Genetic approaches for improvement of the crop potassium acquisition and utilization efficiency
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Potassium (K) is one of the essential macronutrients for higher plants, not only important for plant growth and development, but also crucial for crop yield and quality. The deficiency in K in large areas of arable land worldwide has become a limitation for sustainable development of agriculture, and threatens the world food security. Along with the increased limitation of K fertilizer supply, the genetic improvement of K utilization efficiency (KUE) of crop plants may become a feasible way to solve the problem. K nutrition depends on an underlying relationship with metabolic regulation which together influence crop yield, quality and responses to environmental stress. Manipulation of root architecture together with K transport and distribution within the plant offer great potential to improve KUE.

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Current Opinion in Plant Biology 2015, 25:46–52
This review comes from a themed issue on Physiology and metabolism
Edited by Steven Smith and Sam Zeeman

http://dx.doi.org/10.1016/j.pbi.2015.04.007
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Introduction
As one of the essential macronutrients, potassium (K) plays important roles in many fundamental physiological processes in plant cells, including osmoregulation, enzyme activation and ion homeostasis [1]. Sufficient K supply is required for optimal plant growth and development. Particularly, K⁺ transport across the cell membrane or the endomembrane is related to the photosynthetic regulation [2**,3**] and is also involved in transport of assimilation products [4]. Obviously, sufficient K supply is important for crop yield as well as product quality [5,6].

Soils in most arable fields are deficient in K, such as about 75% of the paddy soils in China [7,8]. K deficiency significantly reduces crop yield, so that K fertilizer must be applied in most areas for crop production. In the last five decades, the global K fertilizer consumption has continuously increased (Figure 1a), and this demand is estimated to further increase from 28.6 Mt (K₂O) in 2012 to 33.2 Mt (K₂O) in 2016 [9]. Asia (especially East and South of Asia), as one of the most important agricultural areas, consumes 44.9% of the world K fertilizer, but Asia lacks K resources for fertilizer supply [9]. As a result, K fertilizer supply in Asia is far lower than the demand, and the gap between supply and demand will be increased to 9.7 Mt (K₂O) in 2016 [9] (Figure 1b). Crop production in Asia has to face a deficit of K fertilizer supply in a long term, which threatens food security for 60% people of world population. In the meanwhile, the price of K fertilizer has rapidly increased in recent years from US$ 165 per ton (KCl) in 2003 to US$ 595 per ton (KCl) in 2013 (Figure 1a, USDA), which results in the remarkable increment of cost for crop production. As one of strategies towards solving the problem of K deficiency for crop production, genetic improvement of crop K utilization efficiency (KUE) has been proposed.

Potassium nutrition assures crop yield and quality, and enhances crop tolerance to environmental stresses
It is known that sufficient K supply is required for maintaining high photosynthesis rate and driving assimilate transport into grains [5]. A recent report showed that the Arabidopsis K⁺ channel TPK3 at the thylakoid membrane modulates the proton motive force (pmf) through ion counterbalancing, which controls photosynthetic light utilization [2**]. The K⁺-efflux antiporters KEA1, KEA2 and KEA3 located at the inner envelope membrane of chloroplasts and the thylakoid membrane respectively regulate the pmf and photosynthesis [3**]. K⁺ transport mediated by K⁺ channel AKT2 (Arabidopsis K⁺ transporter 2) is essential for the assimilate transport from the source to the sink [10,11*]. Obviously, K supply has significant effect on crop yield by regulation of photosynthesis rate and assimilate transport [5]. In addition, the K supply also affects the quality of crop products. In general, high K contents in crop products are welcome for human healthy diet. One example showing the effects of K supply on crop quality is grapevine (Vitis vinifera). K⁺ is the major cation in grape berries and plays important roles during the berry growth and ripening [12]. An optimal K⁺ concentration in berries is crucial for the fermentation of red wine and determines the wine quality [12].

A number of studies have shown that the sufficient K supply may enhance crop plant tolerance to various
environmental stresses [6] (Figure 2). Salinity, as one of the common abiotic stresses, affects about 1/3 of the irrigated land worldwide [13]. Because the salt (Na+) stress not only exerts osmotic stress on living plant cells but also competitively reduces K+ uptake by plant root cells, most terrestrial crop plants are highly sensitive to salt stress [13,14]. However, the high external K+ inhibits the Na+ influx [15], and maintenance of high K+/Na+ ratio in cytosol enhances the crop resistance to salinity [13]. A recent report showed that overexpression of a K+ transporter LeNHX2 (tomato Na+/H+ Exchanger 2) increases the salt tolerance in transgenic tomato [16]. It is not surprising that the K fertilization frequently improves the crop performance on saline soils [17].

The sufficient K supply also contributes to crop tolerance to drought stress. As the most abundant cation content in living plant cells, K+ functions as the important osmolyte and is crucial for the osmoregulation in plant cells. Under severe K-deficiency, the crop plants often show the wilting symptoms because of the disturbed water balance. In the field, an ample K supply would maintain the cell osmolarity and sustain water uptake from the droughted soils [18]. In addition, K+ also plays a central role in the regulation of stomatal movement, which thereby controls the water loss from the stomata [19]. Transporters from Arabidopsis thaliana (At) including AtNHXs (Na+/H+ Exchanger) and AtKUPs (K+ uptake transporter) have been reported to regulate plant responses to drought stress by controlling the K+ homeostasis in guard cells during the stomatal movement [20,21].

K+ ions maintain the cell turgor that drives cell expansion and elongation. The high K+ concentration in cytosol increases the cell turgor leads to the elongation of root hairs [22], which consequently enhances the root capacity for absorbing nutrients and water. In addition, the high cell turgor maintains the plant rigidity and enables the crop resistance against lodging. It has been also reported that sufficient K supply can increase crop resistance to pathogen [23]. In the K-deficient field, crops are more susceptible to fungal infection [8]. The spraying of KCl could suppress the septoria leaf blotch and powdery mildew of wheat by the inhibition of fungal spore germination [24,25]. Recently, Zhou et al. [26] reported that overexpression of the K+ channel GmAKT2 (ortholog of Arabidopsis AKT2 gene in soybean) significantly enhances soybean resistance to the SMV (soybean mosaic virus).
Potential approaches for improvement of crop potassium utilization efficiency

Obviously, increasing the KUE of crop varieties may help to overcome K-deficiency problem. It is known that different plant species as well as different varieties (genotypes) of the same species often show varied K acquisition and utilization efficiencies [27–29], which provides possibilities for selection or genetic modification of crop K nutrition efficiency. First, plant KUE mainly depends on K acquisition capability of plant roots. Obviously, optimizing plant root architecture and root K uptake activity may effectively improve plant KUE. Second, plant KUE is regulated by K transport and translocation in plant tissues and organs, which may also provide possibility for improvement of plant KUE. In addition, selection of the important natural variations or QTLs in crops associated with high KUE may also give us valuable information for genetic improvement of crops.

Optimizing the root architecture

The mineral nutrients are absorbed by the plant root cells, especially via the root hairs. The root architecture and root hair development significantly affect the nutrient absorption, and are plastic and responsive to nutrient availability [30**,31]. The larger root volume (e.g., increasing the length and density of lateral roots and root hairs) increases the root surface area, which may significantly enhance the nutrient absorption (Figure 3).

Recent report showed that a very important rice phosphorus-efficient QTL (quantitative trait locus), Pup1 (phosphorus uptake 1), has been identified as a protein kinase gene named PSTOL1 (phosphorus-starvation tolerance 1). The PSTOL1 enhances the early root growth and increases the rice root volume [32], which not only enables rice to acquire more phosphorus but may also enhance absorption of other nutrients. The investigations in Arabidopsis have revealed that some K⁺ transporters may affect the root growth. K⁺ transporter ZIFL1.1 (Zinc-Induced Facilitator-Like 1.1) affects the primary root elongation and lateral root emergence, perhaps by modulating the polar transport of auxin [33*]. It is known that auxin is the major phytohormone that controls root growth under diverse environmental conditions. It is expected that plant root architecture may be optimized for plant nutrient acquisition by genetically modifying auxin metabolism and transport.

The root growth is reduced under K limitation [30**]. However, the K-deficiency induces the root hair

**Figure 3**

Potential approaches for improvement of crop potassium efficiency. This illustration shows several potential approaches for genetic improvement of crop potassium efficiency. These approaches include optimizing the root architecture (PR, primary root; LR, lateral root; RH, root hair), enhancing the potassium uptake and translocation abilities, coordinating the potassium absorption and translocation with other nutrients, and mining natural variation in KUE.
elaboration, which has been observed in many crops [31].
There are many regulators and genes have been reported
To regulate root hair elongation [34]. Phytohormone ethe-
ylene and ROS (reactive oxygen species) signal are in-
volved in regulation of root hair elongation under low-K
conditions [35]. RAP2.11 (related to AP2 11) encodes an
AP2/ERF (APETAL2A2-domain-containing protein/Eth-
ylene Response Factor) transcription factor in Arabidopsis
and is induced under K-deprived conditions [36]. Over-
expression of RAP2.11 enhances the root hair elongation
[36]. The K⁺ transporter TRH1/AtKUP4 (Tiny Root Hair
Arabidopsis thaliana K⁺ uptake transporter 4) has also
been identified as an essential component controlling root
hair growth by regulating the auxin transport [37,38].

Enhancing the potassium uptake and
translocation

Plants absorb and transport K⁺ ions through K⁺ channels
and transporters that locate at cell membrane [39]. K⁺
channels function as selective pores, through which K⁺
ions diffuse across the membrane with a rapid rate (about
10⁸ ions per second through each channel). K⁺ transport-
ers do not have pore structure. K⁺ ion is bound to a
specific site on the K⁺ transporter and then transported to
the other side of the membrane through a conformational
change of the transporter protein. The K⁺ transport rate
by a transporter (100–1000 ions per second) is much
slower than that through a channel.

The cytoplasmic K⁺ concentration in living plant cells is
relatively stable at approximately 100 mM, while the K⁺
concentrations in soils vary from 0.1 to 1 mM. In higher
plants, there are two main systems mediating the K⁺
uptake: a high-affinity system that functions at low exter-
nal K⁺ concentrations (below 0.2 mM) and a low-affinity
system at high external K⁺ concentrations (above
0.5 mM) [40]. The H⁺-coupled K⁺ transporters mediate
the K⁺ uptake in the high-affinity range, while the K⁺
channels operate in the low-affinity range [41]. So far,
many K⁺ channels and transporters have been identified
in various crop species [39]. In Arabidopsis, the K⁺ trans-
porter HAK5 (high-affinity K⁺ transporter 5) and K⁺
channel AKT1 (Arabidopsis K⁺ transporter 1) conduct
most of the K⁺ uptake [42–44]. Their homologs perform
the similar functions of K⁺ uptake in crops [39]. Increas-
ing the amount and activity of these K⁺ uptake compo-
nents may enhance the crop K acquisition efficiency
(Figure 3).

The homolog genes of K⁺ transporter HAK5 from many
different crop species (such as tomato, barley, pepper,
rice) are induced under K-deficient conditions [45]. It has
been reported that overexpression of HAK5 or the tran-
scription factors that promote HAK5 expression may
increase the root K⁺ uptake and enhance the Arabidopsis
tolerance to K deficiency [36,46]. Recent data has also
revealed that overexpressing the rice K⁺ transporter
OsHAK5 not only increases the rice K⁺ uptake/translo-
cation, but also improves the rice tolerance to salt stress [47].
It’s further hypothesized that overexpression of HAK5
homolog genes in other crop species may also enhance the
crop K uptake efficiency especially under K-limited
conditions.

As a major component for Arabidopsis K acquisition, K⁺
channel AKT1 mediates K⁺ uptake over a wide range of
external K⁺ concentrations (above 10 μM), and is mainly
regulated at post-translational level rather than transcrip-
tional level [48–52]. The K⁺ uptake activity mediated by
AKT1 is regulated by the calcium sensors CBL1/9 and
their interacting protein kinase CIPK23 [52]. Overexpres-
sion of CBL1, CBL9 or CIPK23 all enhance the Arabidopsis
tolerance to K starvation [52]. The similar regulatory
mechanism has been repeatedly reported in many crop
species such as in barley [53], grapevine [54,55], maize
[49] and rice [56**]. It seems that the regulation of AKT1-
like channels via a CBL–CIPK complex might be a
universal mechanism in different plant species. There-
fore, genetic modification of CBL and CIPK gene expres-
sions in crops may be a prospective approach to improve
the crop K uptake efficiency.

Besides the K⁺ uptake from the soils, the K⁺ translocation
from the sources to the sinks in phloem is also crucial for
the crop yield and quality (Figure 3). K⁺ translocation in
phloem facilitates the co-transport of assimilates to grains
or fruits [4], which increases the product yield. K⁺ trans-
location and accumulation in fruits and tubers is benefi-
tial to improve the quality and nutrition of the products,
such as in tomato and potato [6]. A long-term investiga-
tion in wheat and barley demonstrated that most of the K
(about 70%) remains in the straw. And the mature grains
contain a relatively low and constant K content, even the
K supply is gradually increased [6,57]. If the K in straw
could be translocated into grains during the grain filling
stage, it might increase the grain yield and quality. In
higher plants, the K⁺ translocation in phloem is mainly
mediated by the AKT2-like K⁺ channels [10,39]. The post-
translational modification of Arabidopsis K⁺ channel
AKT2 efficiently assists the plasma membrane H⁺-
ATPase in energizing the transmembrane phloem (re)load-
ing processes [11*]. Therefore, elucidating the
regulatory mechanisms of AKT2-like channels in crops
may have importance for improvement of KUE.

Coordinating the K⁺ absorption and
translocation with other mineral nutrients

In plants, the mineral nutrients are absorbed and translo-
cated as their ion forms, some are cations others are
anions. Therefore, the absorption and translocation of
different nutrients should abide by the charge balance
in order to maintain the high transport efficiency. In
plants, K⁺ and NO₃⁻ are the most abundant cation and
anion respectively. The coordinated absorption and
translocation of these two kinds of ions seem to be very important [45, 58] (Figure 3). In Arabidopsis, the protein kinase CIPK23 not only regulates AKT1-mediated K+ uptake [52], but also modulates the activity of nitrate transporter CHL1 that conducts nitrate uptake [59]. The CIPK23 may act as an important node of the plant nutrient regulatory network and facilitate the coordinated uptake of K+ and NO3−. Recently, the crystal structures of CIPK23 and CHL1 proteins have been resolved [60, 61, 62]. One may expect that such a coordinated regulatory mechanism of K+ and NO3− acquisition by CIPK23 may also exist in various crops.

The K+ transporters and nitrate transporters seem to be also co-regulated at the transcriptional level. In Arabidopsis, the K+ deficiency not only induces the K+ transporter genes [45], but also suppresses many nitrate transporter genes [63, 64]. Moreover, this suppression could be relieved after the K resupply [63]. Although the mechanism of this coordinative regulation remains unknown, searching for the pivotal genes encoding key regulators for genetic network of plant nutrient acquisition would be important for genetic improvement of crop nutrient efficiency.

Mining the natural variations for high KUE

The natural genetic variations lead to the diverse genotypes of crops and endow crops with different phenotypes in responses to the environmental stresses. These natural variations or QTLs underlying the various genotypes in crops may contain the valuable resources for the crop improvements. For example, the genotypic differences for K uptake/use efficiency have been observed in many crops, such as in wheat [28] and barley [29]. However, the genetic loci that control these K efficiency differences are not identified yet. Therefore, mining the important natural variations or QTLs in crops associated with high KUE might provide the resources for genetic improvement of crop cultivars (Figure 3).

Along with the rapid development of sequencing technologies and computational methods, GWAS (genome-wide association study) has become a powerful tool for detecting the natural variations and QTLs [65] and has been successfully applied to characterizing many genetic loci that control the crop important agronomic traits, such as flowering time, grain yield, leaf size and disease resistance [65]. It’s believed that GWAS would be an efficient way to identify the genetic loci that control the K nutrition traits and to promote the genetic improvement for crop KUE in future.

Prospects

The K deficiency has become a challenge for the sustainable development of crop production. To genetically improve K acquisition and utilization efficiency in crop plants, we need to further increase our understanding in molecular genetic mechanisms of K use efficiency in crops. So far, most of our knowledge for plant K nutrition comes from the investigations with Arabidopsis. Although Arabidopsis and crop plants might share the similar genetic mechanisms in K nutrition efficiency, the thorough investigations in molecular genetic mechanisms of K nutrition efficiency in various crop plants are urgently required.

Acknowledgements

The research work in authors’ lab was supported by the “973” Project (2011CB100303 to YW; 2012CB114203 to WHW), the NSFC (no. 31270306 to YW; 31121002 to WHW) and the “111” Project (no. B06003) from China.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest


This work shows that the Arabidopsis K+ channel TPK3 is located at the thylakoid membrane and regulates the composition of pmf across the thylakoid membrane via ion counterbalancing. TPK3 controls the size and composition of the pmf, directly affects the light utilization and dissipation. These results indicate the crucial role of K+ channel in plant photosynthesis.


This report shows that the Arabidopsis K+-efflux antiporters KEA1 and KEA2 are located at the inner envelope membrane of chloroplasts, while KEA3 is target to the thylakoid membrane. These three transporters control the chloroplast pH homeostasis and osmoregulation, and consequently influence the pmf across the thylakoid membrane and play fundamental role in photosynthetic regulation.


This study suggests a new function of K+ in plant vascular tissues. The K+ circulating in the phloem serves as a decentralized energy storage that
can be used to overcome local energy limitations. The post-translational modification of Arabidopsis AKT2 K+ channel efficiently assists the plasma membrane H+-ATPase in energizing the transmembrane phloem (re)loading processes.


This research reports the functions of K+ transporters (KUP2, 6, 8) in Arabidopsis responses to osmotic stress. The triple mutants kup2/6/8 exhibited enhanced cell expansion and decreased the survival of drought stress. These K+ transporters might mediate the K+ efflux in Arabidopsis and are regulated directly via an ABA signaling complex.


This study reports that the 26 natural accessions of Arabidopsis adopt two different strategies in root architecture under K+ starvation conditions, arising from a major trade-off between main root and lateral root elongation. The QTL analysis identified some genetic loci that control the K+-specific root architecture traits. The results suggest that identification of K+-specific root architecture genes may provide useful information for genetic improvement of plant K+ uptake efficiency.


In this report, the Zinc-Induced Facilitator-Like 1 (ZIF1L1) was identified as an Arabidopsis H+-coupled K+ transporter that has two isoforms ZIF1L1.1 and ZIF1L1.3. ZIF1L1.1 indirectly modulates the shootward auxin transport at the root tip by regulating the PIN2 abundance at the plasma membrane. ZIF1L1.3 is involved in the drought tolerance by regulating stomatal closure. The results indicate the underlying relationship between K+ transport and auxin transport.


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This work shows that an inward K+ channel OsAKT1 is crucial for the K+ uptake in rice. The lesion of OsAKT1 results in the low-K+-sensitive phenotype and reduction of rice yield. The K+ transport activity of OsAKT1 is positively regulated by the protein kinase OsCIPK23 and the calcium sensor OsCBL1. This work demonstrated an important molecular mechanism of K+ uptake in rice and may provide useful information for the genetic improvement of rice K+ uptake efficiency.


This study presents the crystal structures of the NAF-truncated and pseudophosphorylated kinase domains of CIPK23 and CIPK24 (SO2, salt overly sensitive 2). The structure analysis indicates that CIPK kinase activity necessarily requires the coordinated releases of the activation loop from the active site and of the NAF motif from the nucleotide-binding site. The presented structural information is helpful to elucidate the regulatory mechanism of CIPK protein kinases in plant responses to ionic stress (K deficiency or salt stress).


