingiber officinale* Roscoe) [180], which reduced the ROS formation in plant cells. Zheng et al. [181] suggested that applying a suitable amount of KNO_3 detoxified the ROS through increased SOD, CAT, and POD enzyme activities in *T. aestivum* under salt stress. Jan et al. [182] reported that the SOD, CAT, and ascorbate peroxidase (APX) enzyme activities were enhanced, and 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
<i>Vigna radiata</i>	Drought (25% and 50% field capacity)	3 mM	<ul style="list-style-type: none"> Reduced reactive oxygen species (ROS) production Enhanced the rate of net photosynthesis 	[173]
<i>L. esculentus</i>	60 mM NaCl	5 mM	<ul style="list-style-type: none"> Improved chl content Decreased ROS production Increased dry matter Increased water used efficiency 	[183]
<i>H. rosa-sinensis</i>	Water deficit after 54 days of transplanting	10 mM	<ul style="list-style-type: none"> Increased rate of net photosynthesis, transpiration, and stomatal conductance Improved leaf water content and leaf water relations by decreasing the leaf osmotic potential ($\Psi\pi$) 	[113]
<i>T. aestivum</i>	100 mM NaCl	16 mM	<ul style="list-style-type: none"> Increased superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) activity Reduced the formation of ROS 	[181]
<i>O. sativa</i>	200 mM NaCl	11.8 mM	<ul style="list-style-type: none"> Decreased ROS production Improved photosynthetic performance 	[179]
<i>T. aestivum</i>	Water deficit at milking stage	1.5%	<ul style="list-style-type: none"> Reduced ROS production Improved transpiration and photosynthesis 	[81]
<i>Z. mays</i>	70 mM NaCl	9 mM	<ul style="list-style-type: none"> Increased CAT activity Improved photosynthetic capacity Increased accumulation of K in the leaves 	[139]
<i>Solanum lycopersicum</i>	150 mM NaCl	9 mM	<ul style="list-style-type: none"> 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 	[142]
<i>T. aestivum</i>	8.56 mM NaCl	0.49 mM	<ul style="list-style-type: none"> Increased SOD, CAT, ascorbate peroxidase (APX) activity Improved photosynthetic capacity Reduced ROS formation 	[182]

On the other hand, NADPH-oxidizing enzymes reduce O_2 to O_2^- by using NADPH as an electron donor ([6]; Figure 3). Moreover, the NADPH oxidase activity was substantially enhanced under K deficiency, increasing the NADPH-dependent O_2^- production. Cakmak [6] found that K deficiency increased the NADPH oxidase activity in the cytosol of *P. vulgaris* roots, with a corresponding increase in the NADPH-dependent O_2^- generation, but exogenous K decreased the NADPH oxidase activity. Potassium deficiency is most likely the primary reason for the increased NADPH oxidase and NADPH-dependent ROS formation through the generation of ABA. Peuke et al. [184] experimented with castor (*Ricinus communis*) and found that K deficiency increased the biosynthesis of ABA in roots and increased the translocation of ABA from the roots to the shoots. Moreover, ABA has likewise appeared to be effective at increasing the accumulation of H_2O_2 and O_2^- in plant roots [185,186], but this point needs to be verified in future studies. It is clear that an improvement in the K status maintains the photosynthetic electron transport and inhibits the NADPH oxidase activities, which reduce ROS formation in plants.

7. Interaction of Potassium with Other Biomolecules

Potassium is called the policeman nutrient; it plays an important role in the growth, development, and yield as well as the metabolism of plants. It also has some interactive regulatory functions with other biomolecules [5,9]. Therefore, K deficiency leads to dysfunction in numerous physiological and biochemical processes; for example, in the water balance, enzyme activity, and charge balance, in addition to tolerance to biotic and abiotic stresses [187]. Potassium is also essential for the function and performance of many plant enzymes; at least 60 enzymes require K as a cofactor for activation [188]. These enzymes regulate the vital metabolic mechanisms in arable plants [38,189]. To increase substrate attraction, K binds with the specific binding site of inactive enzymes, resulting in their activation, and these enzymes were involved in various metabolic and physiological mechanisms. Several studies have suggested that the activity of nitrate reductase (NR), RuBisCO, starch synthase, sucrose phosphate synthase, β -amylase, invertase, phosphofructokinase, and pyruvate kinase greatly depends on the K sufficiency of plants [190,191].

Among the biomolecules, carbohydrates have a greater interactive relation with K. When plants obtain enough K, they synthesize large biomolecules; for example, cellulose, starch, protein, etc. As a result, the number of small molecules such as free sugars, amino acids, organic acids, and amides are reduced in the cell while the concentration of phenols increases, and these compounds aid in plant resistance [192] and increase the plant response to abiotic stress [193]. Carbohydrates, mostly in terms of hexose content, are decreased in leaves due to a sufficient K supply, which was transported to another plant organ due to better phloem activity. On the other hand, K deficiency resulted in the decreased activity of pyruvate kinase and/or increased invertase activity that reduces the concentration of starch in leaves because of the inhibition of starch synthase [60].

Potassium has a positive relationship to plant hormone synthesis as well [194]. When the K concentration in the cell is low, JA and auxin biosynthesis are upregulated [195], but ethylene synthesis is increased by two-fold in *Arabidopsis* when the plant is suffering from K-starvation [196], and the other biological functions decreased in the roots and xylem sap, leading to sucrose accumulation. Conversely, the cytokinin concentrations in the leaf and the xylem sap decreased when plants obtained sufficient amounts of K [187,197]. 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* [198]. Exogenously applied K and naphthaleneacetic acid (NAA) can interact significantly to increase the growth and yield of *V. radiata* [199]. A similar result was also obtained by applying K and GA to rice [200] and by applying K and SA to olive trees under salinity [201]. Increased levels of JA, hydroxy-12-oxo-octadecadienoic acids (HODs), and 12-oxo-phytodienoic acid (OPDA) were obtained under K-starved conditions along with the upregulation of the 13-lipoxygenase (LOX) pathway, indicating the transcript levels of several biosynthetic enzymes with K interactions [202]. ABA acts as an important signal-mediated factor during the transduction of the sucrose regulation signal. The ABA content in the seed is negatively correlated with the sucrose content, and the ABA/(Indole acetic acid + GA + cytokinin) ratio is influenced by K nutrition in a way that particularly reduces the ABA content, playing a key role in the increase in the sucrose content, which suggested the K interactions with phytohormones [187].

Polyamines also have a role in a wide range of environmental stresses, and they are involved in various physiological processes. Their concentrations at the cellular level increased under K deficit conditions in oat (*Avena sativa* L.) [203]. When plants face any stress, they accumulate polyamines at a higher concentration. Polyamines have significant interactions with K at the cellular level, and they regulate the plasma membrane K⁺ channel of the guard cells, modulating stomatal regulation [204]. The authors also reported that spermidine, spermine, cadaverine, and putrescine powerfully block the opening and closing of stomata, which provides a link among the stress, the stomatal regulation, and the polyamine level.

8. Potassium-Induced Abiotic Stress Signaling

In a dynamic environment, the K content of the soil may not remain the same over the growing period of a crop. Interestingly, plant roots can sense fluctuations in the K⁺ availability. When the K deficiency is sensed by plant roots, a series of events occurs in the plant at the molecular level to cope with this condition. Some signaling components are involved from the signal perception to the adaptive responses (Figure 4). For example, the Ca²⁺ signaling, ROS, microRNA, membrane potential and phytohormones are the signaling components [25,52]. Under K-deficient conditions, CIPK23 (a protein kinase) activates the K⁺ transporter AKT1 by phosphorylation. The calcium sensors CBL1 and CBL2 regulate the activation of CIPK23 [205]. Later, low K⁺ induces two distinct Ca²⁺ signals that are read by CBL1/9, as observed in *A. thaliana* [206]. The CBL1/9 then regulates the AKT1 by activating CBL1/9-CIPK23 complexes [206]. The overexpression of the type III peroxidase *RCI3* increased the production of ROS as well as the HAK5 expression. However, a mutant lacking this gene exhibited reductions in both ROS production and HAK5 expression, indicating the relationship between the ROS and the low K response [207]. Potassium channels such as NSCC and GORK are very sensitive to ROS. Under saline conditions, the ROS-mediated activation of NSCC and GORK is the primary reason for the K pool reduction in the cytosol [29,208]. A prolonged K deficiency in the cytosol activates different endonucleases and proteases, which in turn causes cell death [29].

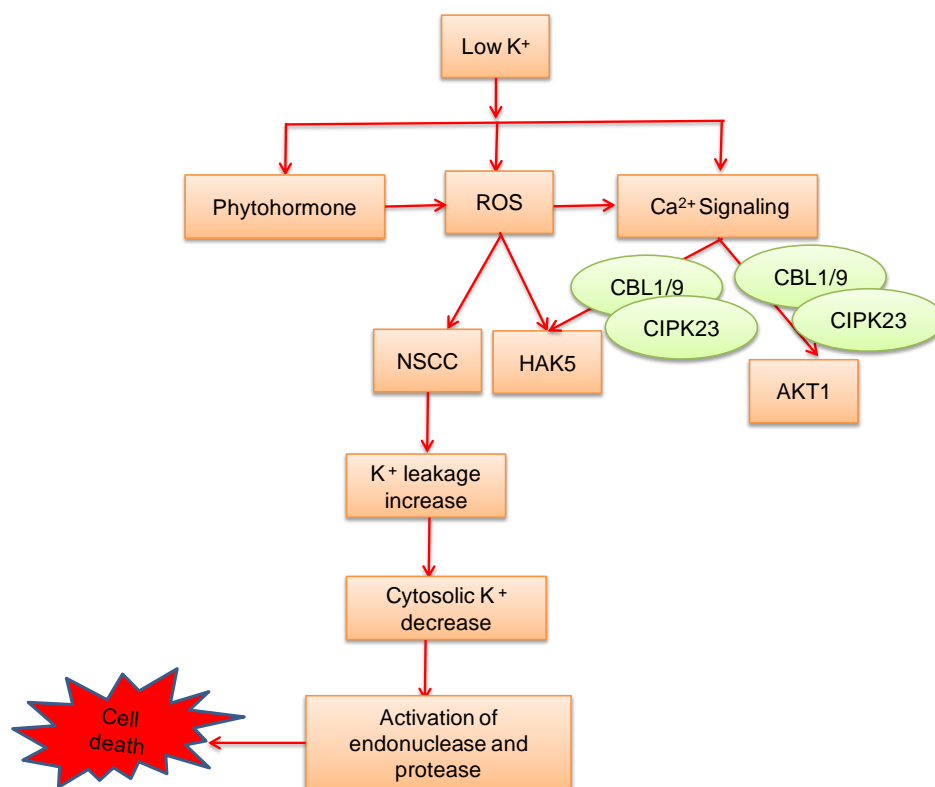


Figure 4. K-induced signaling in the plant. ROS: Reactive oxygen species; NSCC: Non-selective cation channel; HAK5 and AKT1: K⁺ transporter, CBL1/9: calcineurin B-like proteins, CIPK23: A protein kinase.

Phytohormones such as ethylene, auxin, cytokinin, and JA are also involved in low K-induced signaling processes. Under K-deficient conditions, *HAK5* transcription is regulated by the upstream signaling molecule ethylene and ROS [209]. However, the cytokinin content decreases under low K stress to regulate *HAK5* by inducing ROS [209]. A K⁺ transporter in rice has been found to be regulated by JA [210]. The involvement of microRNAs in plant nutrient homeostasis has been reported in many

studies. For example, the gene chip overexpression of *OsmiR399* increased the nutrient contents of the plant, including the contents of K^+ . Under nutrient starvation, *OsmiR399* expression increases [211]. The elucidation of a complex pathway that was induced by K signaling allowed us to engineer the pathway in a way that would ensure the optimum K level in the plant.

9. Conclusions

Potassium is vital for plant survival under both physiological and stress conditions. It is not only a part of the chemical structure but also plays vital regulatory functions 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 animals and human beings. 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., they exert their deleterious effects in crop plants. Important physiological activities including photosynthesis are greatly hampered under most of the abiotic stresses, which lead to increased toxic ROS in the 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 systems which helps to defend some stresses by activating antioxidant defense systems. Thus, this review assesses K involvement in normal plant growth and development, in addition to increasing tolerance/resistance against different stress conditions.

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