



Review

Potassium physiology from Archean to Holocene: A higher-plant perspective

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ABSTRACT

In this paper, we discuss biological potassium acquisition and utilization processes over an evolutionary time-scale, with emphasis on modern vascular plants. The quintessential osmotic and electrical functions of the K^+ ion are shown to be intimately tied to K^+ -transport systems and membrane energization. Several prominent themes in plant K^+ -transport physiology are explored in greater detail, including: (1) channel mediated K^+ acquisition by roots at low external $[K^+]$; (2) K^+ loading of root xylem elements by active transport; (3) variations on the theme of K^+ efflux from root cells to the extracellular environment; (4) the veracity and utility of the “affinity” concept in relation to transport systems. We close with a discussion of the importance of plant-potassium relations to our human world, and current trends in potassium nutrition from farm to table.

“Time is an ocean, but it ends at the shore”

- Bob Dylan

1. Introduction

Potassium (K), an alkali metal (i.e. a Group-1 element in the periodic table), is essential to the function of all living cells (Benito et al., 2002). It was first isolated in 1807 by the British poet-scientist Humphry Davy, shortly before he isolated sodium (Na), a chemically similar alkali metal (Forbes, 1995). Both elements were discovered by use of the dramatic, indeed explosive, new method of electrolysis, in which a massive “voltaic pile” (Volta’s recently invented, prototypical battery) generated an electric current through moistened samples of pure caustic potash (KOH) or caustic soda (NaOH) (Siegfried, 1963; Enghag, 2004). By the end of the century, von Liebig and Ringer had shown potassium to be essential for plants and animals, respectively (Radulov et al., 2014), and, today, it is recognized as a requirement for all life (Danchin and Nikel, 2019).

In aqueous solutions, K loses its lone 4s-orbital valence electron to produce the stable complete-octet K^+ cation, the form in which the

element generally operates in biological systems. In this regard, K differs from most other major elements of life, which function via the formation of highly specific covalent bonds (N, P, S, and, of course, C; Clarkson and Hanson, 1980). As a result, K^+ is a highly mobile, exchangeable ion in living organisms, and these characteristics underlie its common biological significance, as well as its taxon-specific significance. Engaging with the high intrinsic mobility of K^+ is the plethora of K^+ transporters found in all cells and organisms, which catalyze the fluxes of K^+ over short and long distances, and dynamically maintain internal K^+ pools at scales ranging from the vesicular to the whole-plant level.

The topic of potassium in biology is vast. Within the realm of plant potassium biology alone, recent years have seen an explosion in detailed reviews on diverse aspects of the topic, indicative of tremendous current activity in the field (e.g. Li et al., 2018; Hasanuzzaman et al., 2018; Sze and Chanroj, 2018; Nieves-Cordones et al., 2019; Chérel and Gaillard, 2019; Ragel et al., 2019; Sustr et al., 2019; Adem et al., 2020; Srivastava et al., 2020; Sardans and Peñuelas, 2021). Notably, most of these papers focus on the transport of K^+ , between the plant and its external environment, and among compartments within the plant, functions that are quintessential to its character as a mobile osmolyte and electrolyte. While the present paper is no exception, we begin by stepping back from

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the exquisite minutiae of plant K^+ -transport, to take a more panoramic view than is usual, and consider evolutionary turning points in potassium biology since the dawn of life. We then turn to a comparative physiology of K^+ transport in major groups of organisms, with special reference to higher plants (Section 2). This is followed by an overview of K^+ -transport systems in plants, with emphasis on what we suggest are some of the most interesting current concepts and controversies in the field (Section 3). We conclude with a discussion of the agronomic dimensions of plant-K biology, placing it in the context of human society today (Section 4). While full coverage of this large range of topics would require many volumes, this paper is meant to serve as an outline of the fascinating and utilitarian topic of K^+ transport physiology in plants, and also to provide a stimulus for new thinking in this and related fields.

2. Potassium physiology in plants and other life forms: A comparative survey

2.1. Early life and the cellular universality of K^+

The biologically universal functions of potassium fall into two broad categories: (a) the formation and utilization of electrical and osmotic gradients in cells and tissues, and (b) the chemical coordination and activation of enzymes and nucleic acids (Gajdanowicz et al., 2011; Benito et al., 2014; Nieves-Cordones et al., 2016a). A third, and more recently investigated, role for K^+ is as an agent of stress signaling and tolerance, and possibly even of stress-induced metabolic and developmental reprogramming in animals and plants (Amtmann et al., 2008; Adem et al., 2020; Zhao et al., 2020; see Section 3.4). The structural aspects of potassium's participation in fundamental biochemical processes continues to be resolved at ever finer levels, as in the recent study by Rozov et al. (2019), who used X-ray diffraction to map the spatial coordinates of individual potassium ions within the rRNA matrix of the ribosomal decoding center. This ancient and universal interaction is crucial to information transfer between the genetic blueprint and protein synthesis (Auffinger et al., 2016), and is an example of high biological selectivity for K^+ (Danchin and Nikel, 2019; Rozov et al., 2019). In such roles, K is similar to most other nutrient elements, which generally allow for little substitution.

Conversely, many other roles of K are less selective. For example, various monovalent cations (Na^+ , Rb^+ , Cs^+ , and NH_4^+) can substitute for K^+ in the basic functions of osmotic regulation (along with organic "compatible solute" molecules, such as proline, glycine betaine, polyamines, and sugar alcohols; Clarkson and Hanson, 1980; Leigh and Wyn Jones, 1984; Shabala, 2013; White, 2013; Luo et al., 2017), charge balancing (Danchin and Nikel, 2019), and enzyme activation (Nitsos and Evans, 1969; Nieves-Cordones et al., 2016a). In plants, the physicochemical similarities between K^+ and Na^+ (in terms of solubility, ionic character, and atomic and hydrated radii) allow Na^+ to substitute for K^+ to a significant extent when external $[K^+]$ ($[K^+]_{ext}$) or K^+ transport is limiting (Gaymard et al., 1998; Spalding et al., 1999; Subbarao et al., 2003; Battie-Laclau et al., 2014; Kronzucker et al., 2013; Benito et al., 2014; Hedrich and Shabala, 2018; see Section 2.2). This is illustrated by the facultative ability of root cells to take up Na^+ when K^+ is low or unavailable (Horie et al., 2007; Schulze et al., 2012). At higher, saline concentrations, however, the limited capacity of plants to discriminate between Na^+ and K^+ can lead to an over-accumulation of Na^+ and suppression of K^+ uptake, two major factors contributing to sodium toxicity (Aharon et al., 2003; Kronzucker et al., 2013).

Its relative lack of unique functional properties has raised the question as to how K^+ became the predominant cation within all cells, rather than, for example, its abundant "twin", Na^+ (Rodríguez-Navarro, 2000; Mulkidjanian et al., 2012; Benito et al., 2014; Dibrova et al., 2015; Danchin and Nikel, 2019). The question is perplexing, given the widely held assumption that life originated in a Na^+ -rich marine environment during the Archean eon (c. 4 Ga, or billion years ago; Weiss et al., 2018; Raven, 2020). While the ratio of $[Na^+]$ to $[K^+]$ in ocean water is

presently close to 50:1, it may have been even higher in Archean oceans, which are thought to have been 1.5–2 times as sodium-rich as today (Hunt, 1891; Knauth, 1998, 2005; Dibrova et al., 2015; Danchin and Nikel, 2019). Nevertheless, chemical gradients and chemiosmotic energy transduction across membranes are common to all extant cellular life (Lane and Martin, 2012; Benito et al., 2014). If the first cells did maintain a low internal $[Na^+]/[K^+]$ ratio in a marine environment with very high $[Na^+]/[K^+]$, they would have required a mechanism by which steep, opposing, transmembrane ion gradients could be maintained. Such a mechanism would not, however, need to be invoked in the context of an emerging alternative hypothesis: that life did not originate in a marine setting, but in ponds or lagoons on the earth's land surface, in association with surface hydrothermal vents and volcanic activity (Deamer, 2017b; Rimmer and Shorttle, 2019; Deamer and Deamer, 2020). In this "fluctuating hydrothermal field hypothesis" (Deamer, 2017a), vapors from terrestrial Archean volcanoes and related hydrothermal systems, which were enriched in K^+ relative to Na^+ (and also rich in C and N), could alternatively explain high K^+ accumulation in the earliest cells (Mulkidjanian et al., 2012; Danchin and Nikel, 2019; Rimmer and Shorttle, 2019). The hypothesis is supported by the findings that extant terrestrial hydrothermal vents often emit more K^+ than Na^+ (Dibrova et al., 2015), and that the abiotic synthesis of organic macromolecules can take place within their chemical fields of influence (Deamer et al., 2019). In addition, laboratory studies of early-Earth conditions show that cycles of hydration and dehydration (simulating the intermittent dryness of terrestrial environments) can facilitate polymerization of amino and nucleic acids via dehydration reactions, and thus lead to the accumulation of organic polymers hundreds of monomers in length (Da Silva et al., 2015; Rimmer and Shorttle, 2019). Cyclic dehydration and the concentration of synthesized products would be less likely to occur in the sea (Deamer, 2017b), where, in addition, high ionic concentrations could be unfavourable to the self-assembly of fatty acids into proto-cellular vesicles (Milshteyn et al., 2018; Omran and Pasek, 2020).

This unorthodox hypothesis is fairly new, and does face conflicting views (Cartwright and Russell, 2019; Korolev, 2021; Omran and Pasek, 2020). It is fairly well agreed upon, however, that more complex life forms, including the earliest eukaryotic and multicellular lineages, did indeed evolve in marine environments, about 1–1.5 billion years later, and that many lineages subsequently returned to land (Strother et al., 2011; Mulkidjanian et al., 2012; Reinhard et al., 2016). In this setting, the prokaryotic marine ancestors immediately preceding these early eukaryotes would already have evolved a reliable thermodynamically active mechanism able to maintain high $[K^+]$ and low $[Na^+]$ intracellularly, while inhabiting a high- $[Na^+]$, low- $[K^+]$ marine environment (Dibrova et al., 2015). Indeed, phylogenetic and biochemical analyses suggest that electrochemical Na^+ gradients ($\Delta\mu_{Na^+}$) were actively generated in the "last universal common ancestor" of all existing life, the prokaryotic LUCA, as well as its much later descendant LECA (the last universal eukaryotic ancestor; Margulis et al., 2006; Mulkidjanian et al., 2008; Weiss et al., 2016). Moreover, in this "sodium world" (or "sodium economy", as it is sometimes called; Skulachev, 1988; Britto and Kronzucker, 2005; Mulkidjanian et al., 2009; Taylor et al., 2012), the generation of $\Delta\mu_{Na^+}$, using ATP as an energy source, may have constituted the means by which membranes were electrochemically energized in the earliest true cells (Mulkidjanian et al., 2008, 2009; Rodríguez-Navarro and Benito, 2010; Lane and Martin, 2012; Poehlein et al., 2012; Dibrova et al., 2015). Considerable evidence suggests that an alternative, proton (H^+)-based economy was only later established, via the independent (convergent) evolution of Na^+ pumps into H^+ pumps in multiple lineages (Mulkidjanian et al., 2008; a chloride-based economy is also possible, see Raven and Beardall, 2020). These early H^+ pumps may have been used primarily for cellular pH regulation (Raven and Beardall, 2020). Today, H^+ pumps also energize membranes in many organisms, and are universally distributed among the outer cell membranes of both prokaryotes (archaea and bacteria, as well as mitochondria and plastids,

the prokaryote-derived organelles of eukaryotic cells), and non-animal eukaryotes, including plants, fungi, and some protists (Gogarten and Taiz, 1992; Mulikidjanian et al., 2008; Rubio et al., 2017). The common occurrence of a proton economy among sessile organisms may reflect the ubiquity of H^+ in the presence of water, relative to ions such as Na^+ or K^+ , which are more patchily distributed (Sakano, 2001; Wegner and Shabala, 2020). Molecular-phylogenetic evidence for a proton economy evolving subsequent to a sodium economy is corroborated by the advanced adaptations in lipid structure and composition required of proton-tight membranes, such as a higher density of hydrocarbons in the midplane of the lipid bilayer (Deamer, 1987; Mulikidjanian et al., 2008, 2009; Taylor et al., 2012; Muralidhar et al., 2015). Lacking such adaptations, the plasma membranes of animal cells can generate substantial transmembrane potential gradients (although less polarized ones than are found in plants; Pedersen and Palmgren, 2017) via Na^+ and K^+ transport, but are leaky to the much smaller H^+ ions, and, with few exceptions, cannot maintain H^+ gradients (Mulikidjanian et al., 2008).

2.2. K^+ in plants and animals: One ion, divergent functions

Precise control over both intracellular and extracellular pools of Na^+ and K^+ is a fundamental feature of animal physiology, underlying such basic zoological functions as nerve impulses, muscular contraction, and cellular signalling (Glynn, 2002; Maathuis, 2014). Animal cells actively maintain Na^+ and K^+ homeostasis via the Na^+/K^+ -ATPase (the “sodium pump”; Glynn, 2002; Studer et al., 2011), which hydrolyzes one molecule of ATP to drive the export of three Na^+ ions from the cell and the import of two K^+ ions into the cell (Clausen et al., 2017). This asymmetrical exchange results in two important outcomes for the cell: (1) it establishes and maintains a low intracellular $[Na^+]/[K^+]$ ratio and a high extracellular one (within, e.g. blood plasma in vertebrates, or hemolymph in invertebrates); (2) it establishes and maintains an electrical potential difference (voltage) across the plasma membrane (Glynn, 2002; Matchkov and Krivoi, 2016). These two outcomes enable the cell to perform a wide variety of energy-demanding functions, such as the active transport of inorganic ions and organic metabolites across membranes, driven by the steep Na^+ electrochemical gradients that place animals firmly in a “sodium economy” (Lu et al., 2016; Clausen et al., 2017).

The fully fledged Na^+/K^+ -ATPase is exclusive to animals and our closest unicellular relatives, the choanoflagellates (Studer et al., 2011), the two having diverged from a common ancestor in the late Proterozoic Eon (634–604 Ma, or million years ago; Peterson and Butterfield, 2005). The presence of the Na^+/K^+ -ATPase in this ancestor likely contributed significantly to the evolution of multicellularity in the earliest eumetazoans (gastrulating animals, i.e. excluding sponges and other parazoans), as it provided a means of generating and controlling ionic, osmotic, and electrochemical potentials, not only in cells, but also in tissue-bound, extracellular compartments (Studer et al., 2011). These basal adaptations prefigured the development of primordial nerve and muscle cells with resting and action potentials, and the establishment and maintenance of the Na^+ - and K^+ -rich internal environments that enabled faunal invasions of terrestrial environments (Dibrova et al., 2015). The universality of the animal Na^+/K^+ signature can be illustrated by the similarity in Na^+ and K^+ concentrations in the tissues of marine and freshwater fishes, despite their environments varying in $[Na^+]$ by orders of magnitude (Zaman et al., 2015), or by the presence of this signature in the only exclusively terrestrial animal phylum, the Onychophora (“velvet worms”; Campiglia, 1976).

Like all cells, those of vascular plants (i.e. “higher plants”, or tracheophytes) must maintain high K^+ concentrations in the cytosol ($[K^+]_{cyt}$), of around 100 mM (Leigh and Wyn Jones, 1984; Walker et al., 1996; Kronzucker et al., 2003b; Burton, 2010; Rodríguez-Navarro and Benito, 2010; see Section 3.2). Unlike eumetazoans, however, plants do not generally require concentrated, highly regulated pools of Na^+ , K^+ , or other inorganic ions in extracellular compartments such as cortical

apoplast or xylem elements; rather, in most cases these enclose relatively dilute solutions, the compositions of which vary substantially with external supply (Rozema et al., 1981; Drew et al., 1990; Peuke, 2010; White and Karley, 2010; Canales et al., 2018). Indeed, when elevated extracellular solute concentrations do occur, as in plants growing on saline soils, they can provoke osmotic stresses and toxicity (Kronzucker et al., 2013). Moreover, at high external Na^+ concentrations ($[Na^+]_{ext}$), K^+ uptake into root cells can be suppressed or even reversed (resulting in net K^+ efflux; see Section 3.4), while at lower $[Na^+]_{ext}$, K^+ can be partially replaced by Na^+ in K^+ -deficient plants (Shabala and Cuin, 2008; Kronzucker et al., 2013; Battie-Laclau et al., 2014; Wu et al., 2018). Nevertheless, Na is not an essential plant nutrient, except in a small number of C_4 species, which require it in micronutrient amounts (Brownell and Crossland, 1972). Indeed, most plants are Na^+ excluders, to an extent that this trait may have evolved partly as an herbivory-avoidance strategy (Whittaker et al., 1979; cf. Seastedt and Crossley, 1981). As such, Na^+ - K^+ interactions are quite distinct from those in animal cells, where the transport, accumulation, and compartmentation of Na^+ are inextricably bound to that of K^+ .

$[K^+]_{cyt}$ in plant cells can be deleteriously affected by a range of stress factors other than external Na^+ , such as NH_4^+ nutrition (Kronzucker et al., 2003b). It is interesting to speculate as to whether the depression of $[K^+]_{cyt}$ by NH_4^+ might be partially offset by increasing $[NH_4^+]_{cyt}$, and whether the NH_4^+ ion may be able to substitute for some of the roles normally fulfilled by cytosolic K^+ , in particular enzyme optimization functions (Nitsos and Evans, 1969; see above). More broadly, one might ask if the sum of potentially abundant, monovalent, cytosolic cations like NH_4^+ (Kronzucker et al., 2003b), Na^+ (Kronzucker et al., 2013), and Rb^+ (used as a fair, if imperfect, analogue for K^+ in flux and compartmentation experiments; Läuchli and Epstein, 1970; Behl and Jeschke, 1982; Drobner and Tyler, 1998) might be able to complement a suppressed $[K^+]_{cyt}$ to physiologically approximate a “normal” (100-mM $[K^+]_{cyt}$) condition. Related questions may be asked about the extent to which NH_4^+ might replace cytosolic K^+ in plants that are highly tolerant of elevated NH_4^+ (Kronzucker et al., 1997; Chen et al., 2013), relative to plants that readily suffer NH_4^+ toxicity (Britto et al., 2001; Britto and Kronzucker, 2002). As K^+ is central to the alleviation of NH_4^+ toxicity (Szczërba et al., 2008a, b; Balkos et al., 2010; Li et al., 2012), answering these questions may prove to be of substantial practical significance.

While cytosolic Na^+/K^+ concentration ratios ($[Na^+]_{cyt}/[K^+]_{cyt}$) in animal cells are maintained at precise, homeostatically controlled set points, there is no evidence for an analogous, precisely set ratio in plant cells. Nevertheless, discussion of $[Na^+]_{cyt}/[K^+]_{cyt}$ “homeostasis” does appear frequently in the plant literature, where it is presented as a hallmark or critical feature of salinity-stress tolerance (e.g. Ma et al., 2012; Wu et al., 2018; Chérel and Gaillard, 2019; Rubio et al., 2020). Although maintaining this ratio at low values may well be critically important to life in saline environments, the lack of evidence for cytosol-specific, homeostatically managed set points for $[Na^+]_{cyt}/[K^+]_{cyt}$ in plants makes the term “cytosolic $[Na^+]_{cyt}/[K^+]_{cyt}$ homeostasis” imprecise and somewhat misleading. The absence of well-defined set points may be due, in part, to the relative scarcity of measurements of $[Na^+]_{cyt}$ in plants, either in isolation or with concurrent measurements of $[K^+]_{cyt}$, and the few reports that are available are often conflicting (Kronzucker and Britto, 2011). More fundamentally, it may be that precise $[Na^+]_{cyt}/[K^+]_{cyt}$ homeostatic set points are simply absent in plant systems. Indeed, in the case of a plant growing on Na^+ -free media, $[Na^+]_{cyt}/[K^+]_{cyt}$ would be essentially zero (and its inverse undefined). Nevertheless, in the context of Na^+ as a beneficial nutrient (Subbarao et al., 2003; Kronzucker et al., 2013), it might prove worthwhile to measure $[Na^+]_{cyt}/[K^+]_{cyt}$ in species, both glycophytic and halophytic, when they demonstrate improved growth under non-toxic Na^+ regimes. An optimal $[Na^+]_{cyt}/[K^+]_{cyt}$ could perhaps be discovered in such cases, which might assist in understanding the mechanism(s) by which low-to-moderate Na^+ provision can benefit growth (Subbarao et al., 2003; Gattward et al., 2012; Kronzucker et al.,

2013). It should be noted that, on a tissue level, gross Na^+ concentrations and $[\text{Na}^+]/[\text{K}^+]$ ratios are low in most plants, especially in leaves, except under saline (usually toxic) conditions, when Na^+ can be hyper-accumulated (Flam-Shepherd et al., 2018). Because salinity continues to be a major agricultural problem and research focus in plant biology, tissue $[\text{Na}^+]/[\text{K}^+]$ ratios will likely remain an important conceptual tool (e.g. Guo et al., 2019).

At the molecular scale, these kingdom-level physiological distinctions are reflected in a complete absence in vascular plants of the ATP-powered membrane transport of Na^+ or K^+ , either individually, or in a coordinated manner (as with the Na^+/K^+ -ATPase; Morth et al., 2011). Instead, the primary electrochemical energization of the plant plasma membrane is achieved via the H^+ -ATPase-powered pumping of protons out of the cell, which produces an electrochemical H^+ gradient ($\Delta\mu_{\text{H}^+}$), or “proton motive force” (Mitchell, 1961), and thus places plants solidly in a “proton economy” (Rodríguez-Navarro, 2000; Pedersen and Palmgren, 2017; Siao et al., 2020). Thermodynamically “uphill”, active influx of K^+ (and most other ions) into plant cells is coupled energetically to the “downhill” return of H^+ into the cell, while the inwardly negative membrane potential generated by the proton pump also provides electrical attraction for K^+ influx into the cell. It is worth noting that even “passive” K^+ transport at relatively high $[\text{K}^+]_{\text{ext}}$ (i.e. via a channel-mediated uniprot mechanism; see Section 3) can only be sustained by continued membrane repolarization, which makes it ultimately dependent on H^+ -ATPase activity. The energy required for passive K^+ transport, however, is still considerably less than that needed by active H^+/K^+ symport (which entails the balancing of an extra incoming positive charge). A few exceptions to the use of $\Delta\mu_{\text{H}^+}$ to drive secondary active transport in plants can be found in the marine angiosperms (“seagrasses”) *Zostera marina* and *Posidonia oceanica*, which can use the massive electrochemical Na^+ gradients between ocean water and cytosol to drive anion uptake (García-Sánchez et al., 2000; Rubio et al., 2018); others can be found in cation-chloride cotransporters (CCCs; Henderson et al., 2018), and in the Na^+/K^+ symport activity of one subgroup of plant Na^+ transporters (HKT2s; Rubio et al., 1995; see Section 3.1).

The marine algal ancestors of vascular plants, by contrast, engaged in a sodium economy, consistent with their habitats having both a high $[\text{Na}^+]$, and a high pH of around 8.2 (Rodríguez-Navarro and Benito, 2010; Taylor et al., 2012; Muralidhar et al., 2015; Raven and Beardall, 2020). By contrast, terrestrial freshwaters and the soils they permeate are usually orders of magnitude lower in $[\text{Na}^+]$ than marine waters, and frequently lower in pH; these are precisely the conditions that would favor a proton economy (Taylor et al., 2012). The evolutionary transition from marine algae to tracheophytes occurred via a series of green (charophyte) algae, from brackish and fresh waters to dry land, followed by non-vascular-plant intermediates (de Vries and Archibald, 2018). Some lineages may have engaged in both economies, possibly switching between them as dictated by the fluctuating demands of highly variable terrestrial and semi-terrestrial environments (Skulachev, 1988; Taylor et al., 2012; Pedersen and Palmgren, 2017). Co-existing economies can be found in green algae, filamentous fungi, and bryophytes (i.e. the mosses, liverworts, and hornworts, which are non-vascular plants that evolved prior to tracheophytes). Species within all of these groups engage both ATP-powered Na^+ exporters (either animal-like Na^+/K^+ -ATPase antiporters, or Na^+ uniporters known as “ENAs”), and H^+ -ATPases at the plasma membrane (Yao et al., 1992; Rodríguez-Navarro and Benito, 2010; Morth et al., 2011; Taylor 2012).

In vascular plants, however, which first appeared in the mid-Paleozoic Era (between 451 and 493 Ma; Morris et al., 2018), the ability to directly use ATP to generate Na^+ currents and gradients has been completely lost. ENAs present in bryophytes might have been selected against, in tracheophytes, because they do not discriminate between Na^+ and K^+ as effectively as, for example, animal Na^+/K^+ -ATPases do (Benito and Rodríguez-Navarro, 2003). This could result in loss of cellular K^+ through an ENA-mediated K^+ -efflux pathway, leading to

reduced growth under freshwater conditions (Nakayama et al., 2004; Lunde et al., 2007; Pedersen and Palmgren, 2017); still, however, the expression of a bryophyte ENA in rice was able to confer salinity tolerance (Jacobs et al., 2011). In this context, the expression of a more ion-specific, animal-like Na^+/K^+ -ATPase in plant plasma membranes was recently proposed as a potential means of improving plant salt tolerance (Pedersen and Palmgren, 2017). Theoretically, the activity of such pumps in cells of crop plants could assist in the maintenance of electrically polarized membranes and low $[\text{Na}^+]_{\text{cyt}}/[\text{K}^+]_{\text{cyt}}$ under saline conditions (see Section 4).

K^+ transport in animals and plants reflects their respective heterotrophic and autotrophic conditions. Being entirely autotrophic (except in rare cases, such as that of insectivorous plants), plants must allocate a substantial fraction of metabolic energy to the uptake of nutrients that are usually present in soil at low levels, concentrating them by orders of magnitude within various intracellular compartments. In the case of K^+ , soil concentrations can vary widely, from 0.01 mM to as much as 20 mM (Ragel et al., 2019; Srivastava et al., 2020; but see Section 4), but many soils show K^+ deficiency, particularly in highly weathered tropical lands, such as are found in parts of Australia, Latin America, and southern and eastern Asia (Römheld and Kirkby, 2010; Battie-Laclau et al., 2014; Ahmad et al., 2016; Wang et al., 2016b; Srivastava et al., 2020; Section 4). By contrast, cytosolic and vacuolar K^+ concentrations in plant cells are typically about 10^3 to 10^5 times greater than soil concentrations (Walker et al., 1998; Rodríguez-Navarro, 2000; Dreyer and Uozumi, 2011; Coskun et al., 2013a; Pottosin and Dobrovinskaya, 2014; Wang et al., 2016b). High intracellular $[\text{K}^+]$ is sustained by the electrical potential across the membrane, which is fairly close to the equilibrium potential for K^+ (Pottosin and Dobrovinskaya, 2014). At the heterotrophic level, by contrast, eumetazoans absorb nutrients that had been previously concentrated by the organisms they consume and digest. Thus, in humans, the average $[\text{K}^+]$ in the gastrointestinal lumen is about 16 mM (Spencer, 1959), much higher than in a typical soil solution. Accordingly, K^+ absorption by epithelial cells in the gut can be energetically driven solely by the electrochemical gradient for K^+ ($\Delta\mu_{\text{K}^+}$), and is dominated by “passive” K^+ channels, rather than ATP-powered K^+ pumps or other active K^+ transporters (Stone et al., 2016). In human extracellular fluids such as blood plasma, $[\text{K}^+]$ is somewhat lower than in the gut lumen (3.5–5 mM), which is in the operating range of Na^+/K^+ -ATPases (Cheng et al., 2013). Thermodynamic analysis has suggested that these ATPases are nevertheless not capable of mediating K^+ influx from concentrations below 100 μM , a concentration at which plant K^+ transporters excel (Rodríguez-Navarro, 2000). The functional range of K^+ transporters is reflected in their half-maximal activity constants (K_M values, or “affinity constants”; see Section 3.5): 40–300 mM for K^+ channels (Vora et al., 2008), 1–10 mM for Na^+/K^+ -ATPases (Clausen et al., 2017), and much lower (micromolar) values for “high-affinity” H^+/K^+ co-transporters (e.g. 14 μM for AtHAK5-mediated K^+ influx in *Arabidopsis thaliana*; Gierth et al., 2005; Grabov, 2007). Fittingly, animals are enriched in ion channels relative to plants, while plants are enriched in active transporters (Hwang et al., 2016). While homologs of plant H^+/K^+ co-transporters can be found in prokaryotes, algae, and fungi (Grabov, 2007), none have been identified in animals, which is consistent with the limited ability of animal cells to maintain H^+ gradients across the plasma membrane (Corratgé-Faille et al., 2010; Véry et al., 2014; see above). K^+ channels, on the other hand, are found in all domains of life (eubacteria, archaeobacteria, and eukaryotes; Moran et al., 2015), and genes encoding them are found even in viruses (Thiel et al., 2013; Eckert et al., 2019). The predominant voltage-gated K^+ channels in plants are commonly referred to as “Shaker-like” channels (or simply as “plant Shaker channels”), after the shaking-leg phenotype expressed in mutant fruit flies deficient in K^+ -channel activity (Jegla et al., 2018; see Section 3). However, while belonging to the same superfamily, the metazoan and plant forms of these K^+ channels are now understood to be mechanistically distinct, and, while distantly related, derive from different prokaryotic ancestors

(Jegla et al., 2018).

A similar dichotomy exists in terms of the acquisition of water on land. Eumetazoans obtain water either in bulk, directly from the environment, or indirectly through the consumption of other organisms, while most plants must initially extract it from the soil by osmosis. Because K^+ is the dominant osmolyte in plant cells (Haruta and Sussman, 2012; Oosterhuis et al., 2014; Wang et al., 2016a), the concentrative (and dilutive) effects of K^+ transporters are major factors responsible for generating and modifying the large water-potential gradients that usually exist between a plant cell and its immediate, extracellular environment. Such gradients have several profound consequences for the plant. The uptake and accumulation of K^+ (together with a range of charge-balancing anions and compatible solutes) establish low intracellular water potentials, driving water uptake into plant cells and thus keeping the organism hydrated even under arid or saline conditions (Ahmad et al., 2016). The close relationship between the movements of K^+ and water in plants is clearly seen in the positive correlations between K^+ and water uptake, and in the intimate co-regulation and osmotic sensing functions of K^+ transporters and water-conducting aquaporins (Wang et al., 2016a). Current evidence suggests, furthermore, that some ion-conducting aquaporins may osmotically couple the transport of water and K^+ (Tyerman et al., 2021). Water uptake following K^+ accumulation produces an increase in intracellular water pressure, which causes the plasma membrane to appress against the tensile cell walls that restrain it, as in the skin of an inflated balloon. This state of cellular turgor drives cellular expansion growth, which translates into the development of the whole plant (Elumalai et al., 2002; Grefen et al., 2011; Kroeger et al., 2011; Karnik et al., 2017). K^+ transport and accumulation can change rapidly and directly alter cell turgor, shape, and volume, providing a mechanistic basis for macroscopic plant movements such as phototropisms, gravitropisms, and “seismonastics”, as in the touch-sensitive leaflets of legumes like *Mimosa pudica* (the “sensitive plant”; Scorza and Dornelas, 2011) and leaves of carnivorous plants like *Dionaea muscipula* (Venus flytrap; Koler, 1986; Sherry and Galen, 2002; Nieves-Cordones et al., 2016a; Hedrich and Neher, 2018). Microscopically, the opening and closing of stomata, a process critical to photosynthetic gas exchange and water conservation in higher plants, is controlled by massive fluxes of K^+ into and out of stomatal guard cells (respectively). The K^+ fluxes in turn drive water fluxes into and out of the cells by osmosis, resulting in the large and rapid changes in cell size and shape that are critical to stomatal function (Nieves-Cordones et al., 2012; Lawson and Blatt, 2014; Hedrich and Shabala, 2018). In contrast to plant cells, animal cells do not have restraining cell walls, nor are such restraints required to prevent plasmolysis, because intracellular osmolarity is similar to that of the surrounding media (Gilles, 1998). For example, the osmolarity of human blood is about 300 mOsm in both intracellular and extracellular compartments (Cheuvront et al., 2014). Cell shape, expansion, and movement in animals therefore depend on structures and mechanisms other than those involving cell walls, K^+ transport, and turgor pressure (e.g. cytoskeletal elements; Pedersen et al., 2001).

3. K^+ transport systems in plants: An overview, with focus on current questions

3.1. Classifications of K^+ transporters

Ionic fluxes across cell membranes are catalyzed by macromolecular ion-transport systems, which are essential to both the acquisition and the functions of K^+ (Fig. 1). In plants, K^+ transport systems have been intensively characterized, and can be understood in a variety of intersecting ways, in terms of their functional roles, for example, or in terms of the molecular mechanisms that enable and govern these roles. In this section, we present a concise overview of the roles and mechanisms of K^+ transporters across plant cell membranes, interwoven with a selection of important, and at times controversial, topics within the field,

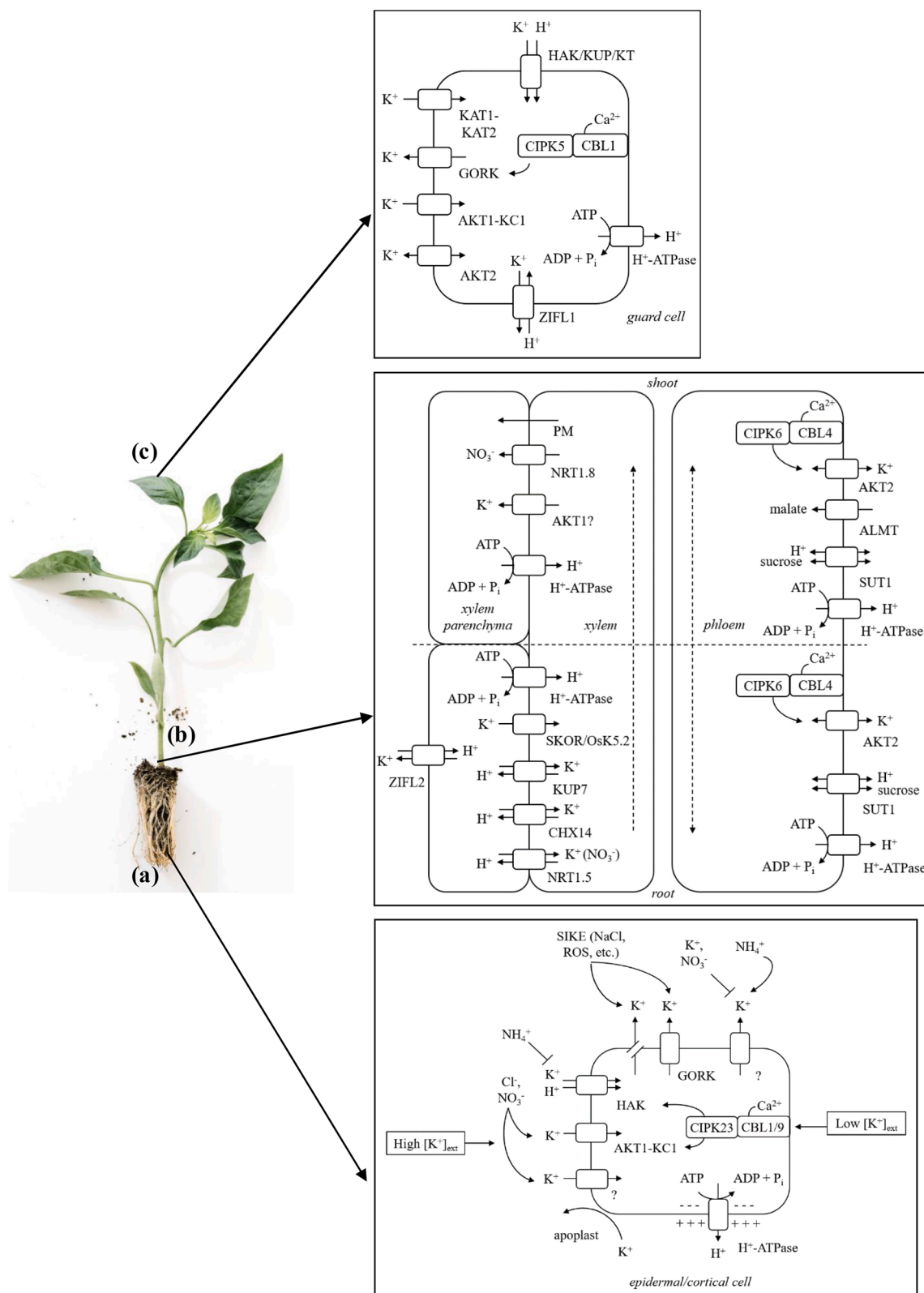
including: channel-mediated K^+ uptake at low $[K^+]_{\text{ext}}$, active K^+ fluxes into the xylem stream, efflux of K^+ from roots, and the “affinity” concept. We hope some of the insights provided here will prove to be interesting and useful to the reader.

Plant K^+ -transport systems can be variously classified in terms of their functional roles. Some are involved in the primary step of K^+ acquisition from the soil, while others enable the secondary circulation of K^+ within the plant, among its organs, tissues, cells, and organelles (note that this use of “primary” and “secondary” is different from the common use in reference to types of active transport; e.g. Raven and Beardall, 2020). Another form of classification is between systems operating at low or at high $[K^+]_{\text{ext}}$ (high- or low-“affinity” transport systems, respectively; see Section 3.5), and a third is between influx systems which transport K^+ into the cell, and efflux systems, which catalyze an outward flux. Many correspondences may be found amongst these categories. For instance, in the case of primary K^+ acquisition, transport is mediated by K^+ -influx systems that must be able to operate at relatively low $[K^+]_{\text{ext}}$ (≤ 1 mM) in most natural and agricultural settings. On the other hand, the diverse systems that circulate K^+ within the plant can variously mediate K^+ influx or efflux, and collectively operate over a wide range of $[K^+]_{\text{ext}}$.

The mechanistic aspects of K^+ transport may also be viewed through multiple lenses. A thermodynamic lens provides a basic distinction between active transport systems, which use metabolic energy to drive trans-membrane fluxes of K^+ against $\Delta\mu_{K^+}$, and passive systems, which transport K^+ down its energy gradient. In plants, active and passive K^+ fluxes map precisely to two distinct types of membrane transport systems, respectively the H^+/K^+ co-transporters (symporters and antiporters), which harness the energy of $\Delta\mu_{H^+}$ to drive active K^+ fluxes, and passive ion channels, which allow K^+ to flow energetically downhill, energized only by $\Delta\mu_{K^+}$, a much weaker gradient than $\Delta\mu_{H^+}$ (Fig. 1).

Seen through the lens of molecular genetics, active K^+ transporters in plants are predominantly H^+/K^+ co-transporters (symporters or antiporters) belonging to two major groups: (1) the HAK (HAK/KUP/KT) family of H^+/K^+ symporters, the largest K^+ -transporter family in plants; this family includes the most important players in K^+ acquisition when $[K^+]_{\text{ext}}$ is low and/or limiting, many of which are rapidly upregulated in response to low $[K^+]_{\text{ext}}$ (Gassman and Schroeder, 1994; Grabov, 2007; Britto and Kronzucker, 2008; Rubio et al., 2008; see discussion below), and (2) the CPA1 (NHX) and CPA2 (CHX/KEA) subdivisions of the monovalent cation/proton antiporter superfamily (CPA), which include transporters involved in osmotic regulation, pH balance, and nutrient mobilization within the plant, through the mediation of K^+/H^+ exchange across membranes of plastids and in the endomembrane and vacuolar systems (Martinoia et al., 2012; Almeida et al., 2017; Khan et al., 2018; Sze and Chanroj, 2018; Wang et al., 2019b; Isayenkov et al., 2020; Tsujii et al., 2020). In addition to the relatively well studied CPA transporters, several H^+/K^+ antiporters belonging to the major facilitator superfamily (MFS) have been recently identified and characterized. These are the nitrate/peptide-transporter family (NPF) member NRT1.5 (Drechsler et al., 2015; Li et al., 2017) and the zinc-induced facilitator-like ZIFL1 and ZIFL2 transporters (Remy et al., 2013, 2015). Interestingly, all three transporters are thought to mediate K^+ efflux from cytosol to apoplast. ZIFL1 mediates K^+ efflux from guard cells, which helps drive stomatal closure (Remy et al., 2013), while ZIFL2 appears to mediate K^+ efflux in cells of the root vasculature, driving K^+ away from the xylem and into the cortical apoplast, under the rare condition of excess K^+ supply (Remy et al., 2015). NRT1.5 also operates in the root vasculature, but on the opposite side of the endodermal divide from ZIFL2, loading K^+ into the xylem (Li et al., 2017; see Section 3.3). These proteins are of additional interest due to their involvement in the transport of other important solutes, such as nitrate (NRT1.5) and the plant hormone auxin (ZIFL1), which suggests that they help to coordinate interactions among potassium and other substances in regulatory and developmental processes.

For both K^+ acquisition and internal K^+ circulation, passive K^+



(caption on next page)

Fig. 1. The nutritional physiology of plasma-membrane K^+ transporters. (A) In roots, epidermal and cortical cells take up K^+ by different transport systems, depending on the external K^+ concentration ($[K^+]_{ext}$). At low $[K^+]_{ext}$ (<0.1 mM), uptake occurs predominately via a H^+/K^+ symport mechanism mediated by high-affinity HAK transporters (e.g. AtHAK5 from *Arabidopsis thaliana* and HvHAK1 from barley; Gierth and Mäser, 2007; Rubio et al., 2010; Coskun et al., 2013a). In the presence of high (>1 mM) external NH_4^+ , HAK transporters are inhibited, and AKT1-KC1 channel complexes can mediate K^+ uptake (given a sufficiently polarized membrane potential, which is ultimately governed by the H^+ -ATPase; see Section 3.2). Other transporters (labelled '?') may contribute to K^+ uptake, including CHX13 (Zhao et al., 2008), HKT2s (Horie et al., 2007), and nonselective cation channels (NSCCs; Caballero et al., 2012), but their roles are poorly understood and may be relatively minor. Both HAK and AKT1-KC1 are activated at low $[K^+]_{ext}$ via phosphorylation by the Ca^{2+} -dependent CBL1/9-CIPK23 complex (Xu et al., 2006; Ragel et al., 2015). At intermediate $[K^+]_{ext}$ (0.1–1 mM), K^+ uptake can occur via a combination of HAK, AKT1-KC1, and unknown or minor pathways, whereas at high $[K^+]_{ext}$ (>1 mM), it is predominately mediated by channels, and stimulated by anions (Cl^- and NO_3^-) via unknown mechanisms (Kochian et al., 1985; Coskun et al., 2013a). Stress-induced K^+ efflux ('SIKE'), produced, for example, in response to salinity and ROS, can occur via membrane disruption or depolarization-activated GORK channels (Shabala et al., 2006b; Britto et al., 2010; Demidchik et al., 2010). In the absence of stress and at $[K^+]_{ext}$ below 1 mM, various degrees of steady-state K^+ efflux take place, via an unknown mechanism which is inhibited by high $[K^+]_{ext}$ and $[NO_3^-]_{ext}$, and stimulated by high NH_4^+ (Coskun et al., 2010). (B) Within the vasculature, xylem K^+ loading in roots usually occurs via SKOR (Gaymard et al., 1998; or OsK5.2 in rice, as reported by Nguyen et al., 2017), KUP7 (Han et al., 2016), CHX14 (Zhao et al., 2015), and NRT1.5 (which also mediates NO_3^- loading; Li et al., 2017). ZIFL2 mediates the release of K^+ away from the xylem apoplast (Remy et al., 2015). Xylem K^+ unloading in shoots is not well understood but may occur via AKT1 (Nieves-Cordones et al., 2019) and/or by endocytosis in pit membranes (labelled "PM"; Botha et al., 2008), while NRT1.8 mediates xylem NO_3^- unloading (Li et al., 2010). Phloem K^+ loading and unloading is predominately controlled by AKT2 and linked to sucrose fluxes (via SUT1; Gajdanowicz et al., 2011; Dreyer et al., 2017) and malate transport (via ALMT-type transporters; Heng et al., 2018). AKT2 is regulated by the Ca^{2+} -dependent CBL4-CIPK6 phosphorylation complex (Held et al., 2011). The cooperative long-distance transport of K^+ , N, and malate is described by the Dijkshoorn-Ben Zioni model (Dijkshoorn et al., 1968; Ben Zioni et al., 1971; see also Coskun et al., 2017). (c) Within guard cells, K^+ influx facilitating stomatal opening is mediated by KAT1-KAT2, AKT1-KC1, and AKT2 channels, and to a lesser extent, HAK transporters (Jezek and Blatt, 2017). K^+ efflux (which facilitates stomatal closure) is predominately mediated by GORK (Hosy et al., 2003; Jezek and Blatt, 2017), which is activated by the Ca^{2+} -dependent CBL1-CIPK5 phosphorylation complex (Förster et al., 2019). ZIFL1 can also mediate K^+ efflux, particularly under drought stress (Remy et al., 2013).

transport can be mediated by voltage-gated Shaker channels, which dominate plasma-membrane K^+ conductances in most cell types (Leb-
audy et al., 2007; Dreyer and Uozumi, 2011; Sassi et al., 2012). Other
passive K^+ conductances are mediated by voltage-independent, tan-
dem-pore potassium channels (TPK/KCO channels, including the K_{ir} -like
channels), which are localized mainly at the tonoplast membrane and
are important for stomatal closure and for vacuole-to-cytosol mobi-
lisation of K^+ when $[K^+]_{ext}$ is low (Walker et al., 1996; Sharma et al.,
2013). Both Shaker and TPK channels have a pore-region GYG (Gly-
Tyr-Gly) motif that is highly conserved in K^+ channels across kingdoms
(Nimigean and Allen, 2011) and forms the core of the selectivity filter
(Demidchik, 2014). In addition to K^+ -specific channels, K^+ fluxes can be
mediated by proteins belonging to several families of non-selective
cation channels (NSCCs). Like Shaker and TPK channels, NSCCs are
involved in tonoplast K^+ transport and in efflux of K^+ from root cells,
possibly to help control membrane potentials and compartmental pH
(Demidchik and Maathuis, 2007; Pottosin and Dobrovinskaya, 2014;
Guo et al., 2016; Chérel and Gaillard, 2019). As their name suggests,
NSCCs display limited substrate discrimination, and some can even
transport anions (Tyerman, 2002). In addition, many are inhibited by
high external $[Ca^{2+}]$, are voltage-insensitive, and exhibit transport
bi-directionality (i.e. poor rectification; Pardo and Quintero, 2002;
Demidchik and Maathuis, 2007; Pottosin and Dobrovinskaya, 2014;
Adams et al., 2019). To guard against the dissipation of crucial cellular
ion gradients, *in-vivo* NSCC activities might need to be restricted to
background currents much or most of the time, relative to the "fore-
ground" currents mediated by dedicated, voltage-gated K^+ channels and
HAK transporters. However, they may be able to act as backup systems
at high $[K^+]_{ext}$, when the dominant pathways are blocked by inhibitors
or genetic disruptions (Demidchik and Maathuis, 2007; Caballero et al.,
2012; Coskun et al., 2016; this backup function may be shared with
ion-conducting icPIP2 aquaporins; Tyerman et al., 2021).

Among the multiplicity of plant K^+ -transport systems, the Shaker-
like channels may be the most functionally diverse, and also the best
studied (for reviews, see Dreyer and Uozumi, 2011; Sharma et al., 2013;
Jegla et al., 2018). By facilitating large, passive fluxes of K^+ across cell
membranes ($\sim 10^2$ times greater than in H^+/K^+ co-transporters; Sassi
et al., 2012), these channels are key agents in the K^+ -dependent regu-
lation of electrical and osmotic homeostasis, and recent studies have
indicated that they may also play a role in cellular signaling processes,
and even act as an important metabolic regulatory switch, in response to
severe stresses caused by, e.g., salinity and reactive oxygen species
(ROS; Demidchik, 2018; Chérel and Gaillard, 2019; Adem et al., 2020;

see Section 3.4). Functional plant Shaker channels take the form of
tetramers composed of four, often non-identical, α -subunits. Each sub-
unit has six transmembrane segments, a transmembrane voltage-sensing
domain at its N terminus, a voltage-gating regulator in the fourth
segment, and a cytosolic regulatory "tail" domain at its C terminus,
which, in some cases, includes an ankyrin regulatory domain (Dreyer
and Uozumi, 2011; Véry et al., 2014; Sánchez-Barrena et al., 2020). The
four subunits collectively form a hydrophobic central pore through
which K^+ may permeate in a highly potassium-selective manner
(Sharma et al., 2013; Sánchez-Barrena et al., 2020).

Some of the functional and regulatory diversity in these channels
arises from variations in the tetramerization of different α -subunits
(Wang et al., 2016b). These subunits are encoded by nine genes in
Arabidopsis thaliana, the products of which are grouped as four main
channel types (Dreyer and Uozumi, 2011; Sharma et al., 2013; Coskun
et al., 2014; Chérel and Gaillard, 2019): (1) inwardly-rectifying
 K^+ -influx (K_{in}) channels, which normally transport K^+ into the cell
when the plasma membrane is electrically hyperpolarized, and are
produced from AKT1 and four other K_{in} -type subunits in *A. thaliana*
(KAT1, KAT2, AKT5, and SPIK); (2) outwardly-rectifying K^+ -efflux
(K_{out}) channels, which release K^+ from the cell when the membrane is
depolarized (GORK and SKOR in *A. thaliana*); (3) weakly rectifying K^+
(K_{weak}) channels, which can operate in either a voltage-gated, K_{in} -like
influx mode ("mode 1" of AKT2 in *A. thaliana*; Dreyer et al., 2017) or in a
bi-directional influx/efflux mode ("mode 2" of AKT2), where the di-
rection of K^+ flow depends on the direction of $\Delta\mu_{K^+}$; and (4) "silent" K^+
(K_{silent}) channels, which do not conduct K^+ currents when expressed on
their own, but play important regulatory roles when forming hetero-
tetramers with K_{in} channel subunits (in *A. thaliana*, KC1 is the sole K_{silent}
subunit; Wang et al., 2016b; see Section 3.2). We note that sometimes
group 1 is split into two groups (depending on the presence or absence of
an ankyrin domain in the cytosolic tail region), and also that the number
of Shaker genes can, to a small degree, vary among species (Véry et al.,
2014; Ragel et al., 2019; Drain et al., 2020).

Members of the HKT family of transport proteins resist simple clas-
sification in terms of active and passive transport. HKT transporters
were originally thought to be important for K^+ acquisition at low $[K^+]_{ext}$
(Rubio et al., 1995), but are now seen mainly as regulators of Na^+
transport between root and shoot, and mediators of root uptake of Na^+
when it substitutes for K^+ under low- K^+ conditions (Horie et al., 2007;
Ali et al., 2020). The HKT transport mechanism in most cases appears to
be a passive, electrogenic uniport (Waters et al., 2013), which is
consistent with structural properties shared between HKTs and

Shaker-like K^+ channels, such as a strong similarity in their selectivity filters (Ali et al., 2020). In the HKT1 subfamily, K^+ transport is restricted due to a steric hindrance in the selectivity filter (Cotsaftis et al., 2012), but in the HKT2 subfamily there might be a limited role for Na^+/K^+ symport activity, at least in monocots and at low external $[Na^+]$ (Rubio et al., 1995; Britto and Kronzucker, 2008; Sassi et al., 2012; Hamamoto et al., 2015; Ragel et al., 2019; Ali et al., 2020). In this role, HKT2 transporters could potentially use a Na^+ gradient to drive the uphill movement of K^+ under low $[K^+]_{ext}$ (Rubio et al., 2005; Oomen et al., 2012; Waters et al., 2013). While this mechanism appears to be engaged when expressed in heterologous systems, however, its activity and significance in *planta* have yet to be demonstrated (Waters et al., 2013).

Lastly, we mention the cation-chloride co-transporters (CCCs), a phylogenetically widespread group which is also found in plants, but has not been as well characterized as other K^+ transporters. While plant CCCs have been shown to mediate secondarily active, electrically neutral co-transport of K^+ , Na^+ , and (2) Cl^- in heterologous systems, and affect plant growth and ion homeostasis (Colmenero-Flores et al., 2007; Chen et al., 2016; Henderson et al., 2018), their *in-planta* functions are poorly understood. Originally proposed to mediate root-shoot translocation, particularly of Cl^- , in *A. thaliana* (Colmenero-Flores et al., 2007), subsequent analyses in *A. thaliana* and grapevine (*Vitis vinifera*) indicated that CCCs could be involved in the functioning of the Golgi complex (Henderson et al., 2015). In rice, OsCCC1 is strongly expressed in root tips and localized to the plasma membrane, and appears to be involved in osmoregulation and cell elongation (Kong et al., 2011; Chen et al., 2016). Loss-of-function CCC mutants in *A. thaliana* exhibit severe growth defects, extensive branching, and loss of shoot apical dominance (Colmenero-Flores et al., 2007). The connection between the growth phenotype and K^+ transport is not understood, but may be related to the influence of K^+ pools on auxin transport and activity (Henderson et al., 2018; Sustr et al., 2019). To our knowledge, CCC-mediation of primary root K^+ uptake has not been demonstrated.

3.2. Channel-mediated K^+ acquisition at low $[K^+]_{ext}$: Is *Arabidopsis* an outlier?

When $[K^+]_{ext}$ is below the concentration at which passive influx into root cells is possible, root K^+ acquisition is almost exclusively conducted by members of the HAK family (Fig. 1C; Gierth and Mäser, 2007; Rubio et al., 2010; Coskun et al., 2013a). As $[K^+]_{ext}$ increases above this threshold, however, the proportion of K^+ influx becomes increasingly shifted to K_{in} channels (Fig. 1C; Coskun et al., 2014). In *A. thaliana*, these two types of transporters are exemplified in AtHAK5 and AtAKT1, which together are responsible for a major share of K^+ influx under most conditions (Gierth and Mäser, 2007; Rubio et al., 2008; Pyo et al., 2010; Coskun and Kronzucker, 2013; Nieves-Cordones et al., 2014; Li et al., 2018). Expression of AtHAK5 and other HAK proteins is strongly increased at low $[K^+]_{ext}$ (Gierth et al., 2005; White and Karley, 2010; Ródenas et al., 2017; Cao et al., 2019), while AKT1 expression appears to be constitutive in most cases (Nieves-Cordones et al., 2016b; cf. Buschmann et al., 2000). Interestingly, transport activity at low $[K^+]_{ext}$ is post-translationally upregulated in both HAK5 and AKT1 as part of a common stress response involving the CBL1–9/CIPK23 signaling/kinase pathway. In this pathway, the perception of low soil $[K^+]$ is communicated via Ca^{2+} -channel-mediated Ca^{2+} signatures, directing the CBL1–9/CIPK23 protein complex to activate K^+ transporters by phosphorylation (Fig. 1; Ragel et al., 2015, 2019; Nieves-Cordones et al., 2016b; Saito and Uozumi, 2020; Srivastava et al., 2020).

It has been shown that channel-mediated K^+ acquisition by *A. thaliana* root cells is feasible at $[K^+]_{ext}$ values as low as 10 μM , provided that plasma-membrane electrical potential ($\Delta\Psi$) can be sufficiently negative in this species (Hirsch et al., 1998; Dreyer and Blatt, 2009; Coskun et al., 2013a, 2014; Ródenas et al., 2017; Rubio et al., 2020). In this regard, however, *A. thaliana* might not be representative of plant behavior more generally. In barley and wheat, for example, the

external $[K^+]$ thresholds for channel-mediated influx (or “minimum concentration”, C_m) were estimated to be ten and thirty times higher than that put forward for *A. thaliana* (100 μM and 300 μM , respectively; Gassman and Schroeder, 1994; Coskun et al., 2013a; see Rubio et al., 2020). A higher C_m could be largely attributed to more positive $\Delta\Psi$ values in barley and wheat. More broadly, plasma-membrane $\Delta\Psi$ values in roots of *A. thaliana* are often (though not always; see below) reported to be much more negative (up to -225 mV; Lew, 1996; Hirsch et al., 1998; Ivashikina et al., 2001) than those reported in most plant species, which typically range between about -100 and -175 mV (Higinbotham, 1973; Sze et al., 1999; Demidchik, 2014; Fig. 2; Supp. Table S1), and can be even more positive when NH_4^+ is a dominant N source (see below). This suggests that the C_m for channel-mediated K^+ influx could be substantially lower in *A. thaliana* than in many or most other species, as can be seen in Fig. 2, which shows the C_m (as predicted by the Nernst equation, assuming a $[K^+]_{cyt}$ of 100 mM) plotted against published values of $\Delta\Psi$ in 16 species. In this survey, the great majority of $\Delta\Psi$ values in species other than *A. thaliana* are more positive than -175 mV, predicting that the C_m for passive K^+ influx should be greater than 100 μM in most cases. This would mean that, in the many wild and agricultural settings where soil K^+ concentrations fall towards, or below, this threshold (Ahmad et al., 2016; especially in K^+ -depletion zones, as discussed in Section 4), K^+ acquisition in the field might only rarely be channel-mediated. Instead, this function would be accomplished mainly by H^+/K^+ co-transporters, which, unlike K_{in} channels, show peak activity at similarly dilute concentrations (Gassmann et al., 1993; Pardo and Quintero, 2002; Nieves-Cordones et al., 2007; Rubio et al., 2020).

This evaluation, however, is complicated by several significant factors. One is the overly simple assumption that plant cells have a uniform $[K^+]_{cyt}$ of 100 mM across species (Shabala et al., 2006b; Szczerba et al., 2006, 2009). While this value is a commonly invoked “ballpark” figure, it can drop significantly in the context of K under K deprivation (Walker et al., 1996, 1998), or under other conditions such as hypoxia (Yemelyanov et al., 2020). It should also be considered that a more precise analysis would use the cytosolic activity of K^+ (A_{K^+}), rather than its concentration, as the preferred input value. In dilute external K^+ solutions, there is little difference between the two, but in the high ionic-strength environment of the cytosol, the activity of K^+ can be 20–30 % lower than its concentration (Dash et al., 2012). That this is the case is suggested by the generally lower values found using ion-selective microelectrodes and fluorescent dyes, which measure K^+ activities, compared to the values found using compartmental tracer analysis and longitudinal ion profiling, which measure K^+ concentrations (Maathuis and Sanders, 1993; Walker et al., 1996; Carden et al., 2003; Cuin et al., 2003; Britto and Kronzucker, 2008). A different input value for cytosolic K^+ would shift the log-linear trendline in Fig. 2 closer to the lower dashed line, which was modeled assuming a cytosolic $[K^+]$ of 75 mM, or to the upper dashed line, drawn assuming a $[K^+]_{cyt}$ of 125 mM. Another typical effect of low $[K^+]_{ext}$ on root cells that should be noted in this context is plasma-membrane hyperpolarization (Szczerba et al., 2006; Amtmann et al., 2008; Britto and Kronzucker, 2008; Chérel et al., 2014; Ahmad et al., 2016), which would also energetically favor channel mediation.

Another complicating factor is that measurement of $\Delta\Psi$ using glass microelectrodes entails a systematic underestimate of plasma-membrane polarization by -20 to -50 mV, due to shunt resistances that lead to membrane-potential dissipation at the impalement site (Goldsmith and Goldsmith, 1978; Gassman and Schroeder, 1994; Hirsch et al., 1998). Although rarely made (Gassman and Schroeder, 1994; Hirsch et al., 1998), corrections for this underestimate would also serve to shift the points downwardly along the Fig. 2 trendline. Interestingly, however, in a study where such corrections were made in root hairs of wheat (Gassman and Schroeder, 1994), the C_m for channel mediation of K^+ influx was nevertheless estimated to be 30 times higher than in *A. thaliana* (as mentioned above), revealing a substantially more positive $\Delta\Psi$ in wheat. Accordingly, the authors acknowledged the fundamental

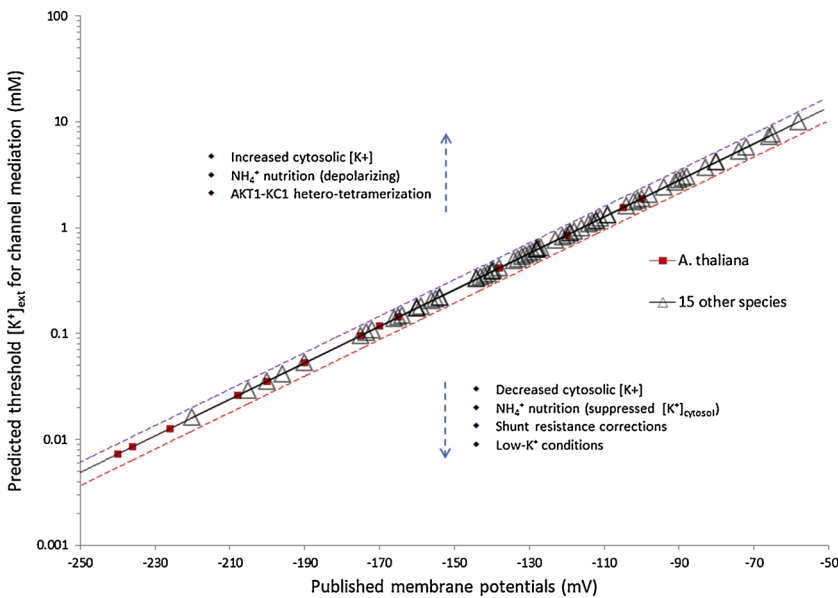


Fig. 2. Predicted threshold $[K^+]_{\text{ext}}$ (or “minimum concentration”, C_m) for channel mediation of K^+ uptake in *Arabidopsis thaliana* (squares) and 15 other plant species (triangles), as a function of root-cell plasma membrane potential ($\Delta\Psi$). Membrane potentials were assembled from 34 publications (see Supp. Table 1 for numerical values and references). Threshold $[K^+]_{\text{ext}}$ was calculated using a variant of the Nernst Equation.

$\Delta\Psi = \frac{RT}{zF} \ln \frac{[K^+]_{\text{ext}}}{[K^+]_{\text{cyt}}}$ in which R , z , and F have their standard meanings, and $[K^+]_{\text{ext}}$ and $[K^+]_{\text{cyt}}$ are the external and cytosolic K^+ concentrations, respectively. T is assumed to be 293 K, and $[K^+]_{\text{cyt}}$ is assumed to be 100 mM (for solid diagonal line; see text for a discussion of this assumption). Arrows indicate conditions under which the K^+ threshold would shift to lower or higher values (see text). Dashed red and blue diagonals refer to predicted threshold $[K^+]_{\text{ext}}$ for cytosolic $[K^+]$ values of 75 and 125 mM, respectively.

importance of proton-coupled “high-affinity” K^+ -uptake mechanisms in plant roots.

A third factor is nitrogen source. Much experimentation on AKT1-mediated K^+ acquisition at low $[K^+]_{\text{ext}}$ has been performed using elevated ammonium ($[NH_4^+] \geq 1$ mM) as an N source. This is because NH_4^+ suppresses H^+/K^+ symport via transporters such as AtHAK5 in *A. thaliana*, thus isolating the channel contribution (Hirsch et al., 1998; Rubio et al., 2008; Coskun et al., 2013a). However, in the absence of NH_4^+ , AKT1 might not play a substantive role in K^+ uptake at low $[K^+]_{\text{ext}}$, but might instead merely serve as a back-up system for HAK-mediated uptake under these conditions (Maathuis and Sanders, 1993; Kochian and Lucas, 1993; Sassi et al., 2012; Coskun et al., 2014). HAK5 and AKT1 itself are both backed up by an additional, as-yet unidentified channel system (Rubio et al., 2010; Caballero et al., 2012; Coskun et al., 2013a, 2014, 2016). Ammonium nutrition could have at least two additional, and opposing, effects on the data points in Fig. 2. The NH_4^+ ion usually causes the plasma membrane to depolarize, either transiently or permanently (Ayling, 1993; Wang et al., 1993; Britto et al., 2001; Szczerba et al., 2006; Coskun et al., 2013a; cf. Nieves-Cordones et al., 2007), which would serve to upwardly shift the points. On the other hand, this shift could be simultaneously opposed by the ability of elevated NH_4^+ to suppress $[K^+]_{\text{cyt}}$ at low to intermediate $[K^+]_{\text{ext}}$ (Kronzucker et al., 2003b; Szczerba et al., 2006), favoring passive K^+ influx.

Lastly, the analysis is affected by an important regulatory dimension to this problem, the heteromultimeric composition of functional plant Shaker channels. Remarkably, even though AKT1 activity in *A. thaliana* is stimulated by phosphorylation at low $[K^+]_{\text{ext}}$, its ability to conduct inward K^+ currents under these very conditions is curtailed due to the heterotetramerization between AKT1 and KC1 (K_{silent}) subunits (Wang et al., 2016b). The AKT1-KC1 complex gates open at membrane voltages substantially more negative (by as much as -70 mV) relative to the AKT1 homotetramer (Dubey et al., 2008; Geiger et al., 2009; Wang et al., 2010). In addition, AKT1-KC1 tetramerization acts to destabilize the pore region at a higher $[K^+]_{\text{ext}}$ than found with AKT1 homomers, causing the pore to change conformation, collapse, and cease to conduct K^+ fluxes (Geiger et al., 2009). This seemingly self-defeating situation can be understood by considering the plant’s overriding need to constrain AKT1-mediated K^+ efflux from the cytosol under low $[K^+]_{\text{ext}}$ conditions, as occurs in the absence of KC1 (Wang et al., 2016b; Adams et al., 2019; but see section 3.4). The negative shift of gating voltage, and collapse of the pore region at a higher $[K^+]_{\text{ext}}$, together contribute to a more stringently valve-like channel behavior (Sharma et al., 2013; Wang

et al., 2016b), which would serve to upwardly shift the points in Fig. 2.

These analytical complications aside, reports of anomalously hyperpolarized membranes in *A. thaliana* have not been explained. While it may be shown that this seeming taxonomic divergence is merely a technical or a statistical artefact, we note that we are not the first to remark upon such a tendency (Nieves-Cordones et al., 2017; Rubio et al., 2020). It may be shown, alternatively, that a high innate capacity to generate very negative membrane potentials in *A. thaliana* contributes to its competitive ability as a ruderal species (Hovick and Whitney, 2019), relative to the less hardy crop species that populate most of the data in Fig. 2. This interesting ecophysiological question has, to our knowledge, not been addressed. On the other hand, $\Delta\Psi$ values measured in *A. thaliana* by some laboratories do fall in line with the preponderance of species examined (e.g. Maathuis and Sanders, 1993; Volkov and Amtmann, 2006; Su et al., 2019), which raises other questions, in particular about technical inconsistencies in measurement among laboratories. In any case, our survey re-affirms the central importance of active, H^+ -coupled K^+ transport under the many soil conditions where concentrations of plant-available K^+ are limiting (also see Section 4).

3.3. Essential plant-internal functions of K^+ transport systems

Within the plant, K^+ channels are critical to the concerted transport of K^+ across membranes and over longer distances, as between roots and shoots or from senescing to growing tissues (Fig. 1). An important example is the K_{out} channel SKOR, which transports K^+ from the cytosol of xylem parenchyma and pericycle cells to the xylem apoplast and, thence, to the leaves (Demidchik, 2014; Huang et al., 2018; Drain et al., 2020). In rice, this function is carried out by the related channel OsK5.2, which also has a role in K^+ efflux from guard cells (Nguyen et al., 2017). In *A. thaliana*, AtSKOR is strongly and specifically expressed in the root vasculature, and its disruption leads to reductions in $[K^+]_{\text{xylem}}$ and shoot K^+ accumulation of about 50 % (Gaymard et al., 1998). However, the remaining 50 % has not been adequately explained, and it is clear that other transporters must play a role in xylem K^+ loading (Elumalai et al., 2002; Alejandro et al., 2007; Li et al., 2017; Drain et al., 2020). This is perhaps most apparent in the legume *Medicago truncatula*, which expresses a single K_{out} channel, showing both GORK-like and SKOR-like activities, and referred to as MtSKOR/GORK (Fedorova et al., 2021). It was recently shown that, although this channel is expressed in the root vasculature, its disruption nevertheless had little or no effect on K^+ translocation to the shoot (Drain et al., 2020). More generally, a

thermodynamic analysis of xylem parenchyma cells, based on a $[K^+]_{\text{cyt}}$ of 100 mM and a plasma-membrane potential of -80 mV (with respect to the xylem apoplast), indicates that passive, channel-mediated xylem K^+ loading can proceed only when $[K^+]_{\text{xylem}}$ is below about 4 mM (White and Karley, 2010). This value is toward the minimum of the 2- to 25-mM range reported for $[K^+]_{\text{xylem}}$ (Marschner et al., 1997; White and Karley, 2010), which suggests that active transporters are required to sustain xylem K^+ loading under many conditions. Above this threshold, a passive SKOR-mediated K^+ leak from the xylem back into parenchyma cells would be energetically feasible, but also at least partially blocked by the $[K^+]_{\text{ext}}$ -dependent positive shift in the channel's gating voltage (Johansson et al., 2006).

Four known active transporters are potential candidates for active xylem K^+ loading, above this 4-mM threshold: the HAK/KUP/KT transporters HAK5 (Yang et al., 2014) and KUP7 (Han et al., 2016), the CHX H^+ / K^+ antiporter CHX14 (Zhao et al., 2015), and the NPF transporter NRT1.5 (Li et al., 2017; Fig. 1b). Expression of these proteins is pronounced in the root vasculature and has been positively correlated with K^+ transport from root to shoot. In *japonica* rice, though, OSHAK5 is thought to function only indirectly in this process, mediating K^+ influx into xylem parenchyma cells, and thereby setting the stage for a subsequent channel-mediated transport of K^+ from parenchyma to xylem (Yang et al., 2014). On the other hand, KUP7, CHX14, and NRT1.5 may all act as active efflux transporters, loading K^+ into the xylem against its electrochemical potential gradient (Drechsler et al., 2015; Han et al., 2016; Li et al., 2017). However, HAK5 and KUP7 appear to be important specifically at low K^+ , suggesting a functional mismatch from the thermodynamics perspective, given that lower $[K^+]_{\text{ext}}$ is associated with a lower xylem $[K^+]$ (White and Karley, 2010; Hasanuzzaman et al., 2018), a condition which would favor channel-mediated, rather than active, xylem K^+ loading. On the other hand, lower $[K^+]_{\text{ext}}$ is generally associated with more negative membrane potentials (Chérel et al., 2014), which could more than compensate for low xylem $[K^+]$. Interestingly, a role for KUP7 and NRT1.5 in active xylem K^+ loading would require both to function as H^+ -coupled antiporters, contrary to the H^+ -symport type normally ascribed to members of these transporter families (Chérel et al., 2014; Li et al., 2017). This poses a mechanistic problem in the case of KUP7 in *A. thaliana*, because this transporter might be involved in H^+ -coupled root K^+ -uptake at low $[K^+]_{\text{ext}}$ (Han et al., 2016), in addition to xylem loading; how would it be able to switch mechanisms between H^+ / K^+ antiport (for xylem loading) and H^+ / K^+ symport (for root acquisition)? In addition, one might ask if KUP7 can also switch affinities, given that it would mediate fluxes from a high cytosolic $[K^+]$ pool in the case of xylem parenchyma cells, but from a dilute pool in a low- K^+ rhizosphere. The fourth candidate, CHX14, on the other hand, is, of course, a member of a designated antiporter family (CHX). Its activation by high $[K^+]_{\text{ext}}$ (Zhao et al., 2015) suggests that this antiporter could very well meet the requirements of an active xylem K^+ loader.

Unlike xylem loading, xylem unloading of K^+ is not well characterized, but AKT1 has been proposed to be one mechanism responsible for this function (Nieves-Cordones et al., 2019). Alternatively, a generic solute transfer mechanism might contribute to K^+ unloading via endocytosis in the pit membranes that are found between metaxylem vessels and xylem parenchyma cells (Botha et al., 2008; Fig. 1b).

The involvement of NRT1.5 in the translocation of both K^+ and nitrate (NO_3^-) from root to shoot (Drechsler et al., 2015; Li et al., 2017) is indicative of the close relationship between the two nutrients (Fig. 1; Kellermeier et al., 2014; Coskun et al., 2017; Li et al., 2017). Nitrate can be the most abundant anion in plant tissues, and its fluxes and accumulation are co-ordinated to some degree with those of K^+ , the two ions contributing to the balance of one another's charge in NO_3^- -fed plants (Casadesús et al., 1995; van Beusichem et al., 1988; Ródenas et al., 2017). In the many species that predominantly reduce NO_3^- to NH_4^+ in the shoot, nitrate must be delivered from root to shoot via the xylem, a passage that is coupled to that of K^+ (Dijkshoorn et al., 1968; Ben-Zioni et al., 1971; Casadesús et al., 1995; see also Coskun et al., 2017). The

co-ordination of long-distance NO_3^- and K^+ fluxes likely involves SKOR (under high NO_3^- supply) as well as NRT1.5, both of which are up-regulated by NO_3^- (Casadesús et al., 1995; Wang et al., 2004; Ragel et al., 2019). Interestingly, the CBL9/CIPK23 signalling/kinase pathway is a key factor in the regulation not only of K^+ uptake via K_{in} channels and HAK transporters (see above), but also of NO_3^- uptake via NRT1.1 (NPF6.3), the most abundant nitrate transporter in roots (Straub et al., 2017). More generally, it is now clear that CBL-CIPK-type mechanisms regulate and integrate a large array of transport systems in the plasma membrane and tonoplast, including systems that mediate NH_4^+ , Na^+ , and Mg^{2+} fluxes, in addition to those of K^+ and NO_3^- (Tang et al., 2020).

Only a fraction of the K^+ translocated via the xylem remains in the shoot; some 40–90 % is circulated back to the root and other parts of the plant via the K^+ -rich phloem (White and Karley, 2010; Coskun et al., 2017; Sustr et al., 2019). Phloem transport of K^+ is accompanied not by NO_3^- as a charge balancer, but by other anions including organic acids, in particular the diprotic acid malate (as described in the “ K_2 -malate shuttle” concept; Ben Zioni et al., 1971; Peuke, 2010; Fig. 1). Shoots regulate K^+ uptake in roots not just by supplying photoassimilates, but also by communicating their K^+ demand via changes in levels of K^+ circulating throughout the plant (Drew et al., 1990; Touraine et al., 1992; Casadesús et al., 1995; Marschner et al., 1997; White and Karley, 2010; Ahmad and Maathuis, 2014; Dreyer et al., 2017; Ródenas et al., 2017).

The K_{weak} channel AKT2 (AKT2/3) is found in sieve elements and companion cells throughout the phloem, and may account for half of the plasma-membrane K^+ permeability in leaf mesophyll (Dennison et al., 2001; Chérel et al., 2002; Dreyer et al., 2017). The operating mode of AKT2 can be switched by phosphorylation from a voltage-gated K^+ -influx mode (mode 1), to a bi-directional mode (mode 2), which is weakly rectifying (or non-rectifying, at physiological membrane potentials), its direction of transport depending on the direction of the K^+ gradient (Sharma et al., 2013; Dreyer et al., 2017). The transport flexibility of AKT2 allows it to function in both phloem K^+ loading in source tissues, and phloem K^+ unloading in sinks (Pilot et al., 2003; Ahmad and Maathuis, 2014), and may even link its activity to whole-plant electrical signaling (Michard et al., 2005). Interestingly, the coordination of the two modes may provide a significant energy source for sucrose loading of phloem cells (Dreyer et al., 2017). In this model, non-phosphorylated, mode-1 AKT2 participates in the unidirectional K^+ -loading of cells in source tissues having high membrane polarization, H^+ -ATPase activities, and respiration rates, while, in mode 2, phosphorylated AKT2 helps to sustain negative plasma-membrane electrical potentials in energetically constrained sinks (e.g. in phloem cells deeply embedded in heterotrophic tissues) by mediating K^+ efflux, which polarizes the membrane (Gajdanowicz et al., 2011; Sandmann et al., 2011; Dreyer et al., 2017). By maintaining negative membrane potentials in sieve elements and companion cells in the phloem, AKT2 can thus participate in the short-term energization of H^+ /sucrose symport without drawing upon local ATP reserves, a system appropriately termed the “potassium battery” (Dreyer et al., 2017; Fig. 1b). Between the K^+ -loading tendency of mode 1 and the sucrose-loading facilitation of mode 2, AKT2 is clearly an important contributor to intracellular osmolarity in the phloem, and thus to the pressure-flow model of phloem transport (Henton et al., 2002).

Another major function of voltage-gated K^+ channels in shoot tissue is the control of stomatal opening and closing (Fig. 1c). The K_{in} channels KAT1 and KAT2 (along with AKT2 and AKT1) cause stomata to open by conducting large influxes of K^+ into the guard cells, lowering the intracellular osmotic potential and drawing in water, which ultimately increases guard-cell turgor and alters cell shape (Pilot et al., 2001; Shin, 2014). KAT1 and KAT2 are activated by a complex sequence of molecular events, involving, in part, the Ca^{2+} -dependent stimulation of the guard-cell plasma-membrane H^+ -ATPase OST2 (AHA1), which results in a rapid hyperpolarization of the membrane that drives K^+ influx (Sirichandra et al., 2009). Interestingly, under saline conditions the

regulatory K_{silent} subunit KC1 is co-expressed with KAT1 and KAT2 in leaves in *A. thaliana*, which leads to the formation of KAT1-KC1 and KAT2-KC1 heterotetramers (Pilot et al., 2003; Jeanguenien et al., 2011). In these tetramers, K^+ conductance is inhibited by 65–95 % relative to KAT1 and KAT2 homo-tetramers, indicating that KC1 probably plays a key role in controlling leaf water loss under salinity. The reverse flux of K^+ across the guard-cell plasma membrane leads to stomatal closure, and is mediated mainly by the K_{out} channel GORK, which is activated by the Ca^{2+} -dependent CBL1-CIPK5 phosphorylation network (Ache et al., 2000; Hosy et al., 2003; Jezek and Blatt, 2017; Förster et al., 2019; Drain et al., 2020).

A striking example of the integration of K^+ -channel function at a whole-plant level can be seen in the influence of the stress hormone abscisic acid (ABA) on channel expression and activity. One of the best-known responses to drought is the host of changes triggered by ABA, including a stimulation of GORK expression and an inhibition of KAT1 expression, as well as the endocytosis and recycling of KAT1 (Sutter et al., 2007). This response leads to decreased stomatal conductance and transpiration, and thus to increased water conservation (Becker et al., 2003; Takahashi et al., 2017). In the root, ABA strongly and rapidly reduces SKOR expression, which lowers K^+ loading into the xylem, and results in elevated solute concentrations (and, therefore, lower water potential) in the root (Gaymard et al., 1998; Pilot et al., 2003; Ma et al., 2020). Increased phloem delivery of K^+ to the root under drought can also be increased by the ABA-stimulated expression of AKT2 in the phloem, and its ABA-triggered de-phosphorylation to mode 1 (Chérel et al., 2002; Pilot et al., 2003; see above).

3.4. K^+ efflux from plant cells: Variations on a theme

The efflux of K^+ across the plant plasma membrane, from cytosol to apoplast, is essential for several critical plant functions. As discussed above, it is a key mechanism directly responsible for stomatal closure via guard-cell turgor loss, the loading of K^+ into xylem elements via xylem parenchyma, and the repolarization of depolarized plasma membranes. In addition, a dramatic episode of stress-induced K^+ efflux (“SIKE”) from root (and shoot) tissues has been frequently observed in response to a wide variety of treatments (Shabala and Cuin, 2008; Demidchik, 2018; discussed below); under normal, long-term, steady-state growth conditions, however, K^+ efflux cannot exceed K^+ influx. K^+ efflux is largely channel-mediated (chiefly via K_{out} channels and NSCCs), and is regulated by multiple mechanisms including K^+ sensing, signaling via hormones, calcium, and ROS, ligand and voltage gating, and phosphorylation (Demidchik, 2014, 2018; Ragel et al., 2019; Adem et al., 2020). K^+ efflux via K_{in} channels is also constrained by the “braking” function of the K_{silent} channel subunit KC1, as discussed earlier. Interestingly, KC1 does not form heteromeric channels with K_{out} subunits (Jeanguenien et al., 2011), which have other mechanisms that strongly counteract the tendency to behave like K_{in} channels when the potential gradient favors K^+ influx (Sharma et al., 2013; Ragel et al., 2019; Adem et al., 2020). A detailed and insightful survey of the multi-faceted physiology of K^+ efflux in plants can be found in a review by Demidchik (2014). In this sub-section, we shall focus specifically on two topics within this area, the radiotracing of K^+ efflux in plants, and SIKE.

The advent of radioisotopic tracers in the mid-20th century made possible the clear separation of unidirectional fluxes (influx and efflux) of K^+ across the plasma membranes of macroalgae (MacRobbie and Dainty, 1958), and, soon afterwards, of vascular plants (Pitman, 1963; Etherton, 1967). These early studies helped form the basis for the methodology of compartmental analysis by tracer efflux (CATE), which has proven to be useful in the measurement not only of unidirectional K^+ fluxes between root cells and the external medium, but also in procuring estimates of K^+ concentrations in the cytosol and vacuole of root cells (Davis and Higinbotham, 1976; Memon et al., 1985; Hajibagheri et al., 1988; Kronzucker et al., 2003b; Coskun et al., 2010). Because the fidelity

of CATE depends on traced pools and fluxes being at (or close to) a long-term steady state, CATE studies provide ample documentation of an efflux phenomenon quite distinct from those mentioned above: that of unidirectional, long-term-steady-state K^+ efflux from root cells to the external medium. This baseline flux occurs simultaneously with the opposing, and normally greater, unidirectional influx of K^+ . The numerical difference between the two is, of course, the net K^+ flux, which is what ultimately determines long-term K^+ acquisition by the growing plant. While unidirectional, steady-state K^+ efflux can be discerned by use of isotopic tracing to monitor K^+ movements (e.g. with $^{42}\text{K}^+$ and $^{86}\text{Rb}^+$), it is inaccessible to methods that report only net fluxes, such as the measurement of changes in external or internal $[\text{K}^+]$, or the use of ion-selective, extracellular, vibrating micro-electrodes (e.g. MIFE, or “Microelectrode Ion Flux Estimation”; Shabala et al., 2006a; and NMT, “Non-invasive Micro-test Technology”; Fan et al., 2018). These methods can only be used to monitor K^+ efflux when the root is undergoing a net loss of K^+ , and, even then, the underlying unidirectional fluxes cannot be disentangled. A condition of net K^+ efflux from the root to the surrounding medium is obviously abnormal and unsustainable for the plant, and may be perceived by the root as a low- K^+ -stress situation, a possibility that could confound experiments examining other forms of stress. Nevertheless, a negative or zero net flux is usually the initial condition in ion-flux experiments using micro-electrodes, desired because it helps to produce an optimal signal-to-noise ratio (Shabala, 2013). Despite these drawbacks, studies based on net K^+ -efflux data have led to important insights into K^+ -efflux-linked stress responses (Demidchik, 2014; Rubio et al., 2020; see below).

A striking feature of steady-state unidirectional K^+ efflux from roots, as measured by radiotracers, is that it can be quite pronounced even when $[\text{K}^+]_{\text{ext}}$ is very low. For instance, in a study on roots of barley (an important model species for tracer-efflux studies), K^+ efflux rates at the near-starvation $[\text{K}^+]_{\text{ext}}$ of 10 μM still ranged from 15 to 50 % of unidirectional K^+ influx (Memon et al., 1985). It is perhaps counter-intuitive that root cells would release K^+ at such low concentrations, which can be growth-limiting, and at which K^+ uptake via H^+/K^+ symport activity can be well below maximum. Moreover, plasma-membrane efflux at low $[\text{K}^+]_{\text{ext}}$ appears to be strictly channel-mediated, and only takes place under low $[\text{K}^+]_{\text{ext}}$ (< 1 mM, “high-affinity” uptake conditions), i.e. when passive K^+ efflux through channels is thermodynamically feasible (Coskun et al., 2010, 2016). The expression pattern and inhibition profile of the K_{out} channel GORK in root tissues suggest that GORK could be a mediator of this steady-state flux, although the baseline flux itself is not depolarization- or ROS-activated (Ivashikina et al., 2001; Demidchik et al., 2010; Coskun et al., 2010). While there is as yet no satisfactory explanation of the functional role of steady-state K^+ efflux in roots, it could be a means by which the continuous fine control of membrane potential, or even $[\text{K}^+]_{\text{cyt}}$, might be achieved (Ragel et al., 2019).

Functional significance aside, steady-state K^+ efflux is important to understand in some experimental settings, as in the measurement of unidirectional K^+ influx into roots, e.g. by $^{42}\text{K}^+$ or $^{86}\text{Rb}^+$ radiotracers. If K^+ efflux is sufficiently large, and the cytosolic K^+ pool turns over rapidly enough, incoming tracer can mix with this pool and be returned to the external medium over the time course of the influx measurement (Siddiqi et al., 1991; Britto and Kronzucker, 2002). The concurrence of tracer influx and efflux can thus lead to an underestimate of the actual unidirectional influx, an error that can be potentially counteracted by the shortening of labeling times (Britto and Kronzucker, 2002). However, this consideration should not pertain to influx measurements made at higher (≥ 1 mM) concentrations, assuming the conclusion by Coskun et al. (2010, 2013a, 2016) is correct, that K^+ efflux from the cytosol of root cells to the external medium is restricted to low- $[\text{K}^+]_{\text{ext}}$ conditions (as mentioned above). Interestingly, above this threshold, a kinetically similar phase of $^{42}\text{K}^+$ efflux is nevertheless observed in CATE experiments (Szczerba et al., 2006; Coskun et al., 2010, 2013a, 2016), but several lines of evidence, including the resistance of this efflux to a wide range of inhibitors (which are very effective against K^+ efflux at low

$[K^+]_{ext}$), strongly suggest that the tracer released in this phase is extracellular (apoplastic) in origin (Fig. 3A; Coskun et al., 2016). If not fully released, apoplastically retained $^{42}K^+$ can become large enough at moderate to high $[K^+]_{ext}$ to cause an overestimate of K^+ influx in short-term unidirectional influx measurements (Coskun et al., 2016), and would invalidate estimates of cytosolic $[K^+]$ arrived at using CATE measurements at the higher end of this concentration range (Szczerba et al., 2006; Demidchik, 2014). Moreover, data corrections accounting for apoplastic K^+ retention at high $[K^+]_{ext}$ suggest that the classic bipartite model of saturating and linear components of transmembrane K^+ influx, as observed with increasing $[K^+]_{ext}$ (Kochian and Lucas, 1982), might be more accurately resolved as a biphasically saturating model, with clear upper limits (Fig. 3B; Coskun et al., 2016). We have applied a similar kind of analysis to re-evaluate the “rapid transmembrane sodium cycling” (RTSC) that appears to occur in roots at high $[Na^+]_{ext}$, interpreting it as largely an extracellular, not a transmembrane, phenomenon (Britto and Kronzucker, 2015; Flam-Shepherd et al., 2018; Santa-María and Rubio, 2018).

As an immediate response to many biotic and abiotic stresses, including pathogen attack, salinity, anoxia, ROS, heavy metals, drought, waterlogging, and temperature extremes, plant cells and tissues undergo SIKE, a dramatic burst in net K^+ efflux that greatly exceeds both steady-state efflux and influx (Shabala et al., 2006b, 2016; Britto et al., 2010; Demidchik, 2014, 2018; Shabala and Pottosin, 2014; Yemelyanov et al., 2020). SIKE has been found to occur in many plant species, in both roots and shoots, and by use of both radiotracer and MIFE techniques (Shabala et al., 2006a; Britto et al., 2010; Coskun et al., 2013b; Liu et al., 2019).

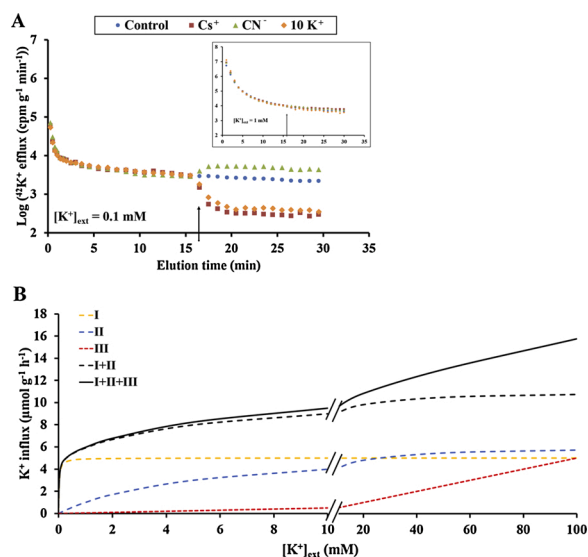


Fig. 3. The emergence of apoplastic K^+ fluxes with rising substrate concentrations in intact barley seedlings. (A) At low $[K^+]_{ext}$ (0.1 mM), $^{42}K^+$ efflux from radioactively loaded roots to the external medium shows sizable responses to a wide range of treatments, including the K^+ -channel inhibitor Cs^+ , the metabolic inhibitor CN^- , and elevated levels (10 mM) of K^+ itself (applied at $t = 16$ min, see arrow). At 1 mM $[K^+]_{ext}$ and above, however, $^{42}K^+$ efflux ceases to respond to these chemical treatments (see inset), revealing a flux that is apoplastic in origin and correlates linearly with $[K^+]_{ext}$. (B) Components of concentration-dependent $^{42}K^+$ influx in intact barley seedlings, determined using mutant and pharmacological analyses. Measured fluxes (solid black trace) can be resolved into three components: (I) a saturable system at low $[K^+]_{ext}$ (predominately mediated by HAK transporters; yellow trace), (II) a second saturable system at higher $[K^+]_{ext}$ (predominately mediated by AKT1 channel complexes and unknown back-up systems; blue trace), and (III) a linear apoplastic flux, which begins to significantly contribute to the total flux at saline concentrations (red trace). Both panels redrawn from Coskun et al., 2016 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

Some of this efflux can be explained as the relatively non-specific leakage of cellular contents due to membrane rupturing, for example from extreme osmotic shock (Nassery, 1979; Cramer et al., 1985; Britto et al., 2010). Where membranes do remain intact, however (as under moderate stress), evidence clearly indicates that SIKE is mediated by ion channels, primarily GORK in roots (and, to a lesser extent, by ROS-activated NSCCs, and, possibly, annexins; Demidchik, 2014; Shabala et al., 2016).

In this context, SIKE is now generally regarded as one component of a network of stress-induced physiological responses, which include membrane depolarization, Ca^{2+} and ROS signaling, protein and lipid phosphorylation, and programmed cell death (PCD; Demidchik, 2014; Shabala et al., 2016). This network has been particularly well studied in the case of NaCl stress. When roots are initially exposed to a sudden elevation in $[Na^+]_{ext}$, the large inwardly directed electrochemical Na^+ gradient drives a significant flux of Na^+ into root cells (possibly via NSCCs), and, within seconds, this causes a large plasma-membrane depolarization (Apse and Blumwald, 2007; Hamam et al., 2019; Su et al., 2019). GORK channels, being depolarization-activated, rapidly respond to this change, and mediate a major portion of the stimulated K^+ efflux. GORK-mediated K^+ efflux is amplified under high NaCl by ROS, produced when $[K^+]_{cyt}$ drops and $[Ca^{2+}]_{cyt}$ rises, thus activating plasma-membrane-bound, ROS-producing NADPH oxidases; it is further augmented by K^+ efflux mediated by ROS-activated NSCCs (Demidchik et al., 2010; Shabala and Pottosin, 2014; Wu et al., 2018; Rubio et al., 2020). The patterns of temporal change and relaxation in SIKE activity vary among species and with the intensity of stress, and some evidence suggests that they can be used as indicators of associated changes in $[K^+]_{cyt}$ (Shabala et al., 2006b; Britto et al., 2010). However, the effect of K^+ efflux on $[K^+]_{cyt}$ is complicated by K^+ replenishment from the vacuole, which has an estimated buffering capacity of 1–7 hours, after which the cell may lose turgor and collapse (Zhao et al., 2020). In some species (*A. thaliana*, *Atriplex lentiformis*, corn, cotton, poplar, quinoa), net K^+ efflux peaks within minutes of salt stress before being rapidly reduced (“Type 1” response), while in others (*Brassica* spp., lucerne, wheat), the flux increases gradually and can persist for several hours at a high level (“Type 3” response; Rubio et al., 2020). These efflux patterns, then, and the implied changes in $[K^+]_{cyt}$, clearly have a genetic component. While they have been likened to “signatures” of signaling agents such as ROS and Ca^{2+} (Shabala, 2017; Rubio et al., 2020; Zhao et al., 2020; see below), however, the meaning, role, and coding mechanisms of such patterns are not known (Rubio et al., 2020).

One of the first consequences of SIKE is the exertion of a repolarizing force on the plasma membrane, which helps to correct the initial depolarization by Na^+ , and illustrates the important role K^+ channels play in the short-term regulation of plasma-membrane potential (Maathuis et al., 1997; Demidchik, 2014; Demidchik et al., 2010; Sharma et al., 2013; Ragel et al., 2019; Dreyer et al., 2021). However, this effect lasts only a few minutes (further repolarization occurs via the H^+ -ATPase; Demidchik, 2014; Shabala, 2017), while net K^+ efflux can persist well beyond this time frame (Rubio et al., 2020). Within half an hour, continued efflux can result in a significant drop in $[K^+]_{cyt}$ (Shabala et al., 2006b), which, while being potentially deleterious, may nevertheless prove to have a positive effect on the stressed plant, at least in the short term and under moderate stress. According to a recent proposal, a significantly lowered $[K^+]_{cyt}$ due to SIKE activity could switch the metabolic state of the cell from one of normal, energy-intensive growth and maintenance (favoring, in particular, anabolic reactions) to one of defense, repair, and acclimation to the imposed stress (a stress-responsive, and more catabolic, state; Demidchik et al., 2014; Chakraborty et al., 2016; Shabala, 2017; Rubio et al., 2020). Energy-demanding enzymes involved in normal cell metabolism would be, it is hypothesized, preferentially inhibited by a drop in $[K^+]_{cyt}$, while enzymes involved in the stress response would either be stimulated or released from inhibition. This differential effect could then allow cellular energy, which can be in short supply under stress, to be diverted

from normal metabolism and towards the stress response (Zhao et al., 2020).

This metabolic switching hypothesis, while intriguing, has not yet been directly demonstrated (Shabala, 2017). Indirect evidence could come in the form of a specific and detailed analysis of preferential (anabolic vs. catabolic) changes in enzyme activity following SIKE activity and/or $[K^+]_{\text{cyt}}$ suppression, or a cost-benefit analysis of sudden, massive K^+ losses from the cell and the whole plant. Findings in this area may resolve the seeming contradiction between the energy-diversion aspect of this hypothesis and the classic suppression of glycolysis under low K^+ (Evans and Sorger, 1966; Armengaud et al., 2009). However, even if the hypothesized adaptive significance of a SIKE-triggered metabolic switch is borne out (which might explain the striking stimulation of GORK expression by NaCl stress in several species; Adem et al., 2014; Chakraborty et al., 2016), it should be kept in mind that SIKE is a two-edged sword, as it has also been negatively correlated with Na^+ tolerance (and K^+ retention) in a wide range of plant species (Chen et al., 2005; Cuin et al., 2008; Wu et al., 2018; Liu et al., 2019; cf. Coskun et al., 2013b). Therefore, any short-term benefit gained from SIKE-generated membrane repolarization or metabolic switching must be seen against a backdrop of potential longer-term harm caused by net K^+ efflux (Chakraborty et al., 2016; Wegner and Shabala, 2020; Zhao et al., 2020). An interesting example in this context is the possible unblocking, by SIKE and suppressed $[K^+]_{\text{cyt}}$, of caspase-like proteases and nucleases, degradative enzymes that are repressed by K^+ and strongly associated with PCD in animal systems; as such, however, these enzymes help to facilitate cellular self-destruction rather than the defense and repair mechanisms relating to a metabolic switch (Demidchik et al., 2010, 2014; Rubio et al., 2020).

Programmed cell death in plants can lead to many different adaptive, genetically preconditioned outcomes that are part of normal growth and development processes, including the production of xylem and aerenchyma, senescence, and the plant hypersensitive response against pathogens (Ma and Berkowitz, 2007; Reape et al., 2008; Shabala, 2009; Buono et al., 2019). PCD-related processes, such as DNA fragmentation (or “laddering”), cytochrome c release, collapse of membrane potential, autophagy, and activation of degradative enzymes, can also be triggered by salt and oxidative stresses, and are therefore likely to coincide with SIKE events (Huh et al., 2002; Lin et al., 2006; Shabala, 2009; Demidchik, 2014; Demidchik et al., 2010; Luo et al., 2017; Wegner and Shabala, 2020; Zhao et al., 2020). Evidence for possible SIKE involvement in PCD can be seen in the delay or suppression of PCD processes in the *gork1-1* mutant (lacking functional GORK channels), and by K^+ -channel blockers and ROS scavengers (Li et al., 2007; Demidchik et al., 2010). However, while the adaptive value of PCD is abundantly clear in plant developmental processes and the hypersensitive response, it is less clear in the case of salinity stress, where cell death can be a net detriment to the plant (Demidchik et al., 2014; Shabala and Pottosin, 2014; Shabala, 2017; Wu et al., 2018). On the other hand, Huh et al. (2002) showed that, although salinity led to a PCD-mediated self-destruction of the primary root in *A. thaliana*, it also led to the proliferation of secondary roots. This resulting change in root architecture, it was argued, could contribute to salinity resistance by modifying water and solute fluxes, as has been shown for drought and anoxia stresses (Jupp and Newman, 1987; Subbaiah et al., 2000). Interestingly, in these studies, the target of cell death was the root apex, where much higher net K^+ efflux (and greater potential for PCD) has been observed, relative to mature regions of the root (Shabala et al., 2016; Wu et al., 2018; Rubio et al., 2020). Another example of a PCD-related process known to provide an adaptive benefit to salt-stressed plants is autophagy, a stress-stimulated, “bulk degradation” process facilitating the breakdown and repurposing of cellular materials (Reape et al., 2008; Luo et al., 2017; Qi et al., 2021). Recently, it was shown that a strong and rapid autophagic response to salt stress in *A. thaliana* can benefit the plant by increasing the activities of three key tolerance processes: 1) clearance of oxidized proteins, 2) vacuolar sequestration of Na^+ (the basis of “tissue

tolerance” to Na^+ stress), and 3) synthesis and accumulation of compatible solutes (Luo et al., 2017). However, it should also be noted that, while autophagy plays a major role in PCD, it is active in routine cellular maintenance processes, and it does not necessarily lead to cell death (Reape et al., 2008), even when stress-induced as in the study by Luo et al. (2017).

Unexpectedly, the role of SIKE in PCD has not been covered in recent reviews focusing on PCD in plants (e.g. Huysmans et al., 2017; Kabbage et al., 2017; Buono et al., 2019; Burke et al., 2020; Qi et al., 2021; Valandro et al., 2020), although it has been the subject of considerable discussion within the ion-transport community for over a decade. This may be related to some insularity among different niches within the plant sciences, but may also point to a need for further conceptual and phenomenological clarification of the SIKE-PCD relationship. In particular, there are very few specific instances of adaptive, “programmable” outcomes of SIKE-induced PCD (the example above from Huh et al., 2002, suggests one, but in this case K^+ efflux was not directly examined). This raises the question as to whether this “PCD” process might at times be more properly referred to as necrosis, which, unlike PCD, is characterized by uncontrolled cell destruction following overwhelming stress (Reape et al., 2008). Lesser degrees or durations of stress could, however, lead to events that more accurately conform to the PCD label, but the distinctions between PCD and necrosis, or between those processes and the hypothetically beneficial, SIKE-controlled, “metabolically switched” state, are not well enough defined at present. It has, however, been suggested that different levels of ROS generation can potentially control cell fate by regulating SIKE (Wu et al., 2018), and also that the restricted duration and tissue localization of SIKE could allow the plant to draw upon the benefits of a transient K^+ loss, while avoiding its detriments (Shabala et al., 2016; Adem et al., 2020; Zhao et al., 2020). More evidence regarding these ideas should prove to be useful for their better evaluation. In particular, it may be asked whether SIKE acts like a signal and/or metabolic switch preferentially in “Type-1” plants (see above), where its duration can be brief, and whether in “Type-3” plants the protracted loss of K^+ may be less like a signal and more like a symptom, or precursor, of serious stress-induced damage.

3.5. The affinity concept: No longer useful? A challenge to a long-held model

The Michaelis-Menten model of enzyme kinetics, with its enzyme-substrate “affinity” concept, has long been embraced by plant scientists as a means of characterizing ion transport across cell membranes. For K^+ , early radiotracer studies provided clear evidence for the existence of distinct high- and low-affinity K^+ -transport systems operating at low and high external $[K^+]$, respectively (Epstein et al., 1963; Kochian and Lucas, 1982; Siddiqi and Glass, 1982; Britto and Kronzucker, 2008). Since then, the distinction between high- and low-affinity systems has become more nuanced, with high-affinity transporters being known to switch to low-affinity states, and vice versa (Hirsch et al., 1998; Fu and Luan, 1998; Liu and Tsay, 2003; Sun et al., 2014; Wang et al., 2015). Three notable examples are AtAKT1, AtKUP1 (Fu and Luan, 1998), and AtNRT1.1 (Sun and Zheng, 2015). The KUP7 transporter, as discussed above, might prove to be another such example, should its dual K^+ -transport function be confirmed (Han et al., 2016).

Recently, an innovative “computational cell biology” study went further, declaring that K^+ channels in plants are inherently of “dual affinity” (Dreyer, 2017). This was concluded *in silico*, in a thermodynamics-based simulation of “wet-lab” (*in-vivo*) investigations of channel-mediated K^+ uptake. The mathematically discovered high-affinity components of these dual-affinity channels were proposed to have been masked in previous *in-vivo* investigations, due to problems related to experimental sampling time. A follow-up to this thought experiment went further still, asserting that the traditional enzyme/substrate-affinity concept has little or no meaning in the context of plant transport systems, and should be revised or discarded

altogether (Dreyer and Michard, 2020). This evaluation is based, in part, on a key *in-silico* outcome: that a simulated K^+ channel, into which no $[K^+]$ dependence or affinity has been pre-programmed, will nevertheless yield multiple, saturating K^+ -uptake curves as $[K^+]_{ext}$ increases, each with its own apparent (but “fake”) affinity. We verified the generation of multiple saturating curves in our own digital simulation, based on the same principles and equations (eqs. 7–10 in Dreyer and Michard, 2020). The same outcome applies both to channel-mediated K^+ uniport and to H^+/K^+ co-transport, and is attributed to $[K^+]_{ext}$ -dependent changes in electrochemical potential gradients driving the K^+ flux; it is built into the thermodynamics. While the curves produced do superficially resemble Michaelis-Menten “isotherms”, they log-transform into straight lines, reflecting the logarithmic relationship between $[K^+]_{ext}$ and the potential energy gradient driving uptake, as seen in the Nernst relationship and related equations. The authors conclude that transporter affinities are attributable to an artefact of data display, which has misled scientists for over half a century.

This critique presents a far-reaching and novel perspective which should be considered by any plant biologist who would assign Michaelis-Menten parameters to a membrane transporter. If the general finding of the critique is accepted, the term “affinity” well may fall into disuse when describing transporter systems (in this paper, we have used it sparingly), and these systems may instead be preferentially classified in different terms, such as those of phylogeny, structure, transport mechanism, or functional range. It may, however, be premature to throw out, with the proverbial bathwater, the entire legacy of Michaelis-Menten modeling of membrane transport. For one thing, precise links between the *in-silico* simulation and the diversity of experimental protocols for measuring transport (e.g. use of electrophysiology, radiotracers, fluorescent dyes, chemical depletion) should be made more explicit. Secondly, *in-silico* studies should be able to provoke hypotheses and predict experimental results *in vivo*, to test their idealized outcomes in the “real world” of wet labs. Notwithstanding the results of the simulation, the activity of any transport protein must eventually approach an upper activity limit (“ V_{max} ”), as the concentration of the transported substrate increases, the kinetics of this approach being dominated by electrical and chemical interactions between enzyme and substrate, and independent of any imposed experimental artefacts. It may be possible for a hybrid solution to emerge, in which the shape of a wet-lab isotherm can be corrected for the side effects of experimentation, to reveal genuine substrate-transporter affinities. In any event, a broader concept of concentration-dependent uptake patterns of K^+ and other nutrients should remain useful in plant science, even if they do not conform precisely to simple Michaelis-Menten formulations, or directly describe the mechanics of transporter-substrate interactions. This concept can be very useful for comparing the ability of plants to abstract nutrients from the environment under varying conditions of nutrient availability, as in nutritional competition scenarios, or ecological succession processes (e.g. Kronzucker et al., 1998, 2003a).

4. Plants, potassium, and people: K in the Holocene

As they grow, plants steadily accumulate K, returning relatively little of it to the soil over the course of their lives; by contrast, animals and other heterotrophs typically consume and excrete potassium in large amounts on a daily basis. In our own species, rates of K intake are approximately balanced by those of excretion (Stone et al., 2016), with the two having an average value of roughly $2 \text{ g person}^{-1} \text{ day}^{-1}$, globally (Iyengar et al., 2002; Stone et al., 2016; NASEM, 2019). This is considerably lower than the average adequate intake (AI) of about $3 \text{ g person}^{-1} \text{ day}^{-1}$ that is recommended in a growing consensus among national and international agencies concerned with human K nutrition (ICRP (International Commission on Radiological Protection), 1980, World Health Organization, 2012, NASEM (National Academies of Sciences, Engineering, and Medicine), 2019; Stone et al., 2016; cf. Strohm et al., 2017). This is about the mass of a US penny, or ~2% of the total K

in an 80-kg person. Actual K intake varies considerably among people of different regions, with intake among Europeans generally exceeding this AI, but intake in the USA falling short at only $2.6 \text{ g person}^{-1} \text{ day}^{-1}$; in many parts of Asia, it is lower still (Iyengar et al., 2002; Stone et al., 2016).

“Adequate” K intake, it should be noted, is not the same as optimal intake, and larger amounts are recommended for some individuals (Weaver et al., 2018). Curiously, human K intake was much higher in prehistoric times ($6\text{--}11 \text{ g day}^{-1}$) than it is today ($1\text{--}3 \text{ g day}^{-1}$), its decline beginning about 5,000 years ago (Young et al., 1995), midway between the start of the Holocene epoch and the present day, or relatively soon after the domestication of cereal grains. This change has been attributed to a major shift in the human diet from one dominated by K-rich fruits, vegetables, and (some) seeds, to one dominated by relatively K-poor foods such as meats and cereal grains. Declining K intake has been accompanied by a similarly large increase in Na intake, a dual tendency that has been linked to increases in cardiovascular disease and other health problems in the modern world (Young et al., 1995; He and MacGregor, 2008; Strohm et al., 2017; Weaver et al., 2018). Not surprisingly, in industrialized societies vegetarians tend to have a significantly higher K intake than the general population (Young et al., 1995). Paradoxically, patients prescribed medications to manage or counteract cardiovascular disease, such as blood-pressure-lowering inhibitors of angiotensin-converting enzyme, can often, as a side effect of the medications’ effects on kidney function, suffer hyperkalemic outcomes (Palmer, 2004), i.e. blood levels of K^+ that exceed normal levels, due to reduced K^+ excretion. Such patients should, therefore, reduce the consumption of K-rich foods.

The vast majority of the potassium consumed by human society, whether in the form of meat or plant material, had to first be taken up by plant roots, via the K^+ -transport systems discussed previously (the contribution of K supplements to human nutrition is minimal). It is no exaggeration to say that life as we know it would not be possible without this remarkable phytological ability. It is also clear that our continued well-being depends on the maintenance of soil K in agricultural fields. Unfortunately, soils are deficient in plant-available K^+ over large regions of the “agrosphere” (Krishna, 2003), either due to characteristics inherent to particular soils, or to unsustainable agricultural practices and other socio-economic factors (Cakmak, 2010; Römhild and Kirkby, 2010; Zörb et al., 2014; Sardans and Peñuelas, 2015; Nieves-Cordones et al., 2016a; Sun, 2018; Srivastava et al., 2020; see Section 2.2), including the high price of K relative to other fertilizers (Schlesinger, 2020). Although supply and demand for fertilizer K have kept pace with the tripling in crop productivity seen globally over the past 60 years (or the recent “anthropocene”, to use a scientifically informal term), the removal of K in general greatly exceeds K inputs (Zörb et al., 2014; Manning, 2015; Dhillon et al., 2019; Schlesinger, 2020), resulting in a “potassium gap” on the global scale (Manning, 2015). For example, it has been estimated that less than half of the K removed from fields in the form of crop residues is replaced by fertilizer, globally (Smil, 1999). Such tendencies will be catastrophic if left unchecked or becomes accelerated by, e.g. increased use of biofuels that is associated with greater removal of plant biomass, and, thereby, K, from agricultural fields than is the case in the harvest of most food crops (Römhild and Kirkby, 2010). More generally, it has been postulated that K may be deficient in as many as 70 % of the world’s ecosystems, and is as limiting a nutrient for plant productivity as are N and P (Sardans and Peñuelas, 2015; Schlesinger, 2020). Even in well fertilized soils, the residence time of K can be very short due to runoff and leaching, from both foliage and soils, especially soils with poor cation-exchange capacities (CEC; Öborn et al., 2005; Römhild and Kirkby, 2010; Zörb et al., 2014; Sun, 2018; Schlesinger, 2020; cf. Goulding et al., 2021). Moreover, rates of potassium loss from soil during litter decomposition can exceed losses of nitrogen and phosphorus, because, unlike those elements, K is not a covalently bound constituent of organic molecules (Sardans and Peñuelas, 2015). While these losses are wasteful, however,

eutrophication via K enrichment is uncommon, compared to that caused by N and P loss from agroecosystems (Wang et al., 2019a; Min et al., 2021), partly because it can be extensively recycled in ecosystems and is retained in clay minerals and biota (Alfaro et al., 2017; Schlesinger, 2020).

Regional examples of soil- K^+ deficiencies abound. In India, the majority of agricultural fields are thought to be K-deficient, due to low K fertilization rates and to the removal of K-rich crop residues and animal manures, which are commonly used for household energy and other purposes in rural areas (Smil, 1999; Römheld and Kirkby, 2010). The situation is even more dire in many croplands of Africa, where K-poor soils are a major factor limiting food production (Sardans and Peñuelas, 2015). Recently, a geographical study on soils and human health patterns in the USA showed strong negative correlations between soil K concentrations and rates of hypertension, obesity, and diabetes among the 48 contiguous states (Sun, 2018). This finding illustrates the strong influence of local soil fertility on human health that can be mediated by K uptake and accumulation in crop plants, even in an age of mass movement of food. Issues such as these have led to renewed attention to plant K requirements in nutrient management programs, which have, at times, been overly focused on nitrogen nutrition (Öborn et al., 2005; Römheld and Kirkby, 2010; Oosterhuis et al., 2014; Schlesinger, 2020). In China, some success in addressing the country's historic soil K deficiencies, as, for example, in an estimated three-quarters of its paddy soils (Rengel and Damon, 2008; Römheld and Kirkby, 2010), has been achieved recently (Liu et al., 2017).

Most of the potassium in soils (90–98 %) is locked up in crystalline form and unavailable to plant roots, except over long time scales as the parent material becomes weathered (Römheld and Kirkby, 2010; Dhillon et al., 2019). Thus, the soil K deficiencies discussed here refer mainly to free K^+ in soil solutions (0.1–0.2%), which is directly available to plant roots, and to exchangeable K^+ (1–2 %), which is electrostatically bound to fixed negative charges on soil particles, but rapidly enters the free-solution K^+ pool as the latter becomes depleted. A fourth phase, of slowly (or non-) exchanging K (1–10%), can slowly buffer these smaller pools. These phases are all dynamic, but change over vastly different time scales, the most rapid changes occurring in soil solution $[K^+]$. Moreover, solution K^+ is not homogeneously distributed within the soil, and when root ion transport activity is high, K^+ can become greatly depleted close to the root surface (to low-micromolar levels; Nieves-Cordones et al., 2016a; Hinsinger et al., 2021). In these K^+ -depletion zones, K^+ -concentration gradients drive the diffusive flux of K^+ from the bulk solution (and, ultimately, from more slowly exchanging K^+ pools) to the plasma membranes of root cells, and constitute the major pathway by which K^+ arrives at the root surface (Ashley et al., 2006; White and Karley, 2010; Lambers and Oliveira, 2019).

How do such root-driven gradients of solution $[K^+]$ relate to plant K requirements, and to characteristics of root K^+ -transport systems? It has long been known that many plant (crop, pasture, and weed) species can achieve maximal productivity at a relatively low K^+ supply, in continuously flowing nutrient solutions where zones of nutrient depletion are minimized. For example, Asher and Ozanne (1967) and Spear et al. (1978) showed that 2–24 μM $[K^+]_{ext}$ was sufficient to maximize growth and yield in eleven plant species (both monocots and dicots), using continuous-flow systems (in the six remaining species studied by Asher and Ozanne, peak growth was met, or nearly met, at $[K^+]_{ext} \leq 95 \mu M$). Incidentally, it is at a similarly low $[K^+]_{ext}$ (10–20 μM) that root exudation of organic compounds, an important mechanism for the mobilization of K^+ from non-exchangeable soil fractions, is activated (Zörb et al., 2014). Interestingly, potassium concentrations of this magnitude are considerably lower than are usually reported for diverse soils (Asher and Ozanne, 1967; Gassman and Schroeder, 1994; White, 2013), raising the question of how the apparent potassium frugality of many plants can be reconciled with widespread concerns over soil-K deficiencies, as discussed above. Part of the answer lies in the soil- $[K^+]$ gradients in the depletion zones surrounding the root, where

root cells can reduce K^+ concentrations to levels below the threshold for maximal plant growth. Of course, the K^+ pools upon which root influx transporters operate are located in these very depletion zones, at concentrations often below adequacy. Strikingly, though, these concentrations are well within the general operating range of active, H^+/K^+ symporters (e.g. AtHAK5), while, on the other hand, they are unlikely to thermodynamically favor the operation of K^+ -influx channels such as AKT1 (see Section 3.2). We note, however, that plants growing in open fields and ecosystems might also have a higher K^+ requirement than sheltered laboratory plants, as they are exposed to more types and greater intensities of stress, against which elevated K^+ can be protective (Cakmak, 2005). Under such conditions, so-called “luxury consumption” of K^+ can allow plants in less controlled settings to accumulate high amounts of K^+ when it is abundant, which may improve plant agro-nomic quality, and act as an “insurance policy” for periods of K^+ deficiency or high stress (Cakmak, 2010; Römheld and Kirkby, 2010; Zörb et al., 2014). We also note that, when transpiration rates are high and K^+ uptake rates are low, the depletion zones can become zones of K^+ accumulation (Ashley et al., 2006).

While increased and improved K-fertilization practices (as well as innovative use of K^+ -solubilizing bacteria; Etesami et al., 2017) are recommended for many soils (Dhillon et al., 2019), plant breeding can approach this problem from the opposite direction, by improving the efficiencies of plant K uptake and K utilization, i.e. the two factors determining K-use efficiency (KUE, in an agronomic sense; White, 2013). K-uptake efficiency depends on the uptake capacity of K^+ -influx transporters, transpiration rates, exudation of organic compounds that release soil K^+ from non-exchangeable fractions, and the modification of root architecture. Utilization efficiency depends on the transport and circulation of K^+ within the plant, its substitution by other ions (like Na^+), and on the K-dependent processes of photosynthesis, carbohydrate translocation, and water balance (White, 2013; Shin, 2014; Zörb et al., 2014). Considerable variability exists among these traits (Rengel and Damon, 2008), suggesting that their optimization could lead the way to crop plants being able to grow at lower $[K^+]_{ext}$.

Electrical polarization and H^+ gradients across the plasma membrane, although centrally important to plant potassium physiology (see Sections 2 and 3), have not yet been closely examined as potential targets for improving K^+ influx at low $[K^+]_{ext}$ (Pedersen and Palmgren, 2017; Liu et al., 2019). However, increased plasma-membrane H^+ -ATPase activity and greater membrane polarization have been linked to acid and salinity tolerance and to the maintenance of K^+ homeostasis under stress (Young et al., 1998; Falhof et al., 2016; Chakraborty et al., 2016; Fan et al., 2018; Wegner and Shabala, 2020; see Section 3.4). In *A. thaliana*, unusually hyperpolarized root cells may provide a naturally occurring example of a highly efficient potassium-acquisition apparatus, shifting the operation of channel-mediated K^+ influx to very low $[K^+]_{ext}$ (as discussed in Section 3.2). Similarly, even a small hyperpolarization due to enhanced H^+ -ATPase activity in epidermal and cortical root cells could result in a significantly lowered threshold for energy-efficient, channel-mediated K^+ influx (i.e. a downward shift of the data points in Fig. 2). It could also increase the amount of energy available for H^+/K^+ symport below this threshold (Huang et al., 2019). On the other hand, H^+ -ATPases are subject to extremely complex regulation, involving pH, ROS, phosphorylation, hormones, protein-protein interactions, transcriptional regulation, and autoinhibition (Hoffmann et al., 2019; Huang et al., 2019; Siao et al., 2020). Constitutive- or over-expression of ATPases can lead to their own downregulation (Gévaudant et al., 2007; Hashimoto-Sugimoto et al., 2013), although increases in H^+ efflux and more polarized membrane potentials have been observed in cases where ATPase expression or activity was increased (Merlot et al., 2007; Niczaj et al., 2016; Xue et al., 2018; Siao et al., 2020). Still, constitutive ATPase expression has, in most cases, led to deleterious side effects, including heat and drought sensitivities, abnormal cell shape, and necrotic lesions (Merlot et al., 2007; Niczaj et al., 2016; Xue et al., 2018), and

unrestricted membrane hyperpolarization can lead to dielectric breakdown of the membrane (Raven, 2020).

A related challenge would be to increase K concentrations in the edible fractions of crop plants. Interestingly, [K] in seeds (including those of cereals) is quite low and has a degree of genetic fixity, compared to that in vegetative tissues (and non-seed fruit tissues), which varies more strongly with soil [K⁺] (Tũma et al., 2004; Zerche and Ewald, 2005; Zörb et al., 2014). Decreases in seed K are part of the seed maturation process, and low seed [K] at maturity can significantly improve germination rates (Zerche and Ewald, 2005). The low K in cereal grains appears to be specific to the endosperm, as embryos show significantly higher levels of K (Mazzolini et al., 1985; Sánchez and Miguel, 1985; Khan et al., 1987; Poersch et al., 2011). Consistent with this idea, the K content of many legume seeds is unusually high, and can be responsive to environmental K (Penny et al., 1976; Tũma et al., 2004; Poersch et al., 2011; White et al., 2021), reflecting that seed-storage tissues in legumes are within the fleshy embryonic cotyledons, rather than the endosperm, as in cereals and many other plants. Thus, while increasing K in cereal grains and most seed crops may prove to be a very difficult enterprise (Tighe-Neira et al., 2018), there may be greater promise in increasing seed K in legumes.

Recently, global K-use efficiency for cereal grains was estimated to be 19 % (Dhillon et al., 2019), reflecting both the low grain-K levels of cereals and the agricultural “mining” of soil K (i.e. usage of cropland soil without replenishment; Römhild and Kirkby, 2010). Similarly, a very rough estimate of “human K-use efficiency” (HKUE) can be calculated on the basis of annual K fertilizer demand (38.7 Mt “K₂O”, an arbitrary and somewhat imaginary standard, equivalent to 32.1 Mt K, projected for 2020 by the FAO, 2019) and average annual K consumption by the global population (5.7 billion kg, at 2 g person⁻¹ day⁻¹ and a current 7.8 billion people). After correcting for the non-fertilizer soil K that contributes to the dietary stream (using as a provisional correction factor the one used by Dhillon et al., 2019; also see Schlesinger, 2020), we can derive an HKUE of about 5%. This rather low value encompasses K losses due to leaching and runoff, plant K-use inefficiencies, and low K content of diets (relative to caloric intake). In addition, much of this low efficiency can be attributed to the flow of K towards agricultural feed for livestock; each day, we provide ourselves with a ration of K, but we also provide a daily ration to the tens of billions of animals raised for human consumption, each of which excretes nearly as much K⁺ as it consumes. The global biomass of livestock was recently estimated to be nearly twice that of global human biomass (Bar-On et al., 2018), suggesting that, in a vegetarian world, HKUE could be nearly triple what it is today. In a more realistic near future, improved recycling of potassium excreted by livestock, back into croplands, has the potential to significantly increase HKUE (Öborn et al., 2005).

5. Concluding remarks

In this Humboldt Review, we have considered a broad range of questions about the function of potassium in living things, with a focus on modern plants and current problems in the field. We have discussed the universality of the K⁺ ion to all cells and how that might have evolved, appraised leading ideas about the molecular physiology of K⁺ transport in plants, and highlighted the inescapable connection between the human diet and the ability of plants to take up and concentrate K⁺. We hope readers have found the exercise to be useful and thought-provoking. A central question for the medium-term future should be asked, regarding how we as a species can deter the already widespread and growing, yet under-discussed and under-publicised, depletion of soil K⁺ by agricultural “mining”, and sustainably achieve potassium sufficiency. Improvements in plant K-use efficiency will likely play an important role in this achievement, as may a reversal of the global trend of increased meat consumption (Godfray et al., 2018). However, greater attention to the replenishment of K-depleted soils by fertilizer or organic matter may be the most urgent, and fundamentally important,

sustainability requirement. Other less pressing, but fascinating “futuristic” topics (not considered here), could involve the evolution of roles of K⁺ in extraterrestrial life, should it be discovered (does K⁺ universality extend beyond Earth?), and the relationships between plant K⁺ and Na⁺ uptake to the sustainability of human life in closed systems, as we continue our travels through the Cosmos (Ushakova et al., 2005; Yamashita et al., 2009).

Declaration of Competing Interest

The authors report no declarations of interest.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.jplph.2021.153432>.

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