Mineral Uptake

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Glossary

Active transport Transport of an ion or solute against its electrochemical potential gradient.
Apoplast The extracellular space in plant tissues.
Casparian strip The hydrophobic barrier in the cell walls of the root endodermis.
Cortex The layers of cells between the root epidermis and the stele.
Cytosol The soluble part of the cytoplasm.
Electrochemical potential Measure of the free energy of an ion or solute in a particular location.
Endodermis The single layer of cells surrounding the stele and separating it from the cortex.
Epidermis The outer cell layer of roots.
H^+ antiporter A cotransporter that couples movement of H^+ down their electrochemical potential gradient to the active transport of an ion or solute in the opposite direction across the membrane.
H^+-coupled cotransporters Transporters that couple the active transport of an ion or compound to the transport of H^+ down their electrochemical potential gradient.
H^+ symporter A cotransporter that couples movement of H^+ down their electrochemical potential gradient to the active transport of an ion or solute in the same direction across the membrane.
Ion channels Regulated protein pores that span membranes and allow passive transport of ions down their electrochemical potential gradients.
Membrane potential Voltage difference across a membrane.
MicroRNA A small noncoding RNA molecule that functions in transcriptional and posttranscriptional regulation of gene expression.
Mycorrhizae Specialized fungi that grow in symbiotic relationships with plant roots.
Passive transport Transport of an ion or solute down the electrochemical potential gradient.
Plasmodesmata Regulated pores that cross cell walls and link the cytoplasms of adjacent cells.
Proteoid roots Cluster of rootlets formed on the main root axes of some species as an adaptation to P or Fe deficiencies.
Reactive oxygen species Chemically reactive molecules containing oxygen.
Rectification The ability of an ion channel to permit transport of ions only in one direction.
Root hairs Tubular outgrowths of root epidermal cells.
Stele The central tissues of the root.
Symplast Linked cytoplasms of adjacent cells, connected by plasmodesmata.
Thermodynamic activity The 'effective' concentration of an ion or molecule in a solution. It is usually lower than the total concentration because of binding or other interactions that occur in the solution.
Xylem The long-distance transport pathway responsible for delivering water and nutrients to the shoot.

Essential Nutrients

In pest- and disease-free conditions with adequate light and water, the growth of plants is determined by the availability of mineral nutrient ions and the ability of roots to capture them. Nutrients are usually taken up by roots as ions. Without these essential nutrients, plants cannot complete their life cycle. Some nutrients (e.g., N, P, and K) are needed in large amounts (macronutrients), whereas others (e.g., Zn, Fe, Co) are required in only trace quantities (micronutrients) (see Table 1).

The concentrations of the mineral elements in plants do not reflect those in the soil because roots selectively absorb nutrients. For instance, Ca and Mg may be present in the soil solution at higher concentrations than K, but the reverse is usually found in plants. Plants grow best when the concentrations of individual nutrients within their tissues fall within certain limits, thus avoiding growth-limiting deficiencies and toxicities. As any particular soil may not be able to supply all nutrients in optimal amounts, plants have evolved mechanisms to enhance the uptake of those that are poorly available. When roots fail to take up optimal amounts of nutrients, plants

Table 1 Essential mineral nutrient elements with typical concentrations in tissues

Element	*Chemical symbol*	*Concentration in plant dry matter (mg kg^{-1})*
Macronutrients		
Nitrogen	N	15 000
Potassium	K	10 000
Calcium	Ca	5000
Magnesium	Mg	2000
Phosphorus	P	2000
Sulfur	S	1000
Micronutrients		
Chlorine	Cl	100
Iron	Fe	100
Manganese	Mn	50
Zinc	Zn	20
Boron	B	20
Copper	Cu	6
Nickel	Ni	0.1
Molybdenum	Mo	0.1

show a range of symptoms including poorer growth, tissue senescence, and, eventually, death.

Root Structure and Delivery of Nutrients to the Shoot

Roots are highly branched. This maximizes their surface area for nutrient absorption and enhances their ability to explore the soil for new sources of nutrients. The structure of the root (see Figure 1(a)) is key to understanding the transport processes that govern the movement of nutrients from the soil solution to the shoot. The epidermis and cortex are the major sites of nutrient and water uptake, while the cell layers of the stele are responsible for loading of nutrients into the xylem vessels for delivery to the shoot. The xylem vessels are hollow pipes connecting the roots with the aerial tissues. Transport up the xylem is by mass flow of solution driven by the transpiration of water from the leaves. The stele is surrounded by the endodermis, which has the hydrophobic Casparian strip in its cell wall. Cells within the roots are linked by plasmodesmata that cross the cell walls and connect the cytoplasms of neighboring cells. Plasmodesmata have a complex

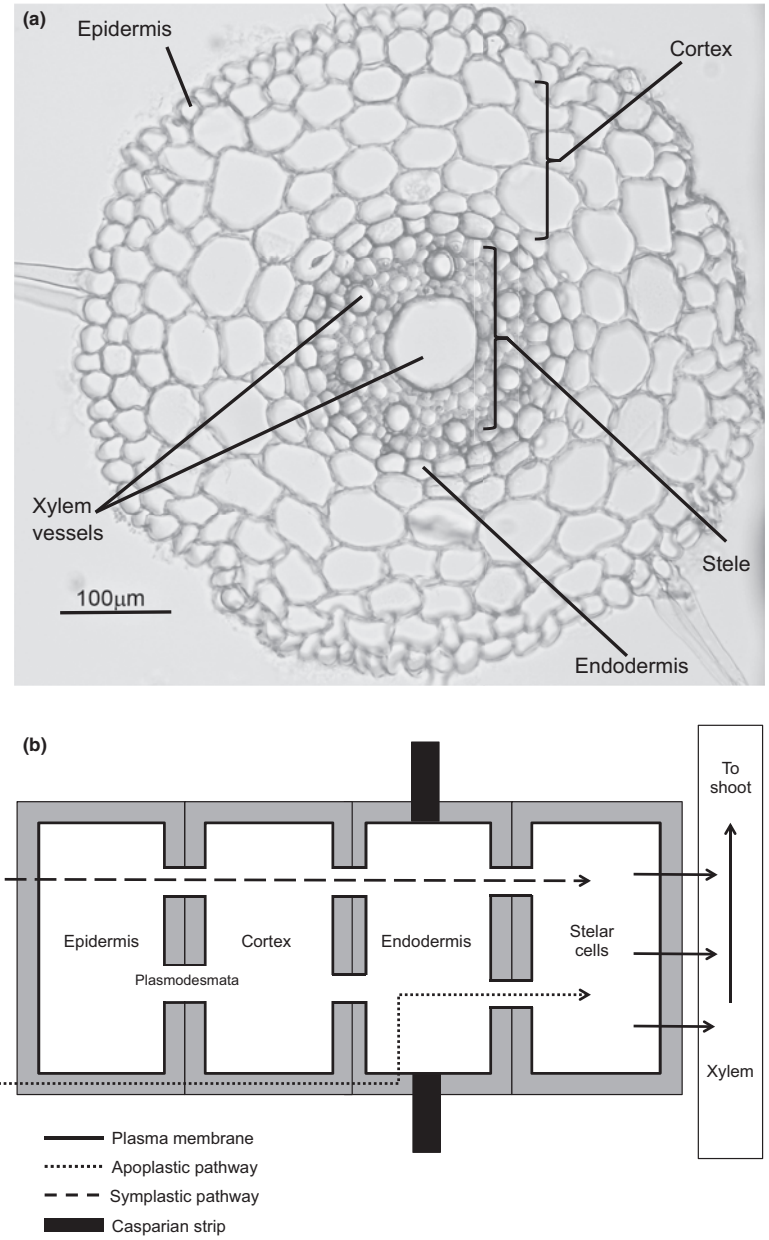

Figure 1 Spatial relationships between different cell types in a root. (a) Cross-section of a wheat root showing the main cell types. (b) Pathways to the stele via the apoplastic (dotted line) and symplastic (dashed line) pathways. The Casparian strip blocks the apoplastic pathway at the endodermis and ions must enter the endodermal cells to reach the stele and xylem vessels. Wheat root cross-section courtesy of Asmini Athman and Matthew Gilliham (University of Adelaide).

internal structure and are regulated transport pathways between cells.

Nutrient ions moving from the soil solution to the root xylem vessels can reach the endodermis by two different routes called the apoplastic and symplastic pathways (see Figure 1(b)). In the apoplastic pathway, ions move through the cell walls (apoplast) of the epidermal and cortical cells without entering a cell. This part of the apoplastic pathway is not particularly ion selective. The apoplast is blocked by the casparian strip, so to enter the stele, ions must cross the plasma membrane of the endodermal cells. An exception to this uptake step occurs in locations where the casparian strip is not present (e.g., root apices) or is disrupted (e.g., where lateral roots form). In the symplastic pathway, ions are taken up into epidermal or cortical cells and move to the stele through the symplast, the system of plasmodesmatally linked cytoplasms. In the main part of the root with a functioning casparian strip, any nutrient that is to be delivered to the stele has to be transported into a cell at some point, in the epidermis, cortex, or endodermis. From the stele, ions are exported out of the cells into the xylem vessels. Hence there are at least two membrane transport processes, one an uptake step and the other an efflux, involved in delivering ions from the soil to the xylem. It is at these points that ion selectivity occurs because the transport proteins in the cell membranes determine which ions are taken up or exported. Root cells may add to the selectivity by retaining some nutrients for their own needs.

Active and Passive Uptake into Roots

For macronutrients, the concentration dependence of their uptake by roots suggests at least two distinct kinetic mechanisms. One operates at low external concentrations (typically below 1 mmol l^{-1}), and the other at higher (>1 mmol l^{-1}). For K^+, at the lower concentrations, uptake is highly selective for K^+ (System 1), whereas at the higher external concentrations, a low affinity mechanism (System 2) operates, which does not discriminate strongly between K^+ and Na^+. These properties suggest that at least two distinct transport processes, with different K^+ and Na^+ selectivities, are operating in K^+ uptake into roots. Similar low- and high-affinity systems also operate for other nutrients.

Root cells usually contain higher concentrations of nutrients than the solution surrounding them. For instance, the roots of barley grown in 1 mmol l^{-1} K^+ contain around 100 mmol l^{-1} K^+. Although this indicates that uptake is against a concentration gradient, defining if this needs the direct input of metabolic energy requires a determination of whether transport is thermodynamically 'downhill' (passive) or 'uphill' (active). Only the latter requires the direct input of energy. Making this assessment requires measurement of an ion's electrochemical potential gradient across the cell's plasma membrane. This is a measure of the difference in free energy between the pools of ions outside and inside a cell. Ions move passively from regions where they have a high electrochemical potential to regions where they have a low electrochemical potential; energy input is required if movement is in the opposite direction. If there is no difference in electrochemical potential, there is thermodynamic equilibrium.

To determine the electrochemical potential gradient of an ion, it is necessary to measure both the voltage difference (membrane potential) between the inside of the cell and the external solution and the thermodynamic activities of the ion in both these locations. Typically, plant cells have a membrane potential of −80 to −150 mV (negative inside the cell with respect to outside) and this provides a driving force for the uptake of cations or efflux of anions. At thermodynamic equilibrium, the membrane potential and thermodynamic activities of ions on each side of a membrane at 20 °C are related by the following equation derived by Walter Nernst, a 1920 Nobel Prize winner:

$$E = \frac{58}{z}\log_{10}\frac{a_o}{a_i}$$

where E is the membrane potential, z is the valency of the ion, and a_o and a_i are the ion's thermodynamic activity outside and inside the cell, respectively. As thermodynamic activities are difficult to measure, most studies use concentrations (i.e., c_o and c_i), although this can lead to inaccuracies at high (>100 mmol l^{-1}) concentrations where values of activities and concentrations diverge. What the Nernst equation shows is that at thermodynamic equilibrium at 20 °C, a membrane potential of −58 mV can be balanced by a 10-fold higher concentration of a monovalent cation (e.g., K^+) in the cell, or a 10-fold lower internal concentration of a monovalent anion (e.g., Cl^- or NO_3^-). For divalent ions (e.g., Ca^{2+} or SO_4^{2-}), a membrane potential of only −29 mV is needed to achieve the same differences in concentration. Hence, simply comparing concentrations inside and outside a cell without knowing the membrane potential does not allow an assessment of the need for active or passive transport.

In hydroponic experiments, the external concentration of an ion is known. The membrane potential can be determined by inserting a voltage-measuring microelectrode into the cell, while internal concentrations can be accurately measured with ion-selective microelectrodes containing a sensor that responds to the concentration of the ion of interest. Such studies for K^+ have shown that uptake in the range of System 1 is active, whereas uptake by System 2 is passive. This is also true for other monovalent cations such as NH_4^+, whereas divalent cations such as Ca^{2+} and Zn^{2+} can usually enter passively even at low external concentrations. Active transport is usually required for uptake of anions such as NO_3^-, SO_4^{2-}, and $H_2PO_4^-$. Table 2 gives a summary of the need for active

Table 2 Role of active and passive uptake in the acquisition of a selection of essential macronutrient ions by plants

Ion	*External concentration (mol l^{-1})*	*Active or passive uptake*	*Probable mechanism*
K^+	<1	Active	H^+ symporter
K^+	>1	Passive	Ion channel
NH_4^+	<0.2	Active	H^+ symporter
NH_4^+	>1	Passive	Ion channel
Ca^{2+}	Most concentrations	Passive	Ion channel
NO_3^-	Most concentrations	Active	H^+ symporter
$H_2PO_4^-$	Most concentrations	Active	H^+ symporter
SO_4^{2-}	Most concentrations	Active	H^+ symporter

and passive transport in the uptake of different macronutrient ions at different external concentrations and the type of transporters that are responsible. For some ions, e.g., Na^+ and Ca^{2+}, their concentrations in plants are much lower than expected from the Nernst equation and active extrusion must be occurring.

Measurement of the electrochemical gradients for K^+ and Cl^- between cells across the root and the xylem vessels has shown that export of these ions into the xylem is energetically downhill. However, for divalent cations such as Ca^{2+} and Zn^{2+}, the electrochemical potential gradients indicate that transport into the xylem must be active. Relatively little is known about the transport processes operating in the stelar cells. Studies of isolated stelar cells have shown that they possess outwardly directed K^+ transporters, as expected if they play a role in the loading of K^+ into the xylem. Transporters for other nutrient ions, including NO_3^-, $H_2PO_4^-$, SO_4^{2-}, and Zn^{2+}, are also present (see section Molecular Identities of Root Ion Transporters).

Energization and Mechanisms of Transport

The physiological principles underlying active and passive ion transport in plants are now understood. Transport at the plasma membrane is energized by an adenosine triphosphate (ATP)–dependent H^+ pump (H^+-ATPase) that catalyzes the outward active transport of H^+. This creates a negative membrane potential and a pH gradient across the plasma membrane (see Figure 2). These differences in voltage and pH drive the uptake of ions through ion channels and H^+-coupled cotransporters.

Ion channels are protein pores that mediate passive transport of ions across membranes. Some channels will only open under conditions that permit transport in one direction (they are said to show rectification). Some ion channels are very selective and transport only particular ions (e.g., K^+ or Ca^{2+}), whereas others are relatively nonselective. However, all ion channels are characterized by very high rates of transport (10^6 to 10^8 ions s^{-1}), which is sufficient to flood or deplete a cell of ions in a very short time. Therefore, ion channels are highly regulated and open only at particular membrane potentials (voltage-gated channels), in the presence of certain chemical effectors (ligand-gated channels), or when phosphorylated.

In root epidermal and cortical cells, K^+ uptake within the range of System 2 is mediated by voltage-gated, K^+-selective channels that permit only inward transport of K^+. Other K^+-permeable channels, such as nonselective cation channels, are also present in roots but their significance in overall K^+ uptake is unknown. Many other channel types have been detected in plants with involvement in the uptake of Ca^{2+}, Zn^{2+}, and Fe^{2+}, and influx or efflux of anions.

Active transport of most ions is mediated by H^+-coupled cotransporters that use the electrochemical H^+ gradient across the plasma membrane to drive the influx or efflux of the ion. Active uptake processes at the plasma membrane are catalyzed by H^+ symporters (H^+ and the ion both move into the cell), whereas active efflux involves H^+ antiporters (H^+ moves in as the ion moves out). Physiological experiments have provided evidence to support the involvement of H^+-coupled cotransporters in the active uptake of K^+, NO_3^-, $H_2PO_4^-$, and Cl^-, and the efflux of Na^+.

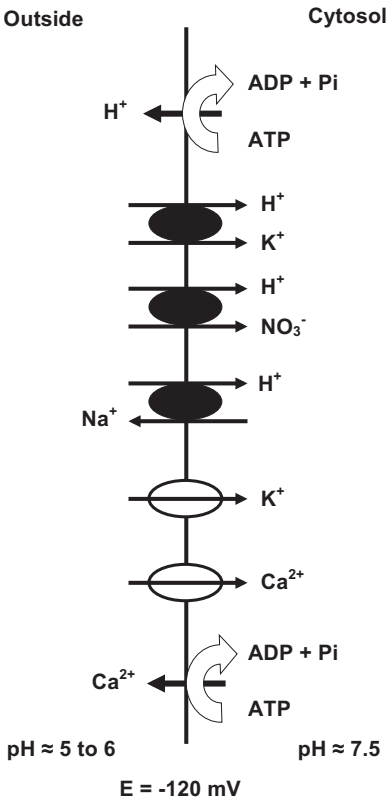

Figure 2 Role of ATP-dependent pumps, H^+-coupled cotransporters, and ion channels in the uptake of some macronutrients at the plasma membrane. The ATP-dependent H^+ pump actively transports H^+ out of the cell and generates a pH gradient and membrane potential across the plasma membrane. These H^+ and electrical gradients are then used to drive the uptake of the other ions either actively via H^+ symporters (e.g., for NO_3^-), or passively through ion channels (e.g., K^+ or Ca^{2+}). Some ions such as Ca^{2+} and Na^+ are at much lower internal concentrations than expected from the Nernst equation and are actively extruded by H^+ antiporters (Na^+) or ATP-dependent pumps (Ca^{2+}). The values of pH and membrane potential (E) are only indicative and may vary considerably with time and environmental conditions.

Hydrolysis of ATP is also directly coupled to the transport of Ca^{2+} out of the cytosol. The concentration of cytosolic free Ca^{2+} is kept very low (below 1 μmol l^{-1}) because it is important in intracellular signaling, with rises in its concentration triggering a range of responses. At typical membrane potentials and prevailing external Ca^{2+} concentrations, there is a massive driving force for the passive uptake of Ca^{2+} across the plasma membrane. There is insufficient energy in the H^+ electrochemical potential gradient for H^+-coupled Ca^{2+} antiporters to maintain a low cytosolic Ca^{2+} concentration. Therefore, ATP-dependent Ca^{2+} pumps (Ca^{2+}-ATPases) operate to transport Ca^{2+} out of the cytosol. There are also heavy metal–ion dependent ATPases (HMAs) that play roles in the transport of micronutrients such as Zn^{2+} and Cu^{2+}, especially between tissues and cellular compartments.

Molecular Identities of Root Ion Transporters

The identification of the proteins responsible for active and passive uptake of ions has progressed rapidly through the use of the yeast, *Saccharomyces cerevisiae*, and other systems to clone genes and characterize their products, and from the analysis of plant genomes. These approaches have shown that plant ion transporters are encoded by large multigene families. Thus any single ion may have multiple proteins involved in its transport. For instance, there are 11 plasma membrane H^+-ATPase genes in *Arabidopsis* and 10 in rice, whereas *Arabidopsis* has 150 genes for cation transporters of which 35 are putative K^+ transporters. There are also multiple genes encoding NO_3^-, NH_4^+, $H_2PO_4^-$, and SO_4^{2-} transporters. For instance, *Arabidopsis* has 14 putative SO_4^{2-} transporters. The cellular location and roles of all the gene products have not yet been completely resolved for any transporter gene family. Thus, of 73 putative nitrate transporters genes in *Arabidopsis*, only 35 have been studied in detail, with 24 confirmed as nitrate transporters. Characterizing the many ion transporters remains a major challenge and is highlighted by attempts to identify genes encoding K^+ transporters.

A number of plant K^+ transporters have been identified by their ability to restore growth of a K^+ transport–deficient yeast mutant under low K^+ conditions. *Arabidopsis* root K^+ transporters identified in this way include AKT1 (an inward voltage-gated K^+ channel), GORK (an outward voltage-gated K^+ channel), SKOR (an outward voltage-gated K^+ channel), members of the HKT family (initially identified as high-affinity K^+ transporters), and members of the KT/KUP/HAK family (relatives of fungal and bacterial H^+:K^+ symporters).

Both AKT1 and SKOR have six membrane-spanning domains (S1–S6), a preponderance of positive charges in S4, considered a voltage-sensing domain, and a hydrophilic region (P-domain) between S4 and S5 that forms part of the ion-conducting pore that determines K^+ selectivity. Despite the structural similarities between AKT1 and SKOR, they transport K^+ in opposite directions, with AKT1 catalyzing uptake and SKOR catalyzing efflux. Thus physiological function cannot be inferred from structure. Localization studies for AKT1 and SKOR have shown that they are expressed in different parts of the root; AKT1 is expressed in epidermal and cortical cells, whereas SKOR is localized in stelar cells. Thus AKT1 provides a route for K^+ uptake and SKOR a pathway for export into the xylem vessels. These functions have been confirmed using *Arabidopsis* mutants with disrupted *AKT1* and *SKOR* genes.

TaHKT2;1 (formerly *TaHKT1*) was first cloned from bread wheat (*Triticum aestivum*) but related genes are present in other plants. Depending on the gene and plant, those in roots are expressed in epidermal, cortical, or stelar cells. The gene product of *TaHKT2:1* was initially characterized as a H^+:K^+ symporter mediating high-affinity active K^+ transport in roots. However, it is now considered a Na^+:K^+ symporter at low external concentrations and mediating just Na^+ transport at higher concentrations. The physiological importance of Na^+-coupled K^+ transport in plants remains unresolved, so the role of HKT proteins in this phenomenon *in planta* has not been confirmed. Other *HKT* genes may be important in Na^+ retrieval from the xylem in roots. This limits Na^+ transport to leaf tissues and helps confer salinity tolerance.

The KT/KUP/HAK proteins form a family of related K^+ transporters with 13 members in *Arabidopsis* and 25 in rice. These proteins have 10 to 14 membrane-spanning domains, and some have a long cytosolic C-terminal domain. The *Arabidopsis HAK5* gene is expressed in roots and its gene product has been shown to mediate high-affinity K^+ transport. Disruption of the *HAK5* gene decreases K^+ uptake by roots in the concentration range of System 1. Other KT/KUP/HAK family members are low- or dual-affinity K^+ transporters.

How K^+ uptake is partitioned between different transporters remains unclear. An explanation that assigns active transport by System 1 to HAK transporters and passive transport by System 2 to ion channels such as AKT1 is supported by calculations that show that HAK5 and AKT1 can account for about 80% of K^+ uptake into *Arabidopsis* roots. However, this simple model is questionable because an *Arabidopsis* mutant lacking a functional *AKT1* gene was found to be compromised in K^+ uptake at 10 μmol l^{-1} external K^+, well below the concentration range for System 2. This was because the root cells in the mutant had very negative membrane potentials and this provided a sufficient driving force for passive K^+ uptake from this low external K^+ concentration.

The identity of proteins responsible for transport from the stele to the xylem vessels is emerging in *Arabidopsis*. SKOR fulfills this role for K^+ and NRT1.5 for nitrate. There are also two stelar transporters identified for $H_2PO_4^-$ and three for SO_4^{2-}. Zinc transport to the xylem in *Arabidopsis* is catalyzed by HMA2 and HMA4, and disruption of the *HMA4* gene in *Arabidopsis halleri*, a Zn hyperaccumulator, decreases Zn concentration in the xylem.

Regulation of Nutrient Uptake

Nutrient acquisition and uptake are regulated to optimize the capture of nutrients needed for growth and reproduction. Under nutrient-deficient conditions, the root:shoot ratio increases to enhance soil exploration and nutrient uptake. When a root system encounters a nutrient-rich patch, lateral roots proliferate to ensure exploitation of the resource. In Arabidopsis, the rate of lateral root elongation in response to localized nitrate is controlled by direct sensing of the nitrate and involves a signaling pathway that depends on the *ANR1* and *AXR4* genes. The nitrogen status of the shoot is also important in controlling root proliferation and may be signaled by long-distance transport of shoot-derived amino acids to the roots. Glutamate is considered a good candidate for the signaling molecule but this has not been proven definitively.

Root hairs and associations with arbuscular mycorrhizal fungi increase the volume of soil exploited around each root, making nutrients with low soil mobilities, such as P and Zn, more accessible. Some species, e.g., lupin, form the so-called proteoid roots when they are deficient in P and/or Fe. These are clusters of small rootlets that grow from the main root axis and secrete citric acid and other chemicals to increase the solubility of P and Fe.

Acquisition of Fe is a major problem for the majority of plants because it is often present in the soil solution at concentrations below those needed to support adequate growth. Therefore, plants have evolved special mechanisms for increasing its

availability. In most species, growth in Fe-deficient conditions results in enhanced acidification of the soil, the secretion of reductants, and an increase in the activity of a reduced form of nicotinamide adenine dinucleotide phosphate (NAD(P)H)–dependent Fe^{3+} reductase in the plasma membrane. Collectively, these increase the solubility of soil Fe^{3+} and the reductase reduces it to Fe^{2+}, which is then taken up through an Fe^{2+}-permeable channel. In grasses, a different mechanism operates involving secretion of specialized Fe^{3+} chelators, phytosiderophores. These are able to solubilize and chelate insoluble Fe^{3+} and deliver it to the root surface where the Fe^{3+}-phytosiderophore complex is taken up.

Increased expression of ion transporter genes are a common response to lack of nutrients. Thus under K-, S-, or P-deficient conditions, the uptake rates of K^+, SO_4^{2-}, and $H_2PO_4^-$ are increased, respectively. At the physiological level these effects appear specific, so lack of S only increases the uptake of SO_4^{2-}. However, at the molecular level, the deprivation of a single nutrient can cause changes in the expression of transporter genes for other nutrients so the specificity is not so clear at this level. The enhanced expression is reversed once the plant reaches sufficiency in a particular nutrient.

All the changes whether they are rapid (transporter gene expression) or longer term (root proliferation) involve signaling systems that sense the need for change and evoke the required response. The signaling pathways are complex and involve many players including but not limited to changes in membrane potential; sensing of soil, root, and shoot ion levels; metabolites; hormones; reactive oxygen species; and long-distance transport of microRNAs. The end result is changes in gene expression that modify the suite of transporters in a cell membrane or reprogram root or shoot development. In some cases, post-translational modification of transporters (e.g., by phosphorylation) to alter their activity may be the end result. Some of the signaling components are common to several nutrients, so other members of the signaling pathway must ensure the outcome is the one needed for a particular nutrient.

Concluding Remarks

The uptake of nutrients is fundamental to the growth of plants and influences their ecological competitiveness and their agricultural productivity. In addition, plants are the major entry point for nutrients into food chains, so the uptake processes in roots are of fundamental importance to the health of humans and other animals. Despite their simple morphology, roots are highly sophisticated organs that can adapt their structure, gene expression, and biochemistry to modify their environment and optimize nutrient uptake. In the future, the challenge is to modify root processes to enhance fertilizer use efficiency and to ensure that plants can meet dietary needs through more nutritious crops.

See also: **Physiology:** Xylem. **Plant Nutrition:** Deficiency Diseases, Principles; Growth and Function of Root Systems; Ion Transport.

Further Reading

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