Potassium

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Abstract Potassium (K) is the most abundant inorganic cation in plants. It is required for the activation of many enzymes, as a cellular osmoticum for rapidly expanding cells, and as a counter cation for anion accumulation and electrogenic transport processes. This chapter describes (1) the symptoms of potassium deficiency and the acclimatory responses of plants to potassium starvation, (2) the mechanisms by which roots acquire K^+ from the soil and K^+ is transported between tissues, and (3) the molecular biology of the transport proteins that catalyse K^+ influx and efflux across the plasma membrane and tonoplast of plant cells to effect K^+ uptake and redistribution within the plant, cell expansion and shrinking, and cytoplasmic K^+ homeostasis.

1 Potassium is an Essential Mineral Element

1.1 Physiological Functions of Potassium

Potassium (K) is the most abundant inorganic cation in plants, comprising up to 10% of a plant's dry weight (Broadley et al. 2004; Watanabe et al. 2007). It is concentrated in growing tissues and reproductive organs, reflecting the vital functions of K^+ in cell metabolism and extension growth. Potassium is required for the activation of many enzymes including those of energy metabolism, protein synthesis and solute transport (Leigh and Wyn Jones 1984; Mengel et al. 2001; Amtmann et al. 2008; Britto and Kronzucker 2008). For optimal performance, K^+ concentrations in metabolically active compartments, such as the cytosol, the nucleus, the stroma of chloroplasts and the matrix of mitochondria, must be maintained at about

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100 to 150 mM (Fig. 1; Leigh and Wyn Jones 1984). Potassium is also required as a counter cation for the neutralisation of fixed negative charges, for the maintenance of trans-membrane voltage gradients, for cytoplasmic pH homeostasis, and for the transport of inorganic anions and metabolites both within and outside the cell (Leigh and Wyn Jones 1984; Mengel et al. 2001; Britto and Kronzucker 2008).

The uptake of K^+ by plant cells, and its accumulation in vacuoles, is the primary driver for their osmotic expansion (Mengel et al. 2001). Rapid cell expansion relies on high mobility of the active osmoticum and, for this reason, only a few other inorganic ions can replace K^+ in this role (Amtmann et al. 2006). However, once cell expansion is over, K^+ can be removed from the vacuole and turgor maintained by less mobile osmotica, such as sugars, organic acids and compatible solutes (Amtmann et al. 2006). The lowest limit for vacuolar K^+ concentration appears to be 10–20 mM, which is thought to reflect a maximum trans-tonoplast voltage of about −40 to −60 mV (Fig. 1; Leigh and Wyn Jones 1984).

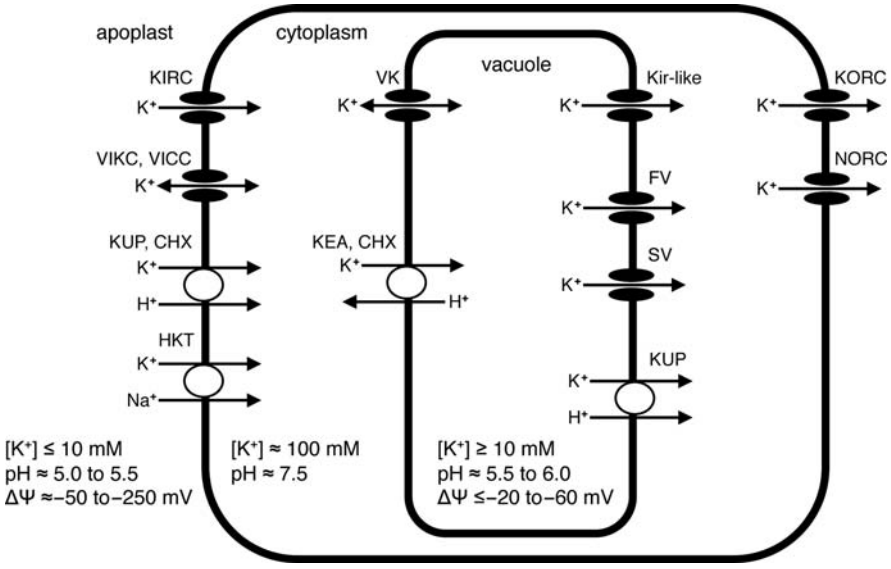

Fig. 1 Electrochemical gradients and subcellular locations of K transporters in a stereotypical cell of *Arabidopsis thaliana*. In the plasma membrane there are inward-rectified K channels (KIRCs) encoded by *AtAKT1*, *AtAKT5*, *AtSPIK*, *AtKAT1*, *AtKAT2*, and *AtKC1*, outward-rectified K channels (KORCs) encoded by *AtSKOR* and *AtGORK*, voltage-independent K^+-channels (VIKCs) encoded by *AtAKT2/3* and *AtTPK4*, voltage-independent cation channels (VICCs) encoded by members of the *AtCNGC* and *AtGLR* gene families, H^+/K^+-symporters (KUPs) encoded by members of the *AtKT/HAK/KUP* gene family, H^+/cation-symporters (CHX), such as *AtCHX13*, and the Na^+/K^+-symporter *AtHKT1*. In the tonoplast there are fast-activating vacuolar (FV) channels, whose genetic identity is unknown, slowly-activating vacuolar (SV) channels, encoded by *AtTPC1*, vacuolar K^+ (VK) channels, encoded by members of the *AtTPK* gene family, Kir-like channels, encoded by *AtKCO3*, H^+/K^+-syporters (KUPs) encoded by members of the *AtKT/HAK/KUP* gene family, and H^+/cation-antiporters (KEA, CHX) encoded by members of the *AtKEA*, *AtCHX* and *AtNHX* gene families

The accumulation of K^+ is essential for the growth of the root system, both for cell expansion in the elongation zone and for the elongation of root hair cells (Dolan and Davies 2004). It is also required for leaf expansion, for the elongation of pollen tubes towards fertile ovules (Mouline et al. 2002) and for the enlargement of fruits and tubers. The rapid accumulation and loss of K^+ by guard cells controls the opening and closing of stomata and, thereby, gas exchange and transpiration (Amtmann and Blatt 2009). The redistribution of K^+ between cells within tissues underpins the bending of roots and coleoptiles in response to gravity (Philippar et al. 1999), leaf movements in sensitive plants in response to shaking and touch, the closing of traps in carnivorous plants, and the diurnal and circadian movements of leaves in response to light signals or an endogenous "clock" (Moran 2007). These cellular phenomena are often attributed to plasma-membrane hyperpolarisation, apoplastic acidification, and an increase in the number and/or activity of transport proteins catalysing K^+ influx across the plant membrane and sequestration in the vacuole. Expanding cells are often characterised by high cytosolic Ca^{2+} concentrations ($[Ca^{2+}]_{cyt}$), and the direction of elongation growth is determined by an elevated $[Ca^{2+}]_{cyt}$ at the apex of the growing cell (White and Broadley 2003; Dolan and Davies 2004; Cheung and Wu 2008; Frietsch et al. 2008). The rapid loss of K^+ from guard cells during stomatal closure (Amtmann and Blatt 2009) and from the shrinking pulvinor cells during leaf movements (Moran 2007), is effected by plasma membrane depolarisation and the opening of K^+ channels that facilitate K^+ efflux from the vacuole and across the plasma membrane. The latter responses appear to be controlled by strictly coordinated temporal changes in both cytosolic pH and Ca^{2+} concentrations through cascades of protein phosphorylation (White 2000; Moran 2007; Amtmann and Blatt 2009).

1.2 Symptoms of Potassium Deficiency

The response of plant growth to increasing K^+ availability follows a hyperbolic relationship and plants can acquire sufficient K^+ for growth from solutions containing micromolar K^+ concentrations, provided the K^+ supply to the roots matches the minimal demand of the plant and NH_4^+ is absent from the rhizosphere (e.g. Asher and Ozanne 1967; Wild et al. 1974; Spear et al. 1978a; Siddiqi and Glass 1983a; White 1993, 1997b). The 'critical' tissue K^+ concentration, at which growth and development attain 90% of their maxima, approximates 5–20 μmol g^{-1} FW (Leigh and Wyn Jones 1984). Shoot tissues reach their critical tissue K^+ concentrations at a lower K^+ supply than root tissues (Fig. 2a, Asher and Ozanne 1967; Spear et al. 1978a; White 1993, 1997b). Tissue concentrations of readily-available cations, such as Na^+, Ca^{2+} and Mg^{2+}, are generally higher when K^+ is in short supply, and lower critical tissue K^+ concentrations are reported when other cations that can be used as cellular osmotica are available to the plant (Johnson 1973; Leigh and Wyn Jones 1984; Barraclough and Leigh 1993). When K^+ is readily available, tissue K^+

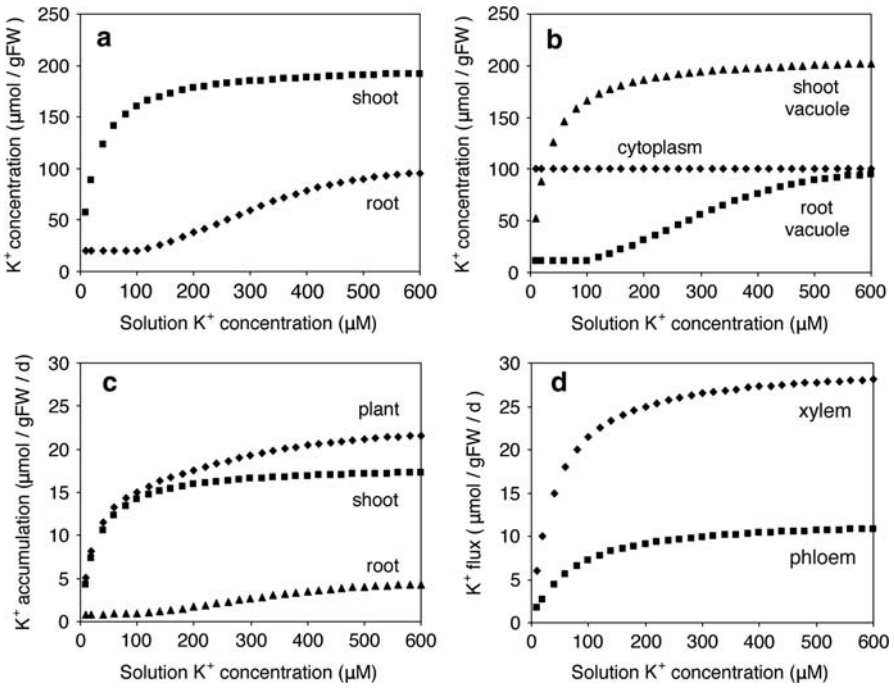

Fig. 2 Potassium nutrition of 14-day old rye plants growing hydroponically. (**a**) Relationships between solution K^+ concentration ($[K^+]_{ext}$) and root (*diamonds*) and shoot (*squares*) K^+ concentrations. (**b**) Predicted relationships between $[K^+]_{ext}$ and vacuolar K^+ concentrations in roots (*squares*) and shoots (*triangles*). These calculations assumed a cytoplasmic volume of 10% containing 100 mM K^+ and no apoplastic contribution (Leigh and Wyn Jones 1984). (**c**) Relationships between $[K^+]_{ext}$ and K^+ uptake (*diamonds*), root K^+ accumulation (*triangles*) and shoot K^+ accumulation (*squares*). (**d**) Relationships between $[K^+]_{ext}$ and K^+ fluxes in the xylem (*diamonds*) and phloem (*squares*). All relationships based on data from White (1993) and White (1997b)

concentrations often exceed those required for maximal growth (Leigh and Wyn Jones 1984).

Plants experiencing mild K-deficiency rarely show overt visible symptoms (Mengel et al. 2001; Fageria 2009). One reason for this is that K^+ is readily redistributed within the plant via the phloem from mature to developing tissues. Plants experiencing more severe K-deficiency exhibit symptoms consistent with the vital functions of this element (Johnson 1973; Bould et al. 1983; Amtmann et al. 2008). They exhibit a scorching along the margins of older leaves. They grow slowly, have short stature and poorly-developed root systems, and are more susceptible to frost damage, pests and diseases. Both leaves and roots of K-deficient plants are short-lived. Stems are weak, and seed and fruit are small and shrivelled. The physiological symptoms of K-deficiency include impaired phloem transport, particularly of sucrose, increased leaf carbohydrate concentrations, a reduction in chlorophyll concentrations and photosynthetic capacity, decreased water content,

decreased turgor, impaired stomatal regulation and reduced transpiration (Cakmak et al. 1994; Mengel et al. 2001; Hermans et al. 2006; Amtmann et al. 2008).

The decline in photosynthesis observed in K-deficient plants appears to be a consequence of sucrose accumulation in leaves and its effects on gene expression (Hermans et al. 2006). Leaves of K-deficient plants accumulate sugars, including sucrose, but rarely starch (Bould et al. 1983; Hermans et al. 2006; Amtmann et al. 2008). Although these solutes can replace K^+ as a cellular osmoticum, this phenomenon is likely to be a consequence of impaired sucrose export from leaves of K-deficient plants, which can be attributed to a requirement for K^+ for loading sucrose into the phloem (Mengel et al. 2001; Deeken et al. 2002; Hermans et al. 2006). An inverse relationship between phloem sucrose concentration and plant K status has been observed across a wide range of nutritional treatments. In addition, concentrations of amide nitrogen, amino acids (lysine, arginine and tyrosine), and polyamines, such as putrescine and agmatine, often increase dramatically in K-deficient plants, and have been used to diagnose K-deficiency in crop plants (Bould et al. 1983).

1.3 Acclimatory Responses to Potassium Starvation

Plants have evolved various morphological and physiological adaptations to acquire K^+ and cope with low tissue K^+ concentrations when this element is in short supply. In contrast to N and P deficiencies, K-deficiency does not generally result in greater biomass partitioning to roots or in major alterations to root architecture (Hermans et al. 2006). However, the expression of genes encoding high-affinity K^+-influx systems increases when plants lack K^+ (e.g. Wang et al. 1998; Shin and Schachtman 2004; Gierth et al. 2005; Hampton et al. 2005; Qi et al. 2008). Increased K^+ uptake is likely to reduce rhizosphere K^+ concentrations and accelerate K^+ diffusion to the root surface and desorption from "exchangeable" binding sites in the soil. Physiological adaptations to low K supply include the replacement of vacuolar K with alternative osmotica, redistribution of K^+ from mature to developing tissues, and reducing plant growth to maintain appropriate tissue K^+ concentrations for cell function.

Amtmann et al. (2006) suggested that fluctuations in apoplastic K^+ concentration and the membrane potential of root cells are most likely to initiate immediate acclimatory responses to reduced K^+ phytoavailability, since cytoplasmic K concentrations ($[K^+]_{cyt}$) are relatively unaffected by K^+ supply (Walker et al. 1996, 1998), and that K^+ channels are the immediate targets for regulating K^+ fluxes (Fig. 3a). The voltage-dependence of both inward rectifying K^+ channels (KIRCs) and outward-rectifying K^+ channels (KORCs) in the plasma membrane of root cells respond to the K^+ gradient between apoplast and cytoplasm, such that they mediate only K^+ influx and K^+ efflux, respectively (White 1997a; Amtmann et al. 2006; Amtmann and Blatt 2009). The opening of these channels determines the direction of K^+ uptake across the plasma membrane, which can be promoted if an appropriate hyperpolarisation of the plasma membrane can be maintained by the activity of the

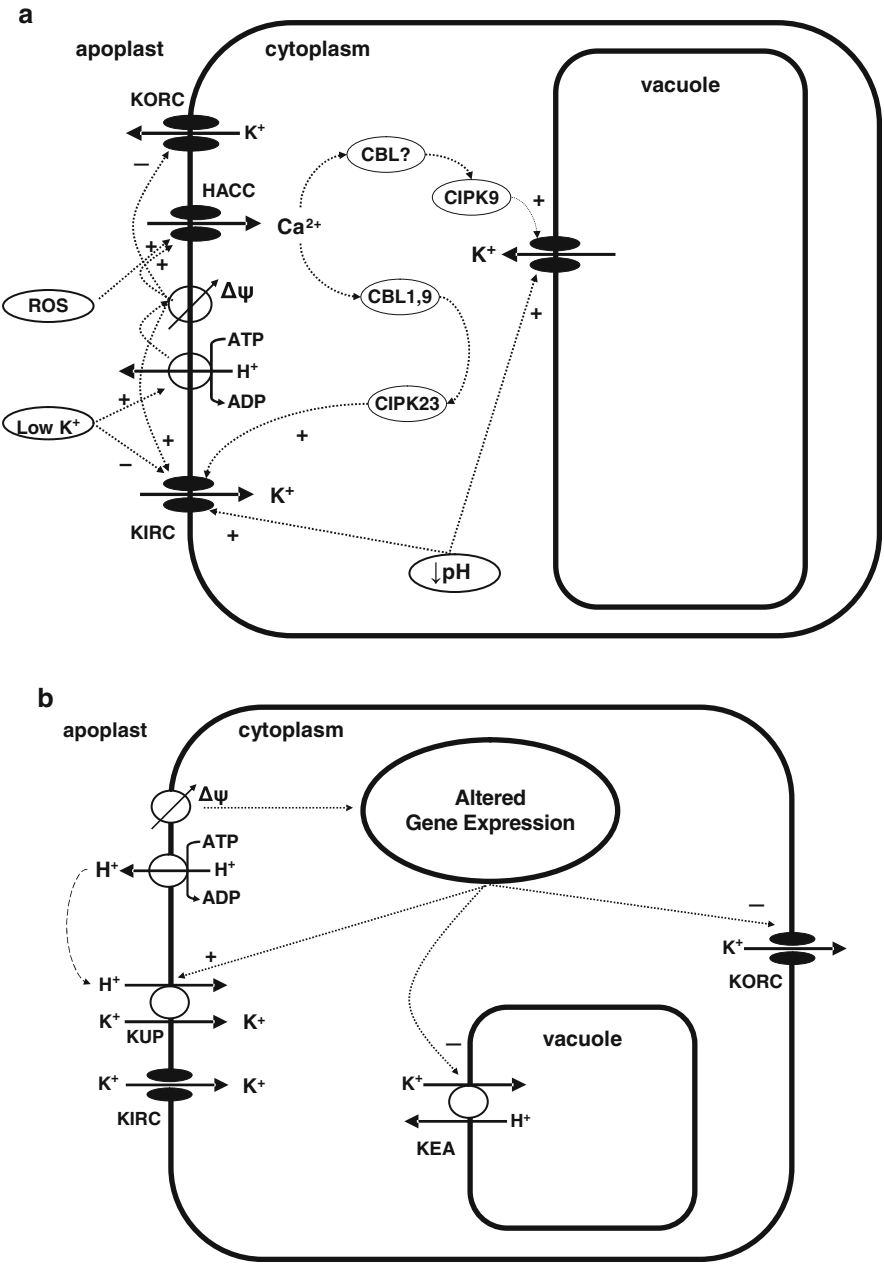

Fig. 3 Immediate acclimatory responses in root cells to reduced K^+ supply. (**a**) *Initial events*. Low external K^+ causes hyperpolarisation of the plasma membrane through reduced K^+ influx and increased activity of the plasma membrane H^+-ATPase. Hyperpolarisation of the plasma membrane results in a greater inward K^+ electrochemical gradient, reduced opening of outward-rectified K^+ channels (KORCs), and increased opening of inward-rectified K^+ channels (KIRCs).

plasma membrane H^+-ATPase (Amtmann et al. 2006; Amtmann and Blatt 2009). The activities of KIRCs and KORCs are regulated by apoplastic and cytosolic pH, and by $[Ca^{2+}]_{cyt}$, both directly and indirectly through posttranslational modification (Amtmann et al. 2006; Amtmann and Blatt 2009). In *Arabidopsis thaliana*, coupling between a calcineurin B-like protein (CBL)-interacting protein kinase (CIPK23) and two upstream Ca^{2+}-binding proteins (CBL1 and CBL9) in tandem with a 2C-type protein phosphatase regulates the activity of AtAKT1, the major K^+ channel involved in nutritional K^+ uptake by roots (Amtmann et al. 2006; Amtmann and Blatt 2009). It is thought that low rhizosphere K^+ concentrations cause plasma membrane hyperpolarisation and initiate the production of ROS through the activity of the NADPH oxidase, AtrbohC. These events increase Ca^{2+} influx through hyperpolarisation-activated Ca^{2+} channels in the plasma membrane and $[Ca^{2+}]_{cyt}$, which results in the phosphorylation and opening of AtAKT1 through the CBL/CIPK23 cascade. In parallel, a CBL/CIPK9 cascade initiated by increased $[Ca^{2+}]_{cyt}$ and subject to transcriptional regulation is thought to open K^+ channels in the tonoplast. A decrease in cytosolic pH, which is associated with decreasing cytosolic K^+ concentrations in particular root cells (Walker et al. 1996, 1998), would also increase K^+ influx through KIRCs and K^+ release from the vacuole. The magnitude and direction of K^+ fluxes across both plasma membrane and tonoplast can also be influenced by heteromerisation of subunits, and interactions with beta-subunits, G-proteins, and 14-3-3 proteins (Zimmermann and Chérel 2005; Gambale and Uozumi 2006; Amtmann et al. 2006; Lebaudy et al. 2007, 2008; Amtmann and Blatt 2009).

In addition to the immediate effects of hyperpolarisation of root cells on the activity of plasma membrane KIRCs and KORCs, it has recently been observed that the expression of genes encoding high-affinity H^+/K^+ symporters, such as *AtHAK5* in *A. thaliana*, is increased in response to prolonged hyperpolarisation of root cells (Fig. 3b; Nieves-Cordones et al. 2008). This serves to increase K^+ uptake by roots over a period of hours to days. The initial signal transduction pathway effecting this

Fig. 3 (continued) Thus, K^+ influx is accelerated. Increased opening of KIRCs is effected both by the more negative membrane potential and by protein phosphorylation coordinated through a cytoplasmic signal transduction cascade involving CBL1, CBL9, and CIPK23, which is initiated by Ca^{2+} influx through hyperpolarisation-activated calcium channels (HACCs). Increased opening of HACCs is promoted by the production of reactive oxygen species (ROS) through the activity of a NADPH oxidase, AtrbohC. Increased cytosolic Ca^{2+} also results in increased opening of vacuolar K^+ channels through a cytoplasmic signal transduction cascade involving CBLs and CIPK9. A decrease in cytosolic pH, which is associated with decreasing cytosolic K^+ concentrations in particular root cells, increases the opening of KIRCs and vacuolar K^+ channels. (**b**) *Altered gene expression*. Prolonged hyperpolarisation of the plasma membrane increases the expression of genes encoding high-affinity H^+/K^+ symporters, such as AtHAK5 in *Arabidopsis thaliana*, thereby increasing root K^+ influx capacity. Also in *A. thaliana*, the expression of genes encoding a putative vacuolar K^+/H^+ antiporter (AtKEA5), the KORC AtSKOR, which is thought to load K^+ into the xylem, and AtAKT2, a KIRC responsible for the recirculation of K^+ from the shoot to the root, are all reduced by low K^+ phytoavailability

could also include $[Ca^{2+}]_{cyt}$ signals. In *A. thaliana*, the expression of genes encoding a putative vacuolar K^+/H^+ antiporter (AtKEA5), the KORC AtSKOR, which is thought to load K^+ into the xylem, and AtAKT2, a KIRC responsible for the recirculation of K^+ from the shoot to the root, are all reduced by low K^+ phytoavailability (Zimmermann and Chérel 2005; Schachtman and Shin 2007). These are thought to maintain the $[K^+]_{cyt}$ of root cells and to restrict long-distance K^+ transport, which might act as a signal of plant K^+ status (Drew et al. 1990; White 1997b; Amtmann et al. 2006; Schachtman and Shin 2007).

Subsequent morphological and physiological adaptations in response to prolonged K^+ starvation could be triggered by an increase in ethylene production, which, together with an increase in ROS, stimulates the initiation and elongation of root hairs (Dolan and Davies 2004, White et al. 2005), and jasmonic acid biosynthesis, which is thought to be responsible for the characteristic accumulation of polyamines observed in K^+-deficient plants and for an increased systemic resistance to particular pests and pathogens (Amtmann et al. 2008). Other K-deficiency symptoms appear to arise as secondary consequences of impaired energy metabolism, redistribution of solutes within the plant and/or reduced growth.

2 The Acquisition and Cellular Distribution of Potassium

2.1 Potassium Acquisition by Plant Roots

The solution K^+ concentration in most soils lies between 0.1 and 1 mM. This represents only 0.1%–0.2% of the total soil K, of which 1%–2% is "exchangeable" K^+, 1%–10% is "non-exchangeable" K^+ associated with clay lattices, and 90%–98% is present as K-minerals (Mengel et al. 2001; Rengel and Damon 2008; Fageria 2009). A large fraction of the total soil K available to plants resides in the topsoil. Diffusion through and mass flow of the soil solution contribute most to the delivery of K^+ to the root surface (Jungk and Claassen 1997). In circumstances when the roots' capacity for K^+ uptake exceeds the rate at which K^+ can be delivered to the rhizosphere, K^+ acquisition by plants is determined by the K^+ concentration gradient between the rhizosphere and the soil solution and by the flow of water to the root. Thus, factors influencing K^+ acquisition by plants include (1) the rate of K^+ uptake across the plasma membrane of root cells, which reduces the K^+ concentration in the rhizosphere solution, (2) the release of non-exchangeable K^+ by root exudates, which increases K^+ concentration and availability in the soil solution, (3) the proliferation of roots into the soil volume, which increases the area for K^+ uptake and also reduces the distance required for K^+ diffusion and water flow, and (4) the transpiration rate of the plant, which drives mass flow of the soil solution to the root (Jungk and Claassen 1997; Rengel and Damon 2008).

Potassium uptake by roots and accumulation by plants are determined by the K^+ uptake capacity of the roots, the K^+ concentration at the root surface, and the

replenishment of rhizosphere K^+. The relationship between root K^+ uptake (plant accumulation) and K^+ concentration in the rhizosphere generally follows the sum of a hyperbolic and a linear function (Fig. 2c; Kochian and Lucas 1988; Leigh and Wyn Jones 1984; Mengel et al. 2001; Britto and Kronzucker 2008). When grown under identical conditions, plant species differ in (a) the relationship between K^+ influx (and accumulation) and rhizosphere K^+ concentration (e.g. Asher and Ozanne 1967; Wild et al. 1974; Spear et al. 1978a, b; Pettersson and Jensén 1983; Steingrobe and Claassen 2000; Jungk 2001; El Dessougi et al. 2002) and (b) the selectivity of monovalent cation accumulation (e.g. Broadley et al. 2004; White et al. 2004). These observations suggest that the complement of proteins catalysing K^+ uptake by root cells differs between plant species. Similarly, genotypes of crop species differ in the relationship between rhizosphere K^+ concentration and K^+ uptake by roots (e.g. Glass and Perley 1980; Siddiqi and Glass 1983a, b; Siddiqi et al. 1987; Chen and Gabelman 1995, 2000; Trehan 2005; Zhang et al. 2007; Rengel and Damon 2008).

2.2 *Thermodynamic Consideration of K^+ Uptake and Distribution in Root Cells*

The hypothesis that K^+ influx to root cells is mediated by distinct "high-affinity" and "low-affinity" transporters, operating at low (<1 mM) and high (>1 mM) rhizosphere K^+ concentrations, respectively, has been modified little since its conception over 50 years ago (Epstein and Bloom 2005; Britto and Kronzucker 2008). However, it is not the "affinity" for K^+ that differentiates K^+ transport mechanisms in the root plasma membrane, but their coupling to pH and voltage gradients (Fig. 1, Gierth and Mäser 2007; Britto and Kronzucker 2008; Karley and White 2009). Electrophysiological studies indicate that K^+ influx across the plasma membrane of root cells occurs against its electrochemical gradient at rhizosphere concentrations less than about 1 mM K^+ (Maathuis and Sanders 1993; Walker et al. 1996). This can be catalysed by H^+/K^+ symporters in the plasma membrane, energized by the pH and voltage gradients generated at the plasma membrane H^+-ATPase, which are capable of accumulating K^+ from rhizosphere solutions containing less than 100 nM K^+ (Fig. 1). At rhizosphere K^+ concentrations above 1 mM, which are common in well-fertilised agricultural soils, K^+ influx to root cells can be energised by the voltage gradient alone and facilitated by K^+ channels. In roots of K-starved plants, K^+ appears to be close to thermodynamic equilibrium across the tonoplast, suggesting that K^+ channels dominate K^+ fluxes across this membrane under these conditions (Maathuis and Sanders 1993; Walker et al. 1996). In K-replete plants, however, which have substantially higher vacuolar K^+ concentrations than K-starved plants, K^+ must be actively transported into the vacuoles of root cells. This is thought to be catalysed by K^+/H^+-antiporters energised by the H^+ gradient generated by the vacuolar H^+-ATPase and/or H^+-PPiase. Potassium efflux from the

vacuole can be mediated by K^+-channels in root cells of both K-starved and K-replete plants.

2.3 *Cellular K^+ Homeostasis*

Cytosolic K^+ concentrations around 100 mM are generally maintained in plant cells to ensure optimal function (Jeschke 1984; Leigh and Wyn Jones 1984, 1986; Memon et al. 1985; Drew et al. 1990; White et al. 1991; Britto and Kronzucker 2008). This is effected by the redistribution of K^+ between vacuolar and cytosolic compartments within the cell and by the redistribution of K^+ from mature and/or senescing tissues to developing tissues within the plant.

In K^+ replete plants, $[K^+]_{cyt}$ is similar in both root and leaf cells, but vacuolar K^+ concentrations in leaf cells are about double those in root cells (Fig. 2b; Cuin et al. 2003). When plants lack K^+, vacuolar K^+ is redistributed to the cytoplasm (Memon et al. 1985; Huang and van Steveninck 1989; Walker et al. 1996, 1998; Cuin et al. 2003). Root tissues require a higher K^+ supply than shoot tissues to achieve their critical K^+ concentration (Fig. 2a), which suggests that root cells might be able to tolerate lower vacuolar K^+ concentrations than shoot cells (White 1993, 1997b). Differences between barley varieties in their ability to mobilise K^+ from the vacuole to the cytoplasm of root cells at low K^+ supply appear to correlate with their sensitivity of growth to K-starvation (Memon et al. 1985). In addition, different cell types within the root and shoot display distinct responses to K-starvation in the redistribution of K^+ between vacuolar and cytosolic compartments. In barley roots, the $[K^+]_{cyt}$ of epidermal cells declines when the vacuolar K^+ activity falls below about 25 mM, but the $[K^+]_{cyt}$ of cortical cells remains constant irrespective of K^+ status (Walker et al. 1996, 1998). The $[K^+]_{cyt}$ in expanding cells of the seminal and nodal roots of barley also declines during K-starvation (Walker et al. 1998), despite higher vacuolar K^+ concentrations being present in cells closer to the root meristem during K^+ starvation, presumably to drive cell expansion and to buffer essential meristematic activities against the vagaries of K^+ supply (Huang and van Steveninck 1989). By contrast, in barley plants under salt stress, $[K^+]_{cyt}$ in leaf epidermal cells can be as low as 15 mM, despite vacuolar K^+ activities of 50 mM, whereas $[K^+]_{cyt}$ in leaf mesophyll cells is maintained at approximately 70 mM, presumably to minimise any detrimental effects on photosynthesis (Cuin et al. 2003). Cellular K^+ concentrations in leaf mesophyll cells also exceed those in epidermal cells in K-starved plants (James et al. 2006).

3 Potassium Transport Within the Plant

At submillimolar rhizosphere K^+ concentrations, K^+ influx to root cells appears to be catalysed by H^+/K^+-symporters, whereas at rhizosphere K^+ concentrations greater than about 1 mM, K^+ influx can be mediated by K^+ channels (Sect. 2.2).

It is noteworthy, however, that unidirectional K^+ influx and K^+ efflux across the plasma membrane of root cells are far greater than the rate of K^+ uptake (accumulation) by the plant (Jeschke 1983; White et al. 1991; Britto and Kronzucker 2008). This is thought to reflect (1) the role of K^+ in charge-balancing fluxes of other ions important for plant nutrition and/or cell signalling and (2) an absolute requirement for $[K^+]_{cyt}$ homeostasis. Rapid K^+ efflux from root cells is effected by depolarisation of the plasma membrane and is mediated by the opening of KORCs (White 1997a; Moran 2007; Amtmann and Blatt 2009). Voltage-insensitive cation channels (VICCs) are also present in the plasma membrane of root cells (White 1997a; Hampton et al. 2005; Demidchik and Maathuis 2007). These channels, which can catalyse both K^+ influx and K^+ efflux from root cells, do not appear to contribute to nutritional K^+ uptake, but are thought to balance electrically other transport processes and, since they also catalyse Ca^{2+} influx, to contribute to cytosolic Ca^{2+} homeostasis and signalling (White and Broadley 2003; Hampton et al. 2005; Demidchik and Maathuis 2007).

The capacity for influx of K^+ and Rb^+, which is often used as a tracer for K^+, to roots increase dramatically with decreasing root K^+ concentration in K-starved plants (e.g. Glass 1976; Pettersson and Jensén 1979, 1983; Wrona and Epstein 1985; White et al. 1987; White 1997b; Shin and Schachtman 2004). Recently, this has been attributed to increased expression of genes encoding high-affinity H^+/K^+ symporters, such as *AtHAK5* in *A. thaliana* and its homologs in tomato (*LeHAK5*), pepper (*CaHAK1*), barley (*HvHAK1*), rice (*OsHAK1*), and other plant species (Hampton et al. 2005; Gierth and Mäser 2007; Nieves-Cordones et al. 2008; Qi et al. 2008). There is some evidence that these transcriptional responses to K-starvation are initiated by the prolonged hyperpolarisation of root cells when rhizosphere K^+ concentrations are low (Nieves-Cordones et al. 2008). However, older experiments on plants whose root systems were divided between solutions with high and low K^+ concentrations demonstrated that roots supplied with high K^+-concentrations have enhanced K^+ uptake in K-starved plants, suggesting that, in addition to cell membrane potential, plant K-status controls K^+ uptake through a systemic signal (Drew et al. 1990). Phloem K^+ concentration and/or K^+ flux have been postulated to be this signal.

Following uptake by epidermal and cortical cells, K^+ is transported symplastically across the root through plasmodesmata to the stelar parenchyma cells, where it is loaded into the xylem (Kochian and Lucas 1988). All regions of the root contribute to loading the xylem with K^+, and it can be estimated that over 90% of the K^+ entering the xylem is delivered through a symplastic route (P.J. White, unpublished calculations). This is consistent with the recent observation that increased suberisation of the root endodermis in the *enhanced suberin 1* (*esb1*) mutant of *A. thaliana* has little effect on shoot K concentration (Baxter et al. 2009). The voltage across the symplast/xylem boundary is about −80 mV (De Boer and Volkov 2003), which allows KORCs to load the xylem with K^+ concentrations up to about 4 mM. Loading the xylem with higher K^+ concentrations through KORCs requires a substantial depolarisation of the stelar parenchyma cells. The xylem K^+ concentration ranges from about 2 to 25 mM, depending upon a variety of factors

(Marschner et al. 1997). Xylem K^+ concentration increases with increasing K^+ concentration in the rhizosphere (Fig. 2d; e.g. Armstrong and Kirby 1979; White 1997b; Peuke et al. 2002). The presence of high concentrations of Na^+, Ca^{2+}, or NH_4^+ in the rhizosphere reduces K^+ uptake and xylem K^+ concentrations (e.g. Munns 1985; Jeschke et al. 1992; Lu et al. 2005). Xylem sap K^+ concentrations are also reduced in P-starved plants (Jeschke et al. 1997). Potassium uptake, xylem K^+ concentration, and K^+ flux to the shoot are all affected by transpiration and also exhibit diurnal cycles driven by illumination (e.g. Armstrong and Kirby 1979; Jeschke 1984; Schurr and Schulze 1995; Macduff and Dhanoa 1996; Macduff et al. 1997; Herdel et al. 2001; Peuke et al. 2001; Malone et al. 2002; Siebrecht et al. 2003; Goodger et al. 2005). Although greater water flow through the xylem reduces sap K^+ concentration, it generally increases K^+ flux to the shoot and K^+ uptake by roots. Both xylem K^+ concentrations and K^+ fluxes to the shoot are reduced in plants during drought, which is thought to be a consequence of (1) reduced expression of genes encoding K^+ channels that load K^+ into the xylem, such as *AtSKOR* in *A. thaliana*, and (2) reduced transpirational water losses through stomatal closure (Gaymard et al. 1998; De Boer and Volkov 2003; Goodger et al. 2005).

The delivery of K^+ within the shoot via the xylem is largely determined by transpirational water flows. The larger vessels are designed for the rapid onward movement of sap, whereas the smaller vessels are important for solute transfer between the xylem and the surrounding tissues. The apoplastic K^+ concentration at the point of xylem unloading approximates 5–20 mM, which allows K^+ to enter the shoot symplast through KIRCs and VICCs in the plasma membrane of the bundle sheath cells of the smaller veins (Keunecke et al. 2001). With the obvious exception of guard cells, which adjust their K^+ concentration to regulate stomatal aperture, and their neighbouring epidermal cells, most cells in leaves of K^+-replete plants appear to have similar K^+ concentrations (Leigh and Storey 1993; Fricke et al. 1994). Potassium is redistributed from mature leaves to developing tissues via the phloem. The K^+ concentration in phloem sap ranges from about 10 to 150 mM, depending upon a variety of environmental factors including K availability (Marschner et al. 1997). The resting potential of the sieve element plasma membrane lies between −150 mV and −50 mV, depending upon plant species, and contains a weakly inwardly-rectifying KIRC with electrophysiological properties resembling AtAKT2/3 of *A. thaliana*, which facilitates K^+ influx to the phloem (Deeken et al. 2002; Hafke et al. 2007). Since phloem K^+ concentrations are lower in plants with lower K-status (Fig. 2d; Mengel and Haeder 1977; Drew et al. 1990; Cakmak et al. 1994; Peuke et al. 2002; Gould et al. 2004), it is thought that phloem K^+ concentration and/or the K^+ flux from the shoot to the root might regulate K^+ uptake by roots in response to shoot K status (Drew et al. 1990; White 1997b; Amtmann et al. 2006). To effect charge balance, concentrations of other cations, such as Na^+, are often increased in the phloem sap of K-starved plants (e.g. Peuke et al. 2002).

In addition to being a putative signal for plant K status, K^+ recirculation within the plant via the phloem serves a number of other functions, such as (1) maintaining

cation-anion balance within the plant, especially when nitrate assimilation occurs in the shoot, (2) enabling the loading of sugars, organic acids, and amino acids into the phloem, (3) contributing to the driving force for mass flow of solution, (4) redistributing K^+ from senescing to developing tissues, (5) meeting the K demand of elongating cells in plants subject to variable rhizosphere K availability, and (6) maintaining high K/Na quotients in sensitive meristematic tissues (Marschner et al. 1997). It has been estimated that up to 90% of the K^+ delivered to the shoot via the xylem is exported back to the root via the phloem (Armstrong and Kirby 1979; Jeschke and Pate 1991; Jeschke et al. 1992, 1995, 1997; Peuke and Jeschke 1993; Marschner et al. 1997; White 1997b; Peuke et al. 2002; Lu et al. 2005).

4 The Molecular Biology of K^+ Transporters

Potassium influx to plant cells can be mediated by cation/H^+ symporters, K^+/Na^+ symporters, and/or K^+-permeable cation channels, such as KIRCs, voltage-independent K^+ channels (VIKCs), and VICCs, depending upon the K^+ electrochemical gradient (Fig. 1, Sect. 2.2). Potassium efflux from plant cells occurs through KORCs and non-specific outward-rectifying cation channels (NORCs). Potassium sequestration in vacuoles can be mediated by cation/H^+ antiporters and/or vacuolar K^+ (VK) channels, while K^+ efflux from vacuoles occurs through fast-activating vacuolar (FV) channels, slowly-activating vacuolar (SV) channels, VK channels, and/or cation/H^+ symporters. Since orthologues of *A. thaliana* genes encoding all these K^+ transporters have been found in every angiosperm species studied to date, this section will summarise the molecular biology of K^+ transporters in plant cells with specific reference to *A. thaliana* (Zimmermann and Chérel 2005; Gambale and Uozumi 2006; Lebaudy et al. 2007; Gupta et al. 2008).

Members of two gene families, the K^+ uptake permeases (*KT*/*HAK*/*KUP*) and the cation-H^+ exchangers (*CHXs*) encode plasma membrane K^+/H^+ symporters (Table 1; Gierth and Mäser 2007; Britto and Kronzucker 2008; Zhao et al. 2008). In *A. thaliana*, AtHAK5, AtKUP1, AtKUP2, AtKUP11 and AtCHX13 have been found in plasma membranes of various cell types and are thought to catalyse K^+ influx to cells at low apoplastic K^+ concentrations (Gierth and Mäser 2007; Qi et al. 2008; Rubio et al. 2008; Zhao et al. 2008). Most genes encoding AtKUPs are expressed in roots, with *AtHAK5* and, occasionally, *AtKUP3* being induced by K-starvation (Shin and Schachtman 2004; Hampton et al. 2005; Gierth et al. 2005; Zimmermann and Chérel 2005; Qi et al. 2008; Rubio et al. 2008). The expression of *AtCHX13* is also increased in roots of K-starved plants (Zhao et al. 2008). It is thought that AtHAK5 dominates nutritional K^+ influx to roots of K-starved *A. thaliana* plants (Gierth et al. 2005; Gierth and Mäser 2007; Qi et al. 2008; Rubio et al. 2008). The KUPs are characteristically inhibited, and transcription of their genes reduced, by NH_4^+, which can serve as a useful pharmacological tool to dissect the physiological roles of these transporters (Bañuelos et al. 2002; Martínez-Cordero et al. 2005; Fulgenzi et al. 2008; Nieves-Cordones et al. 2008;

Table 1 Transport proteins implicated in the uptake and distribution of K^+ between plant organs, cell types, and sub-cellular compartments. See text for details

Gene family	Member	Locus	Membrane	Organ	Proposed mechanism	Putative function (s)
KT/HAK/ KUP	AtKUP1	At2g30070	PM	R,St,L,F,Si	K^+/H^+ symport	K^+ influx
	AtKUP2	At2g40540	PM	R,St,L,F,Si	K^+/H^+ symport	K^+ influx
	AtKUP3	At3g02050		R,L,F,Si		
	AtKUP4	At4g23640	TP	R,L,F,Si	K^+/H^+ symport	
	AtKUP5	At4g33530	TP	R,L,F,Si	K^+/H^+ symport	
	AtKUP6	At1g70300		R,L,F,Si	K^+/H^+ symport	
	AtKUP7	At5g09400	TP	R,L,F,Si	K^+/H^+ symport	
	AtKUP8	At5g12880		R,L,F,Si		
	AtKUP9	At4g19960		R,L,F,Si		
	AtKUP10	At1g31120		R,L	K^+/H^+ symport	
	AtKUP11	At2g35060	PM	L	K^+/H^+ symport	
	AtKUP12	At1g60160	CP	R,L,F,Si		
	AtHAK5	At4g13420	PM, ER	R,L,F,Si	K^+/H^+ symport	nutritional K^+ uptake
HKT/Trk	AtHKT1	At4g10310	PM	R,S	$(K^+)/Na^+$ co-transport	phloem Na^+ recirculation
CPA1	AtNHX1	At5g27150	TP	R,L,St,F,P,Si	Cation/H^+ exchange	vacuolar K^+ and Na^+ accumulation
	AtNHX2	At3g05030	TP	R,L,F	Cation/H^+ exchange	vacuolar Na^+ sequestration
	AtNHX3	At5g55470	TP	F,P	Cation/H^+ exchange	vacuolar Na^+ sequestration
	AtNHX4	At3g06370	TP	R	Cation/H^+ exchange	vacuolar Na^+ sequestration
	AtNHX5	At1g54370	TP,EN	R,L,St,F	K^+/H^+ exchange	vacuolar Na^+ sequestration endosomal pH regulation
	AtNHX6	At1g79610	EN			endosomal pH regulation
	AtSOS1 (AtNHX7)	At2g01980	PM		Na^+/H^+ exchange	Na^+ efflux salt tolerance
	AtNHX8	At1g14660	PM	R,H,L	Li^+/H^+ exchange	Li^+ efflux
CPA2	AtCHX1	At1g16380		P		
	AtCHX2	At1g79400		L,P		
	AtCHX3	At5g22900		P		
	AtCHX4	At3g44900		L,P,Sp		
	AtCHX5	At1g08150		L,P,Sp		
	AtCHX6A	At1g08140		R,P		

	AtCHX7	At2g28170		P		
	AtCHX8	At2g28180		L,P		
	AtCHX9	At5g22910		L,P		
	AtCHX10	At3g44930		P		
	AtCHX11	At3g44920		P		
	AtCHX12	At3g44910		L,P		
	AtCHX13	At2g30240	PM	R,F,Si,P	K^+/H^+ symport	K^+ influx
	AtCHX14	At1g06970		R,L,F,P,Sp		
	AtCHX15	At2g13620		L,P	K^+/H^+ symport (?)	
	AtCHX16	At1g64170		R,L,Sp		
	AtCHX17	At4g23700	EN	R,L,F,P,Sp	K^+/H^+ exchange	K^+ homeostasis cytosolic pH regulation
	AtCHX18	At5g41610		R,L,P,Sp		
	AtCHX19	At3g17630		R,L,P,Sp		
	AtCHX20	At3g53720	EN	R,L,F,P,Sp	K^+/H^+ exchange	K^+ homeostasis cytosolic pH regulation
	AtCHX21	At2g31910	PM	R,L,P,Sp	Na^+/H^+ exchange	xylem Na^+ fluxes
	AtCHX22	At2g37910		P		
	AtCHX23	At1g05580	CP	P	K^+/H^+ exchange	K^+ homeostasis cytosolic pH regulation
	AtCHX24	At5g37060		P		
	AtCHX25	At5g58460		P		
	AtCHX26	At5g01680		L,P,Sp		
	AtCHX27	At5g01690		L,P,Sp		
	AtCHX28	At3g52080		R,P,Sp		
CPA2	AtKEA1	At1g01790	TP (?)	R,L,St,F,Si	K^+/H^+ antiport	vacuolar K^+ accumulation
(KEA)	AtKEA2	At4g00630		R,L,F,Si		
	AtKEA3	At4g04850				
	AtKEA4	At2g19600		R,L,F,Si		
	AtKEA5	At5g51710		R,L,F,Si		
	AtKEA6	At5g11800		R,L,F,Si		
Shaker-type	AtAKT1	At2g26650	PM	R,L,P	K^+ channel (KIRC)	nutritional K^+ uptake
	AtAKT2/3	At4g22200	PM	R,St,L,F,Si	K^+ channel (KIRC)	phloem K^+ loading
	AtSPIK	At2g25600	PM	F,P	K^+ channel (KIRC)	osmotic K^+ influx
	AtAKT5	At4g32500	PM	F,P,Si	K^+ channel (KIRC)	

(*continued*)

Table 1 (continued)

Gene family	Member	Locus	Membrane	Organ	Proposed mechanism	Putative function (s)
	AtKAT1	At5g46240	PM	R,St,L,Si	K^+ channel (KIRC)	osmotic K^+ influx
	AtKAT2	At4g18290	PM	St,L,F	K^+ channel (KIRC)	osmotic K^+ influx
	AtKC1	At4g32650	PM	R,L	K^+ channel subunit	regulation of AtAKT1
	AtSKOR	At3g02850	PM	R,F,P	K^+ channel (KORC)	xylem K^+ loading
	AtGORK	At5g37500	PM	R,St,L,F,P,Si	K^+ channel (KORC)	K^+ efflux for charge compensation
CNGC	AtCNGC1	At5g53130	PM	R,S,F,Si	Cation channel	K^+ influx
	AtCNGC2	At5g15410	PM	R,St,L,F,Si	Cation channel	Ca^{2+} signalling
	AtCNGC3	At2g46430	PM	R,L,F,Si	Cation channel	cation uptake
	AtCNGC4	At5g54250		L,F	Cation channel	Ca^{2+} signalling
	AtCNGC5	At5g57940	PM	R,L,F,Si		
	AtCNGC6	At2g23980		R,L,F,Si		
	AtCNGC7	At1g15990		P		
	AtCNGC8	At1g19780		R,L,F,P,Si		
	AtCNGC9	At4g30560		R,S,F,Si		
	AtCNGC10	At1g01340	PM	R,L,F,Si	Cation channel	K^+ influx
	AtCNGC11	At2g46440	PM	L,F,Si	Cation channel	Ca^{2+} signalling
	AtCNGC12	At2g46450	PM	R,L,F,Si	Cation channel	Ca^{2+} signalling
	AtCNGC13	At4g01010		R,S		
	AtCNGC14	At2g24610		R		
	AtCNGC15	At2g28260		R		
	AtCNGC16	At3g48010		P		
	AtCNGC17	At4g30360		R,L,F		
	AtCNGC18	At5g14870	PM	R,P	Cation channel	Ca^{2+} signalling
	AtCNGC19	At3g17690		R,Si		
	AtCNGC20	At3g17700		S		
GLR	AtGLR1.1	At3g04110		R,St,L,F,Si	Cation channel	Ca^{2+} signalling
	AtGLR1.2	At5g48400		R,St,L,F,Si		
	AtGLR1.3	At5g48410		R,St,L,F,Si		
	AtGLR1.4	At3g07520		R,St,L,F,Si	Cation channel	
	AtGLR2.1	At5g27100		R,St,L		
	AtGLR2.2	At2g24720		R,S		

	AtGLR2.3	At2g24710		R,S		
	AtGLR2.4	At4g31710		R,Si		
	AtGLR2.5	At5g11210		R,St,L,F,Si		
	AtGLR2.6	At5g11180		R		
	AtGLR2.7	At2g29120		R,St,L,Si		
	AtGLR2.8	At2g29110		R,St,L,Si		
	AtGLR2.9	At2g29100		R,St,L		
	AtGLR3.1	At2g17260		R,St,L,F,Si		
	AtGLR3.2	At4g35290		R,St,L,F,Si		Ca^{2+} signalling
	AtGLR3.3	At1g42540	PM (?)	R,St,L,F,Si	Cation channel (?)	Ca^{2+} signalling
	AtGLR3.4	At1g05200	PM	R,St,L,F,Si	Cation channel	Ca^{2+} signalling
	AtGLR3.5	At2g32390		R,St,L,F,Si		
	AtGLR3.6	At3g51480		R,St,L,F,Si		
	AtGLR3.7	At2g32400		R,St,L,F,Si	Cation channel	Ca^{2+} signalling
TPK/KCO	AtTPK1	At5g55630	TP	R,L,F,P,Si	K^+ channel (VK)	cellular K^+ homeostasis
	AtTPK2	At5g46370	TP	R,F,P		
	AtTPK3 (=AtKCO6)	At4g18160	TP	R,L,F,P,Si		
	AtTPK4	At1g02510	PM	R,H,F,P	K^+ channel	K^+ fluxes for charge compensation
	AtTPK5	At4g01840	TP	R,St,L,F,Si		
Kir-like	AtKCO3	At5g46360	TP	R,St,L,F	K^+ channel	vacuolar K^+ release
TPC1	AtTPC1	At4g03560	TP		Cation channel (SV)	vacuolar Ca^{2+} release

PM plasma membrane, *TP* tonoplast, *CP* chloroplast envelope, *EN* endosomal membranes, *ER* endoplasmic reticulum, *R* root, *S* shoot, *L* leaf, *St* stem, *F* flower, *P* pollen, *Si* silique, *Sp* sporophyte

Qi et al. 2008; Rubio et al. 2008). In addition to K^+/H^+ symporters, K^+/Na^+ co-transporters encoded by members of the *HKT*/*Trk* gene family are also found in the plasma membranes of plant cells (Gierth and Mäser 2007). Although, AtHKT1 does not appear to catalyse K^+ transport in *A. thaliana*, homologs in other plant species, including wheat, rice, eucalyptus (*Eucalyptus camaldulensis*), and ice plant (*Mesembryanthemum crystallinum*), do contribute to K^+ influx to plant cells (Gierth and Mäser 2007).

In *A. thaliana*, plasma membrane KIRCs are encoded by several members of the voltage-gated Shaker-type channel family and VIKCs are encoded by *AtAKT2*/*3* and by one member (*AtTPK4=AtKCO4*) of the tandem pore K^+ (*TPK*/*KCO*) channel family (Table 1). The main K^+ channel involved in K^+ nutrition of *A. thaliana* is AtAKT1 (Hirsch et al. 1998; Broadley et al. 2001; Gierth et al. 2005; Rubio et al. 2008) and AtKC1 appears to be a regulatory subunit for AtAKT1 in root hairs (Reintanz et al. 2002; Pilot et al. 2003). *AtAKT2*/*3* is expressed in the phloem and xylem parenchyma and has been implicated in both loading and unloading of the phloem (Deeken et al. 2002). AtKAT1 is primarily responsible for K^+ influx to guard cells and AtKAT2 contributes both to K^+ influx to guard cells and phloem K^+ loading (Zimmermann and Chérel 2005; Lebaudy et al. 2007; Amtmann and Blatt 2009). AtSPIK and AtTPK4 are primarily responsible for the K^+-influx that enables the elongation of pollen tubes (Becker et al. 2004). The VICCs are thought to be encoded by members of the cyclic nucleotide gated channel (*CNGC*) and glutamate receptor (*GLR*) gene families (White and Broadley 2003; Hampton et al. 2005; Demidchik and Maathuis 2007). Many genes encoding CNGCs and GLRs are expressed throughout the plant (Table 1; Chiu et al. 2002; Talke et al. 2003; Hampton et al. 2005; Christopher et al. 2007; Kaplan et al. 2007; Urquhart et al. 2007; Frietsch et al. 2008; Roy et al. 2008), where they are implicated in cytosolic Ca^{2+} homeostasis and signalling (White and Broadley 2003; Demidchik and Maathuis 2007; Stephens et al. 2008; Tapken and Hollmann 2008). Recently, the *A. thaliana* annexin AnxAt1 has also been found to form K^+-permeable channels in artificial lipid bilayers, with channel formation increasing in response to reduced cytosolic pH (Gorecka et al. 2007). It has been proposed that annexins mediate Ca^{2+} influx to plant cells, but they could also mediate K^+ influx (White et al. 2002; White and Broadley 2003; Mortimer et al. 2008, Laohavisit et al. 2009).

Potassium efflux from plant cells, whether to the apoplast or to the xylem, appears to be mediated by both KORCs and NORCs (Fig. 2). These are also encoded by members of the voltage-gated Shaker-type channel family (Table 1). The KORC AtGORK is present in cells throughout the *A. thaliana* plant, where it is thought to be involved in electrical charge compensation, and also dominates K^+ efflux from guard cells during stomatal closure (Ivashikina et al. 2001; Reintanz et al. 2002; Fizames et al. 2004; Lebaudy et al. 2007). The KORC AtSKOR, which is present in the root pericycle and stelar parenchyma, is thought to mediate K^+ loading of the xylem (Gaymard et al. 1998; De Boer and Volkov 2003; Johansson et al. 2006). Genes encoding NORCs are currently unknown.

Several members of the monovalent cation/proton-antiporter (CPA) family, which in *A. thaliana* comprises eight Na^+/H^+-eXchangers (AtNHXs), 28 AtCHXs, six AtKEAs and two AtNHDs resembling NhaD, can mediate K^+ influx to the vacuoles and endosomes of plant cells (Table 1: Sze et al. 2004; Pardo et al. 2006; Gierth and Mäser 2007). These include the cation/H^+-antiporters AtNHX1, AtNHX5, AtCHX17, and AtCHX20, which have all been implicated in cellular K^+ homeostasis and the regulation of cytosolic pH (Cellier et al. 2004; Gierth and Mäser 2007; Padmanaban et al. 2007; Morris et al. 2008), plus AtNHX2, AtNHX3 and AtNHX4 (Pardo et al. 2006; Gierth and Mäser 2007; Jaquinod et al. 2007). Some *AtCHX* genes are expressed exclusively during microgametogenesis or in sporophytic tissue in *A. thaliana*, suggesting that they are specifically involved in maintaining K^+ homeostasis during pollen development and germination (Sze et al. 2004), but most *AtCHX*s are expressed in several tissues (Sze et al. 2004; Padmanaban et al. 2007). Recently, two members of the calcium cation exchanger (CCX) family of transporters (AtCCX3 and AtCCX4) have also been suggested to function as K^+/H^+ exchangers and catalyse K^+ influx to the vacuole (Morris et al. 2008). *AtCCX3* is expressed principally in flowers, whereas *AtCCX4* is expressed throughout the plant (Morris et al. 2008).

Potassium is released from the vacuole through K^+-permeable cation channels. These include (1) fast-activating vacuolar (FV) channels, whose genetic identities are currently unknown (Demidchik and Maathuis 2007), (2) slowly-activating (SV) channels, one of which appears to be encoded by *AtTPC1* in *A. thaliana* (Peiter et al. 2005; Ranf et al. 2008; Gradogna et al. 2009), (3) voltage-independent, Ca^{2+}-activated VK channels, one of which appears to be encoded by *AtTPK1* (=*AtKCO1*) in *A. thaliana* (Bihler et al. 2005; Gobert et al. 2007; Latz et al. 2007) and (4) K^+ channels encoded by other members of the *TPK*/*KCO* and Kir-like (*KCO3*) gene families (Table 1, Zimmermann and Chérel 2005; Voelker et al. 2006; Lebaudy et al. 2007). Several KUPs, such as AtKUP4, AtKUP5 and AtKUP7 have also been found in the tonoplast and might catalyse K^+ efflux from the vacuole (Jaquinod et al. 2007).

5 Summary

Potassium is the most abundant inorganic cation in plants. It is required for the activation of many enzymes in metabolically-active cellular compartments, as a vacuolar osmoticum for rapidly expanding cells, and as a counter cation for anion accumulation and electrogenic transport processes. Plants that lack K have lower water content, impaired stomatal regulation, reduced transpiration, impaired phloem transport, higher leaf carbohydrate concentrations, higher polyamine concentrations, lower leaf chlorophyll concentrations and reduced photosynthetic capacity. Visible symptoms of K-deficiency include scorching along the margins of older leaves, reduced growth, reduced fecundity, and a greater susceptibility to abiotic stresses, pests and diseases. Plants acclimate to low K supply by increasing

their root K^+ uptake capacity, replacing vacuolar K^+ with alternative osmotica, redistributing K^+ from mature to developing tissues, and reducing plant growth to maintain appropriate tissue K^+ concentrations for cellular functions. Potassium is highly mobile within the plant and many genes encoding K^+ transport proteins responsible for distributing K^+ within cells and between tissues are known. It may be possible to use this knowledge of molecular biology to develop crops that utilize K-fertilisers more effectively, to improve both plant and animal nutrition (Karley and White 2009).

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