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Review

The nitrogen–potassium intersection: membranes, metabolism, and mechanism

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ABSTRACT

Nitrogen (N) and potassium (K) are the two most abundantly acquired mineral elements by plants, and their acquisition pathways interact in complex ways. Here, we review pivotal interactions with respect to root acquisition, storage, translocation and metabolism, between the K^+ ion and the two major N sources, ammonium (NH_4^+) and nitrate (NO_3^-). The intersections between N and K physiology are explored at a number of organizational levels, from molecular-genetic processes, to compartmentation, to whole plant physiology, and discussed in the context of both N-K cooperation and antagonism. Nutritional regulation and optimization of plant growth, yield, metabolism and water-use efficiency are also discussed.

Key-words: ammonium; assimilation; efflux; influx; nitrate; nitrogen-potassium interactions; plant productivity; translocation.

INTRODUCTION

Nitrogen (N) and potassium (K) are required for plants to complete their life cycles and are the two nutrients acquired in greatest quantities by roots (Oosterhuis *et al.* 2014). The pathways by which these elements are transported and utilized by plants intersect in significant ways, including the influences exerted by potassium ions on nitrogen nutrition and physiology, and vice versa, in terms of primary uptake of N and K at the root plasma membrane, their transport, accumulation and assimilation within the plant, and the regulation of these metabolic and transport pathways. In this paper, we shall review what is known about these interactions, with special emphasis on mechanistic processes and plant productivity.

A few fundamental distinctions between these essential elements should be made at the outset. Firstly, while potassium is generally available to plants only as a simple monoatomic, monovalent cation, K^+, nitrogen is available in the form of diverse compounds, for example, as cationic ammonium (NH_4^+), anionic nitrate (NO_3^-) or as amino acids, which may be cationic, anionic or zwitterionic, depending on the chemical species and soil pH. In addition, uncharged ammonia, NH_3, is likely to rapidly enter plant root cells from the soil, particularly under conditions of high N supply and/or high pH (Coskun *et al.* 2013b). Because the dominant forms of N available to plants in most soils are the inorganic ions NH_4^+ and NO_3^-, however, they, with the K^+ ion, will make up the central focus of our review.

Another distinction is that K^+ ions, once taken up by plants, remain in this simple ionic state, while N-containing compounds undergo numerous chemical reactions and become covalently bonded within organic molecules throughout the plant. This fundamental difference is reflected in the major physiological roles the two elements play in plants. Nitrogen is an essential constituent of a vast array of metabolites and structural compounds, including proteins, nucleic acids, chlorophyll, co-enzymes, phytohormones and secondary metabolites, while the main functions of K^+ are as a major osmolyte and source of positive charge for electrical homeostasis and enzyme activation (Evans & Wildes 1971; Leigh & Wyn Jones 1984; Britto & Kronzucker 2008; Marschner 2011). Thus, our discussion of the metabolic processes at the intersection of N and K physiology will focus on biochemical pathways involving the transformation of nitrogen.

Thirdly, it is interesting that N enters the terrestrial biosphere chiefly from the atmosphere as a result of enzymatic processes in N_2-fixing soil bacteria (and today, via the industrial Haber–Bosch process), although weathering of bedrock N (itself primarily atmospherically derived), which ties up about 20% of the global N pool, can sometimes produce ecologically significant rates of nitrogen release (Holloway & Dahlgren 2002; Xu *et al.* 2012). By contrast, K^+ must be replenished by weathering of parent rock and release from exchangeable and non-exchangeable sources, if not supplied as fertilizer (Zhang *et al.* 2010).

Soil NH_4^+ concentrations tend to range between 0.1 and 1 mM, while those of NO_3^- tend to be higher, often exceeding 1 mM and reaching 10 mM or even higher following fertilization or a burst of nitrification (Wolt 1994; Crawford & Glass 1998; Owen & Jones 2001; Miller *et al.* 2007). Thus, the molar ratios of soil NO_3^- to NH_4^+ typically range between 10 and 100 (Wolt 1994; Miller *et al.* 2007). In some soils, however, such as rice paddies, bog lands and boreal and montane forests, anaerobic, acidic and reductive conditions reverse this scenario, with NH_4^+ concentrations exceeding those of NO_3^- (Gillman & Bell 1978; Kronzucker *et al.* 1997, 2000). In the case of K^+, soil

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concentrations tend to be similar to those of NH_4^+, or about 0.1–1 mM (Wolt 1994; White, 2013). In some agricultural areas of the world, including China, India and the Philippines, the relatively small K^+ pools are replenished at rates far lower than those of N replenishment, leading to nutritional imbalances, reduced productivity and eutrophication by N runoff (Dobermann *et al.* 1998; Hoa *et al.* 2006; Andrist-Rangel *et al.* 2007; Zhang *et al.* 2010). The concentrations of NO_3^-, NH_4^+ and K^+ in soils can vary greatly, not only over regional scales but even within relatively small patches (Jungk & Claassen 1986; Wolt 1994; Miller *et al.* 2007; Cramer *et al.* 2009). Nitrate levels also tend to show greater heterogeneity in soils and can range over two orders of magnitude across relatively short distances (e.g. 4 m or less; Lark *et al.* 2004), whereas NH_4^+ and K^+ levels tend to vary more narrowly, about one order of magnitude over a similar scale. This is partially due to the negative charge on NO_3^-, which results in a high degree of mobility within soils (Miller & Cramer 2004). Plant roots themselves directly increase soil heterogeneity within the rhizosphere via N-uptake and K-uptake processes, producing zones of depletion (Scherer & Ahrens 1996; Hinsinger *et al.* 2005; Kayser & Isselstein 2005; Moody & Bell 2006; Andrist-Rangel *et al.* 2007).

Soil concentrations of N and K are important not only because plant productivity can be limited by their scarcity but also because their excess can bring about toxicity and repress growth. Thus, optimum growth and yield curves, which can vary greatly with plant species and environmental factors, are typically seen with respect to these nutrients (Asher & Ozanne 1967; MacLeod 1969; Loué 1980; Britto & Kronzucker 2013). The shapes of such curves can be greatly influenced by the presence of other potentially limiting nutrients. In Fig. 1, this type of influence is shown for K supply upon N optima (1a), and vice versa (1b). It is notable that the lowest provision of K (1a) or N (1b) results in a relatively moderate N or K concentration (respectively) required to reach maximum yield (i.e. about 6 mM N or 70 kg ha^{-1} K), but this yield is still much lower than can be reached with higher provision of the companion nutrient.

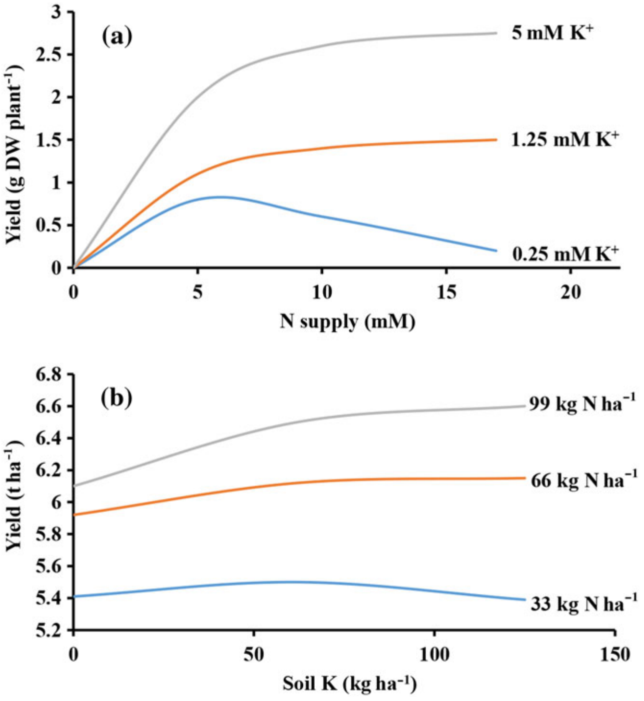

Figure 1. The effect of varying levels of soil K^+ and N on grain yield. (a) The effect of increasing concentrations of N at three K^+ levels on grain yield of barley grown hydroponically (redrawn from MacLeod 1969). (b) The effect of increasing concentrations of K^+ at three N levels on grain yield of maize grown in the field (redrawn from Loué 1980).

TRANSPORT

It is rather remarkable that the transport functions involved in the uptake of NO_3^-, NH_4^+ and K^+ from soil solution, moving these ions across the plasma membrane and into the cytosol of the root cell, share a common feature: all have been characterized using two-mechanism models, which consist of saturable, high-affinity and linear, low-affinity transport systems ('HATS' and 'LATS') generally operating at low and high external substrate concentrations, respectively (Miller *et al.* 2007; Szczerba *et al.* 2009; Zhang *et al.* 2010). For the cations K^+ and NH_4^+, these two types of transport systems mechanistically contend with the two main thermodynamic scenarios encountered by roots engaged in cation uptake: those that require active uptake (HATS conditions) and those that allow passive uptake (LATS conditions). In general, the active uptake of a cationic substrate is driven by an energetic coupling between the passive flow of H^+ down its transmembrane electrochemical potential gradient, and the substrate's thermodynamically 'uphill' influx into the cell, while passive uptake proceeds 'downhill' via ion channels (Hedrich & Schroeder 1989; Szczerba *et al.* 2009; Coskun *et al.* 2013a). It is worth noting that the distinction between HATS and LATS transporters is somewhat blurred, and ion channels can at times function at low substrate concentrations, while active-transporting carriers can operate at high concentrations (see succeeding text). In the case of NO_3^-, it is likely that, under most conditions, uptake is thermodynamically active, because of the inside-negative electrical potential difference across the plasma membrane (Wang *et al.* 2012). The plethora of transport proteins catalysing the fluxes of NO_3^-, NH_4^+ and K^+ under both HATS and LATS scenarios, many of which have been identified at the genetic level, is consistent with the spatially and temporally heterogeneous distributions of these substrates in the soil (see Introduction Section). However, it has been pointed out that the transport of NO_3^- under many field conditions might be catalysed primarily by low-affinity transporters, given the relatively high NO_3^- concentrations in soils, and because the expression and activities of high-affinity NO_3^- transporters become down-regulated as soil $[NO_3^-]$ rises (Miller *et al.* 2007).

One of the best known interactions between N and K physiology in plants is the marked inhibitory effect that NH_4^+ exerts on the high-affinity K^+ uptake system (Smith & Epstein 1964; Deane-Drummond & Glass 1983; Pettersson, 1984; Scherer *et al.* 1984; Vale *et al.* 1987, 1988; Wang *et al.* 1996; Spalding *et al.* 1999; Nielsen and Schjoerring 1998; Santa-María *et al.*, 2000; Szczerba *et al.* 2008a; ten Hoopen *et al.* 2010; Coskun *et al.* 2010, 2013a; Zhang *et al.* 2010). In barley seedlings, the inhibition of K^+ translocation to the shoot by NH_4^+ appears to be even more pronounced than the inhibition of primary K^+ uptake at the plasma membrane, with suppressions as high as 90% (Kronzucker *et al.* 2003; see also below). This inhibition appears to be at least partially reciprocal, resulting in an 'antagonism' between the two ions, with both competitive and non-competitive components. The competitive effects likely arise from the similarities between the two ions, in terms of their hydrated diameters, charge and influence on membrane potentials (Wang *et al.* 1996; ten Hoopen *et al.* 2010). Non-competitive effects include a suppression of NH_4^+ uptake in tobacco seedlings by K^+ that persists even after K^+ removal (Scherer *et al.* 1984), the lack of suppression of NH_4^+ uptake by a wide range of external $[K^+]$ in sweet pepper (Xu *et al.* 2002), a stimulation of NH_4^+ transport by K^+ in *Arabidopsis* (ten Hoopen *et al.* 2010; in addition, see Szczerba *et al.* 2008b, for a LATS-range stimulation), and the inhibition of K^+ uptake by the acidification of the rhizosphere that is associated with NH_4^+ uptake in many species (Findenegg 1987). It has also been shown that the induction, by K^+ starvation, of *AtHAK5* (the gene encoding the dominant component of high-affinity K^+ transport in *Arabidopsis* roots; Gierth & Mäser 2007; Rubio *et al.* 2008; Fig. 2) expression was almost completely suppressed by the presence of only 100 μM NH_4^+ (Qi *et al.* 2008; *cf.* Rubio *et al.* 2008; see Section on Sensing, Signalling and Co-regulation). In another study, it was shown that the removal of NH_4^+ from solutions bathing the roots of barley and *Arabidopsis* plants resulted in dramatic increases (4.5-fold and 6-fold in the two species, respectively) in K^+ uptake (Coskun *et al.* 2013a). Interestingly, this effect occurred under both low-K^+ and high-K^+ conditions and was partially attributed to the hyperpolarization

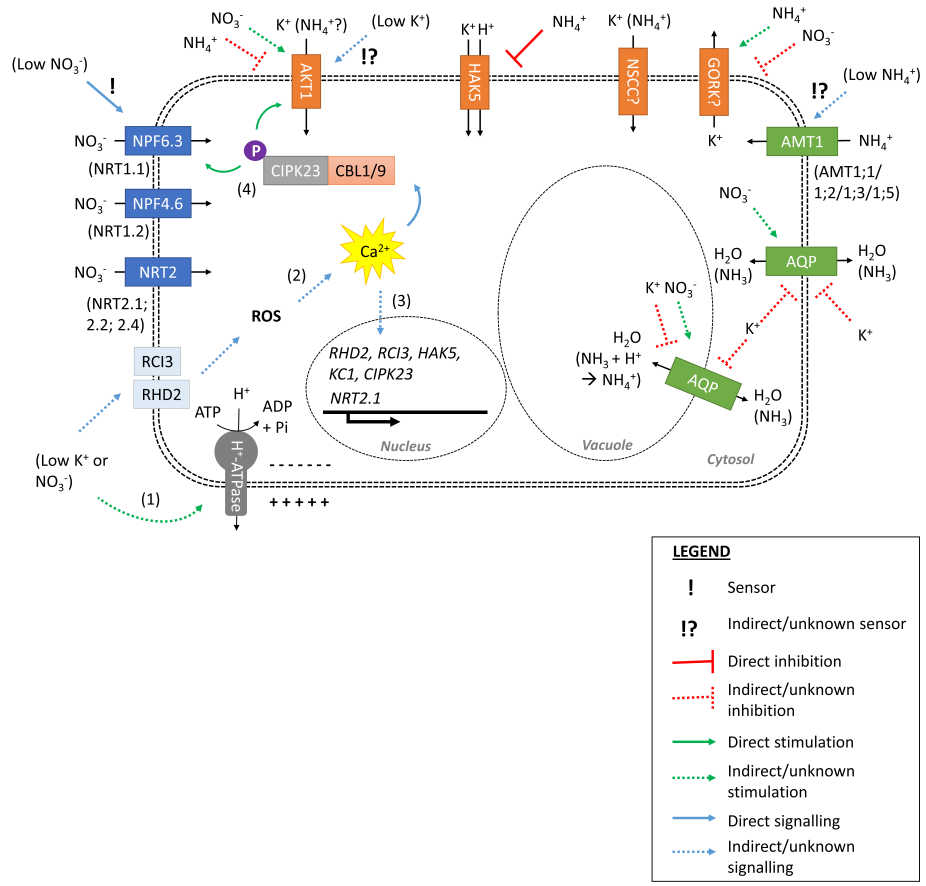

Figure 2. The intersections of K^+, NO_3^-, and NH_3/NH_4^+ transport and regulatory mechanisms in plant root cells. Low external NO_3^- (sensed directly by NPF6.3; Tsay *et al.* 2011) or K^+ triggers (1) the hyperpolarization of the plasma membrane (Britto & Kronzucker 2008; Rubio *et al.* 2014), (2) ROS accumulation (via NADPH oxidase, RHD2, and type III peroxidase, RCI3; Shin & Schachtman 2007) and $Ca2^+$ signalling cascades, which result in (3) the expression of various K^+– and N-related genes (Shin & Schachtman 2007; Tsay *et al.* 2011), and (4) activation of K^+ and NO_3^- transporters (AKT1 and NPF6.3, respectively) by phosphorylation via CBL1/CBL9– CIPK23 complexes (Luan *et al.* 2009; Tsay *et al.* 2009). NH_4^+ inhibits K^+ transport via HAK5 (directly) and AKT1 (indirectly, possibly via effects on membrane potential; Gierth & Mäser 2007; Britto & Kronzucker, 2008; Coskun *et al.* 2014). NH_4^+ also stimulates K^+ efflux (likely via effects on membrane potential; Coskun *et al.* 2010). In contrast, NO_3^- stimulates and inhibits K^+ influx and efflux, respectively, via unknown mechanisms (Coskun *et al.* 2014). Low-affinity NH_3 transport, possibly via aquaporins (AQPs), is inhibited by K^+ through unknown mechanisms (likely related to cell turgor; Coskun *et al.* 2013b). Similarly, water fluxes through AQPs may be K^+–regulated, in addition to being positively regulated by NO_3^- (Cramer *et al.* 2009; Britto *et al.* 2014). K^+ and NH_4^+ transport via non-selective cation channels (NSCCs) is also a possibility (Kronzucker & Britto 2011).

of the plasma-membrane electrical potential that was observed upon NH_4^+ withdrawal.

A lower accumulation of K^+ in NH_4^+-grown (relative to NO_3^--grown) plants is thus partially attributable to the suppression, by NH_4^+, of K^+ influx in the HATS range. However, it may also be due to an enhancement of K^+ efflux by NH_4^+, which has been demonstrated in several studies (Munn & Jackson 1978; Rufty *et al.* 1982; Topa & Jackson 1988; Coskun *et al.* 2010; *cf.* Deane-Drummond & Glass 1983). In the study by Coskun *et al.* (2010), it was shown that NH_4^+-stimulated K^+ efflux in roots of barley could be completely counteracted by the channel-blocking agents tetraethylammonium (TEA^+) and cesium (Cs^+), suggesting that it is catalysed by an as yet unidentified ion channel, possibly a member of the Shaker family of K^+-specific channels. This study also showed that K^+ efflux could be stimulated by the co-presence of NH_4^+ and NO_3^- (as NH_4NO_3), but NO_3^- as the sole N source reduced K^+ efflux, an effect also observed by Pettersson (1984).

A few studies, however, have provided evidence that NH_4^+ can actually stimulate high-affinity K^+ transport under some conditions (Nieves-Cordones *et al.* 2008; Alvarez-Pizarro *et al.*, 2011). These studies have suggested that the stimulation was due to a more electrically hyperpolarized plasma membrane in the presence of NH_4^+, a condition, however, that is rarely seen in other studies (e.g. Coskun *et al.* 2013a; see Section on Sensing, Signalling and Co-regulation). Ammonium-induced hyperpolarization was also inferred in sorghum roots based on an increase in expression of the plasma-membrane H^+-ATPase (Alvarez-Pizarro *et al.* 2011), and such a hyperpolarization was measured in roots of tomato (Nieves-Cordones *et al.* 2008). The latter study suggested that membrane hyperpolarization is a regulatory component of HAK5 expression in tomato (see Section on Sensing, Signalling and Co-regulation).

By contrast, few effects of NH_4^+ on K^+ transport in the low-affinity range have been reported (*cf.* Coskun *et al.* 2013a). However, a study using T-DNA insertion lines showed that transport of K^+ not only via HAK5 but also via AKT1, the dominant low-affinity K^+-specific influx channel in plant roots (Ivashikina *et al.* 2001; Gierth & Mäser 2007; Fig. 2) is sensitive to NH_4^+ (Rubio *et al.* 2008). Nevertheless, the powerful suppression of HAK-mediated K^+ transport by NH_4^+, coupled to the lack of such an effect on AKT1, has been used as a parsing tool to distinguish between the two systems. By this means, it was shown that AKT1, normally associated with LATS, is capable of transporting K^+ at external concentrations as low as 10 μM in *Arabidopsis* (Hirsch *et al.* 1998; Spalding *et al.* 1999), and 100 μM in barley (Coskun *et al.* 2013a), given a sufficiently negative membrane potential. The 'dual-affinity' nature of AKT1 is not unique; it can also be seen in the *Arabidopsis* high-affinity K^+ transporter AtKUP1 (Fu & Luan 1998) and the NO_3^- transporter AtNRT1.1, in which a molecular switch between high-affinity and low-affinity functions via changes in phosphorylation and conformational states has been demonstrated (Ho *et al.*, 2009; Sun *et al.* 2014; Parker & Newstead 2014; see also Section on Sensing, Signalling and Co-regulation).

Nevertheless, some studies have shown effects of NH_4^+ supply on low-affinity K^+ transport. Vale *et al.* (1987) found that both a saturating and a linear phase of [K^+]-dependent K^+ transport in corn were suppressed by NH_4^+, but the latter phase, while kinetically resembling 'classic' low-affinity transport due to its linearity (Szczerba *et al.* 2009), was only investigated between 50 and 200 μM K^+, at which the flux may have still been dominated by HAK systems. An interesting aspect of this study was that the maximal suppression of K^+ influx was seen at 100 μM NH_4^+, with no further suppression seen at 200–500 μM. At higher K^+ and NH_4^+ concentrations (5 and 10 mM, respectively), however, it was clearly demonstrated in a study on barley roots that steady-state NH_4^+ supply can indeed inhibit LATS-range K^+ transport (Coskun *et al.* 2013a). In this study, removal of NH_4^+ during measurement of $^{42}K^+$ uptake resulted in a flux more than twice as high as in control plants (i.e. those in the presence of 10 mM NH_4^+). Moreover, when NH_4^+ was removed and replaced by NO_3^- (also at 10 mM), K^+ influx was more than three times that of controls. Interestingly, the NH_4^+-withdrawal effect was generally short term, and essentially disappeared over a 10 h period, while similar experiments at low K^+ (20 and 100 μM) showed a longer-lasting effect of NH_4^+ withdrawal, resulting in fluxes four to five times higher than control, as well as substantially higher K^+ accumulation, even after 24 h. This suggests that under some conditions, such as that of low K^+ supply, the influence of other ions on K^+ transport may override regulation by internal K^+ status or growth demands. Under other conditions, the reverse may be true, and K^+ uptake and content may be relatively unaffected by the supply of other nutrients (including N), as has been frequently observed (Pitman 1972; Pettersson 1984; Vale *et al.* 1987; Zhang *et al.* 2010).

At least one study has reported the stimulation of low-affinity K^+ uptake under steady-state provision of high (10 mM) NH_4^+, relative to equimolar NO_3^- (Szczerba *et al.* 2008b). At or below 100 μM K^+, the characteristic suppression of K^+ influx by NH_4^+ was observed in this study, but, at 1.5 mM K^+ and above, growth on NH_4^+ pronouncedly stimulated both K^+ influx and accumulation in the shoots of rice plants. Because of the up-regulation of NH_4^+ transport known to occur under high NH_4^+ conditions (e.g. Wang *et al.* 1993; Rawat *et al.* 1999; Cerezo *et al.* 2001), it was suggested that the stimulation of K^+ transport under these conditions was mediated by the enhanced activity of a low-affinity NH_4^+ transporter. However, it should be noted that this effect was found in tropical lowland rice, considered to be an 'ammonium specialist', and might not be common among species sensitive to NH_4^+ toxicity. Moreover, the increased K^+ accumulation found under NH_4^+ nutrition in rice did not always translate into increased growth; maximal growth was found at 1.5 mM K^+, but growth declined by 40% when K^+ was raised to 40 mM (the condition at which the largest stimulation of NH_4^+ transport and accumulation was observed). Under NO_3^- nutrition, the optimal growth concentration was even lower, with a fresh-weight decline of about 20% observed at 1.5 mM K^+ (relative to 100 μM) despite the higher shoot K^+ content in these plants.

It is well known that NH_4^+ nutrition is often associated with substantial declines in tissue levels of essential cations including K^+ as well as Ca^{2+} and Mg^{2+} (Kirkby & Knight 1977; Kurvits & Kirkby 1980; van Beusichem *et al.* 1988); this is a central aspect of the NH_4^+ toxicity syndrome and is largely attributable to the inhibition of fluxes of other cations by NH_4^+ (Britto & Kronzucker 2002). The converse of this is that NH_4^+ toxicity is frequently found to be relieved by an increase in K^+ provision (Lips *et al.* 1990; Cao *et al.* 1993; Britto & Kronzucker 2002; ten Hoopen *et al.* 2010). In addition, elevated K^+ provision can reduce the inhibition of NO_3^- transport by NH_4^+, when N is provided as NH_4NO_3, and improve growth on this mixed-N source (Rufty *et al.* 1982; Hagin *et al.* 1990). The alleviation of NH_4^+ toxicity by K^+ is in part a result of the up-regulation, by increased K^+, of enzymes involved in NH_4^+ assimilation (see Section on Metabolism), but also because of the pronounced, dose-dependent reductions in low-affinity NH_4^+ transport and accumulation brought about by elevated K^+ (Szczerba *et al.* 2008a, b; Balkos *et al.* 2010). This contrasts with high-affinity NH_4^+ uptake via the AMT1 transporter (possibly involving a H^+-NH_4^+ symport mechanism; Ortiz-Ramirez *et al.* 2011; Xu *et al.* 2012), which appears to be quite selective for NH_4^+ and against K^+ (Ninnemann *et al.* 1994). At high (10 mM) NH_4^+, however, a switch in external $[K^+]$ ($[K^+]_{ext}$) from 0.1 to 1.5 mM reduced NH_4^+ influx into barley roots by nearly 60% (Szczerba *et al.* 2008a), with similar results seen in rice (Szczerba *et al.* 2008b; Balkos *et al.* 2010). In addition, elevated $[K^+]_{ext}$ reduced the efflux of NH_4^+ from roots of barley and rice, to an even greater extent than influx, resulting in a lower extent of futile N cycling across the plasma membrane, which has been linked to NH_4^+ toxicity (Britto *et al.* 2001; Chen *et al.* 2013). Interestingly, these effects were seen both instantaneously and over the long term, and, although K^+ elevation did not generally reduce the net flux of NH_4^+ into the plant (indeed, it was substantially increased in rice), the increased metabolism of NH_4^+ resulted in greatly reduced accumulation of this toxic compound (of up to 75–80%) in both barley and rice (Szczerba *et al.* 2008a; Balkos *et al.* 2010; see also Mengel *et al.* 1976). Subsequent work has shown that, under these low-affinity NH_4^+-transport conditions, the major transported species may in fact be the deprotonated, uncharged ammonia molecule (NH_3), which crosses the plasma membrane via aquaporins (Jahn *et al.* 2004; Coskun *et al.* 2013b). The ability of elevated $[K^+]_{ext}$ to greatly diminish transport via aquaporins may reflect the significance of this ion in the area of plant water relations (Quintero *et al.* 2007; Britto *et al.* 2014; see succeeding text).

In contrast to the antagonistic relationship between K^+ and NH_4^+ nutrition, the acquisition rates of K^+ and NO_3^- are often found to be positively correlated, and enhance one another, likely because of improved charge balance (Minotti *et al.* 1968; Blevins *et al.* 1974; Kirkby & Knight 1977; Kurvits & Kirkby 1980; Pettersson 1984; Kochian *et al.* 1985; Le Bot & Kirkby, 1992; Macduff *et al.*1997; Marschner *et al.* 1996; Siebrecht & Tischner 1999; Coskun *et al.* 2013a; Delaire *et al.* 2014) and the activation, by K^+, of enzymes involved in NO_3^- assimilation (Hagin *et al.* 1990; Zhang *et al.* 2010; Roosta & Schjoerring, 2008; Balkos *et al.* 2010; see Section on Metabolism). Thus, it is commonly observed that plants take up and accumulate substantially more K^+ under NO_3^- nutrition than with NH_4^+, or in the presence of other cations such as Mg^{2+}, Na^+ and Ca^{2+} (Ivashikina & Feyziev 1998; Coskun

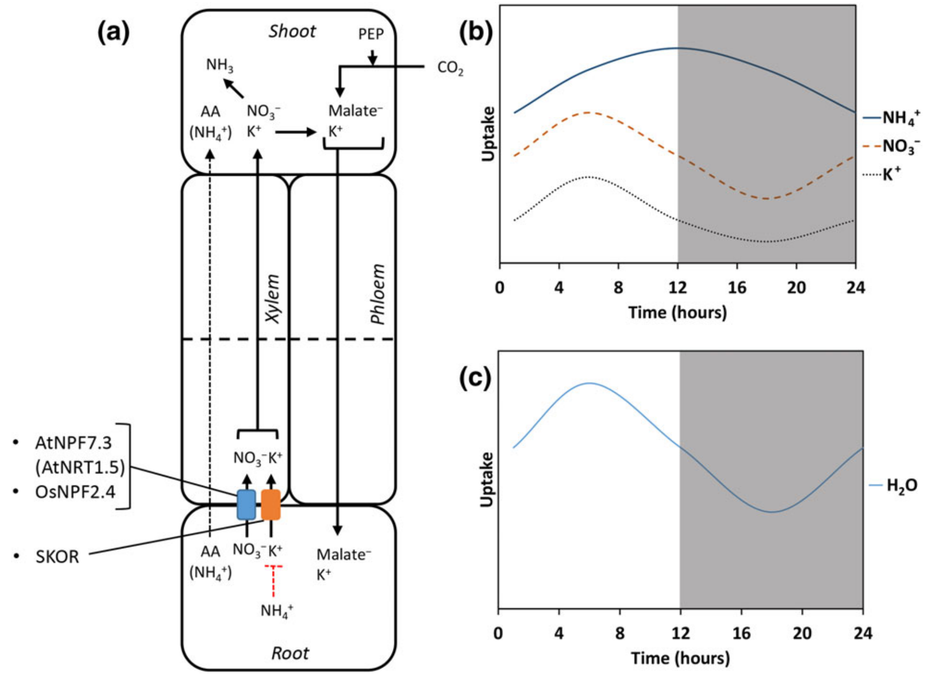

Figure 3. Long-distance K^+ and N transport, and the diurnal regulation of K^+, N, and water uptake. (a) Schematic diagram of K^+ circulation between root and shoot with respect to NO_3^- and malate transport (PEP, phosphoenol pyruvate). NH_4^+ is not translocated from root to shoot to any appreciable extent, but NH_4^+ assimilates (e.g. amino acids, AA) are. NH_4^+ can also be a potent inhibitor of K^+ translocation (based on Dijkshoorn *et al.* 1968; Ben-Zioni *et al.* 1971; Kirkby & Knight 1977; Kronzucker *et al.* 1998; Szczerba *et al.* 2008b). (b and c) The diurnal regulation of K^+, NO_3^-, NH_4^+, and water uptake measured over 24 h (redrawn from Le Bot & Kirkby 1992; Ourry *et al.* 1996).

et al. 2013a). However, the direct influences exerted by one ion on the transport of the other are poorly understood. Nitrate and potassium can both be stored in the vacuole at high concentrations (Martinoia *et al.* 1981; 2007; Walker *et al.* 1996; Oosterhuis *et al.* 2014), where they may electrically balance one another, and can be dynamically retrieved according to plant demand (Blumwald & Poole 1985; Walker *et al.* 1996). The situation for NH_4^+ in the vacuole is less clear. It is not often accumulated in high amounts in plant tissues, except under toxic conditions, under which it may enter the vacuole as NH_3, via aquaporins (Jahn *et al.* 2004; Loqué *et al.* 2005; Martinoia *et al.* 2007; Coskun *et al.*, 2013a, 2013b).

An intriguing example of the co-operative use of K^+ and NO_3^- in plants is what is referred to as the 'Dijkshoorn–Ben Zioni model' of internal ion cycling via the vasculature, in which NO_3^- is transported from root to shoot in the xylem, using K^+ as a counterion (Dijkshoorn *et al.* 1968; Ben Zioni *et al.* 1971; Kirkby & Knight 1977; Pettersson 1984; Touraine *et al.* 1988; Fig. 3a). NO_3^- is reduced and assimilated into amino acids in the shoot, with the concomitant transfer of negative charge to organic (carboxylic) acids. These acids, particularly in the form of malate, are then transported to the roots via the phloem, accompanied by K^+ as counterion, where they are decarboxylated and release HCO_3^- to the external medium. Indeed, it has been estimated that as much as half the K^+ found in the xylem stream is not directly introduced via uptake processes in the root, but comes from recirculated K^+ in the phloem (Engels & Kirkby 2001; Chérel *et al.* 2014).

The Dijkshoorn–Ben Zioni model has proven useful in a large number of studies and provides one of the few mechanisms known to link shoot demand for nutrients with their uptake by the roots (Casadesús *et al.* 1995; Marschner *et al.* 1996). However, its applicability is limited by several conditions and has been contradicted in some studies. Firstly, the model pertains to plants that reduce NO_3^- mainly in the shoot, which is a common but by no means universal occurrence (Pate 1973; Andrews 1986; Touraine *et al.* 1990). Interestingly, a low supply of K^+ can increase the degree of NO_3^- reduction in roots relative to shoots, possibly because of the lack of a xylem-mobile cation to accompany NO_3^- moving to the shoot (Rufty *et al.* 1981; Förster & Jeschke 1993; see Section on Metabolism). Secondly, even when shoot reduction is pronounced, and the upward movement of K^+ as a counterion with NO_3^- is observed, a significant downward recirculation of K-malate in the phloem is not always seen (Kirkby and Knight 1977). This appears to be related to conditions where there is a balanced uptake of cations and anions by roots, as in many herbaceous dicotyledons growing under nutrient-replete conditions (van Egmond 1978; *cf.* Touraine *et al.* 1990). Thirdly, the regulation of diurnal variations in NO_3^- uptake may depend less on the synthesis, transport or addition of malate than on light-dark transitions affecting the shoot (Delhon *et al.* 1996; in addition, see Casadesús *et al.* 1995; Fig. 3b).

Nevertheless, in many cases, the model appears to be fairly robust in terms of the co-ordinated translocation of the two ions from root to shoot. Significant progress in this area includes demonstrations of K^+ and NO_3^- interdependence at the molecular level, in terms of alterations of transporters that load NO_3^- into the xylem, and resulting effects on K^+ translocation (Lin *et al.* 2008; Xia *et al.* 2015; see Section on Sensing, Signalling and Co-regulation). However, it may be possible for other cations, in particular Mg^{2+}, to at least partially substitute for K^+ in the charge balancing of NO_3^- in the xylem (Förster & Jeschke 1993). In addition, there appears to be a regulatory decoupling between the uptake of K^+ and NO_3^- across the plasma membrane, on the one hand, and their translocation to the shoot (Kirkby & Armstrong 1980; Touraine & Grignon 1982; Casadesús *et al.* 1995; Ivashikina & Feyziev 1998).

SENSING, SIGNALLING AND CO-REGULATION

Plants have evolved complex sensing, signalling and regulatory mechanisms to manage the acquisition of ions in fluctuating environments, and key similarities can be found in mechanisms involving K^+ and N transport and assimilation. These similarities include the co-regulation at the transcriptional level of K^+ on N transporters and vice versa, the post-translational modifications of K^+ and N transporters by the same regulatory proteins, as well as more systemic changes, such as in membrane potential, the accumulation of reactive oxygen species (ROS) and phytohormones.

One of the clearest examples of K–N interaction at the transport level, that is, the inhibition of high-affinity K^+ transport via HAK transporters by NH_4^+ (see Section on Transport; Fig. 2), manifests itself at the transcriptional level as well. NH_4^+ has been shown to down-regulate *AtHAK5* and *CaHAK1* transcription in K^+-deprived *Arabidopsis* and pepper plants, respectively (Martínez-Cordero *et al.* 2005; Qi *et al.* 2008). It is well documented that K^+ deprivation leads to hyperpolarization of the root plasma membrane (Etherton & Higinbotham 1960; Maathuis & Sanders 1993; Amtmann *et al.* 2006; Schachtman & Shin 2007; Britto & Kronzucker 2008). It has recently been suggested, based on a correlation analysis, that membrane hyperpolarization could trigger an as yet unknown signalling cascade inducing the expression of high-affinity HAK transporters (*LeHAK5* and *AtHAK5* in tomato and *Arabidopsis*, respectively; Nieves-Cordones *et al.* 2008; Rubio *et al.* 2014). Interestingly, this induction appears to occur even under K^+-replete conditions, contrary to reports indicating that HAK induction is dependent on K^+ starvation (Armengaud *et al.* 2004; Gierth & Mäser 2007; Qi *et al.* 2008). One such condition that has been tested is that of NO_3^- deprivation, in which membrane hyperpolarization was seen to coincide with an increased expression of *AtHAK5* and *LeHAK5* (Rubio *et al.* 2014; see also Wang *et al.* 2001; Shin *et al.* 2005). Perhaps critically, however, it does not coincide with increased root (net) K^+ uptake, in contrast to K^+-deprivation conditions, suggesting a specific regulatory role of low K^+ in HAK5 activity (Rubio *et al.* 2014). Furthermore, intriguingly, Nieves-Cordones *et al.* (2008) found that tomato plants grown in the presence of NH_4^+ displayed hyperpolarized membrane potentials relative to NH_4^+-free conditions and increased *LeHAK5* expression. This is in apparent contradiction to many reports of NH_4^+-induced membrane depolarization, at least in the short term (Ullrich *et al.* 1984; Ayling 1993; Wang *et al.* 1994). In tomato, transcript levels of *LeHAK5* were also found to quickly (2–6 h) decline with membrane depolarization events (e.g. K^+ re-supply, or initial exposure to NH_4^+, Rb^+, vanadate or carbonyl cyanide m-chlorophenyl hydrazone (CCCP); Nieves-Cordones *et al.* 2008). It would be interesting to see whether other means of short-term membrane hyperpolarization (e.g. with bicarbonate (Poole 1969), fusicoccin (Ullrich & Novacky 1990) or NH_4^+ withdrawal from NH_4^+-grown plants (Coskun *et al.* 2013a; see previous text)) would also result in increased *HAK5* expression. Overall, this is an interesting, but as yet speculative, regulatory mechanism that requires further investigation.

Another important link between K^+ and N nutrition is the involvement of calcineurin B-like (CBL)-interacting protein kinase 23 (CIPK23) in high-affinity K^+ and NO_3^- uptake (Xu *et al.* 2006; Ho *et al.* 2009; Ho & Tsay 2010; Castaings *et al.* 2011; Tsay *et al.* 2011; see also Fig. 2). CIPK23 is involved in activating high-affinity uptake of both K^+ and NO_3^- via AKT1 and NPF6.3 (NRT1.1), respectively (Xu *et al.* 2006; Cheong *et al.* 2007; Lee *et al.* 2007; Li *et al.* 2006; Ho *et al.* 2009). Under K^+ deprivation, a Ca^{2+} signalling cascade (triggered perhaps by ethylene and ROS; see succeeding text) results in its binding to CBL1 and CBL9, which in turn activate CIPK23, which phosphorylates and thus activates AtAKT1 (Xu *et al.* 2006; Cheong *et al.* 2007; Li *et al.* 2006; Lee *et al.* 2007; Luan 2009; Wang and Wu 2013). Like AtAKT1, AtNPF6.3 is a dual-affinity transporter, conducting both high-affinity and low-affinity NO_3^- uptake (Wang *et al.* 1998; Liu *et al.* 1999; Liu & Tsay 2003; Ho *et al.* 2009; Tsay *et al.* 2011; Léran *et al.* 2014). At low external nitrate concentrations (i.e. HATS conditions), the same signalling cascade triggers AtCIPK23 to phosphorylate AtNPF6.3 (at T101) and thus switches the transporter into 'high-affinity mode' (Ho *et al.* 2009; Sun *et al.* 2014; Parker & Newstead 2014). By contrast, unphosphorylated AtNPF6.3 functions as a low-affinity transporter (Ho *et al.* 2009; Ho & Tsay 2010). The crystal structure of AtNPF6.3 (AtNRT1.1) and the allosteric effects of phosphorylation have been determined (Sun *et al.* 2014; Parker & Newstead 2014); to our knowledge, such a study has yet to be conducted for *AKT1*. Recently, a developmental role of the CBL1-CBL9-CIPK23-AKT1/NRT1.1 signalling module was proposed, identifying specific parameters related to root system architecture as targets (Kellermeier *et al.* 2014). For example, it was found that under K^+ and NO_3^- deficiency, phosphorylated AKT1 and NRT1.1 stimulate second-order lateral root emergence. This is an important new development because conditions arise that exclude AKT1 and NRT1.1 in high-affinity K^+ and NO_3^- uptake, respectively (e.g. under conditions where high-affinity HAK transporters are functional (Rubio *et al.* 2008; Coskun *et al.* 2013a, 2014) or where high-affinity *NRT2* transporters predominate (Okamoto *et al.* 2003; Wang *et al.* 2012)).

The apparent coupling of K^+ and NO_3^- transport in the xylem (Section on Transport) appears to play out at the molecular level as well. In *nrt1.5* knock-out mutants for a transporter responsible for xylem NO_3^- loading in *Arabidopsis*, K^+ translocation was reduced along with that of NO_3^- (Lin *et al.* 2008). However, a K^+-coupled mechanism for this transporter was ruled out in a heterologous expression system in favour of one of H^+ coupling. Furthermore, K^+ deprivation was shown to down-regulate the expression of *AtNRT1.5* (*AtNPF7.3*), suggesting NO_3^- translocation was controlled by plant K^+ levels (Lin *et al.* 2008). Similar results were found in rice with respect to the nitrate transporter OsNPF2.4 (Xia *et al.* 2015), and other nitrate transporters have been implicated in NO_3^- xylem loading (e.g. AtNPF6.3 (AtNRT1.1), AtNPF2.3; OsNPF2.2 and LeNRT2.3; Léran *et al.* 2013; Taochy *et al.* 2015; Li *et al.* 2015; Fu *et al.* 2015), but their relationships to K^+ nutrition have yet to be elucidated. The expression of the gene for the K^+ xylem-loading transporter SKOR was shown to be up-regulated by nitrate supply (Wang *et al.* 2004), demonstrating a similar response as *AtNRT1.5* and *OsNPF2.4* to K^+ supply. These data strongly support a co-regulation at the level of xylem transport that maintains the balance between NO_3^- and K^+ (Wang *et al.* 2012). It will be interesting to see if such co-regulation at the molecular level exists at the level of primary uptake, where, for example, the stimulation of low-affinity K^+ uptake in the presence of NO_3^- is observed (Kochian *et al.* 1985; Coskun *et al.* 2013a; see Section on Transport; Fig. 2).

In addition to nutritional regulation, K^+ and NO_3^- xylem-loading transporters and root-to-shoot translocation also show diurnal regulation (Fig. 3b). *AtNPF7.3* (*AtNRT1.5*) expression peaked at the night-to-day transition and fell to a minimum at the day-to-night transition (Lin *et al.* 2008). In the legume *Samanea saman*, *SPORK1* (a *SKOR* homolog) expression showed similar diel patterns (Moshelion *et al.* 2002). Such patterns are consistent with xylem loading of NO_3^- and K^+ being highest during the day and lowest during the night (Mattson and Palmer 1988; Schurr & Schulze 1995; Macduff & Bakken 2003; Siebrecht *et al.* 2003), as they are closely tied to transpiration rates (Le Bot & Kirkby 1992; Siebrecht *et al.* 2003; Fig. 3c). Moreover, leaf nitrate reductase (NR) activity (the first enzyme involved in nitrate reduction; Campbell 1999) also rises to a maximum during the first half of the light period (Scheible *et al.* 1997; Lillo *et al.* 2001). This highly suggests a coordinated and concerted mechanism at play related to NO_3^- and K^+ translocation. Insight into the underlying signalling and regulatory network is eagerly anticipated.

K^+ deprivation has been demonstrated to result in strong up-regulation of the nitrate transporters *LeNRT1.2* and *LeNRT2.1* in tomato roots (Wang *et al.* 2001). This parallels the well-documented effects of the induction of high-affinity HAK transporters in response to K^+ deprivation (Martínez-Cordero *et al.* 2005; Gierth & Mäser 2007; Qi *et al.* 2008). By contrast, K^+ deprivation resulted in the *down-regulation* of *AtNRT2.1*, as well as *AtNRT2.3*, and *AtNRT2.6*, in *Arabidopsis* (Armengaud *et al.* 2004). Expression of *AtNRT1.1*, however, was up-regulated with K^+ deprivation in this study. To our knowledge, these discrepancies have yet to be thoroughly investigated or resolved. However, the differences may be the result of varying timeframes of K^+ deficiency in each study, as the responses observed for tomato were made over a relatively short time (within 1–3 h), whereas the responses observed for *Arabidopsis* took place after 2 weeks of K^+ starvation (although re-supply of K^+ resulted in *AtNRT2* genes being up-regulated within 6 h; Armengaud *et al.* 2004). Nevertheless, these reports clearly indicate a 'crosstalk' between the nutritional status of one nutrient and the expression of membrane transporters for the other.

Another common observance to K^+ and NO_3^- deficiency is the accumulation of ROS as a signalling component (Shin & Schachtman 2004; Shin *et al.* 2005; Schachtman & Shin 2007). While the consequences of ROS accumulation are not well understood (Schachtman & Shin 2007), they include the up-regulation of *AtHAK5* and *AtNRT2.1* expression under K^+ and NO_3^- deprivation, respectively (Shin *et al.* 2005; Kim *et al.* 2010, 2012). In contrast to the study by Armengaud *et al.* (2004), *AtNRT2.1* expression was not affected by K^+ deprivation in the study by Shin *et al.* (2005). This may also be due to timing, as K^+ deprivation was maintained for up to 30 h in the latter study, as opposed to 2 weeks in the former. A more comprehensive study on the role of ROS in this crosstalk would be most interesting. Ca^{2+} may be part of this signalling cascade both upstream (Torres & Dangl 2005; Li *et al.* 2006; Lebaudy *et al.* 2007) and downstream (Mori & Schroeder 2004) of ROS production. At least in the case of K^+ deprivation, ethylene acts upstream of ROS (Shin & Schachtman 2004; Jung *et al.* 2009). Mutants defective in ethylene or ROS production, such as ethylene insensitive2-1 (*ein2-1*), an NADPH oxidase (*rhd2*) or a type III peroxidase (*rci3*), all showed reduced *AtHAK5* expression (Shin & Schachtman 2004; Jung *et al.* 2009; Kim *et al.* 2010; Fig. 2). The expression and function of nitrate transporters in these mutants, however, remain unknown.

METABOLISM

Although K^+ itself is not metabolized, it plays a vital role in many aspects of plant metabolism. K^+ is involved in the activity of some 46 enzymes (Evans & Sorger 1966; Leigh & Wyn Jones 1984; Hagin *et al.* 1990; Britto & Kronzucker 2008; Armengaud *et al.* 2009), including as cofactor to such critical enzymes as pyruvate kinase, starch synthase, Rubisco and NR (Beevers & Hageman 1969; Sorger *et al.* 1965; Evans & Sorger 1966; Nitsos & Evans 1966; 1969; Peoples & Koch 1979; Wyn Jones & Pollard 1983). Moreover, K^+ is crucial to protein synthesis, not only with respect to enzyme activation but also to ribosome synthesis and mRNA turnover (Blevins 1985; Evans & Wildes 1971; Pettigrew 2008). Its importance in cellular metabolism is reflected in its high, homeostatically set concentration in the cytosol of ~100 mM (Leigh & Wyn Jones 1984; Walker *et al.* 1996; Kronzucker *et al.* 2003).

The close relationships between K^+ supply and N metabolism is evident from many studies. One such connection involves the partitioning of NR activity between the root and shoot (Blevins *et al.* 1978; Barneix & Breteler 1985; Förster & Jeschke 1993; Casadesús *et al.* 1995; Armengaud *et al.* 2009), which also depends on plant species, external nitrate supply, temperature and light intensity (Pate 1973; Smirnoff & Stewart 1985; Andrews 1986). Generally, with high external K^+ supply, the co-translocation of K^+ and NO_3^- to the shoot increases (Ben Zioni *et al.* 1971; Blevins *et al.* 1978; see Section on Transport; Fig. 3), and both storage of NO_3^- and NR activity increases in leaves, while less N assimilation is found in roots (Blevins *et al.* 1978; Rufty *et al.* 1981). In contrast, with K^+ deprivation, less translocation of NO_3^- is observed, and hence, higher N assimilation occurs in roots (Förster and Jeschke 1993; Rufty *et al.* 1981; Wang *et al.* 2003). Interestingly, this has not been borne out in the model species *Arabidopsis thaliana*; Armengaud *et al.* (2009) observed significant *decreases* in root NR activity, relative to K^+ sufficiency, with prolonged (2 weeks) K^+ deprivation. By contrast, the authors observed significant up-regulation in the activity of key enzymes involved in ammonium assimilation, that is, glutamine synthetase (GS), ferredoxin-glutamine-2-oxoglutarate aminotransferase (Fd-GOGAT) and glutamate dehydrogenase (GDH). It was concluded that the down-regulation of NR (as well as nitrate transporters; Armengaud *et al.* 2004) could be as a result of decreased carbon-skeleton production via the tricarboxylic acid (TCA) cycle (decreased glycolysis and the direct inhibition of pyruvate kinase due to low cytoplasmic K^+ were observed). On the other hand, the up-regulation of GS, GOGAT and GDH was interpreted as a compensatory response to maintain C flux through the TCA cycle and into amino acids and proteins (increased NADP-malic enzyme activity due to low cytoplasmic pH was also observed).

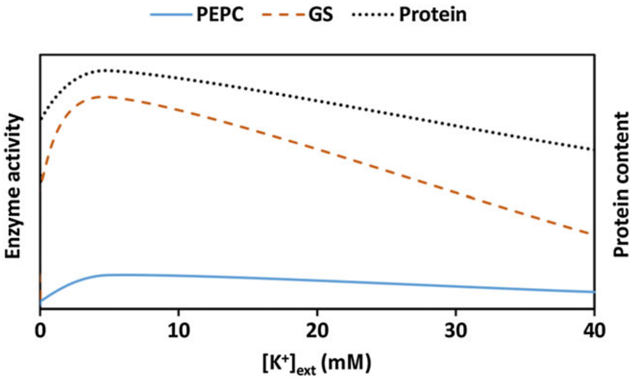

Figure 4. Root enzyme activity and plant protein content as a function of external K^+ ($[K^+]$ext) (redrawn from Balkos *et al.* 2010; see also Roosta & Schjoerring 2008; Pettigrew 2008).

In rice, root GS activity was found to increase with increasing $[K^+]_{ext}$ (again, in apparent contradiction to the *Arabidopsis* model; see previous text), reaching its maximum at 5 mM in an NH_4^+ (10 mM) background (Balkos *et al.* 2010). The same pattern was also observed for phosphoenolpyruvate carboxylase (PEPC) activity, the key anapleurotic C-fixing enzyme, as well as with total protein content (Fig. 4). This corresponded with tremendous gains in plant biomass, with growth 160% higher than NO_3^--grown plants and 220% higher than plants grown at 0.1 mM K^+ (Balkos *et al.* 2010). Similar effects were observed in cucumber, although they were not as dramatic, which may reflect the lower tolerance to NH_4^+ in this species, relative to rice (Roosta & Schjoerring 2008). Other reports of the stimulation of expression and activity of N-assimilatory enzymes by K^+ can be found in Ali *et al.* (1991) and Mohammad & Naseem (2006). Taken together, these findings, including the controversial findings with *Arabidopsis*, point to a distinct reprogramming, by K^+, of C and N metabolism (Armengaud *et al.* 2009; Balkos *et al.* 2010; Pettigrew 2008). A similar reconfiguration of primary (and secondary) metabolic machinery was observed by transcriptomic analysis in *Arabidopsis*, in response to N. After 2 d of N deprivation, the majority of genes associated with photosynthesis, chlorophyll synthesis and plastid protein synthesis were repressed, and those associated with secondary metabolism were induced (Scheible *et al.* 2004).

Lastly, phytohormone responses involving K^+ and N nutrition include auxin and cytokinin (CK) biosynthesis and signalling. Cao *et al.* (1993) showed that growth suppression of *Arabidopsis* seedling roots in the presence of 6 mM NH_4^+ and 20 μM K^+ could be relieved by elevation of K^+ to 200 μM, but not in the presence of supplementary auxin (indole acetic acid) or cytokinin (6-benzylaminopurine) or a combination of the two. Moreover, growth suppression by NH_4^+ was also much less pronounced in auxin-resistant mutants. Cytokinins have been implicated in K^+ and N signalling and the regulation of genes encoding K^+ and N transporters (Brenner *et al.* 2005; Kiba *et al.* 2005; Schachtman & Shin, 2007; Shin 2011; Nam *et al.* 2012). Under low-K^+ stress, root CK levels are reduced, which result in ROS accumulation, root hair growth and *AtHAK5* expression (Nam *et al.* 2012). Similarly, low N results in lowered CK levels (Takei *et al.* 2002, 2004; Scheible *et al.* 2004; Miyawaki *et al.* 2006; Nam *et al.* 2012) that have been linked to increased expression of genes encoding nitrate and ammonium transporters (*NRT2 and AMT1*, respectively; Brenner *et al.* 2005; Kiba *et al.* 2005).

CONCLUSION

On a planet where the human population continues to greatly expand (forecasts estimate growth of up to 12.3 billion by 2100; Gerland *et al.* 2014), ever-increasing demands on the world's agricultural systems are expected to produce immense strains on land, water and nutrient resources in the coming decades. Rapidly changing climates and environmental degradation in many parts of the world will put additional stresses on crop production, while a dangerous feed-forward cycle may play itself out, given that food systems are themselves responsible for 19–29% of anthropogenic greenhouse gas emissions globally (Vermeulen *et al.* 2012). Plant physiologists have applied their knowledge and skills to produce remarkable increases in crop yields over the past century, preventing the starvation of millions, and must be called upon once again to address new challenges.

Clearly, to reduce the amount of new land required to meet growing demands, and thereby reduce strains upon 'marginal' or ecologically fragile environments, the efficiency of crop production will need to be increased. One approach to this would be to precisely determine species-specific and site-specific growth optima with respect to nutrients such as NO_3^-, NH_4^+ and K^+, not only singly, but in relation to one another. In this review, we have discussed some of the key physiological issues pertaining to these relationships, from the often observed antagonism between NH_4^+ and K^+, to the alleviation of NH_4^+ toxicity by K^+, to the co-operative uptake, internal transport and utilization of NO_3^- and K^+. Other interactions, such as those involving synergies and antagonisms between NO_3^- and NH_4^+, and their relationships to K^+ supply, as well as interactions involving other essential macronutrients and micronutrients in optimizing growth and yield, will greatly improve the science of plant nutrition. In addition, the examination of nutrient interactions with water use in plants (and its efficiency), such as the influences of NO_3^- and K^+ on aquaporin and stomatal function (Guo *et al.* 2003; Cramer *et al.* 2009; Fig. 2) and as major osmotica, will become increasingly important as water scarcity and soil salinity become more widespread. Moreover, the world's most important crop species, rice, is also the world's most water consumptive, further highlighting the necessity to understand and optimize plant water use (Hoekstra & Chapagain 2007; Chapagain & Hoekstra 2011; Britto *et al.* 2014).

While the complexities of nutrient sensing, signalling mechanisms and transport regulation cannot be fully unravelled without the benefits of molecular biology, there is still much room for physiological methods in the pursuit of more efficient and productive crop systems (Pettigrew 2008; Cramer *et al.* 2009; Britto *et al.* 2014). This is important in part because of the current public reaction against recombinant DNA technology, particularly in Europe. However, even while 'genetically modified' organisms (GMO) are out of favour, the vast amount of data provided by modern molecular biology (e.g. Armengaud *et al.* 2009) has the potential to inform and direct physiologists and agronomists seeking to improve crop production by nutritional means. These approaches, combined with gradual improvements in remote and local sensing of soil fertility and crop mineral content, and in spatially and temporally precise application of water and nutrients, can help bring about yield increases even in GMO-free zones.

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