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REVIEW

Impact of potassium starvation on the uptake, transportation, photosynthesis, and abiotic stress tolerance

Havza Imtiaz[1] · **Anayat Rasool Mir**[1] · **Francisco J. Corpas**[2] · **Shamsul Hayat**[1]

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Abstract

Potassium (K^+) plays a crucial role in plant homeostasis, and its deficiency significantly impacts photosynthesis, triggering a decrease in growth and crop production. K^+ starvation induced a significant reduction in the net photosynthetic rate, and the drop is associated with resistance of CO_2 diffusion through stomatal conductance, mesophyll conductance, and lowered carboxylase activity of Rubisco, electron transport rate of PSII, and with many biochemical limitations. The complex interaction of all the above factors contributed to limiting photosynthesis under K^+ starved conditions. Low chlorophyll content and poor chloroplast structure may also define photosynthetic processes and causes a decrease in crop growth and productivity under K^+ starvation. Under abiotic stresses such as drought, waterlogging, temperature, salinity, and heavy metal, the application of exogenous K^+ promotes plant tolerance by activating the antioxidant system, which limits the overproduction of reactive oxygen species (ROS), avoiding the associated oxidative damages where other signaling molecules such as nitric oxide (NO) and hydrogen sulfide (H_2S) may involve. The review highlights the decisive role of exogenous and endogenous K^+ in modulating diverse physiological and biochemical processes in a healthy and stressful environment. Furthermore, this review appraises the involvement of K^+ with another signaling molecule in enhancing abiotic stress tolerance in plants. Therefore, this review provides a comprehensive update on the relevance of K^+ in higher plants. Its exogenous application should be a potential tool, especially in crops under adverse environmental conditions.

Keywords Antioxidant · Gasotransmitters · Photosynthesis · Rhizosphere · Oxidative stress

Introduction

Potassium is an essential macronutrient and the most abundant cation in plant cells (Pettigrew 2008; Singh and Reddy 2017). It is only found in its ionic form (K^+) or in weak complexes from which it can be easily exchanged (Marschner 2012). 2.1–2.3% of the earth's crust accounts for potassium; nonetheless, the fraction of soil K^+ available to plants is only 0.1–0.2% (Britzke et al. 2012; Wedepohl 1995), and the availability of K^+ from soil depends on edaphic and some other factors with the capability of plants to take up K^+ (Chérel et al. 2014; Hasanuzzaman et al. 2018; Sardans and Peñuelas 2021). K^+ uptake from root cells and its mobilization into distinct cellular compartments and organs is facilitated by transporters and channels (Ve'ry et al. 2014; Wang and Wu 2015; Raddatz et al. 2020; Lhamo et al. 2021). K^+ in plant cells is carried out by a variety of transporter proteins classified into several families with different structures and transport mechanisms, including channels families such as voltage-dependent shaker-like channels, the tandem-pore (TPK) and two-pore channels (TPC) (Hedrich 2012), and the carrier-like families KT/HAK/KUP (Nieves- Cordones et al. 2014a; Li et al. 2018) HKT uniporters and symporters (Hamamoto et al. 2015), and cation-proton antiporters (CPA).

K^+ participates in many physiological processes, viz., photosynthesis and respiration, enzyme activities, water relations, electrical neutralization, assimilate transport,

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✉ Shamsul Hayat
hayat_68@yahoo.co.in

[1] Plant Physiology Section, Department of Botany, Faculty of Life Sciences, Aligarh Muslim University, Aligarh 202002, India

[2] Group of Antioxidants, Free Radicals, and Nitric Oxide in Biotechnology, Food and Agriculture, Department of Stress, Development and Signaling in Plants, Estación Experimental del Zaidín, Spanish National Research Council (CSIC), 18008 Granada, Spain

osmoregulation, turgor pressure, protein synthesis, ion homeostasis, anion-cation balance, energy transfer, and utilization (Weng et al. 2007; Maathuis 2009; Zou et al. 2011; Houmani and Corpas 2016; Wang and Wu 2017; Ragel et al. 2019; Srivastava et al. 2020; Cui and Tcherkez 2021; Sardans and Peñuelas 2021; Houmani et al. 2022). Furthermore, K^+ indirectly affects plant growth and development (Lu 2016c). All these events can be disrupted by K^+ deficiency which is a type of plant abiotic stress that induces a wide range of responses, including oxidative stress, and results in limited crop growth and productivity (Hafsi et al. 2014; Waqas et al. 2021; Houmani et al. 2022; Johnson et al. 2022). K^+ starvation makes various responses at different stages, viz., morphological, physiological, biochemical, and molecular (Hafsi et al. 2014). K^+ deficiency, also called potash deficiency, leads to decreased chlorophyll content, reducing photosynthetic activity and thus minimizing overall agricultural productivity (Hartt 1969; Pier and Berkowitz 1987; Zhao et al. 2001). Visible symptoms of K^+ deficiency take a long time for expression (Kanai et al. 2011); plant growth is reduced and ceases (Mengel and Kirkby 1987). The first noticeable symptom of K^+ deficiency is mottled or marginal chlorosis which later develops into necrosis primarily at the leaf tips, margins, and between veins. Still, in several monocotyledonous plants, these necrotic lesions first form at the leaf tips and margins and then extend towards the leaf base. These symptoms first appear on mature leaves at the bottom of a plant due to mobilization of K^+ to younger leaves. Stems may be slender, weak, and abnormal short internodal regions of K^+ deficient plants (Taiz et al. 2015). Photosynthesis is influenced by K^+ deficiency in several ways and affects fruit quality and yield (Kumar et al. 2006; Shen et al. 2017; Zhang et al. 2017a, b).

K^+ plays a prominent role in alleviating abiotic stresses, which may have associated with oxidative stress (Trono et al. 2015; Hasanuzzaman et al. 2018; Kumari et al. 2021; Houmani et al. 2022). Plants have evolved strategies to increase K^+ uptake while maintaining ROS homeostasis in response to low K^+ availability. Nicotinamide adenine dinucleotide phosphate oxidase RHD2/RbohC produces H_2O_2, a ROS that regulates K^+ transporters, particularly the high-affinity potassium transporter HAK5, which is induced under these conditions. Thus, ROS plays an essential role in generating K^+ starvation responses at the root level by regulating the expression of the AtHAK5 gene, which encodes a high-affinity K^+ transporter that is activated in response to low K^+ supply (Kim et al. 2010). During the inadequate K^+ response, the member of the type III peroxidase family RCI3 (rare cold-inducible gene 3) also contributes to ROS production (Kim et al. 2010). Furthermore, ROS directly activates the K^+ channels AtGORK and AtSKOR, which are involved in K^+ efflux from cells during stress (Demidchik et al. 2010; GarciaMata et al. 2010; Demidchik 2018). Potassium starvation causes oxidative stress that increases antioxidant and NADPH-generating systems, thus allowing the halophytes to survive (Houmani et al. 2022). Thus, K^+ emerged as a potential anti-stressor molecule due to its protective functions under different plant abiotic stress, viz., salt, drought, temperature, and heavy metal.

The present review focuses on the efficient role of K^+ in improving chlorophyll content, net photosynthetic rate, chloroplast morphology, and ultrastructure. An attempt has been made to cover the contribution of K^+ in increasing enzymatic antioxidant machinery such as catalase (CAT), peroxidase (POX), superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR) in reducing ROS and MDA content and maintaining osmotic content. The current review also highlights the influential role of K^+ in mitigating environmental stresses like salinity, drought, waterlogging, temperature, and heavy metal stress with the help of several signaling molecules. Considering the recent reviews focused on K^+ transporters and channels (Santa-María et al. 2018; Jegla et al. 2018; Ali et al. 2021; Lhamo et al. 2021; Dave et al. 2022), the present assessment will be focused on K^+ deficiency and its effect on photosynthesis and ROS metabolism, and highlighting its possible connections with other signaling molecules such as NO and H_2S.

Potassium in the rhizosphere

In the lithosphere, K^+ is the fourth most abundant element; nonetheless, a low proportion is available for plants (Mengel and Kirkby 1982). Four distinct pools of K^+ in soil: (i) ionic form in soil solution (0.1–0.2%); (ii) exchangeable or readily available (1–2%); (iii) non-exchangeable, slowly available or fixed (fixed in 2:1 clays 1–10%); and, (iv) unavailable or structural (96–99%) (Fig. 1) (Sparks 1987). The first two pools of K^+ are reversible and known to meet the instantaneous demand of growing plants, while the last two are irreversible and known for the long-term supply of K^+ to plants (Askegaard et al. 2003). When the availability of K^+ is low in the soil, the ionic form is the source used by the roots to provide the needs of K^+ for plant growth as well as its replenishment when the soil is deficient in K^+ that is in equilibrium between the interchangeable and non-interchangeable (Hinsinger et al. 2021). Leaching is one of the factors responsible for the K^+ depletion from the reversible pool; therefore, the application of K^+ fertilizer will raise the K^+ availability for plants (Sparks and Huang 1985; Mouhamad et al. 2016). A major portion of K^+ in the soil is in mineral pools such as muscovite, biotite, or feldspars, which are released over a long time due to weathering or breaking down that refills the exchangeable and fixed pool (Römheld and Kirkby 2010; Mouhamad et al. 2016). The exchangeable or readily available K^+ is the fraction of the K^+

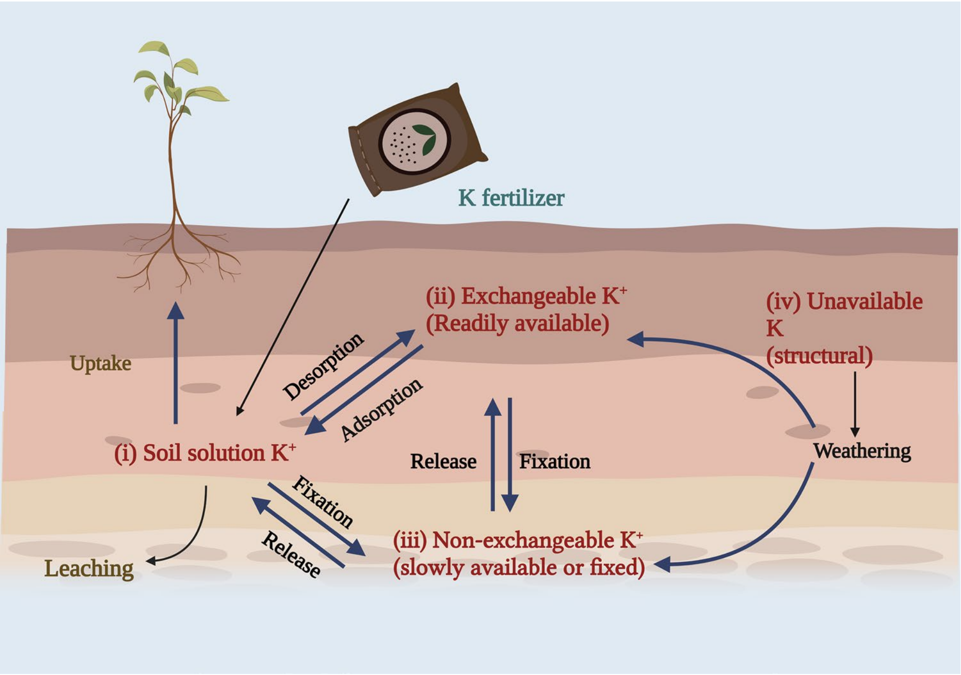

Fig. 1 Interrelationship of various forms of soil K$^+$ (modified from Sparks 1987) which includes (i) ionic form in soil solution (0.1–0.2%); (ii) exchangeable or readily available (1–2%); (iii) non-exchangeable, slowly available or fixed (fixed in 2:1 clays 1–10%); and, (iv) unavailable or structural (96–99%)

that is surface-adsorbed on negatively charged sites of clay minerals and organic matter and in a rapid equilibrium to soil solution (Sardans and Peñuelas 2015). A minor amount of K$^+$ is found in organic matter because it is not a component of biomolecules, thus rapidly and simply leached from leaves because of its high solubility. Hence low fraction of K$^+$ is directly available to plants (Wang et al. 2010a, b; Britzke et al. 2012). Non-exchangeable pool slowly released K$^+$ from the wedge zones of weathered micas and vermiculites when the level of soil solution and readily available K$^+$ decrease by crop removal and leaching (Sparks et al. 1980; Sparks 2000; Mengel and Kirkby 2001). The sequence of availability of K$^+$ for plant uptake and microorganisms is soil solution > readily available (exchangeable) > slowly available (fixed or non-exchangeable) > unavailable (minerals) (Sparks and Huang 1985; Sparks 1987, 2000) (Fig. 1).

K$^+$ uptake and transportation within the plant

To facilitate the uptake and transportation of K$^+$ to different cellular compartments, multiple K$^+$ channels and transporters are found mainly in the cell membrane of plant root cells (Ashley et al. 2006; Coskun et al. 2014). Two discrete kinetic systems accomplished the task of K$^+$ uptake via roots depending on affinity for K$^+$ that switch according to the availability of external K$^+$ i.e. Soil (Epstein et al. 1963): (i) High-affinity system (transporters) activated at the lower level of K$^+$ concentration (<0.2 mmol/L); and (ii) Low-affinity system (channels) activated at a higher level of external K$^+$ concentration (>0.3 mmol/L).

K$^+$ channels comprise three different classes based on their structural characteristics: (i) Shaker-type channels (voltage-dependent); (ii) Two pore channels (TPC); and (iii) Cyclic nucleotide-gated channels (reviewed by Ashley et al. 2006). Shaker-type K$^+$ channels are also classified as (i) Inward rectifying K$^+$ channels, (ii) Outward-rectifying K$^+$ channels, and (iii) Weakly rectifying channels (Lefoulon 2021; Wang and Wu 2013).

K$^+$ transporters include three distinct classes: (i) K$^+$ uptake permease (KT/HAK/KUP); (ii) High-affinity K$^+$ transporter (HKT); (iii) Cation-proton antiporter (CPA) families (Gierth and Mäser 2007; Nieves-Cordones et al. 2014; Ve'ry et al. 2014; Li et al. 2018). The first functionally characterized K$^+$ channels in plants belongings to the Shaker family were the Arabidopsis K$^+$ transporter 1 (AtAKT1) and the K$^+$ channel 1 (AtKC1). They interact to form a heteromeric K$^+$ channel that regulates the AtAKT1 activity, thus preventing K$^+$ leakage under low K$^+$ concentration in root cells (Reintanz et al. 2002; Duby et al. 2008; Geiger et al. 2009; Honsbein et al. 2009; Wang et al. 2010a, b, 2016). Under low K$^+$ concentration, two high K$^+$ affinity root proteins (AKT1and HAK5) mediate the sufficient K$^+$ uptake to support plant growth (Pyo et al. 2010). The transcription level of the *HAK* gene was upregulated in low K$^+$ content (Santa-Maria et al. 1997; Armengaud et al. 2004; Shin and Schachtman 2004; Gierth et al. 2005; Jung et al. 2009; Li et al. 2018), while AtKUP7 participated in K$^+$ uptake in low to moderate external K$^+$ content (~ 0.1 mmol/L) with the effect in translocation from root to shoot (Han et al. 2016).

For long-distance transport, after K^+ absorption into the root cells, K^+ is transported to root stele tissues and then transported to shoots through xylem vessels. The Stelar K^+ Outward Rectifier (SKOR) member of Shaker type outward rectifying K^+ channel in stele tissues mediates K^+ translocation from root parenchyma cells to xylem sap for K^+ transport to shoots (Gaymard et al. 1998; Liu et al. 2006). On the other hand, stomatal movement depends on the K^+ content in the guard cells; thus, the guard cells outward rectifying K^+ channel (GORK) regulates K^+ efflux via membrane depolarization to close the stomata (Ache et al. 2000; Becker et al. 2003; Adem et al. 2020), whereas KAT1 and KAT2 inward channels allow the K^+ influx via membrane hyperpolarization into the guard cell to open the stomata (Schachtman et al. 1992; Pilot et al. 2001; Hosey et al. 2003). The vacuole act as a reservoir of K^+ ions in plant cells, and under K^+ starvation, the ions translocate to the cytoplasm to sustain the K^+ content of the cytoplasm (Walker et al. 1996). To maintain homeostasis, K^+ translocates between the vacuole and cytoplasm; the AtTPK1 channel found in the tonoplast facilitates the K^+ transport necessary for several physiological processes like stomatal movement and seed germination (Czempinski et al. 2002; Gobert et al. 2007). Moreover, tonoplast NHX transporters (AtNHX1 and AtNHX2) act as $Na^+(K^+)/H^+$ antiporters and facilitate K^+ uptake into the vacuole, thus maintaining the K^+ vacuolar pool (Venema et al. 2002; Apse et al. 2003; Bassil et al. 2011; Barragan et al. 2012; Andres et al. 2014). Owing to its high mobile nature, K^+ recirculates between roots and shoots through the xylem and phloem (Ahmad and Maathuis 2014). Plant tissues load the K^+ to phloem with the availability of a sufficient amount of ATP to reach a notable concentration, and K^+ comes to the requiring organs with the flow of sap while it can also return to roots (Jeschke et al. 1985; Dreyer and Blatt 2009). AKT2 inward rectifying channel, another member of the shaker family mainly found in the phloem of both leaves and roots (Deeken et al. 2000; Lacombe et al. 2000b) plays two significant roles in loading of K^+ in source tissues and sink organs, respectively (Gajdanowicz et al. 2011). At the subcellular level, the K^+ Efflux Antiporter (KEA) protein group participates in its homeostasis. In *Arabidopsis*, two KEA subgroups, KEA1-3, are associated with plastid, and KEA4-6 seems to be connected with the endomembrane system (Tsujii et al. 2019; Wang et al. 2019; DeTar et al. 2021). The main K^+ channels and transporters are given in Table 1.

Table 1 General classification of plant K^+ channels and transporters

K^+channels
Shaker-type channels (voltage-dependent)
Inward rectifying K^+ channels
Outward-rectifying K^+ channels
Weakly rectifying channels
Two pore channels (TPC)
Cyclic nucleotide-gated channels
K^+transporters
K^+ uptake permease (KT/HAK/KUP)
High-affinity K^+ transporter (HKT)
Cation-proton antiporter (CPA) family:
CAP 1: Plasma membrane-bound NHX (sodium proton exchanger) and intracellular NHX
CAP2: K^+ Efflux Antiporter (KEA) and cation/H + exchanger (CHX) subfamilies

Impact of potassium on photosynthesis

K^+ affects photosynthesis at various levels and influences various physiological processes, plant metabolism, and osmotic adjustments (Severtson et al. 2016). Under different levels of K^+ photosynthetic capability (Bednarz et al. 1998; Zhao et al. 2001; Basile et al. 2003; Weng et al. 2007; Gerardeaux et al. 2009), physiological and biochemical characteristics of the plants are different (Chartzoulakis et al. 2006). Effects of K^+ starvation on the plant's photosynthetic features are described in Fig. 2.

Chlorophyll

Chlorophyll (Chl) is a light-absorbing green pigment in the chloroplast that converts light to chemical energy in plants (Kalaji et al. 2017). Under K^+ starvation, chlorophyll synthesis is inhibited in *Eucalyptus grandis* (Battie-Laclau et al. 2014). Leaf chlorosis is an early symptom of chlorophyll degradation due to oxidative stress of excessive production of ROS in K^+ deficiency (Cakmak 2005; Lu et al. 2019). Lower chlorophyll content and Chl. a/b ratio is the stress symptoms of chloroplast (Jia et al. 2008), changes in morphology and anatomy of chloroplast were associated with chlorophyll content and photosynthesis capability (Tian et al. 2008; Lu et al. 2019), chlorophyll composition change in low K^+ stress affects the photosynthesis (Jia et al. 2008). Chlorophyll fluorescence gives accurate information about the condition of photosynthetic machinery and mainly of PSII (Sun et al. 2015). Potential quantum efficiency (Fv/Fm), quantum yield of photosystem II (ΦPSII), photochemical quenching (qP), and electron transport rate (ETR) were markedly reduced under K^+ deficiency in *Zea mays* L. (Qi et al. 2019). It has been reported in several studies that total chlorophyll concentration is reduced under K^+ starvation (Bednarz and Oosterhuis 1999; Zhao et al. 2001; Lu et al. 2016b), and the chlorophyll concentration are directly related to photosynthesis (Battie-Laclau et al. 2014). The effect of K^+ starvation on chlorophyll is also presented in Table 2.

Fig. 2 Summary of the main effects on photosynthesis trigger by K^+ starvation. ↑increase and ↓decrease

Chloroplast morphology and ultrastructure

Stabilized morphology and structure of chloroplast contribute resistance to severe impacts of K^+ deficiency stress (Jia et al. 2008; Shao et al. 2016), while changes in morphology and structure are notably associated with chlorophyll content and photosynthetic capacity (Tian et al. 2008; Lu et al. 2019). K^+ facilities the correct organization of grana and stroma lamellae; however, under K^+ deficiency, the ultrastructure is disorganized, and the chloroplast lamella is lopsided, limp, and partly dispersed in the cytoplasm that, triggers a reduction in the number of grana and lamellae (Zhao et al. 2001; Jia et al. 2008). In maize, K deficiency causes a reduction in the number of chloroplasts, which take on an irregular shape, as the outer surface changes from long and oval to elliptical or almost round, thus reducing the length/width ratio. In the corn inbred line 90-21-3, the outer membrane and thylakoids remain the same; the plastoglobule content increases and is swollen. On the other hand, in the inbred line D937, the ultrastructure of chloroplasts was severely damaged with irregular shape and significantly aggregated. At the same time, the swollen plastoglobules and lamellae structure were not typical and mainly scattered in the cytoplasm under K starvation (Qi et al. 2019). In the genotype of *Ipomoea batatas*, leaves showed big starch granules, broken and indistinguishable chloroplast membrane,

Table 2 Impact of K^+ starvation on chlorophyll

Plant species	K^+Concentration	Impact	References
Solanum lycopersicum	155, 232, 310 ppm with 25 µM Cd stress	Reduced chlorophyll content index (CCI)	Naciri et al. (2021)
Vitis vinifera cvs.	K^+deficient	Decreased chlorophyll index, chlorophyll fluorescence, and electron transport	Rogiers et al. (2020)
Triticum aestivum L.	0.02 mM KCl	Inhibited biosynthesis of Chl a and b upto 14.3–20.0%, affected the total content of chlorophyll	Thornburg et al. (2020)
Zea mays L.	K^+deficient	Reduced chlorophyll mainly Chl a	Qi et al. (2019)
Zea mays L.	K^+ deprivation	Reduced 74% chlorophyll	Sitko et al. (2019)
Glycine max L.	0.02 mM (severe) and 0.5 mM (moderate), eCO_2– 800 µmol mol^{-1}	Reduced 80% and ≈25% total chlorophyll at severe K^+ deficiency and moderate K^+ deficiency with eCO_2	Singh and Reddy (2018)
Zea mays L.	0.000, 0.625, 1.250, 2.500 mmol/L	Alleviated Chl a, b, (a + b)	Zhao et al. (2016)
Brassica juncea L.	K^+deficient	Lowered amount of photosynthetic pigments (Chl a,b, and total Chlorophyll)	Ahmad et al. (2014)
Prunella vulgaris L.	0, 1.00, 6.00 and 40.00 mM KCl	Lowest and highest chlorophyll content at 0 and 6.00 mM, respectively, and again dropped at 40.00 mM	Chen et al. (2013)
Carya cathayensis Sarg.	0, 0.4, 1.0, 2.0 and 5.0 mM K^+	Decreased total chlorophyll content but increased Chl a/b ratio at 0 mM	Jin et al. (2011)
Oryza sativa	5 mg K^+ L^{-1}	Reduced 101% Chl a/b ratio and changed chlorophyll composition	Jia et al. (2008)
Zea mays L.	K^+deficient	Increased time and rate of formation and conversion of protochlorophyll and protochlorophyll to chlorophyll, respectively	Lawanson et al. (1977)

grana lamellae limped and distorted, and acute damage in chloroplast ultrastructure under K^+ stress (Tang et al. 2015). In another similar study, the chloroplast blade swelled and acquired a ball shape within lots of starch granules under K^+ deficiency (Wang et al. 2018). However, a slight difference in chloroplast morphology has been observed in *Brassica napus* (Hu et al. 2020). In *Gossypium hirsutum* leaves, poor chloroplast ultrastructure with large starch granules, more and expanded plastoglobuli, little grana, and the thylakoids propels towards periphery likely be the reason for low leaf P_N under low K^+ stress (Zhao et al. 2001).

Net photosynthetic rate

Net photosynthetic rate (P_N) and photosynthetic plant area are the two vital features on which the photosynthetic plant capacity depends. For the enhancement of P_N, researchers have been working to increase the potential of yield (Zhu et al. 2004; von Caemmerer et al. 2012; South et al. 2019) and higher P_N related to higher biomass (Wang et al. 2012). According to several reports, a decline in the rate of photosynthesis is due to a reduction of chlorophyll content, hindrance in PSII activity, and electron transport (non-stomatal) in K^+ deficient plants such as Chinese hickory, cotton, almond tree, and lettuce (Basile et al. 2003; Jin et al. 2011; Wang et al. 2012; Zhang et al. 2017a, b). Table 3 also includes the effects of potassium starvation on the P_N.

Limitations in CO_2 diffusion during photosynthesis

Three major resistances attributed to decrease net CO_2 during photosynthesis under K^+ starvation are (i) reduced stomatal conductance, (ii) reduced mesophyll conductance, and (iii) biochemical limitations.

Stomatal conductance (g_s)

In the stomatal opening, K^+ influx in guard cells is a crucial light-dependent step (Shabala 2003; Inoue et al. 2020), influencing stomatal conductance. It is well documented that the stomatal limitation is associated with K^+ concentrations and the stomatal closure under K^+ starvation and is often considered the main reason behind the reduction of net P_N (Thiel and Wolf 1997; Römheld and Kirkby 2010). Restricted CO_2 diffusion through the stomata and mesophyll cells (stomatal conductance and mesophyll conductance) decreased the carboxylation ability, chlorophyll biosynthesis, and assimilate transport (Singh and Reddy 2017). Compared to mesophyll, the photosynthetic rate is generally limited due to stomatal conductance (g_s) (Jin et al. 2011). Under K^+ starvation, the decrease of g_s coincided with the decline in T and C*i* in soybean (Singh and Reddy 2017). Still, in *Ipomoea batatas* (Tang et al. 2015) and *Eustoma grandiflorum* (Chen et al. 2018), the reduction of g_s, P_N, and T_r is accompanied by no significant change $_{in}$ C*i*. However, a decrease in g_s was

Table 3 Impact of K^+ starvation on the net photosynthetic rate of plants

Plant species	Assayed K^+ concentration	Effect on net photosynthetic rate (P_N)	References
Glycine max L.	K_2SO_4 0 kg ha^{-1} (K0) and K_2SO_4 120 kg ha^{-1} (K120).	P_N alleviated 6.1 ~ 6.9% and 10.9 ~ 15.7% in higher and lower efficiency genotypes, respectively.	Liu et al. (2021)
Nicotiana tabacum	5 mmol L^{-1} and 0.5 K^+ mmol L^{-1}	Combination of grafting under both the treatments reduced the P_N while the *Ci* increases significantly	Hu et al. (2021)
Lactuca sativa L.	LKEC (Na replaced K^+) and LKQM (not replaced Na with K^+)	No change in P_N noticed	Xu et al. (2021)
Raphanus sativus var. *sativus*	K^+ deficient	Alleviated P_N net photosynthetic rate in Suntella F1 cultivar while in Fluo P_N remain maintained	Kusaka et al. (2021)
Brassica napus L.	0 kg K_2O ha^{-1} (K0), 60 kg K_2O ha^{-1} (K60) and 120 kg K_2O ha^{-1} (K120)	Photosynthetic rate highly reduced in lower leaves in compared to middle and upper leaves among K^+ treatments	Hu et al. (2020)
Zea mays L.	K^+ deficient	Higher P_N in K^+-tolerant inbred line and lowered in K-sensitive inbred line	Qi et al. (2019)
Zea mays L. cv.	K^+ deprived nutrient solution	Photosynthetic rate 11% reduced to control, lowest decrease with comparison to other macronutrients deficiency	Sitko et al. (2019)
Eustoma grandiflorum (Raf.) Shin	K^+ deficient nutrient solution comprised –N, –P, –K, –Ca, and –Mg in 1/2 strength of modified Johnson's solution	Decreased P_N	Chen et al. (2018)
Ipomoea batatas L.	0.03 mM for the K^+ deficient and 2.5 mM for the K^+ sufficient treatments	P_N significantly reduced across sweet potato genotypes	Wang et al. (2018)
Brassica napus L.	K^+ deprived	Reduced photosynthetic rate	Lu et al. (2018)
Brassica napus L.	– K (not any fertilizer) and + K (120 kg K_2O ha^{-1}	Only 56.9% of net photosynthesis in – K^+ deficient to + K^+ treatment	Lu et al. (2016a, b, c)
Brassica napus L.	Severe K^+ stress, K^+ treatments like 0 kg K_2O ha^{-1}(K0), 30 kg K_2O ha^{-1} (K30), 60 kg K_2O ha^{-1} (K60) and 120 kg K_2O ha^{-1} (K120).	Slightly decreased rate of photosynthesis under K^+ stress, K^+ supplementation enhanced the mean value 38.8 of H9, while in Z11 it is more enhanced 69.4 in K120 treatment	Lu et al. (2016a, b, c)
Ipomoea batatas [L.] Lam.	Extreme and moderate K^+ deficiency	Reduced P_N in sweet potato cultivars	Tang et al. (2015)
Glycine max (L.) Merr.	0.5 mmol L^{-1} (– K) and 2.5 mmol L^{-1} (control) using KNO_3.	P_N decreased in two varieties, in GD8521 28.7% of decrease while in Tiefeng 40 only 18.2% decrease compared to control	Wang et al. (2015)
Prunella vulgaris L.	0, 1.00, 6.00 and 40.00 mM KCl	Higher P_N at 6.00 mM KCl supplementation, while lowered at all other concentrations	Chen et al. (2013)
Houttuynia cordata Thunb.	0, 1.28, 2.56, 5.31 and 10.26 mM K^+	Alleviated P_N at all treatments, while maximized at 1.28mM K^+	Xu et al. (2011)
Lycopersicon esculentum L. cv. Momotarou	K^+ deficient nutrient medium	Apparent photosynthetic rate (P_0) of the 5th leaf decreased but the rate did not change in younger leaves under K^+deficiency	Kanai et al. (2011)
Gossypium hirsutum L.	K^+ deficient	Only 23% of P_N	Zhao et al. (2001)

accompanied by the increase of C*i* in maize (Qi et al. 2019), cotton (Zhao et al. 2001) constant or enhanced *Ci* in hickory seedlings which might be caused by high mesophyll limitations or low capability of the CO_2 fixation cycle, rather than to stomatal resistance (Jin et al. 2011). Similar findings had been seen in *Prunus dulcis*, *Gossypium hirsutum* L. where stomatal conductance was not the main reason for low $P_{N,}$ and it was reduced via biochemical limitations, little Chl content, poor chloroplast ultrastructure, and restricted saccharide translocation under potassium starvation (Zhao et al. 2001; Basile et al. 2003). The Ji22 genotype of *Ipomoea batatas* L. plants under K^+ deficiency showed a low level of P_N, E, $g_{s,}$ and terrible damage to chloroplast ultrastructure in leaf, suggesting that this genotype faced both photoinhibition and stomatal limitations (Wang et al. 2018). In contrast, an enhancement in the stomatal conductance under moderate K^+ deficiency in a well-irrigated and water-stressed condition may be attributable to dehydration mainly in water-stressed plants, which ultimately leads to impairment of stomatal closure regulation in *Olea europaea* L. (Arquero et al. 2006). In mild K^+ deficiency, stomatal conductance was the main factor contributing to net photosynthesis change. As the K + deficit became more severe biochemical limitations also contributed to stomatal regulations in the cotton (*Gossypium hirsutum* L., cv. Deltapine) plant (Bednarz et al. 1998). There is no significant change in transpiration rate and stomatal conductance with a decrease in chlorophyll content and enhanced anthocyanin pigment under K^+ deprivation in maize plants. Mg deficiency strongly limits the photosynthetic and transpiration rates, stomatal conductance, photosystem II (PSII) performance, chlorophyll, and flavonol content with concomitantly enhanced anthocyanin content. Furthermore, Ca^{2+} deficiency also alleviated the rate of photosynthesis and transpiration, stomatal conductance, and PSII activity, whereas the pigment content was not considerably different compared with the control (Sitko et al. 2019). The primary cause of lower photosynthesis in K^+ starved plants is a subject of debate due to contrasting observations between the plant species.

Mesophyll conductance (g_m)

CO_2 dissolves in the cell walls apoplastic water after diffusion via mesophyll cells' leaf internal air space. Once the CO_2 enters the liquid phase, it is found either as dissolved CO_2 or HCO_3 and further diffuses via the pores of the cell wall, the plasma membrane, the cytosol, the chloroplast envelope and finally reaches the chloroplast stroma, where enzymatic CO_2 fixation took place (Tränkner et al. 2018). Moreover, it is reported that under low K^+ liquid-phase pathways, conductance decreased by reducing the chloroplast exposed surface area per unit leaf area (*Sc*/*S*) and enhancing the resistance of the cytoplasm, thus enhancing the distance between the chloroplast and cell wall and between the adjacent chloroplasts (Lu et al. 2016a, b, c).

Mesophyll diffusion conductance to CO_2 is the main photosynthetic trait. The limitation to photosynthesis impeded by g_m is significant, and under certain conditions like salinity, temperature, nutrients, light, water and tree length and size, leaf structure and aging, cell wall thickness, and chloroplast distribution can be the most significant photosynthetic limitation (Niinemets et al. 2009a; Han 2011; Whitehead et al. 2011; Zhu et al. 2011; Flexas et al. 2012). Quick response to a change of environmental factors might be regulated by another factor like aquaporin conductance (Flexas et al. 2012). In K^+ starved plants, besides g_s, reduced leaf mesophyll cell conductance (g_m) obstructed the diffusion of CO_2 to the chloroplasts (Jin et al. 2011; Battie-Laclau et al. 2014). An alleviated g_m (elevated *L*m) might be an outcome of the decline of intercellular air space due to the accumulation of photosynthate, decreased carbonic anhydrase activity, and aquaporin channel conductance due to limit CO_2 diffusion through mesophyll cells (Cakmak et al. 1994; Zhao et al. 2001; Battie-Laclau et al. 2014; Lu et al. 2016a). It was noted that during photosynthesis, inhibition of net CO_2 assimilation (A_N) resulted due to reduction in CO_2 mesophyll conductance (g_m) neither by maximum quantum use efficiency (F_v/F_m) nor by in vivo Rubisco activity under K^+ starvation. The reduced g_m might be due to variations in the leaf anatomy of *Helianthus annuus* L. under K^+ starvation (Jakli et al. 2017). Leaf area decreased before reduced photosynthetic rates under K^+ starvation, and changes in S/W value before *Sc*/*S* and $D_{chl-chl}$ value were the significant reason for the uneven decline in leaf area and photosynthetic rate in *Brassica napus* plant (Hu et al. 2020). Due to photosynthesis resistance, cucumber leaves were less affected under K^+ starvation than rice, wheat, and rapeseed leaves. All species averaged 50.5% and 53.4% of mesophyll conductance accounted for photosynthetic limiting factors under moderate K^+ and low K^+ conditions, respectively. An increase in leaf hydraulic resistance and R_L (ΔRx and ΔRox, the relative growth of xylem and outside-xylem hydraulic resistance, respectively) simultaneously with the rise in K^+ deficiency were found to be a significant contributor to photosynthetic limitations, and K^+ maintained the leaf photosynthesis and hydraulic conductance through modifications of leaf anatomy (Lu et al. 2019).

Biochemical limitations

The biochemical limitations significantly limit photosynthesis besides stomatal conductance and mesophyll conductance. However, there is considerable discussion on either K^+ starvation inhibits photosynthesis directly by reducing leaf chlorophyll content, obstructing photochemical energy conversion or biochemical processes, or inhibiting CO_2

diffusion from the atmosphere to the site of carbon assimilation in chloroplasts (Jakli et al. 2017). Rubisco is the primary limiting factor of photosynthesis in rice and tobacco leaves (Yang et al. 2004: Weng et al. 2007; Hu et al. 2021). In *Carya cathayensis*, the maximum carboxylation rate of Rubisco ($V_{c,\ max}$) and maximum rate of electron transport (*J*max) were the most sensitive factors (Jin et al. 2011). In *Raphanus sativa*, K^+ starvation reduces the photosynthetic rate by disturbing the balance of H^+ influx into the thylakoid lumen, thus increasing the acidification that leads to triggering the downregulation mechanism, which detaches the LHCII to Photosystem II (PSII) and an increase in energy dissipation, yet without preventing the PQH_2 oxidation at the Cyt *b6f* complex (Kusaka et al. 2021). Similar results were also found in *Glycine max* under K^+ starvation, the maximal fluorescence (*F*m), the maximum quantum efficiency of PSII photochemistry (*F*v/*F*m), actual photochemical efficiency of PSII (*Φ*PSII), photochemical quenching (*q*P), and electron transport rate of PSII (*ETR*) were considerably decreased with Rubisco with minimal fluorescence (Wang et al. 2015).

The relative contribution of all these three limiting factors under K^+ starvation has been explained in the photosynthetic process. It is concluded that the complex interaction of all these factors contributed to limiting photosynthesis. Table 4 illustrates some of these limiting factors under K^+ starvation.

H_2O_2 contents and antioxidant system

In chloroplast thylakoid, PSI and PSII reaction centers are the primary site of reactive oxygen species (ROS) (Asada 2006; Kohli et al. 2019). Several types of stresses trigger the generation of ROS, like nutrient deficiency, high light, high or low temperature, salinity, drought, and pathogen attack (Tripathy and Oelmuller 2012). Due to abiotic stress, stomatal closure limits the CO_2 uptake, which induces the production of H_2O_2 during photorespiration by the peroxisomal glycolate oxidase (Leterrier et al. 2016; Corpas et al. 2020) or singlet oxygen by the reduced photosynthetic electron transport chain (Apel and Hirt 2004; Noctor et al. 2014). If the production of H_2O_2 is prolonged, this will trigger oxidative stress, which is accompanied by altering the cellular redox homeostasis. ROS accumulation disrupts the functioning of the cell and induces the oxidative damage of membrane, lipids, nucleic acid, proteins, and inhibition of enzymes (Mittler 2002; Shahbaz et al. 2008; Ashraf 2009; Akram et al. 2012; Perveen et al. 2010, 2011, 2012). Some evidence indicates that H_2O_2 might function as a signaling molecule under K^+ deficiency (Hernández et al. 2012). Abiotic and biotic stresses are accompanied by the generation of H_2O_2 consequence of

Table 4 Comparative study of mesophyll, stomatal, and biochemical limitation to photosynthesis in K^+ starved condition

Plant species	Low mesophyll conductance (g_m)	Low stomatal conductance (g_s)	References
Glycine max	As the K^+ deficiency became more severe the *L*m enhanced upto 36–59% and *L*s (21–29%), *L*m about 70–80% greater than *L*s	In moderate K^+ deficiency, *L*s and *L*m contributed 15–18% limitation in photosynthesis	Singh and Reddy (2018)
Carya cathayensis Sarg. and *Hickory illinoensis* K.Koch	It accounted for more than 40% and 50% of the total limitation of photosynthesis in pecan and Hickory, respectively	Only accounted up to 20%	Shen et al. (2018)
Brassica napus L.	Main limiting factor of photosynthetic limitations, 33.0% of the total limitations, and as the photosynthesis began to fall B_L replaced it as it reached below 0.78% of leaf K^+ concentration	Only accounted for 23.9% limitation of the total limitations	Lu et al. (2016a, b, c)
Helianthus annuus L.	It is the major limitation of low A_N and might be due to changes in leaf anatomy	Only accounted < 20% of total limitation	Jakli et al. (2017)
Brassica napus L.	Major limiting factor of low photosynthesis	As the K^+ supply increased stomatal limitation and became the major limiting factor	Lu et al. (2016a, b, c)
Eucalyptus grandis	Stomatal conductance increased in the presence of K^+ compared to K^+ deficient	Mesophyll conductance was also higher in + K^+ than to K^+ deficient	Battie-Laclau et al. (2014)
Houttuynia cordata Thunb.		Photosynthetic rate not correlated with limited stomatal conductance	Xu et al. (2011)
Beta vulgaris L.	Mesophyll limitation to CO_2 from 2.8 to 5.3 s per centimeter and decreased photosynthesis in 21 days	First 15 days, stomatal limitations enhanced slowly from 0.3 to 0.5 s cm^{-1} and at 21 days it ultimately reached 1.6 s cm^{-1}	Terry and Ulrich (1973)

the dismutation of superoxide radicals ($O_2^{\bullet -}$) generated by the NADPH oxidase, also known as respiratory burst oxidase homolog (RBOH), which is considered to be the most crucial enzyme responsible for this oxidative burst (Mittler et al. 2004; Sagi and Fluhr 2006; Chapman et al. 2019). Deprivation of K^+ in *Arabidopsis* enhanced ROS accumulation at distinct regions of roots just behind the elongation zone that is active in K^+ uptake and translocation (Shin and Schachtman 2004). Gene RCI3, a member of the type III peroxidase family, is upregulated under K^+ starvation and engaged in ROS production, which affects the regulation of *AtHAK5* expression in *Arabidopsis* roots (Kim et al. 2010). To combat oxidative stress, plants have developed a defense system associated with a noticeable increase in ROS metabolizing enzymes like superoxide dismutase (SOD), catalase (CAT), and enzymes of the ascorbate-glutathione cycles (Mittler 2002; Cakmak 2005; Ashraf 2009; Ahmad et al. 2014; Kohli et al. 2019; Houmani et al. 2022). Many reports suggest that under K^+ starvation, the more vital photosynthetic ability is linked to higher antioxidant enzymes (Chen et al. 2008; Jia et al. 2008).

In *Gossypium hirsutum* L., higher H_2O_2 and ascorbic acid (ASC) activity were observed, which brought about higher malondialdehyde (MDA) content despite the elevated activity of H_2O_2-scavenging enzymes like catalase and peroxidase. However, low dehydroascorbate reductase activity and higher ASC content were attributed to lower ascorbate peroxidase (APX) activity in K + starvation, leading to premature leaf senescence marked by chlorophyll degradation and negative chlorophyll fluorescence (Hu et al. 2016). In *Brassica juncea* plants, initiation of ROS leads to oxidative stress and an increase in antioxidant enzymes like SOD, CAT, APX, and glutathione reductase (GR) under potassium deficiency (Ahmad et al. 2014). Similarly, *Houttuynia cordata* plant showed H_2O_2 accumulation inducing oxidative stress with a concomitant increase of the activity of antioxidant enzymes like CAT and peroxidase to palliate the oxidative damages (Xu et al. 2011) under the deficiency of K^+.

Involvement of K^+ to abiotic stress tolerance and its potential relationship with signal molecules such as NO and H_2S

It was noted that K^+ plays a vital role as an anti-stress agent against different abiotic stresses (Anschütz et al. 2014; Jia et al. 2018; Perelman et al. 2022), such as drought, temperature, salinity, waterlogging, and heavy metal. Furthermore, new evidence supports the correlation between K content with signaling molecules such as NO and H_2S (Zhao et al. 2018; Oliferuk et al. 2020; Lana et al. 2021).

Drought stress

Besides growth and productivity, K^+ was also involved in maintaining cell turgidity, osmotic adjustment, stomatal regulation, aquaporin channel conductivity, cell membrane stability, and detoxification of ROS under drought stress (Wang et al. 2013; Hasanuzzaman et al. 2018; Sehar et al. 2021). Low K^+ alleviated the plant tolerance to drought stress and K^+ absorption (Wang et al. 2013). Reports showed that the K^+ application reduces drought stress consequences, specifically in *Hibiscus rosa-sinensis* (Egilla et al. 2005; Bahrami-Rad and Hajiboland 2017) concluded that applying K^+ under water-stressed and K^+ starved conditions on *Nicotiana rustica* L. induced dehydration avoidance and tolerance by augmenting stomatal resistance and also by the accumulation of organic osmolytes and proline mainly in the young leaves.

In maize, the overexpression of inwardly rectifying K^+ channel 1 (AKT1) facilities the root K^+ uptake but, at the same time, mediates the homeostasis of H_2O_2 and NO, mediating its drought stress tolerance (Feng et al. 2020). More recently, it has proposed a cascade of events associated with the loss of function of chloroplast KEA1 and KEA2 in *Arabidopsis*, which triggered an increased tolerance to drought stress. Thus, the K^+ imbalance in the chloroplasts of this *kea1kea2* mutant causes impairment in chloroplast functions, including photosynthesis and photorespiration pathways associated with an imbalance of ROS and NO metabolism affects stomatal movement causing a higher drought stress resilience (Sánchez-McSweeney et al. 2021) unexpectedly. Thus, this new evidence supports the biochemical crosstalk of K^+ with NO metabolism and other plant gasotransmitters such as H_2S and CO (Zhang et al. 2018; Lana et al. 2021). It should be considered that these signaling molecules participate in a wide range of physiological processes and respond to environmental stresses (Mukherjee and Corpas 2020; Mishra et al. 2021) that would support the benefits exerted by K^+ when it is applied as exogenous. Thus, in tomato seedlings, the exogenous application of K^+ in coordination with endogenous H_2S can regulate H^+-ATPase activity, antioxidant system, sugar metabolism, and redox homeostasis that promote drought tolerance stress (Siddiqui et al. 2021).

Waterlogging stress

Waterlogging is one of the significant abiotic stresses that influence plant growth and yield worldwide (Sasidharan et al. 2018). Waterlogging causes inhibition of soil aeration and limits the supply of oxygen (hypoxia or anoxia) to roots (Amin et al. 2015). A lesser amount of oxygen impeded the respiration process in roots and resulted in a shortage of energy required for nutrient uptake (Boru et al. 2003). In waterlogged conditions, a combined supply of K^+ (foliar and soil) not only improved growth, photosynthetic pigments, and photosynthetic capacity but also mitigated the negative influence of waterlogging in *Gossypium hirsutum* L. (Ashraf et al. 2011). Stomatal closure during early senescence is attributed to alleviating P_N, and during the late senescence stage, low CO_2 assimilation accounted for a low P_N. The supply of K^+ improved the post-anthesis photosynthesis and yield by maintaining the stomatal openings and CO_2 carboxylation capacity by dissipating excess excitation energy, thus reducing the risk of photo-damage in winter wheat at the stem elongation stage under waterlogging conditions (Gao et al. 2021). Recovering root development and yield loss under waterlogged conditions by the combined supply of K^+ and N in *Vigna radiata* L. was observed (Amin et al. 2015).

Temperature stress

Extreme high and low-temperature stress influenced plant growth and development at the whole-plant level, tissue, and cell level, and even at the subcellular level. Direct and indirect injuries due to high and low temperatures reduced the yield (Waraich et al. 2012), inhibited metabolic reactions, and influenced the osmotic and oxidative stresses (Airaki et al. 2012; Wang et al. 2013). Proper plant nutrient management is one of the master strategies for temperature stress tolerance, and K^+ plays a significant role in elevating temperature stress tolerance (Hasanuzzaman et al. 2018). Under chilling and freezing stress, the plant faces dehydration due to the loss of apoplastic water. The application of K^+ under chilling and freezing stress alleviates the freezing-induced cellular dehydration and adjusts the osmotic potential of plant species (Wang et al. 2013). In low K^+ plants, chilling and frost might damage the photosynthetic activities and increase ROS production by reducing the antioxidant activities, thus causing a reduction in plant growth and yield. Exogenous application of high KNO_3 enhanced the antioxidant activities and secondary metabolite transcripts, protecting ROS overproduction and increasing chilling stress tolerance in *Panax ginseng* (Devi et al. 2012). K^+ fertilization augmented the frost tolerance as noted by lowering electrolyte leakage mainly in young leaves of *Albizia plurijuga*, *Cedrela dugesii*, and *Ceiba aesculifolia* (Gómez-Ruiz et al. 2016).

High temperature contributed directly to protein denaturation and aggregation, lipid membrane damage, enzymes inactivation of chloroplast and mitochondria, protein synthesis limitation and degradation, and loss of membrane integrity (Waraich et al. 2012). It also enhanced the leaf senescence and negatively influenced the production of photosynthates, thus reducing the yield (Rahman et al. 2005). In wheat, applying potassium orthophosphate contributed to enhanced yield and quality under heat stress conditions (Rahman et al. 2014). In plants, exogenous application of K^+ might be helpful to the reduced negative influence of heat stress (Waraich et al. 2012). Upregulation of antioxidant enzymes like SOD, POX, CAT, AsA, phenolics, and MDA enhanced heat stress tolerance in cotton (Sarwar et al. 2019).

Salinity stress

Salinity and K^+ starvation are two significant environmental constraints of fields for many crops that generally occur concomitantly and result in loss of plant growth and productivity (Hafsi et al. 2017). Salt stress impedes plant growth, and K^+ deficiency further augments the effects of salinity stress on photosynthetic activity. However, it also displays a mechanism of protecting photosynthetic apparatus by non-photochemical quenching and antioxidant activity. Higher accumulation of phenolic compounds under both stresses might be related to antioxidative defense in *Sulla carnosa* seedlings (Hafsi et al. 2017). In another study, a significant reduction in biomass production under both stresses was noted, and salinity stress impacted more on shoots than roots while potassium starvation the vice versa.

Moreover, the impact of salinity stress on photosynthetic machinery was further enhanced by the deficiency of K^+ with the resistance in CO_2 photo assimilation. Still, it provided an understanding of protecting PSII photodamage and dissipation excess energy in *Hordeum vulgare* (Degl'Innocenti et al. 2009). Oxidative stress is one of the consequences of salinity stress, and the application of K^+ under salinity stress alleviated the ROS production by decreasing the NADPH oxidases activity; however, under low K^+ supply in bean root cells, the movement of NADPH oxidases was up to eightfold higher in plants compared to K^+ sufficient plants (Cakmak 2005). Net uptake rates and translocation of K^+ were reduced under salinity stress, while the impact of salinity stress was enhanced with low K^+ concentration in *Zea mays* L. (Botella et al. 1997). Under salinity stress, plants usually reorganize Na^+ and K^+ contents accompanied by NO accumulation. In *Arabidopsis thaliana* mutants, it has been demonstrated that NO negatively modulates the K^+ channel AKT1, responsible for K^+ uptake, by regulating the biosynthesis of vitamin B6 (Xia et al. 2014). Recently, it has been shown that the overexpression of the K^+, Na^+/H^+ antiporter NHX4 in tomato plants improved the salinity tolerance and increased the yield and quality of its fruits (Maach et al. 2020).

Furthermore, in *Malus hupehensis* seedlings, the pretreatment with H_2S palliates salinity and alkaline stress by regulating the Na^+/K^+ homeostasis because it decreases the root Na^+ content, whereas it increases K^+ content. This was accompanied by an increase in the activity of antioxidant enzymes, including CAT, POX, and SOD which mitigate oxidative stress (Li et al. 2020). On the other hand, in poplar plants under salinity stress, it has been found that exogenous

Table 5 Impact of application of K^+ under salinity stress and K^+ starvation

Plant species	Effect of exogenous K + application	References
Glycine max L.	Application of 2.5% Potassium sulfate positively influenced antioxidant activity, flavonoid, carotenoid, and chlorophyll contents in contrast to potassium chloride. However, the effect was not remarkable compared to fertilizer unsprayed plants thus could not mitigate the negative impact of salinity stress	Adhikari et al. (2020)
Triticum aestivum L.	Alleviated harmful influences of salinity stress and enhanced K^+ content, photosynthetic pigments, photosynthetic efficiency, antioxidant activity (enzymatic and non-enzymatic), and decreased Na^+ content under salinity stress	Rady and Mohamed (2018)
Arachis hypogaea L.	Increased salinity tolerance with regard to water status, biomass production, osmotic adjustment, and maintained ionic balance by excluding Na^+ as a master strategy of enhancing tolerance.	Chakraborty et al. (2016)
Helianthus annuus L.	Enhanced growth and yield, photosynthetic capacity, water use efficiency, and relative water contents	Akram and Ashraf (2011)
Helianthus annuus L.	Increased growth and yield, root K^+, Leaf K^+, K^+/Na^+ ratio	Akram et al. (2007)

H_2S regulates K^+/Na^+ homeostasis in roots through the positive control of the H^+-ATPases (Zhao et al. 2018). Table 5 provides some representative examples of the beneficial effects triggered by the exogenous application of K^+ and how it can mitigate salinity-induced damages (Kumari et al. 2021).

Heavy metal stress

Heavy metal and metalloid stress in the soil is one of the major impediments to the successful establishment and cultivation of crops (Yasin et al. 2018). Metal stress causes a reduction in growth, fruit formation, and development of fruit trees (Worthington 2001; Foyer and Noctor 2005; Lombardi and Sebastiani 2005), and disturbs the biochemical processes, including photosynthetic activity and level of gas exchange, proline production, and K^+ nutrition (Lysenko et al. 2015; Song et al. 2015). However, the K^+ application benefits plant tolerance to different metal stresses (Dhiman et al. 2022). *Prunus persica* seedlings treated with exogenous K^+ (10 mM) not only improved the status of endogenous K^+ but also showed a positive response in alleviating the reduction of zinc-induced photosynthesis and antioxidant defense systems. K^+ application was found to upregulate the transcript level of K^+ uptake genes (*KUP*) engaged in K^+ acquisition, transport, and homeostasis leading to the protection of photosynthesis and the antioxidative defense system (Song et al. 2015).

Moreover, combining K^+ and Ca^{2+} enhanced the antioxidant enzyme activity in Cd stressed faba bean (*Vicia faba* L.) seedlings, leading to enhanced plant growth and productivity (Siddiqui et al. 2012). Similarly, in *Gladiolus grandiflora* L., a combination of K^+ and Si mitigate the Cd stress and enhances the protein and proline accumulation and uptake of mineral nutrients (Ca, Mg, Mn, S, and K) and quantity of total phenolics and flavonoids (Zaheer et al. 2018). Similar results were also observed in *Gladiolus grandiflora* L. under Cd stress by the application of K only (Yasin et al. 2018). An increase in growth, photosynthesis, and nutrient uptake, as well as a reduction in cadmium toxicity, was observed in soybean (Shamsi et al. 2010; Liu et al. 2013) reported that deficiency of K^+ enhanced the antioxidant system, which protects the toxicity of Cd in rice seedlings.

Conclusions and future perspectives

K^+ is an essential macronutrient involved in both physiological and biochemical processes. K^+ starvation is a critical nutritional issue that negatively affects plant growth and yield. This review gives a better understanding of K^+ presence in the rhizosphere and its uptake by roots via several kinds of transporter and channels. It is well documented that K^+ plays a significant role in photosynthesis, chlorophyll content, and chloroplast ultrastructure. Furthermore, K^+ starvation decreased photosynthesis by limiting CO_2 diffusion into and through leaves (g_s, g_m, and biochemical processes). Stomatal resistance, mesophyll resistance, and biochemical limitations are the major factors for the decrease in photosynthesis. Recent investigations also show that K^+ promotes antioxidant defense machinery and osmolyte content, which reduces the oxidative stress produced by ROS and MDA, which further helps attenuate abiotic stress.

K^+ is an essential macronutrient, and its starvation reduces several physiological and biochemical processes, such as photosynthesis, chlorophyll content, and chloroplast ultrastructure. Furthermore, unraveling the contribution of K^+ in modulating genes involved in photosynthesis need to be explored. More studies are required on the genes and signaling molecule that alters plants' metabolic and cellular responses during stress.

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Declarations

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