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Regulation of potassium transport and signaling in plants

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As an essential macronutrient, potassium (K^+) plays crucial roles in diverse physiological processes during plant growth and development. The K^+ concentration in soils is relatively low and fluctuating. Plants are able to perceive external K^+ changes and generate chemical and physical signals in plant cells. The signals can be transducted across the plasma membrane and into the cytosol, and eventually regulates the downstream targets, particularly K^+ channels and transporters. As a result, K^+ homeostasis in plant cells is modulated, which facilitates plant adaptation to K^+ deficient conditions. This minireview focuses on the latest research progress in the diverse functions of K^+ channels and transporters as well as their regulatory mechanisms in plant response to low-K^+ stress.

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Introduction

Potassium (K^+) is one of the essential macronutrients for plant growth and development. In living plant cells, K^+ is involved in many physiological processes, such as osmoregulation, enzyme activation, electrical neutralization, and membrane potential maintenance [1]. As an important inorganic osmolyte, K^+ regulates turgor pressure of plant cells, which controls stomata movement and pollen tube growth [2,3]. K^+ also regulates photosynthesis and subsequent carbohydrate translocation and metabolism, and consequently determines crop yield and quality [4]. In addition, sufficient K^+ supply can enhance the tolerance of crop plants to various biotic and abiotic (e.g. salt and drought) stresses [5]. However, K^+ deficiency in most arable fields has restricted the sustainable development of agriculture production [6]. Facing this challenge, the genetic improvement of crop K^+ utilization efficiency (KUE) is urgently expected, which requires a thorough investigation on the molecular mechanisms of plant responses to K^+ deficiency.

The K^+ uptake by plant root cells as well as K^+ transport inside plants are conducted by a large number of K^+ channels and transporters [7,8]. Thus, investigation on identification and functional characterization of K^+ channels and transporters as well as their regulatory mechanisms has been the focus in this area for the last decade.

Functional identification of potassium transporters

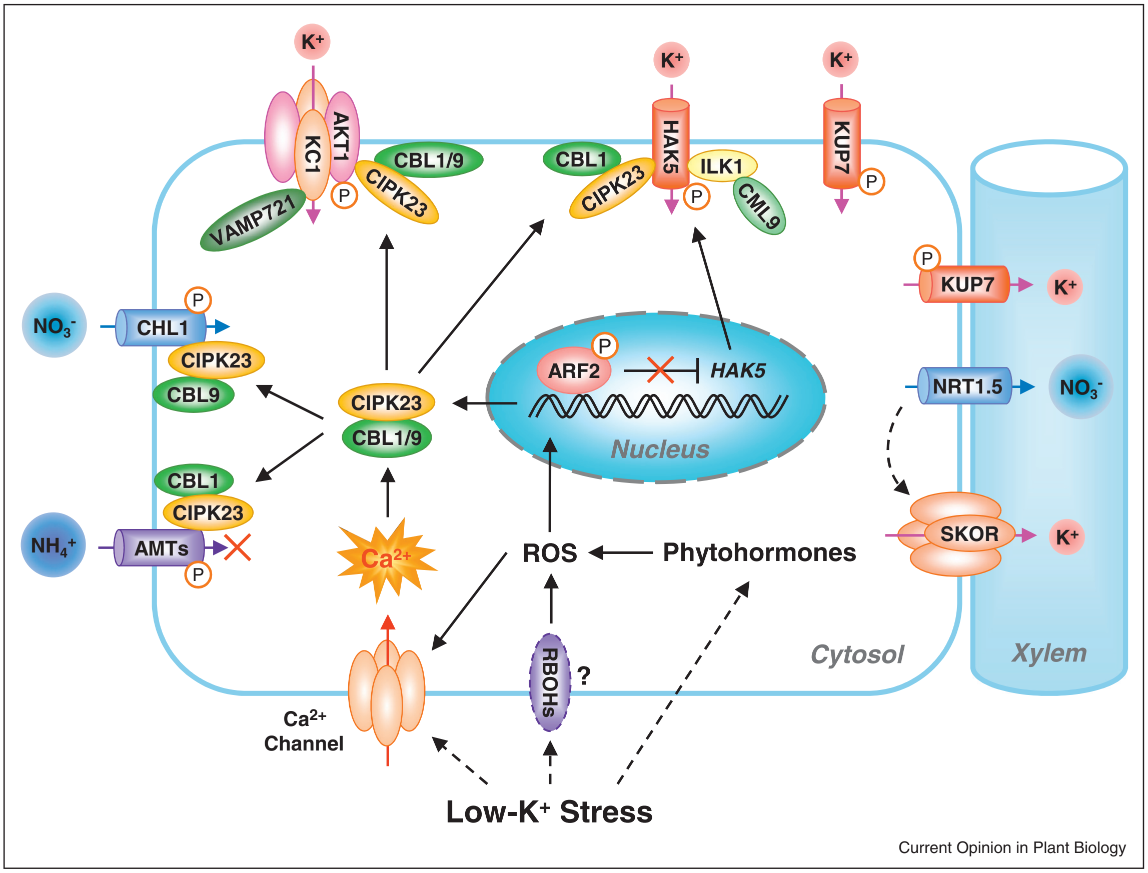
In recent years, many novel K^+ transporters have been functionally identified. They regulate K^+ transport and ion homeostasis in plant cells and exhibit diverse physiological functions in K^+ uptake, photosynthesis, organ development, reproduction, and stress tolerance.

The K^+ transporters from the HAK/KUP/KT family are crucial for K^+ transport and plant development [8]. A recent report showed that AtKUP7 is involved in K^+ uptake in *Arabidopsis* root [9] (Figure 1). AtKUP7 may be an alternative system involved in K^+ uptake besides AtAKT1 channel and AtHAK5 transporter that are two major K^+ uptake components in *Arabidopsis* root [10]. The affinity of AtKUP7 for K^+ transport (about 50–200 μM) is lower than that of AtHAK5 (about 10–20 μM). In addition, AtKUP7 may also mediate K^+ transport into the xylem and subsequently K^+ translocation to shoot [9] (Figure 1).

In rice, three HAK/KUP/KT K^+ transporters, *OsHAK1/5/21*, were characterized. These transporters all participate in K^+ acquisition in rice root, but they operate at different external K^+ conditions [11–13]. OsHAK5 functions in rice K^+ uptake at low K^+ supply level (below 0.3 mM), and is also involved in the K^+ transport from root to shoot in the K^+-deficient rice plants [11]. Comparatively, OsHAK1 regulates the K^+-mediated rice growth within a wide range of K^+ concentrations (0.05–1 mM) [12]. OsHAK21 shows a low-affinity K^+ transport activity when characterized in yeast, but mediates high-affinity K^+ uptake in *Arabidopsis* [13]. In addition, *OsHAK1/5/21* all contribute to rice tolerance to salt stress by maintaining K^+/Na^+ homeostasis [11–13].

Previous studies have indicated that many CHX (cation/H^+ exchanger) members act as K^+ transporters (K^+/H^+ exchanger), and play roles in pH homeostasis [14]. In *Arabidopsis*, AtCHX14 functions as a PM-located K^+-efflux

Figure 1



Signal transduction and ion transporter regulation in *Arabidopsis* responses to low-K^+ stress. Plants are able to perceive external low-K^+ stress and generate low-K^+ signals in plant cells. The signals (Ca^{2+}, ROS, phytohormones, etc.) can be transducted in cytosol, and eventually regulate the downstream targets (particularly K^+ channels and transporters) at transcriptional and posttranslational levels. The "P" represents phosphorylation, and the red "X" indicates inhibition effect. See text for the detail information.

transporter and modulates K^+ homeostasis and K^+ recirculation [15]. AtCHX17 is a K^+-influx transporter localized to prevacuolar compartment, vacuole and the PM in root. AtCHX17 together with AtCHX16/18/19 is required for reproduction and seed development [16]. In rice, OsCHX14 is localized to the ER, and may be involved in the K^+ homeostasis during flowering in rice [17]. A recent report showed that a PM-located cation-chloride cotransporter (OsCCC1) is able to transport K^+, and is involved in cell elongation in rice by maintaining ion homeostasis [18].

It has been known for decades that K^+ plays essential role in photosynthesis, and determines crop yield and grain quality [5,19]. However, little is known about the molecular identification of the K^+ transporters involved in photosynthetic regulation. The recent studies revealed the essential roles of three K^+-efflux antiporters AtKEA1/2/3 in photosynthetic regulation and early chloroplast development in *Arabidopsis*. AtKEA1 and AtKEA2 are located at the inner envelope membrane of chloroplasts, while AtKEA3 localizes to the thylakoid membrane [20]. Both chloroplast development and photosynthesis rate were significantly impaired in the *atkea1,2,3* triple mutant, resulting in stunted growth of mutant plants [20,21]. AtKEA1 and AtKEA2 exhibit polar distribution in small and dividing plastids, which regulates chloroplast development [22]. AtKEA3, as an H^+/K^+ antiporter, mediates H^+ efflux from the thylakoid lumen to the stroma through H^+/K^+ exchange and regulates proton motive force (pmf) across the thylakoid membranes, and consequently regulates photosynthesis as well as photosynthetic acclimation in fluctuating light environments [23•,24].

Low potassium signal sensing and transduction

Plants can sense low-K^+ stress and generate certain signal molecules in plant cells. The signals can be transducted and subsequently trigger downstream responses, and eventually facilitate the plant adaptions to K^+-deficient conditions [7]. Some signal molecules, including Ca^{2+}, ROS, phytohormones, microRNAs, etc., have been