

Potassium transport and use efficiency for sustainable fertigation in protected cropping

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Abstract

The increasing demand for high-quality horticultural produces in global markets has driven the growing crop production under protected cropping, which are usually more efficient in fertilizer use compared to field cultivation. As one of the key macronutrients, available potassium (K⁺) resources have decreased due to the expansion of intensive agriculture and excessive use of K fertilizers. Currently, limited strategies have been adopted to improve crop quality in protected cropping with sustainable use of K⁺ fertigation and its comprehensive understanding at physiological and molecular levels. Therefore, we highlight the importance of optimal use of K⁺ in fertigation in protected cultivation that may also enhance crop quality characteristics. We review different K⁺ channels and transporters from various protein families responsible for K⁺ absorption and distribution across different plant tissues. An analysis of the literature on transcriptome, ionome, proteome and metabolome profiles of crops suggests the crucial roles of K⁺ in maintaining ion homeostasis and modulating stress responses. It reveals that optimal K⁺ fertigation levels in protected cropping not only aids in maintaining the overall crop growth and production but also participates in maintaining the fruit quality. This review can potentially guide crop production and resource use efficiency in protected cropping, contributing to global food security and a better sustainable agricultural and environmental future.

KEYWORDS

crop quality, greenhouse horticulture, membrane transport, omics, soilless cultivation

1 | INTRODUCTION

The demand for agricultural produces is increasing due to rise in global population and greater per capita incomes anticipated through mid-21st century (Tilman et al., 2011). Increasing global population in turn demands to produce more food using different farming systems such as protected cultivation, and hydroponics (Ragaveena et al., 2021). Some problems behind the rise of food cost are due to the cultivation of crops in unfavourable

environmental conditions and increasing price of inputs (e.g., fertilizers, pesticides and energy) that are directly or indirectly related to global climate change. One of the potential solutions is an approach of protected cropping using low- (poly tunnels, net houses, screen houses) medium- (semiautomated polyhouses and glasshouses), and high-tech (highly automated glasshouses) greenhouses to grow different types of crops (Abdalla et al., 2022). Here, we provide an overview of the big potential of protected cropping for sustainable food production.

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Protected cropping covers many fields of science and technology such as agronomy, plant physiology, plant biotechnology, entomology, plant pathology, engineering, computer science, economics and other disciplines (Mahlein et al., 2012). Protected cropping uses low-, medium- and high-tech structures, which act as a guard to crops in a controlled environment and protect them from unfavourable climatic conditions (Morgan, 2021). These protected cropping structures provide viable and efficient means to control internal climatic factors such as light, temperature, humidity, CO₂ and nutrients (Rabbi et al., 2019) and also crop can be isolated from the external climatic and environmental variation such as wind, rain, high solar radiation, drought, soil salinity, pests and diseases (Akter et al., 2022). As a result of which from the past few decades, protected cultivation, has become one of the most popular methods for producing horticultural crops such as tomatoes, cucumbers, capsicums and lettuce both qualitatively and quantitatively (Sabir & Singh, 2013). According to United Nations Food and Agriculture Organisation (FAO 2018), the estimated production of vegetables under protected cultivation is on the rise in key crops such as tomato (182 million tonnes), cucumber (75 million tonnes), eggplant (54 million tonnes).

Appropriate fertigation (fertiliser + irrigation) management in protected cropping is critical for improving crop quality, minimizing water and fertilizer use and reducing leaching beneath root depth (Hasanuzzaman et al., 2018). The optimal utilization of nutrients and water is subject to variation among plant species and their respective developmental stages. Consequently, it is essential to regulate nutrient concentrations for different crop species during specific developmental stages, taking into account the relative proportions required for optimal plant growth and development (Savvas & Gruda, 2018). Electric conductivity (EC) of the nutrient solution is the measure of nutrient availability to the plants and should be regulated according to the plant needs. High EC can result in the reduction of mass flow in plants due to less entry of water inside the root zone and low EC can lead to root cell rupture due to the generation of high imbalance of osmotic gradient across the membrane (Adams & Ho, 1992). Moreover, plant water consumption depends on nutrient assimilation, fertigation levels and the climatic conditions in greenhouses. The ability of plants to selectively take up nutrients according to different nutritional needs at different growth stages optimizes plant growth in a precise manner (Neocleous & Savvas, 2022).

Potassium (K) is one of the most abundant plant nutrients, account for 2.6% in the earth's crust. On average the soil constitutes 0.04%–3% K, but most of the K⁺ in the soil is incorporated in crystal lattice structure of minerals and thus not directly available for plant uptake (Demidchik et al., 2014). Application of K⁺ fertilizer enhances the water holding capacity and the structural stability of soil. K⁺ fertilizer also helps in maintaining the electrolyte concentration in plants under greenhouse environment (Nieves-Cordones et al., 2014). Moreover, the capacity of plants to maintain cytosolic K⁺ at a specific level and alterations in K⁺ concentrations in the vacuoles and apoplast are important factors for the growth and productivity of crops (Shen et al., 2017). To achieve maximum efficiency, it is

essential to deliver of K fertilizer and other nutrients at the appropriate rate, time, and place in the root zone of plant. Crops growing under protected cropping can be a leading approach to minimize fertilizers loss and ensuring adequate nutrient supply at each stage of development. Considering the key role of K⁺ in plant growth, an appropriate supply of this nutrient can maintain adequate photosynthesis and boost off-season production of good-quality fruits (Babla et al., 2023; Maier et al., 2022). Thus, better understanding of K⁺ acquisition efficiency and its transport in plants can contribute to the exploration of biological function of K⁺ in regulating overall plant growth for optimization of the K⁺ fertigation management in protected cropping.

Potassium use efficiency in greenhouse crops is less studied. We review different physiological changes and crop yield in protected cropping caused by high or low K⁺ nutrient concentrations. We further synthesize the insight on K⁺ nutrition connected to important genes, proteins, metabolites, and ions, which provides a basis for understanding essential molecular signalling pathways in response to altered potassium levels in greenhouse crops. This review focuses on understanding the importance of potassium in balancing plant growth by minimizing the dose of K⁺ fertigation can be a primary approach of preserving natural resources and protected biodiversity.

2 | POTASSIUM FERTIGATION MANAGEMENT FOR GREENHOUSE CROPS

In the context of climate change, protected cropping provides an approach to increase food production by utilizing less resources and providing nutritious food to consumers. Fruit quality and yields can be effectively improved by managing the glasshouse environment, including its microclimatic, structural, mechanical and fertigation aspects (Shamshiri et al., 2018). The major environment factors that impact greenhouse crop growth are root zone temperature, moisture, electrical conductivity, nutrient levels, light quality and relative humidity (Maier et al., 2022). Humidity level in greenhouse plays a vital role in controlling the moisture level of plants. High humidity results in suppression of the transpiration and reduces uptake of nutrients including K⁺. In contrast, low humidity increases vapour pressure deficit in leaves that will reduce stomatal opening and photosynthesis (Ahmed et al., 2019). Low light and high light affect greenhouse crop yield that is partial related to the reduced accumulation of K in plant (Babla et al., 2023; He et al., 2022). High and low temperatures influence stomatal movement, which in turn influences growth, transpiration, photosynthesis and yield (Babla et al., 2023; Rabbi et al., 2019). Some modern glasshouse facilities incorporate specialized glass technologies and efficient cooling systems, which have the potential to reduce power use (He et al., 2022). Therefore, these developments can facilitate the protected cropping sector in shifting to a sustainable and cost-effective level of energy efficiency thereby maintaining crop quality, nutritional content and reducing adverse environmental impacts (Figure 1).

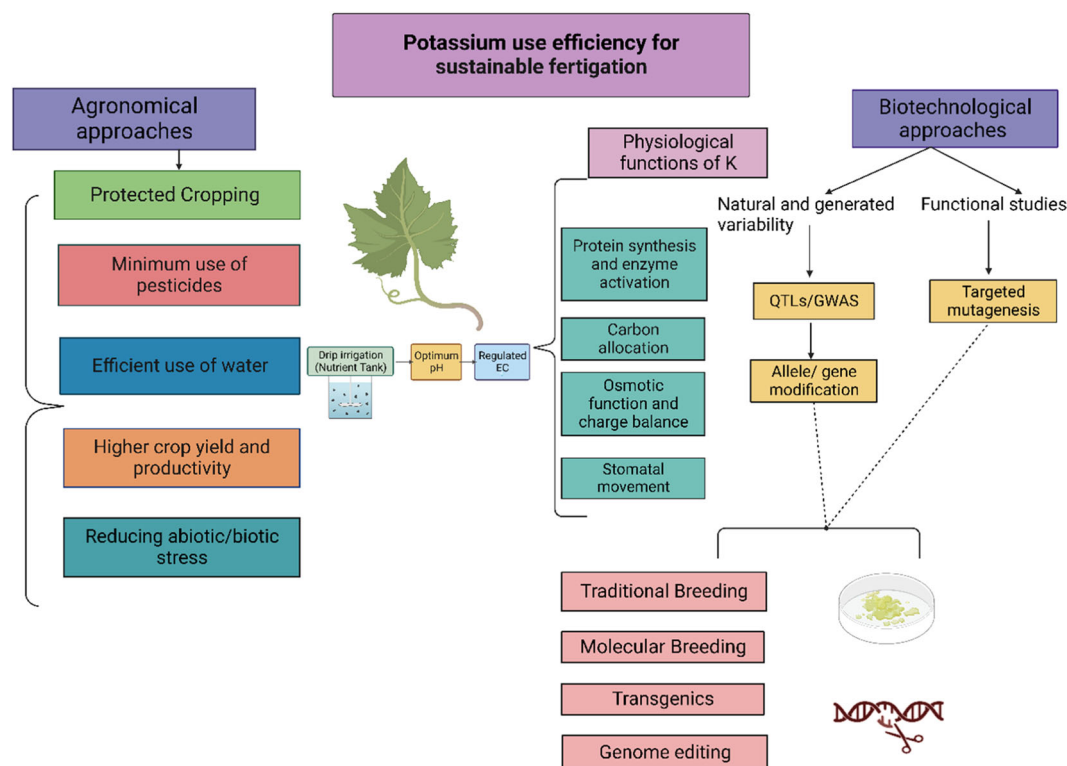


FIGURE 1 Schematic representation of different approaches for sustainable potassium use efficiency. Several potential steps can be taken to grow potassium efficient crop by adopting unique fertigation strategies like drip irrigation and hydroponics under protected cropping. By genetic engineering approaches deeper understanding of potassium-related genes, their translocation, metabolic regulation, ionic response in plants is improving its sustainable use efficiency in maintaining the food security.

2.1 | Potassium fertilizer for crop production in protected cropping

One of the major challenges for agriculture is to increase the crop yield in a resource efficient way. Fertigation regulates crop growth, yield and quality, which is influenced by fertiliser type, concentration and frequency of the application to the plants (Tsafaras et al., 2021). Potassium forms a significant part of salts for the EC in protected cropping, which counterbalances increase and decrease concentration of other ions (Dorai et al., 2001). With respect to fertilizer management, greater K levels stimulate shoot development and enhance fruit production, indicating its increased supply during the fruiting stage facilitates higher yield and productivity in protected crops. K fertilizer application in protected cropping can be managed by monitoring the degree of fertigation in accordance with flower, shoot and root growth of the crop (Wang et al., 2013). Knowing the nutritional status of the plants growing in soilless culture is essential to determine the effectiveness of fertigation management strategies to identify overall growth of plants (Johnson et al., 1985). EC of a solution serves as a measure and the amount of ions available to plants in the root zone is associated with the EC of the nutrient solution (Nemali & van Iersel, 2004). Abrupt, substantial changes to the EC of the root zone can have a detrimental impact on the growth of the roots and plants as well as the quality of the fruits. Correspondingly, optimized nutrient solution and EC considers as a

fundamental route for improved crop production, plant physiology, growth and development of crop. Optimal EC providing a great means of saving fertilisers in large-scale greenhouses (Ding et al., 2018). The concentration of nutrients such as K^+ in the root zone has paramount importance as it directly impacts the plants (Gruda, 2011). Potassium is one of the three most important macronutrients (N, P, K) essential to all plants (Schachtman & Shin, 2007) including vegetable crops in protected cropping. Therefore, optimal K fertigation for a range of crop species significantly improves resource use efficiency and yield in protected cropping.

Almost 40% of the world's K^+ fertilizers are currently used by China, USA, India and other countries to increase crop yield and quality. The largest proportion of K^+ fertilizer use globally is in cereal crops (37%) such as wheat, rice and maize, followed by fruits and vegetables (22%), oilseeds (16%), sugar and cotton (11%) and other crops (14%) (United Nations FAO, 2015). Potassium chloride (KCl) is the major form of fertilizer used these days, but potassium nitrate and potassium sulphate are preferred for the crops that are sensitive to chloride such as vegetables and fruits (Abou-el-Seoud & Abdel-Megeed, 2012). Being a cation molecule potassium comprises 10% of a plant's dry weight. Potassium concentration in plant varies between 0.4% and 4.3% whereas its subcellular distribution of K^+ are around 0.1 mM in apoplast, 100 mM in cytosol, and 50 mM in vacuole (Chen et al., 2012; Hills et al., 2012; Zörb et al., 2014). The minimum

acceptable K^+ content for many crops is between 0.5% and 2% in dry matter. High accumulation of K^+ under regulated environmental conditions enables plants to smoothly perform all photochemical reactions (Ahmad & Maathuis, 2014). When there is an optimal supply of potassium, sink tissues utilised K^+ and photoassimilate in reproductive plant organs for better yield production (Bruns & Ebelhar, 2006). Potassium contributes as a key step regulator in most of the steps of protein synthesis, initiating from activation of enzymes and ending through ribosome synthesis by mRNA turnover during posttranslation process. Therefore, harvest index of the crop is directly related with crop yield and biomass per unit of K^+ applied (Tighe-Neira et al., 2018). In plants, K^+ is a dominant cation for the counterbalance of different anions in intracellular (e.g., cytoplasm, chloroplast and vacuoles) and intercellular (e.g., apoplast, xylem and phloem) spaces (Waraich et al., 2012). Potassium is highly mobile in phloem of plants along with the loading of several photo-assimilates (Schäfer et al., 2018). It is essential to have adequate supply of K^+ redistributes itself toward growing tissues like developing leaves and fruits (Nieves-Cordones et al., 2014). Therefore, optimal supply of K^+ fertilizer owing its fundamental roles towards plant performance could be an important goal for geneticists to develop plants that use K more efficiently.

2.2 | Role of potassium in photosynthesis, yield and quality

K^+ is essential to both the Calvin Benson cycle and the Hill reaction in photosynthesis. Ionic equilibria, electron transport and proton-motive force are the key processes in which K^+ is engaged especially in the Hill reaction, which is primarily connected with the production of NADPH (nicotinamide adenine dinucleotide phosphate hydrogen) and ATP (adenosine triphosphate) (Tighe-Neira et al., 2018). Lack of potassium increases mesophyll resistance and lowers the activity of the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), and ultimately leads in a reduction of total photosynthesis rate (Cakmak, 2000). Some studies suggest that when plants were given a significant amount of K^+ , sucrose content in the leaves increased by several folds (Lu et al., 2017). Therefore, potassium contributes its specific role in plant growth and development by regulating the photosynthetic performance of plants.

The market value of a crop, in terms of both yield and quality, plays a pivotal role in determining the overall crop quality and total yield (Pettigrew, 2008). Potassium is indirectly involved in regulating the protein metabolism of plants. Furthermore, it has been studied that transport of amino acids in plants is enhanced by higher K^+ levels especially when the plant is in its reproductive stages (Bai et al., 2021). Potassium contributes as a key step regulator in most of the steps of protein synthesis, initiating from activation of enzymes and ending through ribosome synthesis by mRNA turnover during posttranslation process. One of the visual phenotypes that can be seen in plants is the reduction in leaf area of plants when K^+ is insufficient to plants (Rengel & Damon, 2008). This leaf area reduction results in lowering

of the photosynthetic efficiency and reduction in canopy light interception (Jordan-Meille & Pellerin, 2004). Potassium is essential for transport of assimilates during photosynthesis which includes sugar transport and metabolism, that ultimately raises crop output and enhanced fruit quality. Accumulation of assimilates and their transport to different plant tissues has been associated with increased yield, fruit size, fruit colour and increased shelf life of fruit (Lester et al., 2010). It has been found that the plant's potassium uptake is higher during vegetative stages whereas in some of plants its uptake has been found to be significant during developmental stages (Rengel & Damon, 2008). Coupling of these factors, K^+ deficiency reduces photo-assimilation efficiency, affecting crop quality and yield.

3 | POTASSIUM TRANSPORT IN PLANTS

Potassium greatly contributes in maintaining the plant growth and metabolism (Wang & Wu, 2013) and membrane potential, anion neutralization and signal transduction (Thornburg et al., 2020). Its concentration in soil ranges from 0.01 to 20 mM, but in cytosolic K^+ concentration ranges from 80 to 100 mM. Plant absorbs K^+ from the soil through its root system and moves in a source-to-sink direction. (Xu et al., 2020). Small changes in cellular K^+ concentration can affect the transcript levels of many K^+ channels and transporters in plants, that affects the direct regulation of potassium sensing in plants (Armengaud et al., 2009). Under potassium deficient conditions plants increase their capacity and affinity to assist the remobilisation and redistribution of stored nutrients to support growth and homeostasis in plants. The overall regulation of potassium is controlled by complex network of gene families encoding shaker type K channels, two-pore K^+ channels, putative K^+/H^+ antiporters, K^+ uptake permease (KUP), high-affinity potassium transporter (HAK/HKT) and potassium transporters (KT) (Feng et al., 2020; Isayenkov et al., 2011; Pettigrew, 2008; Wang et al., 2022). Here, we discuss the roles of the important K^+ transporters in plants (Figure 2).

3.1 | K^+ channels

Shaker-type K^+ channels are mostly found at the plasma membrane and involve K^+ selective voltage-gated channels. These channels activate by voltage-gated currents in the membrane and participates in hyperpolarization and depolarization of membrane in response to K^+ availability (Shabala & Cuin, 2008). Shaker-type K^+ channels operate for low-affinity transport of K^+ and subdivided into three different subfamilies: (1) hyperpolarization-activated inward-rectifying channels (AKT1, KAT1 and KAT2), (2) weakly inward-rectifying channels (AKT2/3), and (3) depolarization-activated outward-rectifying channels (SKOR and GORK) (Shabala et al., 2020). Both AKT1/2 channels are present in roots and thus helps in K^+ uptake into mesophyll cells and root hairs through phloem loading. K^+ absorption in plant roots is

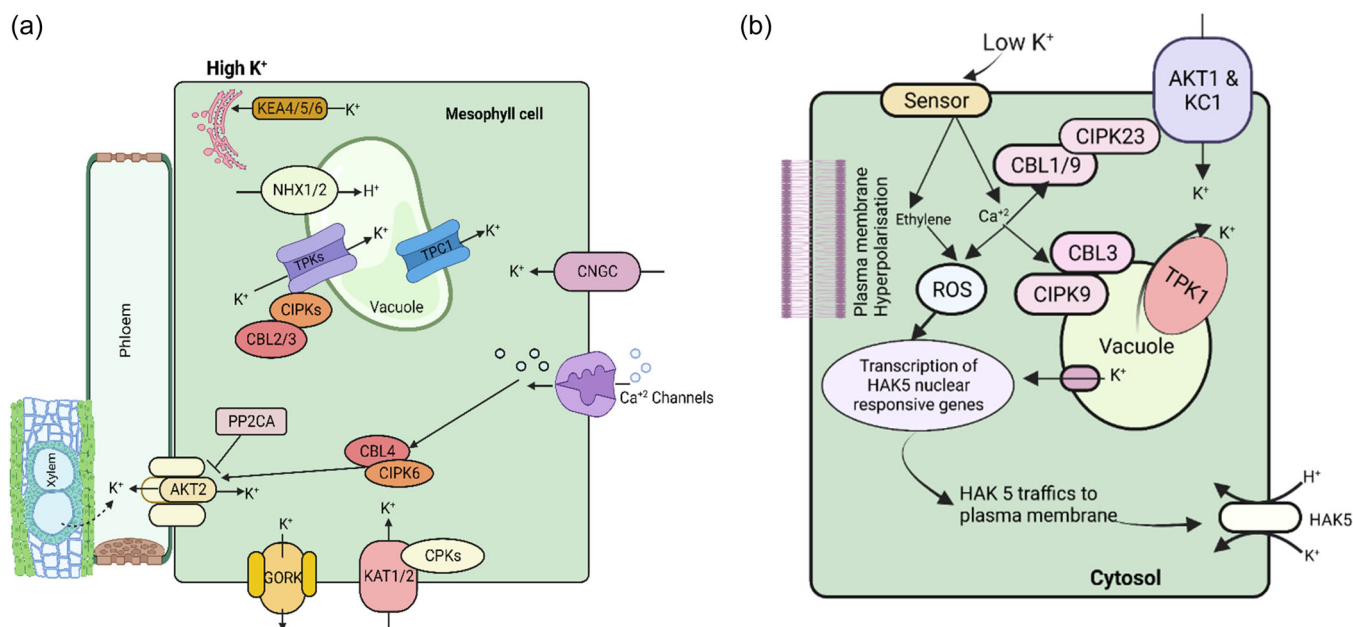


FIGURE 2 Potential mechanism of plant uptake and response at high and low K^+ concentration. At high potassium concentration in plants the outward rectifying channels of K^+ like GORK facilitates the fine-tuning of plasma membrane electric potential and do repolarization of membrane under stress conditions whereas channels like SKOR releases potassium into xylem vessels for its delivery towards the shoots (a). Furthermore, K^+ stored in the vacuole released back into the mesophyll cells by the activation of NHX exchangers, this facilitates K^+ unloading in xylem and activation of AKT 2 channels to release into phloem for its transport towards the roots and allows the assimilation of photosynthates in the phloem sap. On contrary under low K^+ circumstances (b), CIPK23 phosphorylates AKT1, increasing K^+ absorption, and activates high affinity potassium transporters like HAK5, mediated by ROS. This stimulates transcription of HAK5 nuclear responsive genes, which results in increased K^+ absorption under deficit conditions. AKT, Shaker type K^+ channels; CBL2/3, calcium binding like proteins; CIPK6, CBL-interacting protein kinases; CNGC, cyclic nucleotide-gated channel; GORK, guard cell outward rectifying channel; HAK/KUP, high affinity K^+ transporters; KEA4/5/6, potassium antiporters; NHX 1/2, sodium/hydrogen exchanger; PP2CA, phosphatase 2A catalytic subunit; ROS, reactive oxygen species; TPK, tonoplast two pore K^+ channel.

controlled by AKTs when on exogenous $[K^+]$ in the soil is relatively high (Huang et al., 2021; Véry & Sentenac, 2002). In plants when external potassium concentration drops, the permeable pathways for potassium channels get unstable. During that time shaker-type potassium channel 1AKT1 heteromeric proteins collapses and blocks the passage of potassium in unfavourable conditions (Geiger et al., 2009), which in turn activate the high-affinity K^+ transport. GORK (gated outwardly rectifying K^+ channel) and SKOR (stelar K^+ outward rectifier) are considered as two main members of potassium shaker family that help in facilitating the transport of K^+ ions for stomatal regulation and xylem loading, respectively (Mäser et al., 2001; Sharma et al., 2013). For instance, SKOR is triggered by membrane depolarisation and offers a route for K^+ efflux for its function in membrane pericycle and xylem parenchyma of plant cells (Garcia-Mata et al., 2010). When the external concentration of K^+ is high the structural pore region of SKOR interacts with the responsive transmembrane domain of the channel and the channel is stabilized in closed state (Johansson et al., 2006). Thus, SKOR may help in transporting K^+ between tissues under the K^+ deficit conditions to regulate source-to-sink relationship a better yield and quality of greenhouse crops. Whether Shaker Type K^+ channels have these potential functions will require substantial research work in the future.

Potassium transport is also regulated by the two-pore potassium channels (TPK) which in some species named as Kir like channel potassium inward rectifier and in some named as KCO (Dabravolski & Isayenkov, 2021). TPK activity is modulated by cytoplasmic pH, phosphorylation and helps in the membrane trafficking of integral tonoplast proteins to Golgi bodies (Dabravolski and Isayenkov, 2021). TPKs are clustered into two clades with Clade 1 comprises the most recent TPK members found in embryophyte and flowering plants. In Arabidopsis, it has been reported that some of the TPKs are targeted to the plasma membrane, but other TPKs are found to be in tonoplast. For example, TPK1 regulates ABA-dependent stomatal closure by mediating K^+ released from vacuoles with activation via cytoplasmic calcium (Ca^{2+}). TPK1 phosphorylation in the guard cell is mediated by KINASE 7 (KIN7) like receptors that regulates its transport from plasma membrane to the tonoplast in response to ABA (Gobert et al., 2007; Shabala & Pottosin, 2014; Shimazaki et al., 2007). Moreover, sufficient supply of K^+ derives assimilate transport into plant by maintaining a high photosynthesis rate. Regulation of photosynthesis light utilization is controlled by TPKs through ion counterbalancing and proton motive force (Kunz et al., 2014; Wang & Wu, 2015).

3.2 | K^+ transporters

In plants, KUP/HAK/KT transporters, expressed both in tonoplast and plasma membrane, participate in both low- and high-affinity potassium uptake to maintain K^+ homeostasis (Bañuelos et al., 2002). KUP/HAK/KT family mainly clustered into four different groups. Cluster I and II members mainly present in most of the plants (Shabala & Cuin, 2008). Cluster I possesses high affinity potassium during low K^+ availability and Cluster II facilitates potassium efflux from plants and localized in tonoplast of plant cell (Mäser et al., 2001). Evolutionary analysis of these plant transporters revealed their possible origin from streptophyte algae (Chen et al., 2017; Feng et al., 2020). For instance, the proton-driven H^+/K^+ co-transporter HAK5 is responsible for potassium uptake at external K^+ concentration below 0.01 mM as discussed in Figure 2, whereas, HAK5 and AKT1 both participate in potassium uptake is in between 0.01 and 0.05 mM (Grabov, 2007).

K^+/H^+ antiporters (also called Na^+/H^+ antiporters, NHXs) mediate secondary active transport across the membrane and derives by maintaining electrochemical difference in plant cells, acting as key regulators in osmotic adjustment of plant under stress conditions particularly salinity (Shabala et al., 2020). The regulation of NHXs on cell-specific activity of potassium by accumulating in root tissues and controls the salinity tolerance in plants (Shabala et al., 2016). It mainly mediates K^+ influx in exchange of H^+ efflux from vacuoles and

maintains intracellular pH of plants. Some of the studies also revealed that K^+/H^+ antiporters also help in maintaining ionic homeostasis in plants under saline conditions. Essential cellular processes like regulation of pH in organelles of the secretory pathway relies on the presence of K^+/H^+ antiporters using the readily available K^+ in vacuole (Bassil & Blumwald, 2014; Chen et al., 2007). Evolutionary analysis revealed that their origin found to be from chlorophyte algae and streptophyte algae (Cai et al., 2017). Further study confirmed that K^+/H^+ transporters translocate K^+ from root to shoot under low K^+ conditions.

HKT transporters are another type of high-affinity K^+ transporters and were first found in wheat. Proteins of HKT functions generally in alkali cation transport system and help in maintaining osmotic regulation in plants in response to salinity (Platten et al., 2006). In plants, Clade 1 HKTs (Figure 3) mediate the Na^+ transport and activates Na^+ selective transporters at both low and high availability of K^+ and Clade 2 HKTs are also selective for K^+ (Han et al., 2018; Mian et al., 2011). For instance, HKT1 in the root stele, results in the reduction of Na^+ and in the increase of K^+ concentration in the shoots of plants under salinity stress (Uozumi et al., 2000) and HKTs undergo depolarization of plasma membrane and activates K^+ efflux channels which in turn releases K^+ into the xylem (Chen et al., 2016).

However, studies on K^+ channels and transporters are still limited for vegetable crops, particularly in the context of protected cropping.

Regulatory role of HKT transporters in plants

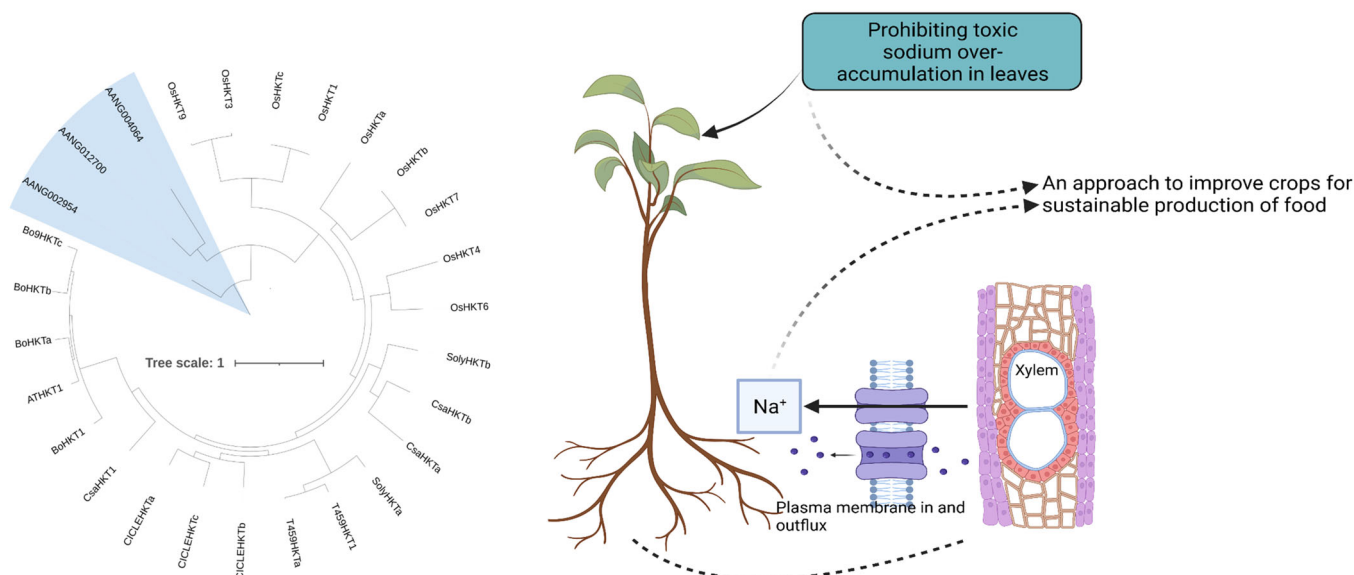


FIGURE 3 Function and phylogenetic analysis of HKT proteins in seven different species. By using protein sequences of seven different vegetable species phylogenetic tree was obtained by ClustalW multiple sequence alignment including different HKT groups. Genes included in HKT1 were found in *Arabidopsis thaliana*, *Capsicum annuum*, *Oryza sativa japonica* and *Brassica oleracea* and *Cucumis sativus* (ATHKT1, CsaHKT1, T459HKT1, BoHKT1 and OsHKT1). HKT 3, 4, 7, 6 and 9 were only found in *O. sativa japonica* (OSHKT3, OSHKT4, OSHKT7, OSHKT6 and OSHKT9) whereas HKT-like proteins were present in *Cucumis sativus*, *Capsicum annuum*, *Solanum lycopersicum*, *Oryza sativa japonica* and *Citrus clementina* (CsaHKTa, CsaHKTb, SolyHKTa, SolyHKTb, T459HKTa, OsHKTa, OsHKTb, CICLEHKTa, CICLEHKTb and CICLEHKTc), *Anthoceros angustus* (AANG002954 AANG004064 AANG012700 as the Outgroup). HKT transporters are selective mainly for Na^+ and protects the plant from stress by inhibiting excess accumulation of Na^+ in leaves.

Given the rapid advancement in protected cropping technologies, it is suggested that we should investigate the K^+ transport in greenhouse vegetables to understand their roles in K use efficiency, source-to-sink relationship, and fruit quality, contributing to the improvement of vegetables with better adaptation to protected cropping environment.

4 | OMICS PERSPECTIVE OF POTASSIUM USE EFFICIENCY IN PLANTS

4.1 | Transcriptomics perspective of potassium use efficiency in plants

Recent development and advancement in technology has developed greater insight towards high throughput sequencing, high-resolution mass spectrometry and different biological processing technologies to explore different cellular phenomena in plants (Chen et al., 2017; Zhang et al., 2022). Transcriptomics can improve our understanding on gene network that activates signalling transduction pathways (Kunz et al., 2014). Under potassium deficit conditions plants activates different calcium-binding proteins and their target kinases such as CBLs and CIPKs to regulate AKT1 in crops, which can be a good approach to improve K^+ transport efficiency for crop yield and quality (Chen et al., 2021). Ethylene is necessary for the formation of root systems. When plants are exposed to low- K^+ stress, both ethylene synthesis and transcription of ethylene-related genes enhances root hair elongation and primary root development. Ethylene signalling responds to low potassium with significant transcriptional changes and plays a positive role towards its uptake and regulation in root zone areas (Li et al., 2006). Some of the auxin transcriptional activators like ARF genes (auxin-responsive factor) controls low potassium-dependent lateral root development through auxin signalling (Shin et al., 2007). Moreover, sufficient K^+ reduces the accumulation of amino acid and lipid metabolic products by reducing lipid peroxidation. Adequate supply of K^+ promotes antioxidant-related transcript expression (e.g., genes associated with glutathione-S-transferase production becomes highly expressed), which activates the antioxidant defence system in plants (Zhang et al., 2021). In summary, there has been rapid advancement in transcriptome research in response to plant K^+ nutrition as it relates to global food security, especially when it comes to identifying traits more promptly.

4.2 | Proteomics perspective of potassium use efficiency in plants

Proteins are vital in response to abiotic stresses and such as low and high K^+ concentrations, involving in shaping the final phenotype of plant (Bazargani et al., 2011; Kamal et al., 2012; Rollins et al., 2013). Proteomics provide useful information in terms of protein functional groups participating in signalling, metabolism and stress response.

Potassium availability in plants leads modifications in synthesis and metabolism of proteins in response to its deficit and excess ratios (Kamal et al., 2012). Under optimum supply of K^+ , differentially expressed proteins include Ubiquinone-NADH dehydrogenase, mitochondrial dicarboxylate/tricarboxylate transporter, γ -aminobutyrate transaminase that are involved in controlling the cellular-like mitochondrial metabolism in plant (Ahmad & Maathuis, 2014). Recent studies revealed that increased K^+ content in leaves of plant is associated with increase in sucrose synthesis proteins like UDP-sugar pyro phosphorylase, HHL1 (hypersensitive to high light 1), NADPH quinone oxidoreductase (Amo et al., 2023). Low K^+ induces proteins like peptidases, ribosomal proteins, signal recognition particle proteins, chloroplast ribosome binding factor that are involved in secondary metabolism of plants (Cui et al., 2019). Activities of proteins like Rubisco, ATP synthase, Calvin cycle enzymes are significantly reduced when potassium availability is low (Alseekh & Fernie, 2018). Whereas lack of K^+ availability is linked with loss in ATP generation which reduces proteins of photosynthesis and photorespiration like glutamate glyoxylate, rubisco activase and sucrose phosphatase transketolase, thus halts growth of plants (Zeng et al., 2015) and Aconitase, cytochrome c oxidase, 3-isopropylmalate dehydratase inhibits mitochondrial metabolism in cotton (Zhang et al., 2021). In this regard, differential supply of potassium has significant impact on proteomics of plants. Thus, the contribution of proteomics to understand the crop complexity regarding different factors participating in plant growth will be a prospective in improvement of crop breeding programs as well.

4.3 | Metabolomics perspective of potassium use efficiency in plants

The important role of metabolites and the factors governing metabolic variations among plants provides an insight to understand plant physiology and biology for better crop improvement in terms of yield and quality (Hong et al., 2016; Nakabayashi & Saito, 2015; Shen et al., 2023). Proteomics and metabolomics are both based on three technologies: fractionation to simplify complex mixtures; mass spectrometry (MS) of individual peptides and metabolites for their identification and quantification and bioinformatics analyses of observed data to correlate with genomic or metabolite databases (Singh et al., 2016). By integrating metabolomics and proteomics, it is feasible to reveal the changes of metabolic and protein composition in a plant, tissue and/or cell that allow plants to exhibit phenotypic plasticity. For example, proteins associated with carbohydrate metabolism and proteins associated with carotenoid biosynthesis can be jointly analysed for better understanding of changes during plant development (Raza et al., 2022). In regard to past studies, it has been revealed that high and low efficiency of potassium utilization can have the direct impact on plant metabolites (Jo et al., 2022). It has been studied that high, low and medium concentrations of potassium affect biomass and yield of crops via some metabolic responses such as the low availability of potassium-affected glycolysis (de Bang

et al., 2021) and some catabolic processes to increase of polyamines like putrescine (Armengaud et al., 2009). Amino acid and nucleotide metabolism are also closely connected with plant stress tolerance (Shen et al., 2017). However, under reduce K^+ the modifications in amino acid metabolism leads to decrease in some of the essential amino acids like asparagine and serine (Zhang et al., 2022), which also affected the accumulation of certain organic acids (Serra et al., 2015). Therefore, metabolomics study is providing mechanisms and characteristics of different metabolites thereby establishing a direct link between plant phenotype and genotype so that multi-omics data can be fully and efficiently used in crop improvement.

4.4 | Ionic perspective of potassium use efficiency in plants

The distribution and transport of different elements mediated by xylem and phloem transportation system known to have dependency between each of them in relation to growth of plant (Du et al., 2020; Salt et al., 2008; Watanabe et al., 2016). Ionomics, or the study of the ionome, entails quantitative and simultaneous evaluation of the elemental composition as well as changes in this composition in response to physiological stimuli, developmental status and genetic alterations in plants (Ali et al., 2021). The fruit/leaf ratio for the concentration of each element may reflect its mobility in the phloem and the efficiency of xylem transport of the element into the fruit. In line with this high amount of K^+ participates in regulating ionic balance in leaf tissue by being ionically associated with organic anions (i.e., malate, malonate and aspartate) (Singh et al., 2013). Ionic profiling revealed that B (Boron) and Zn (Zinc) participates in stomatal opening whereas Mn (Manganese) and Cd (Cadmium) helps in its closure (Cui et al., 2019). Ionic study on wheat under salinity stress unveil that for maintaining Na/K^+ ratio at K^+ accumulation, Ca^{2+} mediates its role to reduce any stress-induced injury (Watanabe et al., 2022). K^+ deficiency in plants causes oxidative stress, leading up in over-reduction of the photosynthetic electron transport chain and high accumulation of cations (Zeng et al., 2015). K^+ deficiency rises the expression of HAK5, this transporter of potassium also transports Ca^{2+} with itself efficiently and regulates pH and homeostasis (Du et al., 2020). Low K^+ supply in plants also coordinates with Mg due to their functional similarity in translocating the ions towards root zone, osmoregulation and enzyme activation (Cotrim, 2022). Furthermore, research regarding ionic response in relation to Low K^+ stress in wheat revealed that Ca (calcium), Mg (magnesium) and Na (sodium) contents increases significantly in the shoot and root tissues (Xiao-Li et al., 2008). These findings indicated that these cations substitute K^+ to carry out specific physiological and metabolic functions in plants under low K^+ situations (Ma et al., 2012). In broader sense ionomics is an approach of quantifying elemental changes, influencing genetic, metabolic and developmental changes in plant tissue or target organs.

4.5 | Integration of omics profiling for potassium use efficiency in plants

The strategies of integrating metabolomics, transcriptomics proteomics and ionomics are to gain better understanding of the links between plant performance and molecular regulators (genes, proteins, ions and metabolites) that holds pivotal roles in plant biology. Therefore, multi-omics approaches provide an insight into such complex and intricate processes when plants are under different environmental stresses (Xiao et al., 2021). Therefore, ionomics and transcriptomics could be an important research approach to understand element-gene and element-environment relationship of physiological and biochemical function of certain genes associated with K^+ (Raza et al., 2022). Furthermore, by integrating metabolomics and transcriptomics, we can also reveal the relationship between genotype and phenotype of an organism, by unveiling the role of essential genes participating in specific metabolic pathways regulated by K^+ (Deshmukh et al., 2014). Some studies revealed the response of different Differentially expressed genes (DEGs) and metabolites in wheat under low K^+ (potassium) conditions. Genes like *TraesCS4B02G047400* and *TraesCS4A02G063800* encoding for glutamine synthetase (GS) regulate glutamate metabolism in plants (Ma et al., 2012; Xiao-Li et al., 2008; Zhao et al., 2020). Identification of candidate genes of K^+ transporters with their associated proteins and metabolites will provide an interesting approach to understand the plant response and its integrated mechanisms for crop improvement in terms of yield and quality in protected cropping.

5 | CONCLUSIONS

Some of the future crop improvement targets are shifting towards plant species and varieties that require low nutrient inputs and are resilient to stresses as well as adaptation to greenhouse and indoor cropping systems. This shift in plant breeding is due to the side effects of extensive fertilizer use and its high cost and the increasing impact from climate change. As a result, a comprehensive understanding of how K^+ is retained and better utilised in plants and the mechanisms involved in K^+ transport will be achieved via the multidisciplinary approaches. The new knowledge of K^+ transport system and its efficient use in agriculture will help researchers to proceed translational research like molecular breeding and genome editing to feasibly develop K^+ efficient crops. This potential translational research will help farmers to transfer alleles of interest, to crops of interest, thus allowing sustainable recirculation system of nutrients for the crop growth. This will also create new genotypes growing under protected cropping in nutrient efficient manner for better yield, quality and economic benefits to growers and consumers in the future.

AUTHOR CONTRIBUTIONS

Sonali: Conceptualization; writing—original draft; visualization. **Samsul Huda:** Writing—review and editing, funding acquisition. **Vijay**

Jayasena: Writing—review and editing; supervision. **Talaat Ahmed:** Writing—review and editing. **Zhong-Hua Chen:** Conceptualization; writing—original draft, review and editing; funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

This is a review article that does not contain any new data.

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Not applicable.

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