Tansley review

Molecular membrane separation: plants inspire new technologies

Authors for correspondence:
Caitlin Byrt
Email: *caitlin.byrt@anu.edu.au*

Samantha McGaughey
Email: *samantha.mcgaughey@anu.edu.au*

Annamaria De Rosa* (iD)**, Samantha McGaughey*** (iD)**, Isobel Magrath** (iD) **and Caitlin Byrt** (iD)

Division of Plant Science, Research School of Biology, Australian National University, 2601, ACT, Acton, Australia

Contents

Summary

Plants draw up their surrounding soil solution to gain water and nutrients required for growth, development and reproduction. Obtaining adequate water and nutrients involves taking up both desired and undesired elements from the soil solution and separating resources from waste. Desirable and undesirable elements in the soil solution can share similar chemical properties, such as size and charge. Plants use membrane separation mechanisms to distinguish between different molecules that have similar chemical properties. Membrane separation enables distribution or retention of resources and efflux or compartmentation of waste. Plants use specialised membrane separation mechanisms to adapt to challenging soil solution compositions and distinguish between resources and waste. Coordination and regulation of these mechanisms between different tissues, cell types and subcellular membranes supports plant nutrition, environmental stress tolerance and energy management. This review considers membrane separation mechanisms in plants that contribute to specialised separation processes and highlights mechanisms of interest for engineering plants with enhanced performance in challenging conditions and for inspiring the development of novel industrial membrane separation technologies. Knowledge gained from studying plant membrane separation mechanisms can be applied to developing precision separation technologies. Separation technologies are needed for harvesting resources from industrial wastes and transitioning to a circular green economy.

*These authors contributed equally to this work.

I. Introduction

During the evolution of plants, there was selective pressure to achieve energy efficient precision in membrane separation control to maintain the cellular and organelle homeostasis required for essential biological processes (Hwang *et al.*, 2016). Heterogeneity in the chemical composition of soil across the globe meant that plants were challenged to adapt to different soil solution compositions in different geographical areas (van der Ent *et al.*, 2013). Soil solution compositions with excess amounts of heavy metals, minerals and salts can present a challenge to plant growth by limiting the uptake of essential nutrients, and causing toxicity and oxidative stress (Ali *et al.*, 2019).

Plant adaptation to challenging soil solution compositions can include strategies such as avoidance via root architecture changes; biomodification or detoxification; adopting symbiotic relationships with soil microbes; and enhanced uptake followed by sequestration of undesirable molecules in membrane bound compartments such as the vacuole (Khare *et al.*, 2017). There have been many studies of adaptation mechanisms where transcriptomic, proteomic, metabolomic and ionomic approaches were deployed to investigate the genetic and physiological basis of adaptation (Baxter *et al.*, 2012; Singh *et al.*, 2016; Stein *et al.*, 2017). These types of studies revealed that some adaptation strategies involve uptake and sequestration of undesirable elements, and these strategies require specialised membrane separation mechanisms (Yang *et al.*, 2005; Verbruggen *et al.*, 2009). Plant membrane separation processes enable undesirable elements to be distinguished from desirable elements and create the potential for undesirable elements to be effluxed from the plant or compartmentalised in the vacuole or in specific cells (Conde *et al.*, 2011; Pasricha *et al.*, 2021). These processes are important for the survival of life on Earth, and life has evolved a suite of transport proteins that enable this selective separation across different membranes to maintain cellular and organelle homeostasis. For example, of the *c.* 25 500 proteins encoded by the Arabidopsis genome, *c.* 34% contain a transmembrane domain and are classified as membrane proteins, and 7% of the 25 500 proteins contain at least four transmembrane domains and could fulfil a transport function (Schwacke *et al.*, 2003; Tang *et al.*, 2020).

Plants, and plant–symbiotic relationships, influence global cycling of carbon, water and nutrients (Silva & Lambers, 2021). The membrane separation processes within plants and plant symbiosomes contribute to the ecosystem services plants provide such as cleaning water, capturing carbon dioxide, cooling land surfaces, moderating the climate and providing food, feed, fibre, fuel and habitats (Fig. 1) (Paasonen *et al.*, 2013; Ellison *et al.*, 2017; Jasechko, 2018; Zhang, 2020). For example, plant transpiration is estimated to be responsible for 60–90% of terrestrial evapotranspiration (Jasechko *et al.*, 2013; Good *et al.*, 2015; Lian *et al.*, 2018; Nelson *et al.*, 2020), plants absorb half of the solar energy that reaches land surfaces, and each year plants capture and fix around one-third of emissions of carbon dioxide.

Demand for the services plants provide is increasing as population growth continues (Maja & Ayano, 2021), but the area of arable land available for plant primary productivity is limited and at risk of degradation (Prăvălie *et al.*, 2021). In future, it may be possible to use and remediate land with suboptimal soil composition if plants are selected and engineered to better tolerate challenging soil constraints and climatic conditions (Clemens *et al.*, 2002; LeDuc & Terry, 2005; Rylott & Bruce, 2022). Plant mechanisms for managing excess metals, minerals and salts are also a source of inspiration for developing biotechnological strategies to manage natural resources and waste. This review considers examples of membrane separation mechanisms that plants use to tolerate challenging environments and explores the potential application of these mechanisms in crop engineering and in advancing the development of novel membrane separation technologies. Selected examples of the types of molecules that plants take up and manage, and the types of plant cell membrane mechanisms that are involved in transporting these molecules are included in this review. The examples of molecules and mechanisms included do not constitute a comprehensive list of either the molecules that plants take up or the respective mechanisms involved in the complement of plant separation processes. Future research is needed to identify the additional plant separation mechanisms and to connect the relationships between plant selective mechanism structures and their respective functions in molecular separation.

II. Environment and genetics influence plant ionomes

1. Examples of metals, mineral, nutrient and salt molecules found in soil solutions

Soil solutions across the globe vary in the concentrations of metals, minerals and nutrients that they contain. Some metals and minerals can be toxic to plants when present in excess and there are many nutrients that are essential for plants to draw up because they are required for plant growth (Table 1). The identities of the many molecular mechanisms in plants that enable the uptake and separation of different metals, minerals and nutrients are of interest for improving crop performance and nutrition, phytoremediation strategies, and informing the development of novel membrane biotechnologies (Pilon-Smits, 2005; Schroeder *et al.*, 2013; Mazzolai *et al.*, 2014; Darestani *et al.*, 2019; Gill *et al.*, 2021; Roorkiwal *et al.*, 2021; Kafle *et al.*, 2022).

2. Learning from plant ionomic data

Plant tissue ionomes represent the outcome of plant uptake, separation, partitioning and accumulation of nutrients, metals and minerals (Pita-Barbosa *et al.*, 2019). The ionome refers to the mineral nutrient and trace element composition of an organism (Salt *et al.*, 2008). It is a product of the plant's environment, such as the chemical composition of the soil in which the plant is grown, and the plant's genetics, such as the encoded regulatory systems and mechanisms that influence the uptake of molecules from the soil solution, the plant's developmental stage and regulation of ion transport within the plant (Baxter, 2010; Baxter & Dilkes, 2012). Plant ionomes differ between species, within species and within different plant tissues of any given species. This can be seen in the
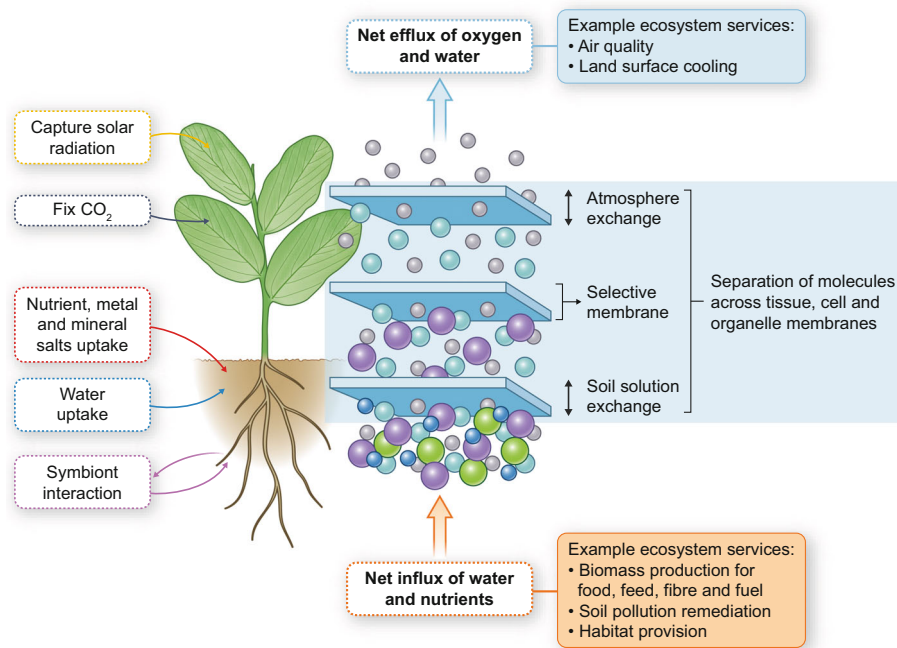
Fig. 1 Plants in collaboration with symbiotic soil microbes contribute services that sustain life. Plants influence global carbon, nutrient (orange dashed box and arrow) and hydrological cycles (blue dashed box and arrows), they fix atmospheric carbon dioxide (CO_2; grey dashed box and arrow), generate net oxygen and clean water (light blue dashed box), capture radiation (yellow dashed box and arrow), cool land surfaces (small blue shaded box) and deliver food, feed, fibre, fuel and habitat (orange shaded box); and this involves exchanges with the soil and atmosphere (large blue shaded box). These services depend on plant photosynthesis, energy conversions, metabolism and membrane separation capability (selective separation of molecules across tissue, cell and organelle membranes). Investigating the molecular mechanisms plants use to achieve their membrane separation functions is key to determining how to improve plant water and nutrient use efficiency, improve crop performance, devise strategies for land remediation and generate biotechnological tools that can be used to address major global challenges such as harvesting resources from wastewater and ensuring food, energy, water and climate security in future.

Table 1 Selected examples of essential nutrient ions plants require (desirable) and ions that share similar charge that can be problematic (undesirable) when present in excess.

	Essential or desirable ions commonly taken up by plants	Ions that can be problematic or undesirable when present in excess
Monovalent cations	K^+, NH_4^+, Na^+ (for C₄)	Na^+, NH_4^+ (in excess), Rb^+, Cs^+, Li^+
Monovalent anions	NO_3^-, $H_2PO_4^-$, $H_2BO_3^-$, Cl^-	$H_2BO_3^-$ (in excess)
Divalent cations	Ca^{2+}, Mg^{2+}, Co^{2+}, Cu^{2+}, Zn^{2+}, Fe^{2+}	Cd^{2+}, Pb^{2+}, Ni^{2+}, $Co(H_2O)6^{2+}$, Zn^{2+}
Divalent anions	HPO_4^{2-}, MoO_4^{2-}, SO_4^{2-}	CrO_4^-
Trivalent cations	Fe^{3+}	Al^{3+}

Abbreviations for ions: aluminium (Al^{3+}), ammonium (NH^{4+}), boric acid ($H_2BO_3^-$), cadmium (Cd^{2+}), calcium (Ca^{2+}), cesium (Cs^+), chloride (Cl^-), chromate (CrO_4^{2-}), cobalt (Cu^{2+}), copper (Co^{2+}), dihydrogen phosphate ($H_2PO_4^-$), hexaaquacobalt(II) ($Co(H_2O)6^{2+}$), hydrogen (H^+), hydrogen phosphate (HPO_4^{2-}), hydroxide (OH^-), iron (ferrous cation Fe^{2+}, ferric cation Fe^{3+}), lead (Pb^{2+}), lithium (Li^+), magnesium (Mg^{2+}), molybdate (MoO_4^{2-}), nickel (Ni^{2+}), nitrate (NO^{3-}), potassium (K^+), rubidium (Rb^+), sodium (Na^+) sulfate (SO_4^{2-}), zinc (Zn^{2+}). Plants can vary in relation to which elements are essential, for example Na^+ is required for C₄ plants (Brownell & Crossland, 1972), but not for C₃ plants, although Na^+ can be useful for osmotic adjustment for all plants (Munns *et al.*, 2020b). Boron, taken up as $H_2BO_3^-$, is an example of an essential nutrient that is also toxic when in excess (Raven, 1980), and Zn^{2+} is essential but can inhibit H^+/OH^- channels (Al Khazally & Bielby, 2012). This list provides a collection of examples but it is not a comprehensive list of elements taken up by plants. Plants also absorb other compounds, for example plants absorb urea (CH_4N_2O) and hydrolyse it to ammonium using urease (Witte, 2011), and plants can take up Rare Earth Elements (REEs, see Box 1; Ding *et al.*, 2005). Desirable and undesirable elements and molecules present in soil solutions can share characteristics, such as their size and charge. Distinguishing between different ions that are similar in size and charge is important for ensuring resources and waste are managed efficiently.

data from two studies on Arabidopsis ionomes (Fig. 2). In one study, Stein *et al.* (2017) measured the leaf ionome of 1972 *Arabidopsis halleri* samples, paired with the ionome of the soil where each plant grew (Fig. 2a). *Arabidopsis halleri* is a metal hyperaccumulator, able to accumulate levels of zinc, cadmium and

sometimes lead at concentrations an order of magnitude higher than other plants. Stein *et al.* (2017) found that there was large intraspecies variation in the levels of these metals in the plant tissue, which was only partially explained by variation in the soil ion content. This shows that there is intraspecies genetic variation in
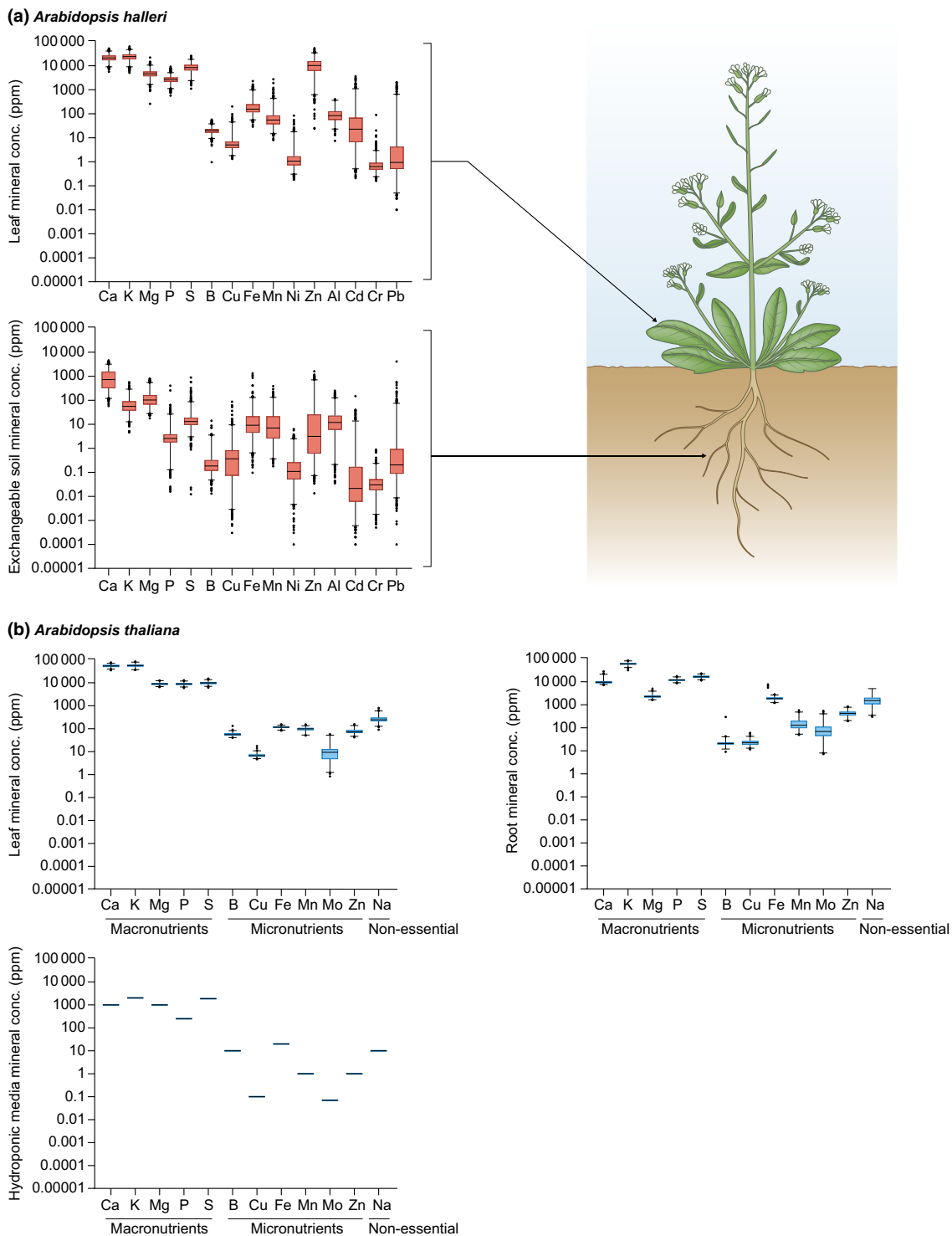
Fig. 2 Element concentrations in Arabidopsis tissue samples compared with growth environment. Element concentration values as parts per million (ppm) dry weight are plotted using a box and whiskers graph where the central horizontal line shows the median value, the box shows the 25th/75th percentiles, the whisker bars show 1st/99th percentiles and outliers are plotted as black circles. (a) Concentration of macronutrients, micronutrients and some non-essential elements found in *Arabidopsis halleri* (l.) leaves and the exchangeable mineral concentration of these elements in corresponding soil samples ($n = 1972$). Raw data reported by Stein *et al*. (2017) were plotted using GRAPHPAD PRISM. (b) Concentration of macronutrient, micronutrient and some non-essential elements found in *Arabidopsis thaliana* (L.) leaves, roots and hydroponic growth media ($n = 96$). Raw data reported by Baxter *et al*. (2012) were plotted using GRAPHPAD PRISM (v.8.0.0 for Windows; GRAPHPAD Software, San Diego, CA USA, www.graphpad.com). Abbreviations for units: parts per million (ppm), concentration (conc.), and for elements: calcium (Ca), copper (Cu), boron (B), iron (Fe), magnesium (Mg), manganese (Mn), molybdenum (Mn), potassium (K), phosphorus (p), sodium (Na), sulphur (S), zinc (Zn).

how the ionome is controlled. The authors found that the tissue levels of zinc, cadmium and lead were not strongly correlated despite these metals being chemically similar and sharing some similar transport pathways in plants (Kraemer, 2009). *Arabidopsis halleri*'s ability to differentially accumulate these elements indicates that this species has selective molecular mechanisms capable of differentiating between and separating these similar metals.

The second study, by Baxter *et al.* (2012), measured the leaf and root ionome of 96 *Arabidopsis thaliana* accessions grown in artificial hydroponic media (Fig. 2b). Growing plants in controlled conditions is a useful way to identify how much ionomic variation between plants is due to genetic variation rather than environment. Baxter *et al.* (2012) found that within the measured *A. thaliana* samples, there was variation of greater than an order of magnitude in the levels of some micronutrients – most notably sodium and molybdenum – suggesting intraspecies genetic variation how these elements are managed. There was little correlation between the root and leaf ionomes of the plants. This shows that the ion movement and accumulation within plants is under tissue-specific regulation.

These types of ionomic studies, which allow the identification of relatively extreme ionomic profiles within some types of Arabidopsis accessions, have led to genomic analysis and identification of molecular mechanisms associated with differences in ionome profiles (Shariatipour *et al.*, 2021). Similarly, variation in the ionomes of 526 rice (*Oryza sativa*) accessions was used for a genome-wide association study to identify 72 loci associated with ionomic variations. Key candidates included *OsHKT1;5* influencing sodium and Os-MOLYBDATE TRANSPORTER 1;1 influencing molybdenum (Yang *et al.*, 2018). Clearly, ionomic studies can provide an excellent resource for progressing towards understanding the molecular mechanisms plants use to control element uptake and distribution.

III. Strategies for molecular membrane separation and their biological relevance

Plant membrane separation occurs at the root epidermal cell membrane where the roots meet the soil, across layers of root cortex cells, at passage cells within the Casparian strip, between different plant tissues and between cell cytoplasm and organelle membrane boundaries (Lynch *et al.*, 2021). Cell membranes can separate specific molecules from mixtures because they can have different permeability through the membrane to different molecules. The membrane permeability is influenced by the membrane lipid composition and the embedded proteins in the membrane (Gumbart *et al.*, 2005). Cell membranes contain many different types of proteins such as transporters, pumps and channels. Selective membrane proteins can differentiate between molecules based on the charge number, polarity, size and molecular mass of the molecules (Lepoitevin *et al.*, 2017).

Modular sorting of soluble molecules can occur in plant cells through compartmentation processes, with various compartments acting as reservoirs or repositories of vital molecules or toxic solute dumping sites (Fig. 3). The major cellular compartment is the vacuole, occupying 90% of the volume of plant cells, with membranes packed with specific proteins to enable cellular sorting

and trafficking mechanisms (Tan *et al.*, 2019). Plants modularise separation steps. Molecular mechanisms such as aquaporins that are capable of contributing to bulk solute update are used to move relatively large volumes of bulk solutions and this function is coordinated with increasingly selective layering of separation steps.

1. Selective uptake of nutrients

Plants require a minimum of 14 inorganic mineral elements for their growth, development and reproduction, but the soil composition of these essential nutrients can vary widely (Marschner, 2012). Essential nutrients can be classed broadly into macronutrients such as nitrogen (N), phosphorous (P) and potassium (K), which are generally observed in plants at concentrations > 0.1% of plant dry tissue weight, and micronutrients such as iron (Fe), zinc (Zn) and boron (B), generally making up < 0.01% of dry tissue weight (Maathuis, 2009; Samota *et al.*, 2017). Membrane transporters are central to plants taking up nutrients from soil, translocation to shoots and their distribution to different organs and tissues (Sasaki *et al.*, 2016). There are membrane transporter mechanisms with very specific substrate transport roles, and other mechanisms involved in transporting many different substrates, and the nomenclature of different membrane transport mechanisms is often not a useful guide to their role or roles (David *et al.*, 2019; Tyerman *et al.*, 2021). As well as being responsible for the transport and partitioning of nutrients throughout plant tissues, membrane transporters may also have key roles in nutrient sensing (Dreyer *et al.*, 2022). Nutrient sensing is important to ensure the plant can dynamically respond to external nutrient availabilities and trigger additional nutrient transport mechanisms such as vacuolar sequestration or translocation to other tissues. Computational cell biology simulations have suggested that two different transporter types for the same nutrient are needed for homeostatic control (Dreyer, 2021). Therefore, a cell gains flexible control in managing nutrient concentrations through the activity of a combination of transporter types energised by different processes (Dreyer, 2021) (with transporter activity regulation being not linked to differences in their affinity) (Dreyer & Michard, 2020).

Nitrogen is important for plant nutrition The ancestors of land plants, green algae like Characeae, take up ammonium ions (NH_4^+) and methylamine ($CH_3NH_3^+$) when in need of nitrogen and the rate of transport falls if nitrogen is not needed (Walker *et al.*, 1979). Plants can take up nitrogen (N) from the soil in several forms, such as nitrate (NO_3^-), NH_4^+ and organic molecules (amino acids) (Fan *et al.*, 2017). In some herbaceous plants, the majority of nitrogen is assimilated as NO_3^- which is subsequently reduced to NH_4^+ (Morere-Le Paven *et al.*, 2011). The external concentration of nitrogen can fluctuate greatly in the soil and distinct mechanisms for nitrogen uptake occur in plants depending on the external availability of nitrogen (NO_3^- or NH_4^+) in the soil. Such mechanisms include the use of low-affinity transport systems (LATS), such as the Nitrate Transporter 1 (NRT1) gene family in high nutrient concentrations (mM range), whereas in low nutrient concentrations (µM range), they utilise high-affinity transport
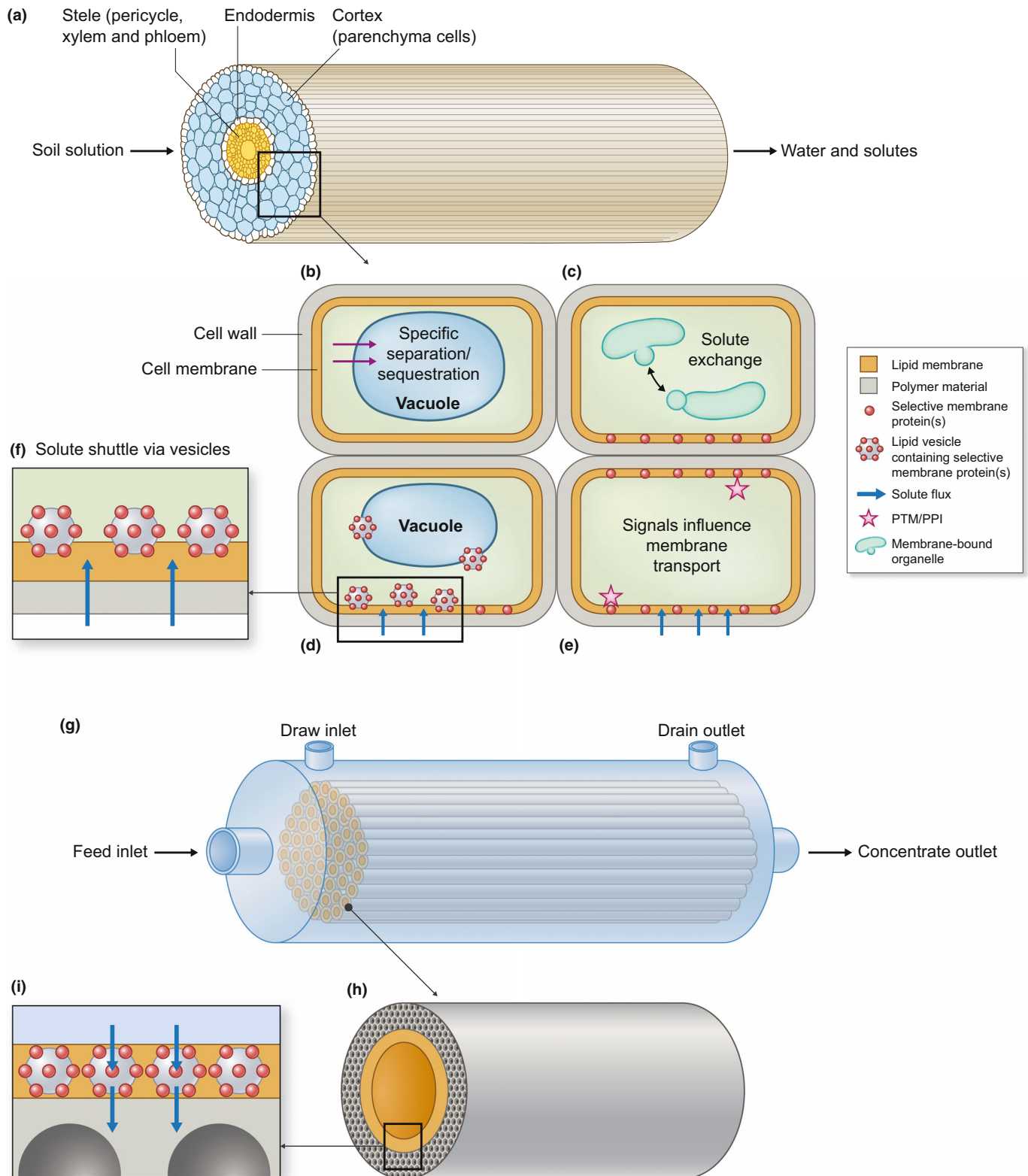
systems (HATS), such as NRT2 transporters, scavenging ions to maintain a normal uptake rate (as reviewed in Fan *et al.*, 2017). Some transporters such as Arabidopsis AtNRT1.1 and *Medicago truncatula* MtNRT1.3, traditionally thought to act in LATS, have been shown to have dual-affinity properties, with their mode of action dependent on external nitrate concentrations. For example, in high nitrate, AtNRT1.1 functions as a low-affinity nitrate transporter, and in low nitrate it functions as a nitrate sensor, with

Fig. 3 Overview of features of plant and industrial membrane separation structures. (a) Plant tissues, such as the root section shown, are made of files of cell layers where cells are bound by a selective plasma membrane (PM) and supporting cell wall, made of mostly cellulosic or lignocellulosic polymers, along with other cell wall components. Plant vasculature comprised of xylem and phloem vessels connect distant plant tissues to facilitate long-distance solute movement whereas other cell types (e.g. root cortex, pericycle) include many files of cells in each layer. Cell wall structures can influence solute passage but most of the selectivity is determined by mechanisms in the PM. Cells share many common features of membrane function (represented individually in parts b–f), that influence plant cell permeability to different solutes and enable the separation of different molecules, though these examples are not comprehensive or specific (for some specific examples, see: Delsart, 2017; Byrt *et al.*, 2018). (b) Tonoplast-localised membrane proteins influence the transport of molecules in and out of the vacuole. (c) Cytoplasmic streaming influences solute exchange between the cytoplasm and organelles. Endoplasmic reticulum can form plasmodesmal sphincters, potentially enabling flux between cells (Rinne & Schoot, 2004). (d) Plants have intracellular and extracellular vesicles and these vesicles can shuttle solutes, proteins and a range of other molecules (Hwang & Robinson, 2009; Yáñez-Mó *et al.*, 2015; Ueda *et al.*, 2016). (e) Posttranslational modifications (PTMs), protein–protein interactions (PPI) and signalling molecules can influence the localisation of transport mechanisms and alter their functions, including their substrate permeability (Saito & Uozumi, 2020). (f) Plants use vesicles containing membrane proteins, such as aquaporins, for trafficking and intercellular communication (Martinez-Ballesta *et al.*, 2018). Plants also have extracellular vesicles with key roles in moving cargo which are not represented in this diagram (Cai *et al.*, 2021). (g) Representation of the structure of typical hollow fibre membranes. Many systems include outer-selective polymer structures and inner-selective biomimetic thin film composite hollow fibre polyamide membranes, where the membranes consist of thin and dense layers that are porous and selectively permeable (Porter *et al.*, 2020). Different types of hollow fibre membranes are used for a range of applications such as extracting clean water from dirty water, desalination, microfiltration, pervaporation, isotope/gas separation and distillation (Fane *et al.*, 2015; Lau *et al.*, 2022). The specific application determines which liquids move in and out of feed and draw inlets and drain and concentrate outlets (h) The hollow fibres are tube-like consisting of an ultrathin dense selective lipid membrane layer that is mechanically supported on an outer layer of a highly porous substrate of various compositions, where use of organic molecules is ideal because they can be low cost, easily processable and scalable (Sanahuja-Embuena *et al.*, 2019; Lau *et al.*, 2022). (i) The structure in each fibre can include proteoliposomes carrying selective membrane proteins, such as embedded aquaporins which can improve the selectivity, where the proteoliposome lipid vesicles are embedded in a lipid membrane attached to a supporting polymer material (Yilmaz & Özkan, 2022). Polymer materials in separation systems can in some cases contain cellulose similar to the supporting material in plant cell walls. The systems in plants that include cell wall polymer supportive layers, lipid membranes and vesicles containing selective membrane proteins (f) are a source of inspiration for optimising membrane separation technology structures (i). Key: lipid membranes in plants (a–f) and in separation technologies (g–i) are represented in dark yellow; polymer structures and materials are represented in grey; selective membrane proteins are represented as red circles, lipid vesicles containing selective membrane proteins are represented as grey circles containing smaller red circles; the direction of solute flux relative to internal structures is represented with blue arrows (f, d, e, i), whereas black arrows represent the main directions of flow of solutes relative to plant and separation technology structures (a, g); posttranslational modifications (PTMs), protein–protein interactions (PPI) and signalling processes are represented by pink stars; organelles and organelle interactions are represented by green shaded shapes with green outlines; tissues in the stele (pericycle, xylem and phloem) are shaded yellow in part (a); endodermis surrounds the stele; cortex (parenchyma cells) are shaded in light blue in part (a); vacuoles (part b) have dark blue outlines; hollow space for solute flow (in g, h, i) are black.

kinase-mediated AtNRT1.1 phosphorylation resulting in activation of several other high-affinity transporters such as NRT2s (Morere-Le Paven *et al.*, 2011; Rashid *et al.*, 2018). Recently in rice, an aquaporin from the PIP subfamily OsPIP1;3 was reported to facilitate transport of NO_3^- when expressed in HEK cells indicating that aquaporins may also contribute to nitrogen uptake and transport (Liu *et al.*, 2020).

In addition to the regulation of high- and low-affinity transporters, plants are able to modulate the localisation of transporters when nitrogen is in excess. For example, plasma membrane (PM)-localised ammonium transporter AtAMT1;3 is internalised through clustering/endocytosis removing the active transporter from the PM and preventing ammonium uptake in ammonium toxicity conditions (Wang *et al.*, 2013). To adapt to soil constraints, plants may implement polar localisation of AMT1 mechanisms to optimise control of the movement of ammonium, and AMT regulation is adjusted during plant development (Konishi & Ma, 2021; Esmaeilzadeh-Salestani *et al.*, 2022).

Phosphorus is a finite resource that must be carefully managed Phosphorous (P) is a macronutrient required by all organisms as a building block of nucleic acids and a component of biological membranes. Plants take up P from the soil primarily in the form of inorganic phosphate (Pi). However, P is the least available macronutrient as it easily complexes with metal ions within the soil solution (Shen *et al.*, 2011). To overcome P availability challenges, plants have evolved several strategies for P uptake, and

subsequent translocation throughout the plant (Puga *et al.*, 2017; Prathap *et al.*, 2022). Pi transport is facilitated by multiple P transporters localised on the plasma and intracellular membranes, summarised recently by Wang *et al.* (2021). P concentrations in leaves are highly variable in different plant species (Suriyagoda *et al.*, 2023).

The regulation of Pi homeostasis in plants is complex and involves many mechanisms influencing tissue level, cellular and subcellular regulation of pools of Pi (Kanno *et al.*, 2016). In Arabidopsis, two high-affinity P transporters AtPHT1;1 and AtPHT1;4, localised to the distal root tip, were found to account for up to 75% of Pi uptake (Shin *et al.*, 2004). The transport of P from xylem-to-phloem in Arabidopsis was influenced by a SULTR-like Phosphorus Distribution Transporter (AtSPDT/AtSULTR3;4; Ding *et al.*, 2020). In cereals, the grains are a major P sink (60–85% total plant P) and SPDTs are involved in allocating P to the grain. For example, loss of rice SPDT function resulted in a 20% reduction of P in the grain (Yamaji *et al.*, 2017). A barley (*Hordeum vulgare*) Pi/H^+ cotransporter HvSPDT, observed to be localised in nodes of reproductive and vegetative tissues, was recently identified as the primary mechanism responsible for distribution of P to grains (Gu *et al.*, 2022). In arsenic hyperaccumulator plants like *Pteris vittate*, there are P transporter encoding genes that were reported to specifically influence P transport, such as *PvPht1;2*, and other P transporter genes encoding mechanisms that transport both P and arsenic, such as *PvPht1;3* and *PvPht1;4* (Cao *et al.*, 2018; Han *et al.*, 2022).

P homeostasis is tightly regulated and influenced by kinase and phosphatases which pause and remobilise P transport, respectively, in response to plant Pi requirements and external Pi conditions (Wang *et al.*, 2021). For example, PHT transporters are subject to multiple levels of post-translational regulation that influence PHT exit from the endoplasmic reticulum (ER), trafficking to the PM, and protein stability in the PM in response to external Pi conditions (Bayle *et al.*, 2011). PHT1 internalised from the PM into endosomes is either recycled in low Pi conditions or targeted for vacuolar degradation in high Pi conditions (Bayle *et al.*, 2011). In rice, the kinase OsCK2 phosphorylates PHT transporters to inhibit their trafficking from ER to PM (Chen *et al.*, 2015) while the protein phosphatase type 2C (PP2C) protein phosphatase OsPP95 interacts with OsPT2 and OsPT8 and dephosphorylates OsPT8 to promote OsPT2 and OsPT8 trafficking from the ER to the PM (Yang *et al.*, 2020).

During Pi starvation, plants increase their capacity to take up Pi and reduce nitrate uptake capacity (Ai *et al.*, 2009). In both Arabidopsis and maize (*Zea mays*), this response is coordinated by a GARP-type transcription factor NITRATE-INDUCIBLE, GARP-TYPE TRANSCRIPTIOANL REPRESSOR1.2 (NIGT1.2). NIGT1.2 upregulates the transcription of Pi transporter genes PHT1;1 and PHT1;4 and downregulates the gene expression of nitrate transporter NRT1.1 under Pi stress conditions (X. Wang *et al.*, 2020). Plants even adjust their mechanisms for managing Pi transport seasonally to account for seasonal changes in Pi availability (Kurita *et al.*, 2022).

Potassium is essential for all living cells Potassium (K$^+$) fulfils many critical functions in plants from osmotic balance maintenance, regulation of cell membrane potential to driving transport processes and metabolic processes, and K$^+$ serves as an enzymatic cofactor and influences turgor generation for cell expansion and guard cell aperture control (Dreyer & Uozumi, 2011; Srivastava *et al.*, 2020). In typical soil conditions, the K$^+$ concentration is between 10 and 100 μM, whereas the optimal K$^+$ concentration in plant cell cytoplasm ranges between 100 and 200 mM (Wyn Jones & Pollard, 1983; Schroeder *et al.*, 1994; Sharma *et al.*, 2013); to maintain required K$^+$ concentrations in cells plants employ a complex K$^+$ transport system (Ragel *et al.*, 2019). There are two major pathways for K$^+$ uptake and translocation, these are also often pathways for Na$^+$; one is mediated largely by selective ion transporters, and the other is mediated largely by ion channels (Britto & Kronzucker, 2008). Different pathways may be active under different external K$^+$ conditions and different mechanisms can have different K$^+$ affinities (Nieves-Cordones *et al.*, 2014).

Similar to nitrogen, potassium is taken up from the soil by the two-mechanism model of HATS and LATS and the different mechanisms have distinct transport energetics (Britto & Kronzucker, 2008). Under high soil K$^+$ concentrations (≥0.5 mM), K$^+$ uptake is predominately carried out by low affinity inwardly rectifying K$^+$ channels (e.g. AKT1; Hirsch *et al.*, 1998), whereas under low K$^+$ concentrations (below 0.1 mM) high-affinity transporters are active (e.g. HAK1 and HAK5; Grabov, 2007). Potassium channels in plants are generally either voltage-gated (e.g. AKT1) or voltage independent (e.g. TPKs; Isayenkov *et al.*, 2011)

and can be specific for K$^+$ or non-selective (Britto & Kronzucker, 2008; Dreyer & Uozumi, 2011). Non-selective cation channels (NSCCs) is the umbrella term describing transmembrane channel proteins found in both animal and plant cells that are generally permeable to a wide range of cations but with a heterogeneity of other kinetic, energetic and regulatory characteristics (Demidchik & Maathuis, 2007). NSCCs have been implicated in both K$^+$ and Na$^+$ flux in roots. Under normal conditions, NSCCs function primarily in K$^+$ uptake and transport systems (Pottosin & Dobrovinskaya, 2014); however, root electrophysiological studies suggest that NSCCs also facilitate the majority of Na$^+$ influx in saline conditions (for review, see Kronzucker & Britto, 2011). There are three major K$^+$ transporter families in plants, the KT/HAK/KUP, the TRK/HKT and the CPA cation proton antiporter families and members of these transporter families generally make up the HATS that operate under normal or low K$^+$ conditions (reviewed in Gierth & Mäser, 2007). In Arabidopsis roots, HAK5 and AKT1 are the primary mechanisms for K$^+$ uptake from the soil, mediating the majority of K$^+$ absorption (Gierth *et al.*, 2005; Pyo *et al.*, 2010). However, the full complement of potassium transport mechanisms is not yet known. When both AKT1 and HAK5 were knocked out in Arabidopsis as the two primary K$^+$ uptake transport proteins, an unknown mechanism contributed to K$^+$ uptake under high K$^+$ conditions (Rubio *et al.*, 2010); recent reports of K$^+$ permeable ion channel aquaporins (Qiu *et al.*, 2020; Tran *et al.*, 2020) reveal that these channels could be contributing to K$^+$ nutrition (Tyerman *et al.*, 2021), although this is yet to be confirmed *in planta*.

Potassium transporters are tightly regulated to ensure exquisite control over cell potassium homeostasis from nutrient sensing leading to transcriptional changes, to post-translational modification or protein heterotetramerisation to enable modulation of transport activity (reviewed in Wang & Wu, 2013, 2017). The gene expression of many K$^+$ transporters is regulated in response to K$^+$ deficiency (Ashley *et al.*, 2006), for example high-affinity K$^+$ transporter HAK5 is transcriptionally upregulated in response to low K$^+$ conditions under the control of a MYB transcription factor MYB77 (Feng *et al.*, 2021). The activity of several K$^+$ transporters has been reported to be regulated by phosphorylation (Wang & Wu, 2013), often in response to low K$^+$ stress. For example, under K$^+$ deficit, two Ca^{2+} sensors, AtCBL1 and AtCBL9, activate the kinase CIPK23 which phosphorylates AtAKT1 to increase its activity (Xu *et al.*, 2006). Activation by phosphorylation has also been reported for HAK5 (Ragel *et al.*, 2015; Scherzer *et al.*, 2015), and stomatal outwardly rectifying K$^+$ channel GORK (Van Kleeff *et al.*, 2018). Transport activity inhibition by dephosphorylation mediated by phosphatases was reported for GORK (Lefoulon *et al.*, 2016) and for AKT1 (Lee *et al.*, 2007). The activity of AtAKT1 is also negatively regulated by its heterotetramerisation with another K$^+$ channel subunit AtKC1 (Duby *et al.*, 2008; Wang *et al.*, 2010).

Potassium homeostasis is intricately linked to plant nutrient status, salt stress tolerance and cell energy status. There is emerging evidence of integrated control between K$^+$ and N nutrition (reviewed in Ruffel, 2018, Srivastava *et al.*, 2020). For example, expression of N transporters was significantly affected by deficient

K^+ conditions and in Arabidopsis a low-affinity NO_3^- transporter (NRT1.5) was found to function as a H^+/K^+ antiporter, effluxing K^+ from the root parenchyma cells to the xylem (Li *et al.*, 2017). The maintenance of a high cytosolic $K^+ : Na^+$ is widely considered a major determinant of salt tolerance (Munns & Tester, 2008) and is contributed to by K^+ and Na^+ channels and transporters alike (see *Salt stress*, Amtmann & Beilby, 2010). For example, a positive correlation was found between K^+ uptake and salt tolerance in several wheat (*Triticum aestivum* L.) cultivars (Cheng *et al.*, 2015). Halophytic ('salt tolerant') plants can be characterised by their ability to maintain sufficient $K^+ : Na^+$ within their cells (Shabala & Cuin, 2008; Flowers *et al.*, 2015) tolerating much higher Na^+ tissue concentrations through the use of several membrane separation mechanisms and in general a higher selectivity for K^+ uptake (Flowers & Colmer, 2008). Potassium is a molecule of importance related to cell energy regulation. For example, a 'rechargeable K^+ battery' has been described, which can influence sucrose loading in phloem under conditions where H^+-ATPase activity is limited; and cycling of K^+ in phloem and surrounding cells via the K^+ channel ATK2 can generate electro-chemical gradients to energise the PM for other transport processes (Gajdanowicz *et al.*, 2011; Dreyer *et al.*, 2017). If plants are struggling to maintain phloem pressure due to sucrose being limited K^+ can be used to help adjust hydrostatic pressure, supporting flow in the phloem (Babst *et al.*, 2022).

Resource separation involves coordinated regulation of mechanisms varying in selectivity Plants have many complex mechanisms for nutrient uptake and translocation, but the membrane separation systems for managing target molecules can be imperfect with respect to their selectivity. Where there are undesirable toxic solutes chemically similar to desirable nutrients, the undesirable solutes can be taken up and translocated throughout the plant inadvertently. Examples of this include excess Na^+ uptake via systems for K^+ uptake (Kronzucker & Britto, 2011, and above), and communal mechanisms for silicon and arsenic uptake (Ma *et al.*, 2008; Zhao *et al.*, 2009). Silicon, a beneficial solute, for most plant species particularly in stress response (for review and references within see: Coskun *et al.*, 2019), is taken up from the soil solution and translocated throughout the plant by a cooperative and imperfectly selective membrane transport system (Ma & Yamaji, 2006, 2015; Ma *et al.*, 2007). This cooperative transport system was first identified and characterised in rice, where rice requires silicon to maintain stable and high yields, but homologues of the transporters have since been reported in several other species (e.g. barley Yamaji *et al.*, 2012; Chiba *et al.*, 2009), maize (Mitani *et al.*, 2009a,b), tomato (*Solanum lycopersicum L*; Mitani-Ueno & Ma, 2021) and cucumber (*Cucumis sativus*; Sun *et al.*, 2017).

In rice, silicon transport is facilitated by two aquaporin channel proteins Lsi1 (OsNIP2;1; Ma *et al.*, 2006) and Lsi6 (OsNIP2;2; Yamaji *et al.*, 2008) localised to the root and shoot, respectively, and two known active transporters Lsi2 (ion transporter superfamily; Ma *et al.*, 2007) and Lsi3 (ion transporter superfamily; Huang *et al.*, 2022) localised to root tissue though different cell types. In roots, Lsi1-, Lsi2- and Lsi3-mediated silicon uptake occurs through polar localisation and specialised transport activity; neutral silicic

acid is passively transported into root cells from the external environment via the channel protein aquaporin Lsi1 (NIP2;1); then active efflux transporters Lsi2 and Lsi3 mediate silicon loading into the xylem for root-to-shoot translocation. However, both Lsi1 and Lsi2 are also known to facilitate the uptake, transport and translocation of the toxic solute arsenic (Ma *et al.*, 2008; Konishi *et al.*, 2022). Mutations to both Lsi1 and Lsi2 significantly decreased arsenic uptake and its accumulation in shoot and grain tissues (Ma *et al.*, 2008). Improvements to silicon transporter selectivity through protein engineering could be an approach to retain the benefits of silicon nutrition to plant growth and yield while minimising toxicity impacts of arsenic to both plants and humans (Clemens, 2019).

2. Dealing with stress

Environmental stress has been a selective pressure driving plants to evolve specialised molecular separation mechanisms. Element toxicity is one type of stress that limits plant growth and yield (Dudka & Miller, 1999). Depending on the species, element toxicity can also have major human health impacts, for example arsenic accumulation in rice (Zhao *et al.*, 2010; Clemens & Ma, 2016). In plants, element toxicity disrupts essential cellular processes such as photosynthesis, protein synthesis and enzymatic reactions as a consequence of the over-accumulation of some elements (Singh *et al.*, 2016). Plants employ several detoxification strategies to manage high toxic element concentrations that rely on the separation of the toxic species across membranes, a process which is facilitated by transport proteins (Volkov & Beilby, 2017). Strategies to manage the distribution of toxic elements within cells and between the shoots and roots include the following: (i) restriction of influx into the cell or translocation throughout the plant (exclusion and retrieval); (ii) the export of excess ions, such as from the root to the rhizosphere (extrusion); and (iii) compartmentation and/or hyperaccumulation of these ions into vacuoles.

Salt stress Salinity is a geographically widespread example of a soil constraint that can cause toxicity problems for plants, and salinisation of agricultural soils is increasing globally (Hassani *et al.*, 2021). Excess salt concentrations in soil solutions can result in cellular toxicity problems, where Na^+ tends to be the toxicity causing element in many plant species, and Na^+ influences whether plants can maintain a suitable gradient for water and nutrient uptake and retention (Jones & Gorham, 2002). The primary strategy for crop plant salt stress tolerance is the maintenance of low intracellular Na^+ concentrations, whereas halophytic plants can accumulate and sequester salt ions (Flowers *et al.*, 2015; Van Zelm *et al.*, 2020).

Crop plant roots must exclude 97–98% of the Na^+ and Cl^- present in saline soils or these ions would quickly accumulate to toxic levels (Munns *et al.*, 2020b). Membrane separation mechanisms circumvent/prevent toxic accumulation of Na^+ by direct Na^+ extrusion from the root epidermis into the soil environment, retrieval of Na^+ from the xylem sap in the root to prevent root–shoot translocation and shoot Na^+ accumulation, and sequestration of Na^+ into cell vacuoles (for recent review, see: Van

Zelm *et al.*, 2020). Several transporters have been identified as contributing to these mechanisms of salt stress tolerance and adaptation.

The Salt Overly Sensitive (SOS) pathway constitutes a key mechanism for salt tolerance through sodium extrusion from the plant into the rhizosphere contributing to the maintenance of low cellular Na^+ concentrations (Ji *et al.*, 2013). The pathway involves salt stress sensors, signalling intermediates and regulatory proteins (Liu & Zhu, 1998; Halfter *et al.*, 2000) that coordinate the control and downstream activity of the PM-localised NHX-family Na^+/H^+ antiporter SOS1 (Lin *et al.*, 2009; Quintero *et al.*, 2011). The SOS1 transporter is activated by phosphorylation mediated by the SOS2/SOS3 kinase complex (Qiu *et al.*, 2002) and works in combination with PM-H^+ATPase to maintain a sufficient proton gradient (Gévaudant *et al.*, 2007; Bose *et al.*, 2015; Miranda *et al.*, 2017) so that the pathway functions as an Na^+ exclusion module which has been observed in many glycophyte and halophyte species. SOS1-mediated Na^+ extrusion from the root-to-rhizosphere was reported for epidermal cells of the root tip (Shi *et al.*, 2002). Meristematic cells lack large vacuoles and are not connected to vascular tissues which limits the type of mechanisms they can deploy to manage excess Na^+. The overexpression or knock-out (KO) of SOS1 has been shown to influence salt tolerance in Arabidopsis (Shi *et al.*, 2003; Yang *et al.*, 2009), tobacco (*Nicotiana tabacum*; Yue *et al.*, 2012), rice (El Mahi *et al.*, 2019) and maize (Zhou *et al.*, 2022). However, the activity or lack thereof of SOS1 does not always confer salt tolerance or sensitivity respectively; when *sos1* loss of function Arabidopsis experienced mild salt stress (25 mM NaCl), these plants accumulated less shoot Na^+ compared with wild type (WT), whereas under severe salt stress (100 mM NaCl), *sos1* mutants accumulated more shoot Na^+ compared with WT (Shi *et al.*, 2002). Similarly, *sos1* mutants were reported to have reduced accumulation of Na^+, within the external [Na^+] range of 5–75 mM (Ding & Zhu, 1997).

There is limited evidence that the salt tolerance of halophytic species is related to more efficient or different SOS1 activity compared with glycophytes, and salt tolerance in halophytic species is not always associated with an increased rate of Na^+ efflux (Britto & Kronzucker, 2015). SOS1 has been identified in the halophytic relative of Arabidopsis *Eutrema salsuginea* (previously known as *Thellungiella salsuginea*) and knock-down of SOS1 resulted in a salt-sensitive phenotype, and Na^+ accumulated preferentially in the root xylem parenchyma cells displacing cytosolic K^+ (Oh *et al.*, 2009). Halophytism of *E. salsuginea* was attributed to increased *SOS1* expression rather than hyper-functioning SOS1 (Oh *et al.*, 2009), but a comparative study between Arabidopsis and *E. salsuginea* found that Na^+ influx in the root was significantly less in *E. salsuginea*, whereas Na^+ efflux was greater in Arabidopsis (Wang *et al.*, 2006). In halophytic *Salicornia spp.*, SOS1 was observed to have constitutively high expression (Yadav *et al.*, 2012; Katschnig *et al.*, 2015). High salinity can sometimes impair the proton pumping that is needed to power Na^+/H^+ antiport, and some organisms exhibit Na^+ efflux powered directly by Na^+-ATPase activity, for example in salt-tolerant Characeae, some bryophytes and *Tetraselmis algae* (Whittington & Bisson, 1994; Balnokin *et al.*, 1997; Benito & Rodríguez-Navarro, 2003; Matalin

et al., 2021; Phipps *et al.*, 2021a,b; Beilby *et al.*, 2022). Rice lines capable of producing greater biomass in saline conditions were created previously by expressing a *Physcomitrella patens* Na^+-ATPase indicating that there is scope to further explore how manipulating Na^+-ATPase function influences plant performance in saline conditions (Jacobs *et al.*, 2011). The contribution of SOS1 to salt tolerance in general and to overall plant energetics has been given consideration in previous studies. If extrusion of one Na^+ from the root by SOS1 requires one H^+ to be similarly extruded by H^+-ATPase, based on the root Na^+ effluxes measured (or calculated) this would consume more energy in the form of ATP than is produced by the maximal respiration of the root (Britto & Kronzucker, 2009; Munns *et al.*, 2020a). This inefficiency highlights that the use of SOS1 is only one option among a range of mechanistic options contributing to salt stress response and management of Na^+ transport in plants.

The retrieval of Na^+ from root xylem to surrounding cell layers, enabling control of Na^+ translocation to the shoot to reduce shoot Na^+ accumulation, is a well-characterised mechanism contributing to salt stress adaptation and tolerance (Assaha *et al.*, 2017). The High-Affinity Potassium Transporter (HKT) protein family has been reported to contribute to this type of Na^+ retrieval mechanism (Hamamoto *et al.*, 2015). There are HKTs with roles in K^+ nutrition and HKT isoforms capable of Na^+ uniport (Class I), some HKTs contribute to Na^+ and K^+ symport (Class II – present only in monocots; and rice HKT2;1 is class II but is a Na^+ transporter: Horie *et al.*, 2001) (Riedelsberger *et al.*, 2021). HKT function has been linked to salt tolerance traits in many species (including halophytes: Ali *et al.*, 2021), for example HKT1;5 function in wheat (Byrt *et al.*, 2007) and rice (Ren *et al.*, 2005) was associated with salt tolerance. HKTs possess a selectivity filter located at the pore entry G/S-G-G-G where the difference in selectivity between Class I and Class II HKTs has been attributed to this serine–glycine sequence polymorphism (Mäser *et al.*, 2002), and this structural feature is therefore an important determinant of function in salt tolerance mechanisms. Recent studies have also identified additional residues influencing HKT function and conferral of salt tolerance. In HvHKT1;5, a leucine to proline substitution at position 189 (L189P) was found to perturb its PM localisation and Na^+ transport function (Houston *et al.*, 2020). Similarly, two HKTs identified in major shoot Na^+ exclusion loci in wheat *Triticum monoccocum* and *Triticum aestivum* differed in their Na^+ affinity through a single amino acid difference (Xu *et al.*, 2018). Engineering of higher Na^+-affinity HKTs, combined with their cell type specific overexpression (Møller *et al.*, 2009), can influence Na^+ retrieval, Na^+ shoot exclusion and plant salt tolerance.

High-Affinity Potassium Transporters work in concert with other mechanisms. A HKT isoform previously identified in maize as functioning in Na^+ retrieval from the xylem was recently found to work cooperatively with a Na^+ selective transporter from the HAK family. ZmHAK4 was identified by GWAS as conferring variation in shoot Na^+ exclusion and salt tolerance in maize plants, accounting for *c.* 11% of shoot [Na^+] variation (Zhang *et al.*, 2019). ZmHAK4 is preferentially expressed in the root stele and xylem parenchyma cells, localised to the PM, and is Na^+ selective (Zhang *et al.*, 2019). Single ZmHAK4 and ZmHKT1 CRISPR KO lines

differed in their root and shoot Na$^+$ content. The ZmHAK4 KO had greater shoot but lower root Na$^+$ content than WT under all test conditions, whereas the ZmHKT1 KO differed from WT under extreme conditions (120 and 150 mM NaCl) only. This suggests that this cooperative mechanism acts under different salinity conditions, where ZmHAK4 is a primary mechanism for Na$^+$ root to shoot translocation under relatively low Na$^+$ conditions (up to 50 mM) (despite having lower Na$^+$ affinity than HKT1, HAK4 transcript levels were 35-fold higher), whereas HKT1 is a key mechanism used under relatively high Na$^+$ conditions. Dual-affinity mechanisms are also described for nutrient uptake (See *Selective uptake of nutrients*).

Another mechanism that plays a central role in plant salt tolerance is Na$^+$ compartmentalisation within cells. Once inside the plant cell, compartmentation of Na$^+$ ions can occur through vacuolar sequestration by transporters localised in the tonoplast (vacuole membrane). A key transporter class example is the vacuolar Na$^+$/H$^+$ antiporters (NHXs, Group I); their Na$^+$ sequestration activity has been shown to increase in response to salt stress, reviewed by Horie & Schroeder (2004) and Keisham *et al.* (2018).

Selective Na$^+$ compartmentation can also extend to a 'tissue-level' accumulation, for example several grass species such as wheat, barley and sorghum (*Sorghum bicolor*) have been shown to load excess Na$^+$ into older tissues, such as old blades and leaf sheaths, to protect young tissues from toxicity upon salt stress (Wei *et al.*, 2003; Netondo *et al.*, 2004; Huang *et al.*, 2006; Rahnama *et al.*, 2011).

Halophytic ('salt tolerant') plants can withstand higher and longer exposure to salt stress than glycophytic plants. Halophytes are capable of osmotically adjusting to maintain a positive turgor pressure in soils containing more than 200 mM NaCl. These plant types have developed improved transporter-mediated cellular uptake and compartmentation of Na$^+$ and Cl$^-$ ions to ensure monovalent ions concentrations are maintained within tolerable limits, reducing toxicity (Cheeseman, 1988; Jones & Gorham, 2002; Hao *et al.*, 2021). A subset of halophytes (also known as recretohalophytes) are capable of not only compartmentalising Na$^+$ ions intracellularly, but also secreting excess salt from their leaves through specialised cellular (i.e. salt bladder) or multicellular structures (i.e. salt gland) (Flowers *et al.*, 2015). Salt-secreting structures can vary in cell number and complexity, with dicotyledonous plants generally having more complex multi-cellular structures sunken in the leaf epidermis, and mangrove species such as *Avicennia marina* having combinations of 8–12 collecting and secretory cells within the salt gland structure (as reviewed by Yuan *et al.*, 2016). Proteomics studies identified a multitude of PM (e.g. NHX and ATPases) and tonoplast-localised (Potassium transporters and V-type proton ATPase) transporters associated with Na$^+$ secretion through mangrove salt glands (Tan *et al.*, 2015). Identified transporter candidates also included aquaporin channel proteins belonging to both the PM- and tonoplast-localising subfamilies (PIPs and TIPs, respectively), potentially implicating them in regulating water and ion transport at both these cellular locations (Natarajan *et al.*, 2021; Guo *et al.*, 2022). Aquaporins may contribute to mechanisms in halophytes, such as mangroves, that enable them to thrive in

---

Box 1   Plants can take up and accumulate rare earth elements (REEs).

This feature is of interest for phytoextraction of these types of resources and for engineering membrane separation technologies (Bashiri *et al.*, 2022; H. Chen *et al.*, 2022; Okoroafor *et al.*, 2022). Rare earth elements (REEs) include holmium (Ho), erbium (Er), thulium (Tm), ytterbium (Yb), lutetium (Lu), gadolinium (Gd), yttrium (Y), terbium (Tb), dysprosium (Dy), neodymium (Nd), europium (Eu), lanthanum (La), cerium (Ce), praseodymium (Pr), promethium (Pm), samarium (Sm) and scandium (Sc) (De Boer & Lammertsma, 2013). Plants have been observed to fractionate different REEs to different tissues (Ding *et al.*, 2005).

---

osmotically challenging environments, such as growing in seawater (Coopman *et al.*, 2021). Resolving how plants achieve control over separating salt and water molecules can contribute to technological advances, such as inspiring novel desalination technologies (Kim *et al.*, 2016; Y. Wang *et al.*, 2020).

Metal toxicity   Among the many different types of metal and element ions, some are useful for plants and others are not. For example, metal ions such as Co, Cu, Fe, Mn, Ni and Zn are required as co-factors for executing diverse enzymatic reactions essential for plant growth, whereas others such as As, Cd and Pb have no known functions for plant growth. Although some metals are essential for cell functioning, excess concentrations can result in toxicity due to cellular stress and oxidative damage. Therefore, sorting of desirable vs undesirable metals and elements is essential for plants' survival (see Table 1 and Box 1).

To deal with the uptake of heavy metals from the soil, plants can distribute heavy metals to different target areas, such as deposition in cell walls or sequestration in vacuoles. Within cells, cytoplasmic ligand binding is also an important survival strategy, enabling long-distance transport of metals and decreasing metallic toxic effects in the cytoplasm (recently reviewed in Jogawat *et al.*, 2021).

There are a multitude of strategies occurring in plants which present a coordinated approach to sort, redistribute and sequester metals through membrane separation processes, specifically using membrane transporters for cellular and organellar redistribution of metals (Kim *et al.*, 2002, 2006, 2009; Song *et al.*, 2003, 2010a,b; Lee *et al.*, 2005; Li *et al.*, 2022). Studying these mechanisms has the potential to inform the development of novel technologies for separating metals (Fig. 3).

Plants can perform modular separation across various cellular membranes. The PM is the first membrane barrier molecules cross when moving into the cell, and the PM of root epidermal cells may benefit from using less selective transporters because this helps in facilitating the entry of a range of metals into the cell where they can then be sorted. Plasma membrane-localised and poorly selective cation transporters such as ZRT/IRT-like (ZIP) have broad substrate specificity for a multitude of heavy metals such as Zn, Co, Cd, Mn and Ni (Korshunova *et al.*, 1999). ZIPs can therefore provide a low-specificity uptake mechanism for heavy metals, where subsequent more precise separation is achieved by the use of

other transporter types, such as specific vacuolar sequestration mechanisms. For example, transporters in the Iron-regulated Protein (IREG) family mediate specific vacuolar sequestration of Ni inadvertently taken up by IRT1 in roots (Schaaf *et al.*, 2006).

Further strategies adopted by plants to deal with metal ions include the collaboration of membrane-associated signalling molecules, calcium-dependent protein kinases (CPK) and metal transporters, with CPKs acting as sensors catalysing the activation/inactivation of specific transporters to control selective separation across membranes. For example, CPK31 interacts with AtNIP1;1, an aquaporin involved in As uptake, where CPK31 activates AtNIP1;1-mediated As uptake (Ji *et al.*, 2017).

Within the plant kingdom, there are plants which can grow in highly metalliferous soils, accumulating relatively high metal concentrations *in planta*. Hyperaccumulator plants can sequester toxic heavy metal elements *in planta*, without the plant showing toxicity symptoms. Such species are able to bioaccumulate heavy metals such as Ni, Zn, Cd, Pb, Co, Cu, Mn, Cr, Se and As, to concentrations 100–1000 times higher than other plants (van der Ent *et al.*, 2013; Lange *et al.*, 2017). Hyperaccumulation strategies have evolved multiple times in the plant Kingdom, as such there might be different strategies adopted by plants to survive metalliferous soils conditions with some species capable of hyperaccumulating more than one element (Reeves *et al.*, 2018). Different compartmentation strategies have been observed in plants for dealing with specific metals. For example, in dealing with Cd, hyperaccumulator species *Thlaspi caerulescens* partitions 35% Cd in the cell wall and remainder in cells/vacuoles (Cosio *et al.*, 2005), whereas tobacco plants accumulate virtually all Cd in vacuoles (Vogeli-Lange & Wagner, 1990). In the Cd/Zn hyperaccumulator, *Sedum plumbizincicola* HMA3 was involved in conferring Cd tolerance (Liu *et al.*, 2017). HMA3 mechanisms are also relevant in cereals. For example, a Sorghum ionomics study and QTL analysis identified Cd transporter SbHMA3s as a key mechanism controlling low Cd seed accumulation by sequestering excess Cd in roots, and *OsHMA3* influences Cd accumulation in rice, and overexpression of rice *OsHMA3* in wheat decreased Cd accumulation in wheat grains (Ueno *et al.*, 2010; L. Zhang *et al.*, 2020; Wahinya *et al.*, 2022).

Hyperaccumulator plants can be used to extract metals from metal-rich soils and wastes, a process termed phytomining or agromining (Brooks *et al.*, 1998; van der Ent *et al.*, 2013, 2015). In the order of 0.2%, angiosperms can hyperaccumulate heavy metal ions (Baker & Whiting, 2002). Metals may be harvested from the plant biomass through smelting to produce bio-ores (Novo *et al.*, 2017). Phytomining to capture metals from wastes is considered to be a strategy of growing importance to transitioning to a circular economy (Dinh *et al.*, 2022). A growing number of studies are emerging that assess the potential of different plant species to contribute to phytomining. For example, a list of plant species that are of interest for harvesting Au, Ag, Pd, Pt and Rh were tabled by Dinh *et al.* (2022) in an analysis of phytomining processes and opportunities, and the gold hyperaccumulation in 17 different plant species was compared by Kurniawan *et al.* (2022) revealing species such as *Typha angustifolia* and *Cyperus haspan* growing around gold mining tailings dams that can accumulate

0.56 mg kg^{-1} gold in dry biomass. The range in gold accumulation in plant shoot samples from the 17 species was 0.44–0.63 mg kg^{-1} and the authors estimate that the most notable species with phytomining potential, *Typha angustifolia* and *Cyperus haspan* could potentially yield in the order of 2.9 g ha^{-1} Au dry weight (Kurniawan *et al.*, 2022).

Plant interactions with soil microorganisms and herbivores influence the capability of plants to take up and manage metal extraction and the potential benefits of hyperaccumulation, respectively (Zubair *et al.*, 2016). For example, rhizobacteria can influence the availability of metals like nickel in the soil. Previous studies reported that the presence of *Microbacterium arabinoga-lactanolyticum* increased *Alyssum murale* nickel uptake into the shoot by 32.4% (Abou-Shanab *et al.*, 2003). *A. murale* can accumulate Ni and Co to above 1000 μg g^{-1} dry weight (Tappero *et al.*, 2007). Hyperaccumulation of some metals like nickel or arsenic may be an advantage to some plants in relation to preventing herbivory (Palomino *et al.*, 2007). For example, arsenic accumulation in the fern *Pteris vittate* was reported to limit grasshopper feeding damage (Rathinasabapathi *et al.*, 2007). *Pteris vittate* can accumulate several 1000 mg as per kg (Zhenyan, 2022). An SLC13-like AsIII effluxer called PvAsE1 is implicated in As translocation via xylem loading contributing to *P. vittate* As hyperaccumulation (Zhenyan, 2022). The mechanisms plants have evolved to manage soils with challenging metal content are relevant to informing the design of systems for separating metals from metal-rich wastewater sources.

3. Membrane structures and regulation

Controlling membrane metal, mineral and nutrient permeability is important for all cellular life and it is also important for developing precision membrane separation technologies (Mulkidjanian *et al.*, 2009). Living cells can adjust cell and organelle metal, mineral and nutrient content and transport through processes such as vesicle transport, changing inter-organelle dynamics and the form of substrate molecules, and by controlling membrane protein functions via post-translational modification (Fig. 3).

Plants have heterogeneous populations of intracellular and extracellular vesicles, which are lipid bilayer-enclosed spheres that have roles in exchanging molecules between organelles, cells, tissues and the external environment including exchange of molecules with other organisms such as microbes (He *et al.*, 2021; Urzì *et al.*, 2021). Combining vesicular membrane structures into membrane separation technologies has aided technological development (Perry *et al.*, 2015). For example, vesicles with embedded aquaporins are attached to polymer layers on porous support substrates to optimise forward and reverse osmosis membrane technology functions (Perry *et al.*, 2015; Fig. 3).

One of the strategies living cells use to influence membrane permeability to important substrates is to convert the form of the substrates following transport to help maintain favourable electrochemical gradients. This can be achieved by changing the form of the substrate during or directly after the membrane transport step. Some types of membrane transport mechanisms are all-in-one units for transport and substrate conversion but other mechanisms

require multiple parts, such as transporter-enzyme complexes, to achieve the transport and conversion of substrates. For example, some types of plant channels can add or remove protons from ammonia or ammonium ions, respectively, during the transport of these substrates across cell membranes (Kirscht *et al.*, 2016). Whereas for molecules such as carbon dioxide living cells pair transport components with enzymes such as carbonic anhydrase to enable them to switch the form of molecule between carbon dioxide and bicarbonate (Reithmeier, 2001). In the field of advancing membrane separation capability, there has been limited investigation of the potential for using diverse plant transporter–enzyme complexes to inform the development of novel components for precision separation applications.

Native cell environment influences the structure and function of membrane proteins (Robertson, 2018). This means that the endogenous function of a protein may not always be replicated when the protein is present in a different membrane environment, but many membrane transport mechanisms can retain function when expressed in an alternative system, such as a heterologous expression systems or artificial membranes (Opekarova & Tanner, 2003). For example, expression of plant metal transporters in yeast cells was reported to increase yeast cell metal accumulation. Engineered yeast strains expressing plant metal transporter and tracking pathway mechanisms caused yeast to sequester metals at concentrations 10–100 times more than established thresholds for chromium, arsenic and cadmium (Sun *et al.*, 2019). Membrane proteins are also subjected to testing following reconstitution in lipid bilayers assuming that their function in their endogenous environment can be recreated in an alternative membrane environment (Kimelberg, 1976). Many membrane proteins have features that living cells can use to turn them on and off, and to alter their permeability to different substrates (Schönichen *et al.*, 2013; Qiu *et al.*, 2020). For the purpose of advancing separation technologies, adjustment of membrane protein functional switches, such as residues subject to post-translational modifications, may contribute to providing consistency in the permeability properties of the proteins.

IV. Bioengineering selective membrane separation technologies

Molecules that are important for plants are important for food and energy security. Half of the global population depends on fertiliser nitrogen for access to sufficient food (Dawson & Hilton, 2011). Urea and ammonium are important sources of N for plants and important molecules for the emerging hydrogen economy (Lan *et al.*, 2012), and urea is an important additive influencing diesel engine emissions (Demir *et al.*, 2022). P and Fe are essential plant nutrients and used in lithium–iron–phosphorus batteries (Roy *et al.*, 2022). In rare earth elements (REEs) deposits, the REEs are often bound to P, and REEs are important for batteries, electronics and magnets (Wang & Liang, 2014; Yang *et al.*, 2017). The plant micronutrient boron is also relevant to the future of battery technologies, as boron can improve battery thermal stability (Zhang *et al.*, 2021). It is essential that important molecules like N and P are recycled for future food and energy security. The

efficiency of use, reuse and recycling of these types of resources can be improved by changing resource management approaches and by implementing technologies that contribute to separating these resources from wastes, such as membrane separation technologies. Membrane separation technologies are important tools for addressing metal, mineral, nutrient and water resources security challenges and environmental challenges (T. Chen *et al.*, 2022).

The features and characteristics of plant and microbe cell membrane transport mechanisms are relevant to engineering membrane separation solutions and novel biotechnologies for improving resource management (Lee *et al.*, 2003; Bhuiyan *et al.*, 2011). Plant and microbial organisms can be used directly in phytomining systems and knowledge about the molecular mechanisms diverse organisms use to control membrane permeability can be used to advance separation technologies. For example, aquaporins are used in a range of membrane technology systems to improve membrane flux and adjust the specificity of the separation (Zhao *et al.*, 2012; Tang *et al.*, 2013; Nabeel *et al.*, 2020). There are subsets of aquaporins with high water permeability and high rejection of other molecules which have been embedded in technologies for use in water desalination (Güvensoy-Morkoyun *et al.*, 2022) and wastewater reuse applications (Tang *et al.*, 2013). There is scope for using a greater diversity of plant and microbe membrane transport mechanisms to further advance the function of separation technologies and for creating biomaterials for wastewater treatment applications (Pervez *et al.*, 2020). Tapping into these selective membrane transport protein resources could be aided by developing catalogues of diverse plant membrane transport protein sequence, structure and permeability information (Hooper *et al.*, 2017; Newport *et al.*, 2019).

The demand for membrane systems capable of ion-selective functions is growing due to resource demand exceeding supply and

---

Box 2 Precision separation technology can be created by mimicking the modular nature of plant separation functions.

Modular systems offer the flexibility to use different types of separation technologies to achieve different functions at different process steps. Similarly, plants use different strategies and mechanisms in different tissues, cells and organelles to optimise separation of molecules. Embedding of selective proteins in membrane technologies is one example of a type of separation technology (Fig. 3). There has been limited testing of pairing of different combinations of separation technologies to optimise for different separation functions. Multi-modular systems where graphene filter modules, metal organic framework modules and protein-embedded membrane separation modules are brought together in a combination of organisational units can enable processing of raw materials and wastes such that different valuable components can be isolated at different steps in processing of input solutions (T. Chen *et al.*, 2022). Successful development of modular systems requires input from the target mining, manufacturing, agricultural, food or energy industries into which these systems will be applied to ensure specificity in conversion of input solutions to re-usable output products matches industry needs.
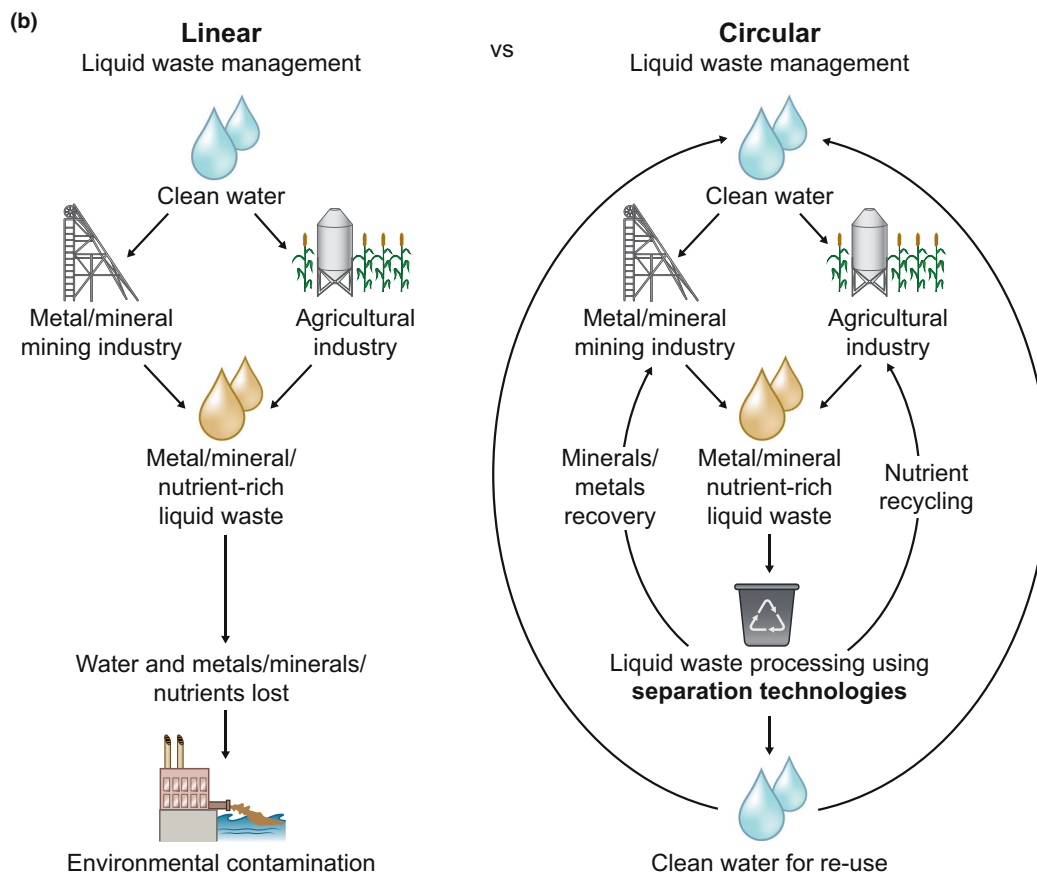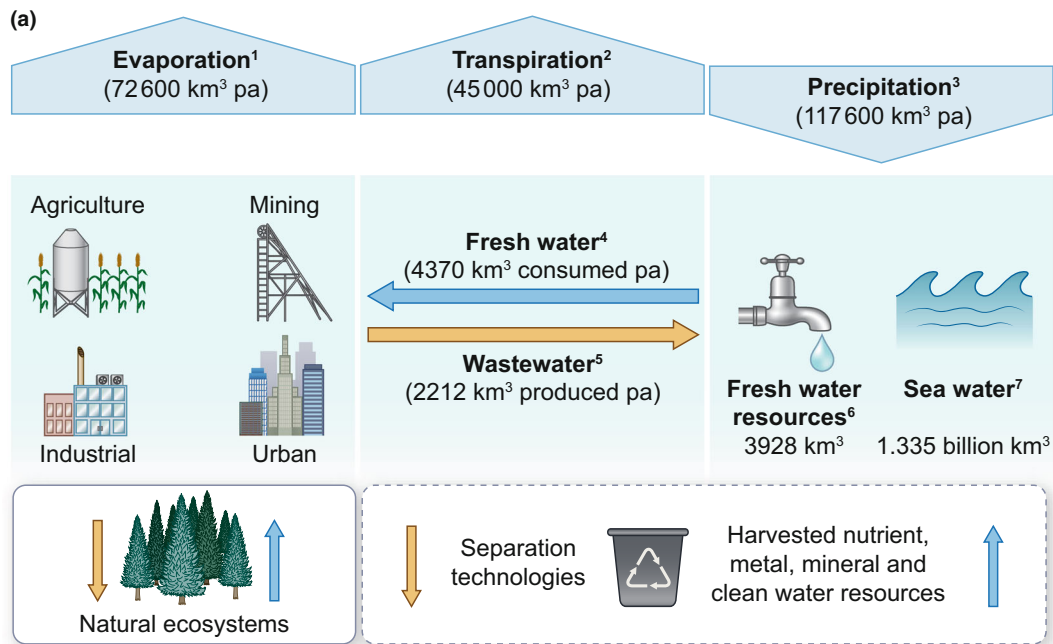
the large amounts of waste being generated around the world requiring processing (DuChanois *et al.*, 2021). There is great diversity in waste and raw material compositions which means that diversity in the function of separation technologies is required.

Separation can be achieved mechanically, biologically or chemically. There is a growing demand for the development of more sophisticated modular separation systems where consecutive separation and processing steps enable multiple resources to be

Fig. 4 Schematic representation of the role for separation technologies in recycling resources from wastewater in the context of global annual fluxes of water and management options. Each year more than 100 000 kilometres cubed (Km^3) of water (blue shaded arrows) moves between the atmosphere and Earth's crust via three processes: evaporation, transpiration through plants and precipitation (values per annum are approximate and derived from: [1]the difference between transpiration data from [2]Evaristo *et al*. (2015) and precipitation data from [3]Schneider *et al*. (2017), and data from [4]Jaramillo & Destouni (2015), [5,6]Smol (2022) and [7]Qadir *et al*. (2022).) (a). Healthy natural plant and microbe ecosystems play key roles in the cycles that enable fresh water resources to be replenished (Jasechko, 2018). Fresh water resources are consumed in human activities such as agriculture, mining, industrial activities and to support urban environments, and wastewater (yellow shaded arrows) is produced. A greater volume of freshwater is consumed per annum (p.a.) than the volume of fresh water resources that can be replenished by natural ecosystems. The volume and composition of the wastewater produced by human activities exceeds the capacity and capability, respectively, of the cleaning functions of natural ecosystems. Development and deployment of separation technologies that enable harvest of nutrient, metal, mineral and clean water resources from wastewater is required for future water and resource security, to prevent natural ecosystems from being further overwhelmed by wastewater and to enable transition from linear to circular liquid waste management (b) (Tarpeh & Chen, 2021). For examples of types of molecules that plants separate that may be relevant to engineering novel industrial separation technologies, see Table 1. Abbreviations: cubic kilometres (km^3), per annum (p.a.). Bin with the universal recycling symbol in the dashed box in part (a) represents where separation technologies can be used to process wastewater to harvest clean water and nutrient, metal and mineral resources to return these resources into circulation rather than releasing industrial wastewater into natural ecosystems (solid box). Droplet shapes in part (b) represent either clean water (blue shading) or wastewater (yellow shading).

retrieved from raw materials and wastes during processing (Box 2). Retrieval of nutrient, metal, mineral and clean water resources from wastes is important for building a sustainable future, supporting agricultural productivity and the capability to supply renewable energy needs and meet climate change mitigation goals.

Current commercially available membrane separation technologies can be used to harvest clean water from various wastewater sources, but the nutrient, metal and mineral resources within those sources of wastewater remain as undifferentiated waste. Reuse of those resources requires them to be relatively pure. Capture of purified sources of resources from waste requires development of precision separation technologies that are adapted to efficiently separate out target nutrient, metal and mineral resources from complex fluids whilst also generating clean water (Fig. 4). Efficient separation of these types of resources is a function that plants and microbes provide in natural ecosystems. Recreating these types of plant and microbe functions in technologies that can be used to manage waste from human activities is the challenge ahead.

V. Conclusions

Within the plant Kingdom resides a wealth of untapped selective membrane transport mechanism resources that can be retrieved and studied to inform crop improvement, phytoremediation strategies and advance industrial membrane separation capability. Sequence-structure–function information is needed to progress our understanding of the membrane protein structure and permeability relationships for mechanisms of interest, and to facilitate the identification and engineering of mechanisms relevant to advancing crop improvement and novel separation technologies. The synthetic biology revolution is offering the possibility of applying systematic design approaches to engineering the selectivity and permeability of molecular mechanisms, making it easier to resolve structure and function relationships and create mechanisms with fit-for-purpose functions (Lu *et al*., 2018; Cravens *et al*., 2019; Freemont, 2019).

Future research directions in this area are expected to include applying computational design and synthetic biology approaches to re-engineer the properties of candidate selective separation mechanisms to optimise the function of these mechanisms for use in industrial applications such as harvesting resources from wastes

(Xu *et al*., 2020). Membrane protein structure and function relationship information is required for developing artificial selective membrane structures that mimic the functions of transmembrane transport mechanisms found in nature (Z. Zhang *et al*., 2020). Functional testing and re-engineering of the selective separation processes found in nature are expected to contribute to enabling the development of precision systems for harvesting and reusing resources from liquid wastes.

Competing interests

AM, CB and SM serve as co-Directors of Membrane Transporter Engineers Pty Ltd (ABN 75649462617).

Author contributions

ADR and SM contributed equally to this work.

ORCID

Caitlin Byrt [ID] https://orcid.org/0000-0001-8549-2873
Annamaria De Rosa [ID] https://orcid.org/0000-0002-2610-9149
Isobel Magrath [ID] https://orcid.org/0000-0002-9065-2015
Samantha McGaughey [ID] https://orcid.org/0000-0001-6133-0415

References

Abou-Shanab R, Angle J, Delorme T, Chaney R, Van Berkum P, Moawad H, Ghanem K, Ghozlan H. 2003. Rhizobacterial effects on nickel extraction from soil and uptake by *Alyssum murale*. *New Phytologist* 158: 219–224.

Ai P, Sun S, Zhao J, Fan X, Xin W, Guo Q, Yu L, Shen Q, Wu P, Miller AJ. 2009. Two rice phosphate transporters, OsPht1; 2 and OsPht1; 6, have different functions and kinetic properties in uptake and translocation. *The Plant Journal* 57: 798–809.

Al Khazally S, Bielby MJ. 2012. Zinc ions block H^+/OH^- channels in *Chara australis*. *Plant, Cell & Environment* 55: 1380–1392.

Ali A, Raddatz N, Pardo JM, Yun DJ. 2021. HKT sodium and potassium transporters in *Arabidopsis thaliana* and related halophyte species. *Physiologia Plantarum* 171: 546–558.

Ali MA, Fahad S, Haider I, Ahmed N, Ahmad S, Hussain S, Arshad M. 2019. Oxidative stress and antioxidant defense in plants exposed to metal/metalloid toxicity. In: *Reactive oxygen, nitrogen and sulfur species in plants: production, metabolism, signaling and defense mechanisms*. Hoboken, NJ, USA: John Wiley & Sons, 353–370.

Amtmann A, Bielby MJ. 2010. The role of ion channels in plant salt tolerance. In: Demidchik V, Maathuis F, eds. *Ion channels and plant stress responses. Signaling and communication in plants*. Berlin & Heidelberg, Germany: Springer.

Ashley M, Grant M, Grabov A. 2006. Plant responses to potassium deficiencies: a role for potassium transport proteins. *Journal of Experimental Botany* 57: 425–436.

Assaha DV, Ueda A, Saneoka H, Al-Yahyai R, Yaish MW. 2017. The role of Na^+ and K^+ transporters in salt stress adaptation in glycophytes. *Frontiers in Physiology* 8: 509.

Babst BA, Braun DM, Karve AA, Frank Baker R, Tran TM, Kenny DJ, Rohlhill J, Knoblauch J, Knoblauch M, Lohaus G. 2022. Sugar loading is not required for phloem sap flow in maize plants. *Nature Plants* 8: 171–180.

Baker AJ, Whiting SN. 2002. In search of the holy grail: a further step in understanding metal hyperaccumulation? *New Phytologist* 155: 1–4.

Balnokin Y, Popova L, Gimmler H. 1997. Further evidence for an ATP-driven sodium pump in the marine alga *Tetraselmis (Platymonas) viridis*. *Journal of Plant Physiology* 150: 264–270.

Bashiri A, Nikzad A, Maleki R, Asadnia M, Razmjou A. 2022. Rare earth elements recovery using selective membranes via extraction and rejection. *Membranes* 12: 80.

Baxter I. 2010. Ionomics: the functional genomics of elements. *Briefings in Functional Genomics* 9: 149–156.

Baxter I, Dilkes BP. 2012. Elemental profiles reflect plant adaptations to the environment. *Science* 336: 1661–1663.

Baxter I, Hermans C, Lahner B, Yakubova E, Tikhonova M, Verbruggen N, Chao D-Y, Salt DE. 2012. Biodiversity of mineral nutrient and trace element accumulation in *Arabidopsis thaliana*. *PLoS ONE* 7: e35121.

Bayle V, Arrighi J-F, Creff A, Nespoulous C, Vialaret J, Rossignol M, Gonzalez E, Paz-Ares J, Nussaume L. 2011. *Arabidopsis thaliana* high-affinity phosphate transporters exhibit multiple levels of posttranslational regulation. *Plant Cell* 23: 1523–1535.

Bielby MJ, Bisson MA, Schneider SC. 2022. How Characean algae take up needed and excrete unwanted ions-an overview explaining how insights from electrophysiology are useful to understand the ecology of aquatic macrophytes. *Aquatic Botany* 181: 103542.

Benito B, Rodríguez-Navarro A. 2003. Molecular cloning and characterization of a sodium-pump ATPase of the moss *Physcomitrella patens*. *The Plant Journal* 36: 382–389.

Bhuiyan MSU, Min SR, Jeong WJ, Sultana S, Choi KS, Song WY, Lee Y, Lim YP, Liu JR. 2011. Overexpression of a yeast cadmium factor 1 (YCF1) enhances heavy metal tolerance and accumulation in *Brassica juncea*. *Plant, Tissue and Organ Culture* 105: 85–91.

Bose J, Rodrigo-Moreno A, Lai D, Xie Y, Shen W, Shabala S. 2015. Rapid regulation of the plasma membrane H^+-ATPase activity is essential to salinity tolerance in two halophyte species, *Atriplex lentiformis* and *Chenopodium quinoa*. *Annals of Botany* 115: 481–494.

Britto D, Kronzucker H. 2015. Sodium efflux in plant roots: what do we really know? *Journal of Plant Physiology* 186: 1–12.

Britto DT, Kronzucker HJ. 2008. Cellular mechanisms of potassium transport in plants. *Physiologia Plantarum* 133: 637–650.

Britto DT, Kronzucker HJ. 2009. Ussing's conundrum and the search for transport mechanisms in plants. *New Phytologist* 183: 243–246.

Brooks RR, Chambers MF, Nicks LJ, Robinson BH. 1998. Phytomining. *Trends in Plant Science* 3: 359–362.

Brownell P, Crossland C. 1972. The requirement for sodium as a micronutrient by species having the C_4 dicarboxylic photosynthetic pathway. *Plant Physiology* 49: 794–797.

Byrt CS, Munns R, Burton RA, Gilliham M, Wege S. 2018. Root cell wall solutions for crop plants in saline soils. *Plant Science* 269: 47–55.

Byrt CS, Platten JD, Spielmeyer W, James RA, Lagudah ES, Dennis ES, Tester M, Munns R. 2007. HKT1; 5-like cation transporters linked to Na^+ exclusion loci in wheat, Nax2 and Kna1. *Plant Physiology* 143: 1918–1928.

Cai Q, He B, Wang S, Fletcher S, Niu D, Mitter N, Birch PR, Jin H. 2021. Message in a bubble: shuttling small RNAs and proteins between cells and interacting organisms using extracellular vesicles. *Annual Review of Plant Biology* 72: 497–524.

Cao Y, Sun D, Chen J-X, Mei H, Ai H, Xu G, Chen Y, Ma LQ. 2018. Phosphate transporter PvPht1; 2 enhances phosphorus accumulation and plant growth without impacting arsenic uptake in plants. *Environmental Science & Technology* 52: 3975–3981.

Cheeseman JM. 1988. Mechanisms of salinity tolerance in plants. *Plant Physiology* 87: 547–550.

Chen H, Chen H, Chen Z. 2022. A review of *in situ* phytoextraction of rare earth elements from contaminated soils. *International Journal of Phytoremediation* 24: 557–566.

Chen J, Wang Y, Wang F, Yang J, Gao M, Li C, Liu Y, Liu Y, Yamaji N, Ma JF. 2015. The rice CK2 kinase regulates trafficking of phosphate transporters in response to phosphate levels. *Plant Cell* 27: 711–723.

Chen T, Wei X, Chen Z, Morin D, Alvarez SV, Yoon Y, Huang Y. 2022. Designing energy-efficient separation membranes: knowledge from nature for a sustainable future. *Advanced Membranes* 2: 100031.

Cheng D, Wu G, Zheng Y. 2015. Positive correlation between potassium uptake and salt tolerance in wheat. *Photosynthetica* 53: 447–454.

Chiba Y, Mitani N, Yamaji N, Ma JF. 2009. HvLsi1 is a silicon influx transporter in barley. *The Plant Journal* 57: 810–818.

Clemens S. 2019. Safer food through plant science: reducing toxic element accumulation in crops. *Journal of Experimental Botany* 70: 5537–5557.

Clemens S, Ma JF. 2016. Toxic heavy metal and metalloid accumulation in crop plants and foods. *Annual Review of Plant Biology* 67: 489–512.

Clemens S, Palmgren MG, Krämer U. 2002. A long way ahead: understanding and engineering plant metal accumulation. *Trends in Plant Science* 7: 309–315.

Conde A, Chaves MM, Gerós H. 2011. Membrane transport, sensing and signaling in plant adaptation to environmental stress. *Plant and Cell Physiology* 52: 1583–1602.

Coopman RE, Nguyen HT, Mencuccini M, Oliveira RS, Sack L, Lovelock CE, Ball MC. 2021. Harvesting water from unsaturated atmospheres: deliquescence of salt secreted onto leaf surfaces drives reverse sap flow in a dominant arid climate mangrove, *Avicennia marina*. *New Phytologist* 231: 1401–1414.

Cosio C, Desantis L, Frey B, Diallo S, Keller C. 2005. Distribution of cadmium in leaves of *Thlaspi caerulescens*. *Journal of Experimental Botany* 56: 765–775.

Coskun D, Deshmukh R, Sonah H, Menzies JG, Reynolds O, Ma JF, Kronzucker HJ, Bélanger RR. 2019. The controversies of silicon's role in plant biology. *New Phytologist* 221: 67–85.

Cravens A, Payne J, Smolke CD. 2019. Synthetic biology strategies for microbial biosynthesis of plant natural products. *Nature Communications* 10: 1–12.

Darestani M, Locq J, Millar GJ. 2019. Powering reversible actuators using forward osmosis membranes: feasibility study and modeling. *Separation Science and Technology* 54: 128–142.

David R, Byrt CS, Tyerman SD, Gilliham M, Wege S. 2019. Roles of membrane transporters: connecting the dots from sequence to phenotype. *Annals of Botany* 124: 201–208.

Dawson CJ, Hilton J. 2011. Fertiliser availability in a resource-limited world: production and recycling of nitrogen and phosphorus. *Food Policy* 36: S14–S22.

De Boer M, Lammertsma K. 2013. Scarcity of rare earth elements. *ChemSusChem* 6: 2045–2055.

Delsart C. 2017. Plant cell wall: description, role in transport, and effect of electroporation. In: Miklavcic D, ed. *Handbook of electroporation.* Cham, Switzerland: Springer International Publishing AG, 489–509.

Demidchik V, Maathuis FJ. 2007. Physiological roles of nonselective cation channels in plants: from salt stress to signalling and development. *New Phytologist* **175**: 387–404.

Demir U, Kozan A, Özer S. 2022. Experimental investigation of the effect of urea addition to fuel on engine performance and emissions in diesel engines. *Fuel* **311**: 122578.

Ding G, Lei GJ, Yamaji N, Yokosho K, Mitani-Ueno N, Huang S, Ma JF. 2020. Vascular cambium-localized AtSPDT mediates xylem-to-phloem transfer of phosphorus for its preferential distribution in Arabidopsis. *Molecular Plant* **13**: 99–111.

Ding L, Zhu J-K. 1997. Reduced Na$^+$ uptake in the NaCl-hypersensitive sos1 mutant of *Arabidopsis thaliana. Plant Physiology* **113**: 795–799.

Ding S, Liang T, Zhang C, Yan J, Zhang Z. 2005. Accumulation and fractionation of rare earth elements (REEs) in wheat: controlled by phosphate precipitation, cell wall absorption and solution complexation. *Journal of Experimental Botany* **56**: 2765–2775.

Dinh T, Dobo Z, Kovacs H. 2022. Phytomining of noble metals: a review. *Chemosphere* **286**: 131805.

Dreyer I. 2021. Nutrient cycling is an important mechanism for homeostasis in plant cells. *Plant Physiology* **187**: 2246–2261.

Dreyer I, Gomez-Porras JL, Riedelsberger J. 2017. The potassium battery: a mobile energy source for transport processes in plant vascular tissues. *New Phytologist* **216**: 1049–1053.

Dreyer I, Li K, Riedelsberger J, Hedrich R, Konrad KR, Michard E. 2022. Transporter networks can serve plant cells as nutrient sensors and mimic transceptor-like behavior. *Iscience* **25**: 104078.

Dreyer I, Michard E. 2020. High-and low-affinity transport in plants from a thermodynamic point of view. *Frontiers in Plant Science* **10**: 1797.

Dreyer I, Uozumi N. 2011. Potassium channels in plant cells. *The FEBS Journal* **278**: 4293–4303.

Duby G, Hosy E, Fizames C, Alcon C, Costa A, Sentenac H, Thibaud JB. 2008. AtKC1, a conditionally targeted Shaker-type subunit, regulates the activity of plant K$^+$ channels. *The Plant Journal* **53**: 115–123.

Duchanois RM, Porter CJ, Violet C, Verduzco R, Elimelech M. 2021. Membrane materials for selective ion separations at the water–energy nexus. *Advanced Materials* **33**: 2101312.

Dudka S, Miller W. 1999. Accumulation of potentially toxic elements in plants and their transfer to human food chain. *Journal of Environmental Science & Health Part B* **34**: 681–708.

El Mahi H, Pérez-Hormaeche J, De Luca A, Villalta I, Espartero J, Gámez-Arjona F, Fernández JL, Bundó M, Mendoza I, Mieulet D. 2019. A critical role of sodium flux via the plasma membrane Na$^+$/H$^+$ exchanger SOS1 in the salt tolerance of rice. *Plant Physiology* **180**: 1046–1065.

Ellison D, Morris CE, Locatelli B, Sheil D, Cohen J, Murdiyarso D, Gutierrez V, Van Noordwijk M, Creed IF, Pokorny J. 2017. Trees, forests and water: cool insights for a hot world. *Global Environmental Change* **43**: 51–61.

van der Ent A, Baker AJM, Reeves RD, Chaney RL, Anderson CWN, Meech JA, Erskine PD, Simonnot M-O, Vaughan J, Morel JL *et al.* **2015.** Agromining: farming for metals in the future? *Environmental Science & Technology* **49**: 4773–4780.

van der Ent A, Baker AJ, Reeves RD, Pollard AJ, Schat H. 2013. Hyperaccumulators of metal and metalloid trace elements: facts and fiction. *Plant and Soil* **362**: 319–334.

Esmaeilzadeh-Salestani K, Bahraseman MRS, Tohidfar M, Khaleghdoust B, Keres I, Mõttus A, Loit E. 2022. Expression of AMT1;1 and AMT2;1 is stimulated by mineral nitrogen and reproductive growth stage in barley under field conditions. *Journal of Plant Nutrition*: 1–13. doi: 10.1080/01904167.2022.2067764.

Evaristo J, Jasechko S, McDonnell JJ. 2015. Global separation of plant transpiration from groundwater and streamflow. *Nature* **525**: 91–94.

Fan X, Naz M, Fan X, Xuan W, Miller AJ, Xu G. 2017. Plant nitrate transporters: from gene function to application. *Journal of Experimental Botany* **68**: 2463–2475.

Fane AG, Wang R, Hu MX. 2015. Synthetic membranes for water purification: status and future. *Angewandte Chemie International Edition* **54**: 3368–3386.

Feng CZ, Luo YX, Wang PD, Gilliham M, Long Y. 2021. MYB77 regulates high-affinity potassium uptake by promoting expression of HAK5. *New Phytologist* **232**: 176–189.

Flowers TJ, Colmer TD. 2008. Salinity tolerance in halophytes. *New Phytologist* **179**: 945–963.

Flowers TJ, Munns R, Colmer TD. 2015. Sodium chloride toxicity and the cellular basis of salt tolerance in halophytes. *Annals of Botany* **115**: 419–431.

Freemont PS. 2019. Synthetic biology industry: data-driven design is creating new opportunities in biotechnology. *Emerging Topics in Life Sciences* **3**: 651–657.

Gajdanowicz P, Michard E, Sandmann M, Rocha M, Corrêa LGG, Ramírez-Aguilar SJ, Gomez-Porras JL, González W, Thibaud J-B, Van Dongen JT. 2011. Potassium (K$^+$) gradients serve as a mobile energy source in plant vascular tissues. *Proceedings of the National Academy of Sciences, USA* **108**: 864–869.

Gévaudant F, Duby G, Von Stedingk E, Zhao R, Morsomme P, Boutry M. 2007. Expression of a constitutively activated plasma membrane H$^+$-ATPase alters plant development and increases salt tolerance. *Plant Physiology* **144**: 1763–1776.

Gierth M, Mäser P. 2007. Potassium transporters in plants–involvement in K$^+$ acquisition, redistribution and homeostasis. *FEBS Letters* **581**: 2348–2356.

Gierth M, Mäser P, Schroeder JI. 2005. The potassium transporter AtHAK5 functions in K$^+$ deprivation-induced high-affinity K$^+$ uptake and AKT1 K$^+$ channel contribution to K$^+$ uptake kinetics in Arabidopsis roots. *Plant Physiology* **137**: 1105–1114.

Gill RA, Ahmar S, Ali B, Saleem MH, Khan MU, Zhou W, Liu S. 2021. The role of membrane transporters in plant growth and development, and abiotic stress tolerance. *International Journal of Molecular Sciences* **22**: 12792.

Good SP, Noone D, Bowen G. 2015. Hydrologic connectivity constrains partitioning of global terrestrial water fluxes. *Science* **349**: 175–177.

Grabov A. 2007. Plant KT/KUP/HAK potassium transporters: single family–multiple functions. *Annals of Botany* **99**: 1035–1041.

Gu M, Huang H, Hisano H, Ding G, Huang S, Mitani-Ueno N, Yokosho K, Sato K, Yamaji N, Ma JF. 2022. A crucial role for a node-localized transporter, HvSPDT, in loading phosphorus into barley grains. *New Phytologist* **234**: 1249–1261.

Gumbart J, Wang Y, Aksimentiev A, Tajkhorshid E, Schulten K. 2005. Molecular dynamics simulations of proteins in lipid bilayers. *Current Opinion in Structural Biology* **15**: 423–431.

Guo Z, Ma D, Li J, Wei M, Zhang L, Zhou L, Zhou X, He S, Wang L, Shen Y. 2022. Genome-wide identification and characterization of aquaporins in mangrove plant *Kandelia obovata* and its role in response to the intertidal environment. *Plant, Cell & Environment* **45**: 1698–1718.

Güvensoy-Morkoyun A, Velioğlu S, Ahunbay MGK, Tantekin-Ersolmaz SBL. 2022. Desalination potential of aquaporin-inspired functionalization of carbon nanotubes: bridging between simulation and experiment. *ACS Applied Materials & Interfaces* **14**: 28174–28185.

Halfter U, Ishitani M, Zhu J-K. 2000. The Arabidopsis SOS2 protein kinase physically interacts with and is activated by the calcium-binding protein SOS3. *Proceedings of the National Academy of Sciences, USA* **97**: 3735–3740.

Hamamoto S, Horie T, Hauser F, Deinlein U, Schroeder JI, Uozumi N. 2015. HKT transporters mediate salt stress resistance in plants: from structure and function to the field. *Current Opinion in Biotechnology* **32**: 113–120.

Han R, Chen J, He S, Dai Z, Liu X, Cao Y, Ma LQ. 2022. Arsenic-induced up-regulation of P transporters PvPht1; 3–1; 4 enhances both As and P uptake in As-hyperaccumulator *Pteris vittata. Journal of Hazardous Materials* **438**: 129430.

Hao S, Wang Y, Yan Y, Liu Y, Wang J, Chen S. 2021. A review on plant responses to salt stress and their mechanisms of salt resistance. *Horticulturae* **7**: 132.

Hassani A, Azapagic A, Shokri N. 2021. Global predictions of primary soil salinization under changing climate in the 21st century. *Nature Communications* **12**: 6663.

He B, Hamby R, Jin H. 2021. Plant extracellular vesicles: Trojan horses of cross-kingdom warfare. *FASEB BioAdvances* **3**: 657–664.

Hirsch RE, Lewis BD, Spalding EP, Sussman MR. 1998. A role for the AKT1 potassium channel in plant nutrition. *Science* **280**: 918–921.

Hooper CM, Castleden IR, Tanz SK, Aryamanesh N, Millar AH. 2017. SUBA4: the interactive data analysis centre for Arabidopsis subcellular protein locations. *Nucleic Acids Research* **45**: D1064–D1074.

Horie T, Schroeder JI. 2004. Sodium transporters in plants. Diverse genes and physiological functions. *Plant Physiology* 136: 2457–2462.

Horie T, Yoshida K, Nakayama H, Yamada K, Oiki S, Shinmyo A. 2001. Two types of HKT transporters with different properties of Na^+ and K^+ transport in *Oryza sativa*. *The Plant Journal* 27: 129–138.

Houston K, Qiu J, Wege S, Hrmova M, Oakey H, Qu Y, Smith P, Situmorang A, Macaulay M, Flis P. 2020. Barley sodium content is regulated by natural variants of the Na^+ transporter HvHKT1; 5. *Communications Biology* 3: 1–9.

Huang S, Spielmeyer W, Lagudah ES, James RA, Platten JD, Dennis ES, Munns R. 2006. A sodium transporter (HKT7) is a candidate for *Nax1*, a gene for salt tolerance in durum wheat. *Plant Physiology* 142: 1718–1727.

Huang S, Yamaji N, Sakurai G, Mitani-Ueno N, Konishi N, Ma JF. 2022. A pericycle-localized silicon transporter for efficient xylem loading in rice. *New Phytologist* 234: 197–208.

Hwang I, Robinson DG. 2009. Transport vesicle formation in plant cells. *Current Opinion in Plant Biology* 12: 660–669.

Hwang J-U, Song W-Y, Hong D, Ko D, Yamaoka Y, Jang S, Yim S, Lee E, Khare D, Kim K. 2016. Plant ABC transporters enable many unique aspects of a terrestrial plant's lifestyle. *Molecular Plant* 9: 338–355.

Isayenkov S, Isner J-C, Maathuis FJ. 2011. Membrane localisation diversity of TPK channels and their physiological role. *Plant Signaling & Behavior* 6: 1201–1204.

Jacobs A, Ford K, Kretschmer J, Tester M. 2011. Rice plants expressing the moss sodium pumping ATPase PpENA1 maintain greater biomass production under salt stress. *Plant Biotechnology Journal* 9: 838–847.

Jaramillo F, Destouni G. 2015. Local flow regulation and irrigation raise global human water consumption and footprint. *Science* 350: 1248–1251.

Jasechko S. 2018. Plants turn on the tap. *Nature Climate Change* 8: 562–563.

Jasechko S, Sharp ZD, Gibson JJ, Birks SJ, Yi Y, Fawcett PJ. 2013. Terrestrial water fluxes dominated by transpiration. *Nature* 496: 347–350.

Ji H, Pardo JM, Batelli G, Van Oosten MJ, Bressan RA, Li X. 2013. The salt overly sensitive (SOS) pathway: established and emerging roles. *Molecular Plant* 6: 275–286.

Ji R, Zhou L, Liu J, Wang Y, Yang L, Zheng Q, Zhang C, Zhang B, Ge H, Yang Y. 2017. Calcium-dependent protein kinase CPK31 interacts with arsenic transporter AtNIP1; 1 and regulates arsenite uptake in *Arabidopsis thaliana*. *PLoS ONE* 12: e0173681.

Jogawat A, Yadav B, Narayan OP. 2021. Metal transporters in organelles and their roles in heavy metal transportation and sequestration mechanisms in plants. *Physiologia Plantarum* 173: 259–275.

Jones GW, Gorham J. 2002. Intra- and inter-cellular compartmentation of ions. In: Läuchli A, Lüttge U, eds. *Salinity: environment – plants – molecules*. Dordrecht, the Netherlands: Springer.

Kafle A, Timilsina A, Gautam A, Adhikari K, Bhattarai A, Aryal N. 2022. Phytoremediation: mechanisms, plant selection and enhancement by natural and synthetic agents. *Environmental Advances* 8: 100203.

Kanno S, Arrighi J-F, Chiarenza S, Bayle V, Berthomé R, Peret B, Javot H, Delannoy E, Marin E, Nakanishi TM. 2016. A novel role for the root cap in phosphate uptake and homeostasis. *eLife* 5: e14577.

Katschnig D, Bliek T, Rozema J, Schat H. 2015. Constitutive high-level SOS1 expression and absence of HKT1; 1 expression in the salt-accumulating halophyte *Salicornia dolichostachya*. *Plant Science* 234: 144–154.

Keisham M, Mukherjee S, Bhatla SC. 2018. Mechanisms of sodium transport in plants–progresses and challenges. *International Journal of Molecular Sciences* 19: 647.

Khare D, Mitsuda N, Lee S, Song WY, Hwang D, Ohme-Takagi M, Martinoia E, Lee Y, Hwang JU. 2017. Root avoidance of toxic metals requires the GeBP-LIKE 4 transcription factor in *Arabidopsis thaliana*. *New Phytologist* 213: 1257–1273.

Kim D-Y, Bovet L, Kushnir S, Noh EW, Martinoia E, Lee Y. 2006. AtATM3 is involved in heavy metal resistance in Arabidopsis. *Plant Physiology* 140: 922–932.

Kim K, Kim H, Lim JH, Lee SJ. 2016. Development of a desalination membrane bioinspired by mangrove roots for spontaneous filtration of sodium ions. *ACS Nano* 10: 11428–11433.

Kim YY, Choi H, Segami S, Cho HT, Martinoia E, Maeshima M, Lee Y. 2009. AtHMA1 contributes to the detoxification of excess Zn (II) in Arabidopsis. *The Plant Journal* 58: 737–753.

Kim YY, Yang YY, Lee Y. 2002. Pb and Cd uptake in rice roots. *Physiologia Plantarum* 116: 368–372.

Kimelberg HK. 1976. Protein-liposome interactions and their relevance to the structure and function of cell membranes. *Molecular and Cellular Biochemistry* 10: 171–190.

Kirscht A, Kaptan SS, Bienert GP, Chaumont F, Nissen P, De Groot BL, Kjellbom P, Gourdon P, Johanson U. 2016. Crystal structure of an ammonia-permeable aquaporin. *PLoS Biology* 14: e1002411.

Konishi N, Huang S, Yamaji N, Ma JF. 2022. Cell-type-dependent but CME-independent polar localization of silicon transporters in rice. *Plant and Cell Physiology* 63: 699–712.

Konishi N, Ma JF. 2021. Three polarly localized ammonium transporter 1 members are cooperatively responsible for ammonium uptake in rice under low ammonium condition. *New Phytologist* 232: 1778–1792.

Korshunova YO, Eide D, Gregg Clark W, Lou Guerinot M, Pakrasi HB. 1999. The IRT1 protein from *Arabidopsis thaliana* is a metal transporter with a broad substrate range. *Plant Molecular Biology* 40: 37–44.

Kraemer U. 2009. The dilemma of controlling heavy metal accumulation in plants. *New Phytologist* 181: 3–5.

Kronzucker HJ, Britto DT. 2011. Sodium transport in plants: a critical review. *New Phytologist* 189: 54–81.

Kurita Y, Kanno S, Sugita R, Hirose A, Ohnishi M, Tezuka A, Deguchi A, Ishizaki K, Fukaki H, Baba KI. 2022. Visualization of phosphorus re-translocation and phosphate transporter expression profiles in a shortened annual cycle system of poplar. *Plant, Cell & Environment* 45: 1749–1764.

Kurniawan R, Henny C, Satya A. 2022. Identification of potential phytoaccumulator plants from tailings area as a gold phytomining agent. *Journal of Ecological Engineering* 23: 169–181.

Lan R, Irvine JT, Tao S. 2012. Ammonia and related chemicals as potential indirect hydrogen storage materials. *International Journal of Hydrogen Energy* 37: 1482–1494.

Lange B, van der Ent A, Baker AJM, Echevarria G, Mahy G, Malaisse F, Meerts P, Pourret O, Verbruggen N, Faucon MP. 2017. Copper and cobalt accumulation in plants: a critical assessment of the current state of knowledge. *New Phytologist* 213: 537–551.

Lau HS, Lau SK, Soh LS, Hong SU, Gok XY, Yi S, Yong WF. 2022. State-of-the-art organic-and inorganic-based hollow fiber membranes in liquid and gas applications: looking back and beyond. *Membranes* 12: 539.

LeDuc DL, Terry N. 2005. Phytoremediation of toxic trace elements in soil and water. *Journal of Industrial Microbiology and Biotechnology* 32: 514–520.

Lee J, Bae H, Jeong J, Lee J-Y, Yang Y-Y, Hwang I, Martinoia E, Lee Y. 2003. Functional expression of a bacterial heavy metal transporter in Arabidopsis enhances resistance to and decreases uptake of heavy metals. *Plant Physiology* 133: 589–596.

Lee M, Lee K, Lee J, Noh EW, Lee Y. 2005. AtPDR12 contributes to lead resistance in Arabidopsis. *Plant Physiology* 138: 827–836.

Lee SC, Lan W-Z, Kim B-G, Li L, Cheong YH, Pandey GK, Lu G, Buchanan BB, Luan S. 2007. A protein phosphorylation/dephosphorylation network regulates a plant potassium channel. *Proceedings of the National Academy of Sciences, USA* 104: 15959–15964.

Lefoulon C, Boeglin M, Moreau B, Véry A-A, Szponarski W, Dauzat M, Michard E, Gaillard I, Chérel I. 2016. The Arabidopsis AtPP2CA protein phosphatase inhibits the GORK K^+ efflux channel and exerts a dominant suppressive effect on phosphomimetic-activating mutations. *Journal of Biological Chemistry* 291: 6521–6533.

Lepoitevin M, Ma T, Bechelany M, Janot J-M, Balme S. 2017. Functionalization of single solid state nanopores to mimic biological ion channels: a review. *Advances in Colloid and Interface Science* 250: 195–213.

Li H, Yu M, Du X-Q, Wang Z-F, Wu W-H, Quintero FJ, Jin X-H, Li H-D, Wang Y. 2017. NRT1. 5/NPF7. 3 functions as a proton-coupled H^+/K^+ antiporter for K^+ loading into the xylem in Arabidopsis. *Plant Cell* 29: 2016–2026.

Li L, Zhu Z, Liao Y, Yang C, Fan N, Zhang J, Yamaji N, Dirick L, Ma JF, Curie C. 2022. NRAMP6 and NRAMP1 cooperatively regulate root growth and manganese translocation under manganese deficiency in Arabidopsis. *The Plant Journal* 110: 1564–1577.

Lian X, Piao S, Huntingford C, Li Y, Zeng Z, Wang X, Ciais P, McVicar TR, Peng S, Ottlé C. 2018. Partitioning global land evapotranspiration

using CMIP5 models constrained by observations. *Nature Climate Change* **8**: 640–646.

Lin H, Yang Y, Quan R, Mendoza I, Wu Y, Du W, Zhao S, Schumaker KS, Pardo JM, Guo Y. 2009. Phosphorylation of SOS3-LIKE CALCIUM BINDING PROTEIN8 by SOS2 protein kinase stabilizes their protein complex and regulates salt tolerance in Arabidopsis. *Plant Cell* **21**: 1607–1619.

Liu H, Zhao H, Wu L, Liu A, Zhao FJ, Xu W. 2017. Heavy metal ATPase 3 (HMA3) confers cadmium hypertolerance on the cadmium/zinc hyperaccumulator *Sedum plumbizincicola*. *New Phytologist* **215**: 687–698.

Liu J, Zhu J-K. 1998. A calcium sensor homolog required for plant salt tolerance. *Science* **280**: 1943–1945.

Liu S, Fukumoto T, Gena P, Feng P, Sun Q, Li Q, Matsumoto T, Kaneko T, Zhang H, Zhang Y. 2020. Ectopic expression of a rice plasma membrane intrinsic protein (OsPIP1; 3) promotes plant growth and water uptake. *The Plant Journal* **102**: 779–796.

Lu P, Min D, Dimaio F, Wei KY, Vahey MD, Boyken SE, Chen Z, Fallas JA, Ueda G, Sheffler W. 2018. Accurate computational design of multipass transmembrane proteins. *Science* **359**: 1042–1046.

Lynch JP, Strock CF, Schneider HM, Sidhu JS, Ajmera I, Galindo-Castañeda T, Klein SP, Hanlon MT. 2021. Root anatomy and soil resource capture. *Plant and Soil* **466**: 21–63.

Ma JF, Tamai K, Yamaji N, Mitani N, Konishi S, Katsuhara M, Ishiguro M, Murata Y, Yano M. 2006. A silicon transporter in rice. *Nature* **440**: 688–691.

Ma JF, Yamaji N. 2006. Silicon uptake and accumulation in higher plants. *Trends in Plant Science* **11**: 392–397.

Ma JF, Yamaji N. 2015. A cooperative system of silicon transport in plants. *Trends in Plant Science* **20**: 435–442.

Ma JF, Yamaji N, Mitani N, Tamai K, Konishi S, Fujiwara T, Katsuhara M, Yano M. 2007. An efflux transporter of silicon in rice. *Nature* **448**: 209–212.

Ma JF, Yamaji N, Mitani N, Xu X-Y, Su Y-H, Mcgrath SP, Zhao F-J. 2008. Transporters of arsenite in rice and their role in arsenic accumulation in rice grain. *Proceedings of the National Academy of Sciences, USA* **105**: 9931–9935.

Maathuis FJ. 2009. Physiological functions of mineral macronutrients. *Current Opinion in Plant Biology* **12**: 250–258.

Maja MM, Ayano SF. 2021. The impact of population growth on natural resources and farmers' capacity to adapt to climate change in low-income countries. *Earth Systems and Environment* **5**: 271–283.

Marschner P. 2012. *Marschner's mineral nutrition of higher plants, 3rd edn.* London, UK: Academic Press.

Martinez-Ballesta MC, Garcia-Ibañez P, Yepes-Molina L, Rios JJ, Carvajal M. 2018. The expanding role of vesicles containing aquaporins. *Cell* **7**: 179.

Mäser P, Hosoo Y, Goshima S, Horie T, Eckelman B, Yamada K, Yoshida K, Bakker EP, Shinmyo A, Oiki S. 2002. Glycine residues in potassium channel-like selectivity filters determine potassium selectivity in four-loop-per-subunit HKT transporters from plants. *Proceedings of the National Academy of Sciences, USA* **99**: 6428–6433.

Matalin DA, Khramov DE, Shuvalov AV, Volkov VS, Balnokin YV, Popova LG. 2021. Cloning and characterization of two putative P-type ATPases from the marine microalga *Dunaliella maritima* similar to plant H+-ATPases and their gene expression analysis under conditions of hyperosmotic salt shock. *Plants* **10**: 2667.

Mazzolai B, Mattoli V, Beccai L, Sinibaldi E. 2014. Emerging technologies inspired by plants. In: *Bioinspired approaches for human-centric technologies.* Cham, Switzerland: Springer Nature.

Miranda RDS, Mesquita RO, Costa JH, Alvarez-Pizarro JC, Prisco JT, Gomes-Filho E. 2017. Integrative control between proton pumps and SOS1 antiporters in roots is crucial for maintaining low Na+ accumulation and salt tolerance in ammonium-supplied Sorghum bicolor. *Plant and Cell Physiology* **58**: 522–536.

Mitani N, Chiba Y, Yamaji N, Ma JF. 2009a. Identification and characterization of maize and barley Lsi2-like silicon efflux transporters reveals a distinct silicon uptake system from that in rice. *Plant Cell* **21**: 2133–2142.

Mitani N, Yamaji N, Ma JF. 2009b. Identification of maize silicon influx transporters. *Plant and Cell Physiology* **50**: 5–12.

Mitani-Ueno N, Ma JF. 2021. Linking transport system of silicon with its accumulation in different plant species. *Soil Science and Plant Nutrition* **67**: 10–17.

Møller IS, Gilliham M, Jha D, Mayo GM, Roy SJ, Coates JC, Haseloff J, Tester M. 2009. Shoot Na+ exclusion and increased salinity tolerance engineered by cell type–specific alteration of Na+ transport in Arabidopsis. *Plant Cell* **21**: 2163–2178.

Morere-Le Paven M-C, Viau L, Hamon A, Vandecasteele C, Pellizzaro A, Bourdin C, Laffont C, Lapied B, Lepetit M, Frugier F. 2011. Characterization of a dual-affinity nitrate transporter MtNRT1. 3 in the model legume *Medicago truncatula*. *Journal of Experimental Botany* **62**: 5595–5605.

Mulkidjanian AY, Galperin MY, Koonin EV. 2009. Co-evolution of primordial membranes and membrane proteins. *Trends in Biochemical Sciences* **34**: 206–215.

Munns R, Day DA, Fricke W, Watt M, Arsova B, Barkla BJ, Bose J, Byrt CS, Chen ZH, Foster KJ. 2020a. Energy costs of salt tolerance in crop plants. *New Phytologist* **225**: 1072–1090.

Munns R, Passioura JB, Colmer TD, Byrt CS. 2020b. Osmotic adjustment and energy limitations to plant growth in saline soil. *New Phytologist* **225**: 1091–1096.

Munns R, Tester M. 2008. Mechanisms of salinity tolerance. *Annual Review of Plant Biology* **59**: 651–681.

Nabeel F, Rasheed T, Bilal M, Li C, Yu C, Iqbal HM. 2020. Bio-inspired supramolecular membranes: a pathway to separation and purification of emerging pollutants. *Separation & Purification Reviews* **49**: 20–36.

Natarajan P, Murugesan AK, Govindan G, Gopalakrishnan A, Kumar R, Duraisamy P, Balaji R, Shyamli PS, Parida M. 2021. A reference-grade genome identifies salt-tolerance genes from the salt-secreting mangrove species *Avicennia marina*. *Communications Biology* **4**: 1–10.

Nelson JA, Pérez-Priego O, Zhou S, Poyatos R, Zhang Y, Blanken PD, Gimeno TE, Wohlfahrt G, Desai AR, Gioli B. 2020. Ecosystem transpiration and evaporation: insights from three water flux partitioning methods across FLUXNET sites. *Global Change Biology* **26**: 6916–6930.

Netondo GW, Onyango JC, Beck E. 2004. Sorghum and salinity: I. Response of growth, water relations, and ion accumulation to NaCl salinity. *Crop Science* **44**: 797–805.

Newport TD, Sansom MSP, Stansfeld PJ. 2019. The MemProtMD database: a resource for membrane-embedded protein structures and their lipid interactions. *Nucleic Acids Research* **47**: D390–D397.

Nieves-Cordones M, Alemán F, Martínez V, Rubio F. 2014. K+ uptake in plant roots. The systems involved, their regulation and parallels in other organisms. *Journal of Plant Physiology* **171**: 688–695.

Novo LAB, Castro PML, Alvarenga P, da Silva EF. 2017. *Phytomining of rare and valuable metals. Phytoremediation.* Cham, Switzerland: Springer, 469–486.

Oh D-H, Leidi E, Zhang Q, Hwang S-M, Li Y, Quintero FJ, Jiang X, D'urzo MP, Lee SY, Zhao Y et al. 2009. Loss of halophytism by interference with SOS1 expression. *Plant Physiology* **151**: 210–222.

Okoroafor PU, Kunisch N, Epede MN, Ogunkunle CO, Heilmeier H, Wiche O. 2022. Phytoextraction of rare earth elements, germanium and other trace elements as affected by fertilization and liming. *Environmental Technology & Innovation* **28**: 102607.

Opekarova M, Tanner W. 2003. Specific lipid requirements of membrane proteins: a putative bottleneck in heterologous expression. *Biochimica et Biophysica Acta (BBA)-Biomembranes* **1610**: 11–22.

Paasonen P, Asmi A, Petäjä T, Kajos MK, Äijälä M, Junninen H, Holst T, Abbatt JP, Arneth A, Birmili W. 2013. Warming-induced increase in aerosol number concentration likely to moderate climate change. *Nature Geoscience* **6**: 438–442.

Palomino M, Kennedy PG, Simms EL. 2007. Nickel hyperaccumulation as an anti-herbivore trait: considering the role of tolerance to damage. *Plant and Soil* **293**: 189–195.

Pasricha S, Mathur V, Garg A, Lenka S, Verma K, Agarwal S. 2021. Molecular mechanisms underlying heavy metal uptake, translocation and tolerance in hyperaccumulators-an analysis: heavy metal tolerance in hyperaccumulators. *Environmental Challenges* **4**: 100197.

Perry M, Madsen SU, Jørgensen T, Braekevelt S, Lauritzen K, Hélix-Nielsen C. 2015. Challenges in commercializing biomimetic membranes. *Membranes* **5**: 685–701.

Pervez M, Balakrishnan M, Hasan SW, Choo K-H, Zhao Y, Cai Y, Zarra T, Belgiorno V, Naddeo V. 2020. A critical review on nanomaterials membrane bioreactor (NMs-MBR) for wastewater treatment. *NPJ Clean Water* **3**: 1–21.

Phipps S, Delwiche CF, Bisson MA. 2021a. Salinity-induced changes in gene expression in the Streptophyte alga chara: the critical role of a rare Na$^+$-ATPase. *Journal of Phycology* **57**: 1004–1013.

Phipps S, Goodman CA, Delwiche CF, Bisson MA. 2021b. The role of ion-transporting proteins in the evolution of salt tolerance in charophyte algae. *Journal of Phycology* **57**: 1014–1025.

Pilon-Smits E. 2005. Phytoremediation. *Annual Review of Plant Biology* **56**: 15–39.

Pita-Barbosa A, Ricachenevsky FK, Flis PM. 2019. One "OMICS" to integrate them all: ionomics as a result of plant genetics, physiology and evolution. *Theoretical and Experimental Plant Physiology* **31**: 71–89.

Porter CJ, Werber JR, Zhong M, Wilson CJ, Elimelech M. 2020. Pathways and challenges for biomimetic desalination membranes with sub-nanometer channels. *ACS Nano* **14**: 10894–10916.

Pottosin I, Dobrovinskaya O. 2014. Non-selective cation channels in plasma and vacuolar membranes and their contribution to K$^+$ transport. *Journal of Plant Physiology* **171**: 732–742.

Prathap V, Kumar A, Maheshwari C, Tyagi A. 2022. Phosphorus homeostasis: acquisition, sensing, and long-distance signaling in plants. *Molecular Biology Reports* **49**: 8071–8086.

Prăvălie R, Patriche C, Borrelli P, Panagos P, Roşca B, Dumitraşcu M, Nita I-A, Săvulescu I, Birsan M-V, Bandoc G. 2021. Arable lands under the pressure of multiple land degradation processes. A Global Perspective. *Environmental Research* **194**: 110697.

Puga MI, Rojas-Triana M, De Lorenzo L, Leyva A, Rubio V, Paz-Ares J. 2017. Novel signals in the regulation of Pi starvation responses in plants: facts and promises. *Current Opinion in Plant Biology* **39**: 40–49.

Pyo YJ, Gierth M, Schroeder JI, Cho MH. 2010. High-affinity K$^+$ transport in Arabidopsis: AtHAK5 and AKT1 are vital for seedling establishment and postgermination growth under low-potassium conditions. *Plant Physiology* **153**: 863–875.

Qadir M, Smakhtin V, Koo-Oshima S, Guenther E. 2022. Global water scarcity and unconventional water resources. In: *Unconventional water resources.* Cham, Switzerland: Springer, 3–17.

Qiu J, McGaughey SA, Groszmann M, Tyerman SD, Byrt CS. 2020. Phosphorylation influences water and ion channel function of AtPIP2; 1. *Plant, Cell & Environment* **43**: 2428–2442.

Qiu Q-S, Guo Y, Dietrich MA, Schumaker KS, Zhu J-K. 2002. Regulation of SOS1, a plasma membrane Na$^+$/H$^+$ exchanger in *Arabidopsis thaliana*, by SOS2 and SOS3. *Proceedings of the National Academy of Sciences, USA* **99**: 8436–8441.

Quintero FJ, Martinez-Atienza J, Villalta I, Jiang X, Kim W-Y, Ali Z, Fujii H, Mendoza I, Yun D-J, Zhu J-K. 2011. Activation of the plasma membrane Na/H antiporter Salt-Overly-Sensitive 1 (SOS1) by phosphorylation of an auto-inhibitory C-terminal domain. *Proceedings of the National Academy of Sciences, USA* **108**: 2611–2616.

Ragel P, Raddatz N, Leidi EO, Quintero FJ, Pardo JM. 2019. Regulation of K$^+$ nutrition in plants. *Frontiers in Plant Science* **10**: 281.

Ragel P, Ródenas R, García-Martín E, Andrés Z, Villalta I, Nieves-Cordones M, Rivero RM, Martínez V, Pardo JM, Quintero FJ. 2015. The CBL-interacting protein kinase CIPK23 regulates HAK5-mediated high-affinity K$^+$ uptake in Arabidopsis roots. *Plant Physiology* **169**: 2863–2873.

Rahnama A, Poustini K, Tavakkol-Afshari R, Ahmadi A, Alizadeh H. 2011. Growth properties and ion distribution in different tissues of bread wheat genotypes (*Triticum aestivum* L.) differing in salt tolerance. *Journal of Agronomy and Crop Science* **197**: 21–30.

Rashid M, Bera S, Medvinsky AB, Sun G-Q, Li B-L, Chakraborty A. 2018. Adaptive regulation of nitrate transceptor NRT1. 1 in fluctuating soil nitrate conditions. *Iscience* **2**: 41–50.

Rathinasabapathi B, Rangasamy M, Froeba J, Cherry RH, McAuslane HJ, Capinera JL, Srivastava M, Ma LQ. 2007. Arsenic hyperaccumulation in the Chinese brake fern (*Pteris vittata*) deters grasshopper (*Schistocerca americana*) herbivory. *New Phytologist* **175**: 363–369.

Raven J. 1980. Short-and long-distance transport of boric acid in plants. *New Phytologist* **84**: 231–249.

Reeves RD, Baker AJ, Jaffré T, Erskine PD, Echevarria G, van der Ent A. 2018. A global database for plants that hyperaccumulate metal and metalloid trace elements. *New Phytologist* **218**: 407–411.

Reithmeier RA. 2001. A membrane metabolon linking carbonic anhydrase with chloride/bicarbonate anion exchangers. *Blood Cells, Molecules, and Diseases* **27**: 85–89.

Ren Z-H, Gao J-P, Li L-G, Cai X-L, Huang W, Chao D-Y, Zhu M-Z, Wang Z-Y, Luan S, Lin H-X. 2005. A rice quantitative trait locus for salt tolerance encodes a sodium transporter. *Nature Genetics* **37**: 1141–1146.

Riedelsberger J, Miller JK, Valdebenito-Maturana B, Piñeros MA, González W, Dreyer I. 2021. Plant HKT channels: an updated view on structure, function and gene regulation. *International Journal of Molecular Sciences* **22**: 1892.

Rinne PL, Schoot CVD. 2004. Cell-cell communication as a key factor in dormancy cycling. *Journal of Crop Improvement* **10**: 113–156.

Robertson JL. 2018. The lipid bilayer membrane and its protein constituents. *Journal of General Physiology* **150**: 1472–1483.

Roorkiwal M, Pandey S, Thavarajah D, Hemalatha R, Varshney RK. 2021. Molecular mechanisms and biochemical pathways for micronutrient acquisition and storage in legumes to support biofortification for nutritional security. *Frontiers in Plant Science* **12**: 682842.

Roy JJ, Rarotra S, Krikstolaityte V, Zhuoran KW, Cindy YDI, Tan XY, Carboni M, Meyer D, Yan Q, Srinivasan M. 2022. Green recycling methods to treat lithium-ion batteries E-waste: a circular approach to sustainability. *Advanced Materials* **34**: 2103346.

Rubio F, Alemán F, Nieves-Cordones M, Martínez V. 2010. Studies on Arabidopsis athak5, atakt1 double mutants disclose the range of concentrations at which AtHAK5, AtAKT1 and unknown systems mediate K$^+$ uptake. *Physiologia Plantarum* **139**: 220–228.

Ruffel S. 2018. Nutrient-related long-distance signals: common players and possible cross-talk. *Plant and Cell Physiology* **59**: 1723–1732.

Rylott EL, Bruce NC. 2022. Plants to mine metals and remediate land. *Science* **377**: 1380–1381.

Saito S, Uozumi N. 2020. Calcium-regulated phosphorylation systems controlling uptake and balance of plant nutrients. *Frontiers in Plant Science* **11**: 44.

Salt DE, Baxter I, Lahner B. 2008. Ionomics and the study of the plant ionome. *Annual Review of Plant Biology* **59**: 709–733.

Samota M, Navnage N, Bhatt L. 2017. Role of macro and micronutrient in development and growth of plant. *Trends in Biosciences* **10**: 3171–3173.

Sanahuja-Embuena V, Khensir G, Yusuf M, Andersen MF, Nguyen XT, Trzaskus K, Pinelo M, Helix-Nielsen C. 2019. Role of operating conditions in a pilot scale investigation of hollow fiber forward osmosis membrane modules. *Membranes* **9**: 66.

Sasaki A, Yamaji N, Ma JF. 2016. Transporters involved in mineral nutrient uptake in rice. *Journal of Experimental Botany* **67**: 3645–3653.

Schaaf G, Honsbein A, Meda AR, Kirchner S, Wipf D, Von Wirén N. 2006. AtIREG2 encodes a tonoplast transport protein involved in iron-dependent nickel detoxification in *Arabidopsis thaliana* roots. *Journal of Biological Chemistry* **281**: 25532–25540.

Scherzer S, Böhm J, Krol E, Shabala L, Kreuzer I, Larisch C, Bemm F, Al-Rasheid KA, Shabala S, Rennenberg H. 2015. Calcium sensor kinase activates potassium uptake systems in gland cells of *Venus flytraps*. *Proceedings of the National Academy of Sciences, USA* **112**: 7309–7314.

Schneider U, Finger P, Meyer-Christoffer A, Rustemeier E, Ziese M, Becker A. 2017. Evaluating the hydrological cycle over land using the newly-corrected precipitation climatology from the Global Precipitation Climatology Centre (GPCC). *Atmosphere* **8**: 52.

Schönichen A, Webb BA, Jacobson MP, Barber DL. 2013. Considering protonation as a post-translational modification regulating protein structure and function. *Annual Review of Biophysics* **42**: 289–314.

Schroeder JI, Delhaize E, Frommer WB, Guerinot ML, Harrison MJ, Herrera-Estrella L, Horie T, Kochian LV, Munns R, Nishizawa NK. 2013. Using membrane transporters to improve crops for sustainable food production. *Nature* **497**: 60–66.

Schroeder JI, Ward JM, Gassmann W. 1994. Perspectives on the physiology and structure of inward-rectifying K$^+$ channels in higher plants: biophysical implications for K$^+$ uptake. *Annual Review of Biophysics and Biomolecular Structure* **23**: 441–471.

Schwacke R, Schneider A, van der Graaff E, Fischer K, Catoni E, Desimone M, Frommer WB, Flugge U-I, Kunze R. 2003. ARAMEMNON, a novel database for Arabidopsis integral membrane proteins. *Plant Physiology* **131**: 16–26.

Shabala S, Cuin TA. 2008. Potassium transport and plant salt tolerance. *Physiologia Plantarum* **133**: 651–669.

Shariatipour N, Heidari B, Ravi S, Stevanato P. 2021. Genomic analysis of ionome-related QTLs in *Arabidopsis thaliana*. *Scientific Reports* **11**: 1–14.

Sharma T, Dreyer I, Riedelsberger J. 2013. The role of K^+ channels in uptake and redistribution of potassium in the model plant *Arabidopsis thaliana*. *Frontiers in Plant Science* **4**: 224.

Shen J, Yuan L, Zhang J, Li H, Bai Z, Chen X, Zhang W, Zhang F. 2011. Focus issue on phosphorus plant physiology: phosphorus dynamics: from soil to plant. *Plant Physiology* **156**: 997–1005.

Shi H, Lee B-H, Wu S-J, Zhu J-K. 2003. Overexpression of a plasma membrane Na^+/H^+ antiporter gene improves salt tolerance in *Arabidopsis thaliana*. *Nature Biotechnology* **21**: 81–85.

Shi H, Quintero FJ, Pardo JM, Zhu J-K. 2002. The putative plasma membrane Na^+/H^+ antiporter SOS1 controls long-distance Na^+ transport in plants. *Plant Cell* **14**: 465–477.

Shin H, Shin HS, Dewbre GR, Harrison MJ. 2004. Phosphate transport in Arabidopsis: Pht1; 1 and Pht1; 4 play a major role in phosphate acquisition from both low-and high-phosphate environments. *The Plant Journal* **39**: 629–642.

Silva LC, Lambers H. 2021. Soil-plant-atmosphere interactions: structure, function, and predictive scaling for climate change mitigation. *Plant and Soil* **461**: 5–27.

Singh S, Parihar P, Singh R, Singh VP, Prasad SM. 2016. Heavy metal tolerance in plants: role of transcriptomics, proteomics, metabolomics, and ionomics. *Frontiers in Plant Science* **6**: 1143.

Smol M. 2022. Chapter 1 – circular economy approach in the water and wastewater sector. In: Stefanakis A, Nikolaou I, eds. *Circular economy and sustainability, vol. 2.* Amsterdam, the Netherlands: Elsevier, 1–19.

Song W-Y, Choi KS, Kim DY, Geisler M, Park J, Vincenzetti V, Schellenberg M, Kim SH, Lim YP, Noh EW. 2010a. Arabidopsis PCR2 is a zinc exporter involved in both zinc extrusion and long-distance zinc transport. *Plant Cell* **22**: 2237–2252.

Song W-Y, Ju Sohn E, Martinoia E, Jik Lee Y, Yang Y-Y, Jasinski M, Forestier C, Hwang I, Lee Y. 2003. Engineering tolerance and accumulation of lead and cadmium in transgenic plants. *Nature Biotechnology* **21**: 914–919.

Song W-Y, Park J, Mendoza-Cózatl DG, Suter-Grotemeyer M, Shim D, Hörtensteiner S, Geisler M, Weder B, Rea PA, Rentsch D. 2010b. Arsenic tolerance in Arabidopsis is mediated by two ABCC-type phytochelatin transporters. *Proceedings of the National Academy of Sciences, USA* **107**: 21187–21192.

Srivastava AK, Shankar A, Nalini Chandran AK, Sharma M, Jung K-H, Suprasanna P, Pandey GK. 2020. Emerging concepts of potassium homeostasis in plants. *Journal of Experimental Botany* **71**: 608–619.

Stein RJ, Höreth S, De Melo JRF, Syllwasschy L, Lee G, Garbin ML, Clemens S, Krämer U. 2017. Relationships between soil and leaf mineral composition are element-specific, environment-dependent and geographically structured in the emerging model *Arabidopsis halleri*. *New Phytologist* **213**: 1274–1286.

Sun GL, Reynolds E, Belcher AM. 2019. Designing yeast as plant-like hyperaccumulators for heavy metals. *Nature Communications* **10**: 1–12.

Sun H, Guo J, Duan Y, Zhang T, Huo H, Gong H. 2017. Isolation and functional characterization of CsLsi1, a silicon transporter gene in *Cucumis sativus*. *Physiologia Plantarum* **159**: 201–214.

Suriyagoda LDB, Ryan MH, Gille CE, Dayrell RLC, Finnegan PM, Ranathunge K, Nicol D, Lambers H. 2023. Phosphorus fractions in leaves. *New Phytologist* **237**: 1122–1135.

Tan W-K, Lim T-K, Loh C-S, Kumar P, Lin Q. 2015. Proteomic characterisation of the salt gland-enriched tissues of the mangrove tree species *Avicennia officinalis*. *PLoS ONE* **10**: e0133386.

Tan X, Li K, Wang Z, Zhu K, Tan X, Cao J. 2019. A review of plant vacuoles: formation, located proteins, and functions. *Plants* **8**: 327.

Tang C, Zhao Y, Wang R, Hélix-Nielsen C, Fane A. 2013. Desalination by biomimetic aquaporin membranes: review of status and prospects. *Desalination* **308**: 34–40.

Tang R-J, Luan M, Wang C, Lhamo D, Yang Y, Zhao F-G, Lan W-Z, Fu A-G, Luan S. 2020. Plant membrane transport research in the post-genomic era. *Plant Communications* **1**: 100013.

Tappero R, Peltier E, Gräfe M, Heidel K, Ginder-Vogel M, Livi K, Rivers ML, Marcus MA, Chaney R, Sparks DL. 2007. Hyperaccumulator *Alyssum murale*

relies on a different metal storage mechanism for cobalt than for nickel. *New Phytologist* **175**: 641–654.

Tarpeh WA, Chen X. 2021. Making wastewater obsolete: selective separations to enable circular water treatment. *Environmental Science and Ecotechnology* **5**: 100078.

Tran STH, Horie T, Imran S, Qiu J, McGaughey S, Byrt CS, Tyerman SD, Katsuhara M. 2020. A survey of barley PIP aquaporin ionic conductance reveals Ca^{2+}−sensitive HvPIP2; 8 Na^+ and K^+ conductance. *International Journal of Molecular Sciences* **21**: 7135.

Tyerman SD, McGaughey SA, Qiu J, Yool AJ, Byrt CS. 2021. Adaptable and multifunctional ion-conducting aquaporins. *Annual Review of Plant Biology* **72**: 703–736.

Ueda M, Tstsumi N, Fujimoto M. 2016. Salt stress induces internalization of plasma membrane aquaporin into the vacuole in *Arabidopsis thaliana*. *Biochemical and Biophysical Research Communications.* **474**: 742–746.

Ueno D, Yamaji N, Kono I, Huang CF, Ando T, Yano M, Ma JF. 2010. Gene limiting cadmium accumulation in rice. *Proceedings of the National Academy of Sciences.* **107**: 16500–16505.

Urzì O, Raimondo S, Alessandro R. 2021. Extracellular vesicles from plants: current knowledge and open questions. *International Journal of Molecular Sciences* **22**: 5366.

Van Kleeff P, Gao J, Mol S, Zwart N, Zhang H, Li K, De Boer A. 2018. The Arabidopsis GORK K^+-channel is phosphorylated by calcium-dependent protein kinase 21 (CPK21), which in turn is activated by 14-3-3 proteins. *Plant Physiology and Biochemistry* **125**: 219–231.

Van Zelm E, Zhang Y, Testerink C. 2020. Salt tolerance mechanisms of plants. *Annual Review of Plant Biology* **71**: 403–433.

Verbruggen N, Hermans C, Schat H. 2009. Molecular mechanisms of metal hyperaccumulation in plants. *New Phytologist* **181**: 759–776.

Vogeli-Lange R, Wagner GJ. 1990. Subcellular localization of cadmium and cadmium-binding peptides in tobacco leaves: implication of a transport function for cadmium-binding peptides. *Plant Physiology* **92**: 1086–1093.

Volkov V, Beilby MJ. 2017. Editorial: salinity tolerance in plants: mechanisms and regulation of ion transport. *Frontiers in Plant Science* **8**: 1795.

Wahinya FW, Yamazaki K, Jing Z, Takami T, Kamiya T, Kajiya-Kanegae H, Takanashi H, Iwata H, Tsutsumi N, Fujiwara T et al. 2022. Sorghum ionomics reveals the functional SbHMA3a allele that limits excess cadmium accumulation in grains. *Plant and Cell Physiology* **63**: 713–728.

Walker N, Beilby M, Smith F. 1979. Amine uniport at the plasmalemma of charophyte cells: I. Current-voltage curves, saturation kinetics, and effects of unstirred layers. *The Journal of Membrane Biology* **49**: 21–55.

Wang B, Davenport RJ, Volkov V, Amtmann A. 2006. Low unidirectional sodium influx into root cells restricts net sodium accumulation in *Thellungiella halophila*, a salt-tolerant relative of *Arabidopsis thaliana*. *Journal of Experimental Botany* **57**: 1161–1170.

Wang L, Liang T. 2014. Effects of exogenous rare earth elements on phosphorus adsorption and desorption in different types of soils. *Chemosphere* **103**: 148–155.

Wang Q, Zhao Y, Luo W, Li R, He Q, Fang X, Michele RD, Ast C, Wirén NV, Lin J. 2013. Single-particle analysis reveals shutoff control of the *Arabidopsis* ammonium transporter AMT1;3 by clustering and internalization. *Proceedings of the National Academy of Sciences, USA* **110**: 13204–13209.

Wang X, Wang H-F, Chen Y, Sun M-M, Wang Y, Chen Y-F. 2020. The transcription factor NIGT1. 2 modulates both phosphate uptake and nitrate influx during phosphate starvation in Arabidopsis and maize. *Plant Cell* **32**: 3519–3534.

Wang Y, He L, Li H-D, Xu J, Wu W-H. 2010. Potassium channel α-subunit AtKC1 negatively regulates AKT1-mediated K^+ uptake in Arabidopsis roots under low-K^+ stress. *Cell Research* **20**: 826–837.

Wang Y, Lee J, Werber JR, Elimelech M. 2020. Capillary-driven desalination in a synthetic mangrove. *Science Advances* **6**: eaax5253.

Wang Y, Wang F, Lu H, Liu Y, Mao C. 2021. Phosphate uptake and transport in plants: an elaborate regulatory system. *Plant and Cell Physiology* **62**: 564–572.

Wang Y, Wu W-H. 2013. Potassium transport and signaling in higher plants. *Annual Review of Plant Biology* **64**: 451–476.

Wang Y, Wu W-H. 2017. Regulation of potassium transport and signaling in plants. *Current Opinion in Plant Biology* **39**: 123–128.

Wei W, Bilsborrow PE, Hooley P, Fincham DA, Lombi E, Forster BP. 2003. Salinity induced differences in growth, ion distribution and partitioning in barley

between the cultivar Maythorpe and its derived mutant Golden Promise. *Plant and Soil* **250**: 183–191.

Whittington J, Bisson MA. 1994. Na$^+$ fluxes in Chara under salt stress. *Journal of Experimental Botany* **45**: 657–665.

Witte C-P. 2011. Urea metabolism in plants. *Plant Science* **180**: 431–438.

Wyn Jones R, Pollard A. 1983. Proteins, enzymes and inorganic ions. In: *Encyclopedia of plant physiology. New series.* New York, NY, USA: Springer.

Xu B, Waters S, Byrt CS, Plett D, Tyerman SD, Tester M, Munns R, Hrmova M, Gilliham M. 2018. Structural1 variations in wheat HKT1; 5 underpin differences in Na$^+$ transport capacity. *Cellular and Molecular Life Sciences* **75**: 1133–1144.

Xu C, Lu P, Gamal El-Din TM, Pei XY, Johnson MC, Uyeda A, Bick MJ, Xu Q, Jiang D, Bai H. 2020. Computational design of transmembrane pores. *Nature* **585**: 129–134.

Xu J, Li H-D, Chen L-Q, Wang Y, Liu L-L, He L, Wu W-H. 2006. A protein kinase, interacting with two calcineurin B-like proteins, regulates K$^+$ transporter AKT1 in Arabidopsis. *Cell* **125**: 1347–1360.

Yadav NS, Shukla PS, Jha A, Agarwal PK, Jha B. 2012. The SbSOS1 gene from the extreme halophyte *Salicornia brachiata* enhances Na$^+$ loading in xylem and confers salt tolerance in transgenic tobacco. *BMC Plant Biology* **12**: 1–18.

Yamaji N, Chiba Y, Mitani-Ueno N, Feng Ma J. 2012. Functional characterization of a silicon transporter gene implicated in silicon distribution in barley. *Plant Physiology* **160**: 1491–1497.

Yamaji N, Mitatni N, Ma JF. 2008. A transporter regulating silicon distribution in rice shoots. *Plant Cell* **20**: 1381–1389.

Yamaji N, Takemoto Y, Miyaji T, Mitani-Ueno N, Yoshida KT, Ma JF. 2017. Reducing phosphorus accumulation in rice grains with an impaired transporter in the node. *Nature* **541**: 92–95.

Yáñez-Mó M, Siljander PR-M, Andreu Z, Bedina Zavec A, Borràs FE, Buzas EI, Buzas K, Casal E, Cappello F, Carvalho J. 2015. Biological properties of extracellular vesicles and their physiological functions. *Journal of Extracellular Vesicles* **4**: 27066.

Yang J, Torres M, McManus J, Algeo TJ, Hakala JA, Verba C. 2017. Controls on rare earth element distributions in ancient organic-rich sedimentary sequences: role of post-depositional diagenesis of phosphorus phases. *Chemical Geology* **466**: 533–544.

Yang M, Lu K, Zhao F-J, Xie W, Ramakrishna P, Wang G, Du Q, Liang L, Sun C, Zhao H. 2018. Genome-wide association studies reveal the genetic basis of ionomic variation in rice. *Plant Cell* **30**: 2720–2740.

Yang Q, Chen Z-Z, Zhou X-F, Yin H-B, Li X, Xin X-F, Hong X-H, Zhu J-K, Gong Z. 2009. Overexpression of SOS (salt overly sensitive) genes increases salt tolerance in transgenic Arabidopsis. *Molecular Plant* **2**: 22–31.

Yang X, Feng Y, He Z, Stoffella PJ. 2005. Molecular mechanisms of heavy metal hyperaccumulation and phytoremediation. *Journal of Trace Elements in Medicine and Biology* **18**: 339–353.

Yang Z, Yang J, Wang Y, Wang F, Mao W, He Q, Xu J, Wu Z, Mao C. 2020. PROTEIN PHOSPHATASE95 regulates phosphate homeostasis by affecting phosphate transporter trafficking in rice. *Plant Cell* **32**: 740–757.

Yılmaz H, Özkan M. 2022. Micropollutant removal capacity and stability of aquaporin incorporated biomimetic thin-film composite membranes. *Biotechnology Reports* **35**: e00745.

Yuan F, Leng B, Wang B. 2016. Progress in studying salt secretion from the salt glands in recretohalophytes: how do plants secrete salt? *Frontiers in Plant Science* **7**: 977.

Yue Y, Zhang M, Zhang J, Duan L, Li Z. 2012. SOS1 gene overexpression increased salt tolerance in transgenic tobacco by maintaining a higher K$^+$/Na$^+$ ratio. *Journal of Plant Physiology* **169**: 255–261.

Zhang L, Gao C, Chen C, Zhang W, Huang X-Y, Zhao F-J. 2020. Overexpression of rice OsHMA3 in wheat greatly decreases cadmium accumulation in wheat grains. *Environmental Science & Technology* **54**: 10100–10108.

Zhang M, Liang X, Wang L, Cao Y, Song W, Shi J, Lai J, Jiang C. 2019. A HAK family Na$^+$ transporter confers natural variation of salt tolerance in maize. *Nature Plants* **5**: 1297–1308.

Zhang R. 2020. Cooling effect and control factors of common shrubs on the urban heat Island effect in a southern city in China. *Scientific Reports* **10**: 17317.

Zhang X, Guo W, Zhou L, Xu Q, Min Y. 2021. Surface-modified boron nitride as a filler to achieve high thermal stability of polymer solid-state lithium-metal batteries. *Journal of Materials Chemistry A* **9**: 20530–20543.

Zhang Z, Huang X, Qian Y, Chen W, Wen L, Jiang L. 2020. Engineering smart nanofluidic systems for artificial ion channels and ion pumps: from single-pore to multichannel membranes. *Advanced Materials* **32**: 1904351.

Zhao FJ, Ma JF, Meharg A, McGrath S. 2009. Arsenic uptake and metabolism in plants. *New Phytologist* **181**: 777–794.

Zhao XQ, Mitani N, Yamaji N, Shen RF, Ma JF. 2010. Involvement of silicon influx transporter OsNIP2; 1 in selenite uptake in rice. *Plant Physiology* **153**: 1871–1877.

Zhao Y, Qiu C, Li X, Vararattanavech A, Shen W, Torres J, Helix-Nielsen C, Wang R, Hu X, Fane AG. 2012. Synthesis of robust and high-performance aquaporin-based biomimetic membranes by interfacial polymerization-membrane preparation and RO performance characterization. *Journal of Membrane Science* **423**: 422–428.

Zhenyan H. 2022. Characterization of a novel arsenite long-distance transporter from arsenic hyperaccumulator fern *Pteris vittata*. *New Phytologist* **233**: 2488–2502.

Zhou X, Li J, Wang Y, Liang X, Zhang M, Lu M, Guo Y, Qin F, Jiang C. 2022. The classical SOS pathway confers natural variation of salt tolerance in maize. *New Phytologist* **236**: 479–494.

Zubair M, Shakir M, Ali Q, Rani N, Fatima N, Farooq S, Shafiq S, Kanwal N, Ali F, Nasir IA. 2016. Rhizobacteria and phytoremediation of heavy metals. *Environmental Technology Reviews* **5**: 112–119.