Plant Nutrition 1: Membrane transport and energetics, potassium nutrition, and sodium toxicity – Teaching Guide

Overview - Plant nutrition concerns: 1) the availability of nutrients in the soil along with the effects of soil microbes on their availability, 2) nutrient uptake from the external environment, across plasma membranes and into plant cells, 3) in some cases, the assimilation of the nutrient into organic molecules, 4) the distribution and redistribution of nutrients throughout the plant, and 5) homeostatic regulation of these processes. In this first of three lessons spanning the topic of Plant Nutrition, we examine primarily the energetics and mechanisms of nutrient uptake and transport. These processes are particularly well illustrated by an examination of the essential nutrient potassium (K), and the closely related element sodium (Na). We also examine the challenges associated with providing plants with sufficient K to support vigorous growth, and the detrimental effects of sodium accumulation in soils. Finally, we examine efforts to improve the salinity tolerance of crop plants.

Learning objectives
By the end of this lesson the student should be able to:

- Evaluate the energetic and kinetic properties of the three types of transport proteins: pumps, channels and carriers
- Summarize the role of proton pumps in plant nutrition
- Distinguish between a concentration gradient and an electrochemical gradient and identify circumstances in which the electrochemical gradient is more relevant
- Summarize the roles of potassium in plants
- Identify three factors that contribute to increasing soil salinity and three strategies to address the problems of soil salinity
- Outline the contributions of two different transporters to plant salinity tolerance

Study / exam questions (understanding and comprehension)

- Compare and contrast a pump, channel and carrier.
- What is the primary electrogenic plant plasma membrane pump?
- Protons are usually more abundant in which: the cytoplasm or the apoplast?
- Explain how the electrochemical gradient determines the movement of ions across membranes.
- Genes encoding PM-H⁺-ATPases are expressed particularly highly in phloem companion cells and root epidermal cells – why?
- What are the roles of proton pumps that reside in endomembranes?
- K is an unusual essential element in that it does not form covalent bonds in the plant. Describe three essential functions of K.
- Why do farmers add potassium to soils?
• Draw a graph that illustrates biphasic potassium uptake at various concentrations of soil K+. What does the shape of this graph suggest about the mechanisms of potassium uptake?

• List four ways that plants exclude sodium from the cytoplasm of their cells.

• One of the reasons that soil salinity is a problem is because Na is physically similar to K. Explain what their positions in the periodic table tell us about these two elements.

• Describe three factors that are contributing to the increasing prevalence of saline soils.

• What are halophytes and how might they be important in developing plants with increased salinity tolerance?

• Summarize how high external Na+ promotes K+ efflux from root cells.

Discussion questions (engagement and connections)

• Plants have three major classes of proton pumps. How widespread are each of these families? What can you surmise about their evolutionary origins? Why do you think plants have so many types of proton pumps?

• Which proton pump is most similar to the ATP synthases found in plastids and mitochondria? In what ways are the different types of proton pumps found in plant cells similar and different?

• Explain the statement “low-affinity potassium channels consume the energy equivalent of pumping one proton”. In what way does the transport of K+ through a channel consume energy? (Hint – how does it affect the membrane potential?)

• Trace the flow of a potassium ion from the soil to the vacuole of a guard cell. What is the smallest number of membranes that must be crossed? Can you suggest candidates for the transporters involved in each stage of the ion’s journey?

• Ion channels are highly regulated. Choose one and learn what you can about its regulation by gene expression, post-translational modification, sensitivity to voltage or small molecules etc. How do these different forms of regulation support its function in the plant?

• In 2003, the Nobel Prize in Chemistry was awarded jointly to Roderick MacKinnon, who studied the structural and mechanistic selectivity of ion channels. Watch his Nobel Lecture and summarize our understanding of how an ion channel permits one but not another ion to traverse it (http://www.nobelprize.org/mediaplayer/index.php?id=550).
Increasingly, HKTs are being implicated as important contributors to salinity tolerance. How do different alleles affect salt tolerance – is the mechanism primarily gene copy number, gene expression level, ion selectivity or other? Here are a few papers to help you address these questions:


Compare and contrast how plants and animals are able to exclude or excrete sodium and so live in saline environments. Here’s an article that looks at both types of organisms:


Salt glands are important secretory organs for several halophytes and those in mangroves have been studied for many years. Thomson et al (1969) is a classic paper that describes their anatomy. Examine the micrographs and identify each of the subcellular structures. How does salt gland anatomy support its function? What do you think is the mechanism that moves the salt through the gland?

  You can read more about different mechanisms for dealing with leaf salt here: http://plantsinaction.science.uq.edu.au/edition1/?q=content/17-3-1-devices-manage-leaf-salt

Although tracheophytes do not produce sodium pumps (Na⁺-ATPases), these enzymes are present in other lineages including bryophytes. Recently, a Na⁺-ATPase identified from moss was introduced into rice plants (references below). If you were to design a salt-tolerant plant based on the de novo introduction of a Na⁺-ATPase, which cell types and membranes would you want to insert the pump into and why?

- Summarize the experiments that led to the identification of the wheat *Nax1* and *Nax2* genes. Explain how their gene products contribute to salinity tolerance.
Lecture synopsis

PLANT NUTRITION: INTRODUCTION (1 - 10)
Plants are autotrophs (self-feeders) that obtain most of their nutrients in the form of inorganic molecules, which they take up from their surroundings and assemble into organic compounds and macromolecules. C, H and O are assimilated from carbon dioxide and water. The remaining elements that make up a plant are often referred to as mineral elements and are usually assimilated from soil. As the plant extracts nutrients from the soil, it has to be replenished using animal manures or inorganic fertilizers. Fertilizers can be expensive and cause environmental and health problems, so they must be used efficiently and sensibly.

NUTRIENT UPTAKE AND TRANSPORT: OVERVIEW (11 - 23)
Plants usually accumulate nutrients to levels much higher than in the surrounding soil, and this occurs through a process of active transport by way of specialized transport proteins which include pumps (ATPases), channels and transporters. Transport can be passive or active. A cell may expend 1/3 of its metabolic energy on transport. In animal cells, much of this is expended by the Na+/K+ ATPase that couples the transport of Na⁺, K⁺ and ATP hydrolysis. These activities occur separately in plants; much of the energy needed for nutrient uptake and transport comes from proton pumps, and Na⁺ and K⁺ are moved via several different families of transporters. Proton pumps are electrogenic in that they produce a charge gradient across the membrane as well as a proton gradient; these are combined together in what is described as an electrochemical gradient. The electrochemical gradient across a membrane is much like the energy stored in a battery; in both cases, the stored energy can be harnessed to drive some other reaction or do work, and the energy stores can be recharged again and again. The membrane potential ($E_m$) is a measure of the electrical potential energy stored across a membrane, and can be measured by measuring the difference in voltage between the inside of a cell and the solution surrounding it.

ENERGIZING THE MEMBRANE: PLANT H⁺-ATPASES AND H⁺-PPASES (24 - 41)
Plasma membrane proton ATPases (25 – 31)
Plasma membrane proton ATPases (PM H⁺-ATPases) have been described as “master enzymes” and “powerhouses for nutrient uptake”. These enzymes are essential for nutrient uptake as well as for many diverse plant functions, from active transport to cell elongation, osmoregulation and stomatal function. Plant PM H⁺-ATPases are part of a large family of P-type ATPases, all of which form a covalent enzyme-phosphate bond during the reaction cycle. As protons are pumped out, the inside of the membrane becomes more negatively charged relative to the outside. The pump action also produces a proton gradient (pH gradient) across the membrane, with the outer side being more acidic (pH often <5) than the inside (pH approximately 7.5). The resulting electrochemical gradients support transport of other solutes.

Vacuolar pumps: Vacuolar H⁺-ATPase and Vacuolar H⁺-PPase (32 – 40)
Two types of proton pumps are resident in the vacuolar or endomembranes, the vacuolar proton-ATPase (VH⁺-ATPase), which hydrolyzes ATP to provide the energy for proton pumping, and the vacuolar proton pyrophosphatase (H⁺-PPase), which hydrolyzes pyrophosphate as an energy source. VH⁺-ATPase is a large, multisubunit enzyme that shares its evolutionary roots with the F-ATPases found in prokaryotes, mitochondria and chloroplasts, and uses the same rotational catalysis mechanism. By establishing an
The electrochemical gradient across the membranes, the VH⁺-ATPase energizes endomembranes, maintains the correct pH of intracellular compartments, and is involved in regulating membrane trafficking. Phenotypes associated with decreased VH⁺-ATPase activity include decreased growth rate, male sterility, and altered nutrient storage capabilities.

The H⁺-PPase pump is formed as a monomer that is encoded by three genes. Increasing the expression level of AVP1 can lead to increased drought or salinity tolerance, increased phosphate accumulation, increased plant biomass, accelerated fruit ripening, among other effects, demonstrating the diverse and important roles of this type of proton pump.

SODIUM AND POTASSIUM – THE “TWINS” (42)
Sodium and potassium are both monovalent cation forming alkali metals in the same column of the periodic table. However, potassium is one of the most essential elements for plant nutrition, whereas at elevated levels sodium is toxic. As we show, potassium’s essentiality is due mainly to its ability to act as an osmotic agent, charge balance and enzyme cofactor, whereas in most cases sodium’s toxicity is due to its similarity but inability to substitute for potassium.

POTASSIUM UPTAKE, TRANSPORT AND HOMEOSTASIS (43 – 63)
Potassium reserves (44 – 46)
Potassium is mined from deep underground deposits. It is present in several compounds that are collectively called “potash”. Almost half of the global reserve of potash is found in a single deposit in the Canadian province of Saskatchewan. As there is no substitute for potassium in plant or animal cells, global food production relies on the continual mining and distributing of potash.

Potassium is an essential macronutrient (47)
Potassium is an essential nutrient in plants and in all living cells, and it is not incorporated into other molecules but instead functions as an unconjugated ion. It has essential roles in water and ionic balance, but it also is a cofactor for some enzymes.

Potassium uptake (48 – 59)
Plants take up potassium from soils against a steep concentration gradient. Transport energy is supplied indirectly by the electrochemical gradient and can occur through channels or co-transporters. Classic studies by Epstein and colleagues identified a biphasic potassium uptake response that has different kinetic properties at low and high [K⁺]. When potassium is scarce, a high-affinity system is required for uptake, whereas when potassium is abundant, a low-affinity system is sufficient. To a first approximation, potassium / proton co-transporters such as HAK5 are involved in high-affinity transport, and potassium channels such as AKT1 are involved in low affinity uptake.

Potassium co-transporters (50)
All plant genomes studied to date contain KT/KUP/HAK genes encoding high-affinity potassium (HAK) transporters. HAK transporters are responsible for much of the high-affinity K⁺ uptake in roots. Other less-specific types of potassium transporters or putative transporters have been identified.

Potassium channels (51 – 57)
The low affinity K⁺ uptake system that dominates at high external potassium levels (1 mM and above) is generally assumed to occur through potassium channels. Plants have at least two families of multimeric potassium channels, the voltage-gated Shaker-type K⁺ channels
(Kv) and the voltage independent channels. Shaker channels were the first plant K+ channels identified at the molecular level, and are the best characterized of plant transporters. Shaker channels form as tetramers, and in both Arabidopsis and rice nine genes encode Shaker subunits. Using the Arabidopsis nomenclature, AKT1 and KAT1 are largely responsible for K+ influx, and SKOR and GORK for K+ efflux.

**Flux through Kv channels – voltage driven and voltage gated (53 - 57)**

Ion flux through Kv channels is voltage driven and voltage gated. Voltage driven means that when the channels are open, current flow and direction depend on the membrane voltage potential ($E_m$) relative to the equilibrium potential of potassium ($E_K$). Voltage gated means that the channels open and close in a voltage-sensitive manner. Many other factors contribute to the activity of potassium channels and transporters, and our understanding of these owes much to studies carried out on guard cells.

**Regulation of potassium transport: The guard cell model (58 – 59)**

Because guard cell function is to change size as they open and close the stomatal pore, their major metabolic activity involves moving ions in and out across the plasma and vacuolar membranes, in order to drive the osmotic flow of water and therefore alter cell turgor and size. Membrane currents, ion fluxes, pH and ion concentrations can be measured using microelectrodes and pH sensitive dyes, and genetic mutants and chemical inhibitors can be introduced to selectively disrupt some activities. As a result of countless studies, it is clear that the activities of ion channels and transporters and proton pumps are extensively coordinated through a network of interactions.

**Potassium homeostasis (59 – 61)**

When K+ is depleted from the environment surrounding a root, the membrane potential of the root epidermal cells becomes hyperpolarized because of a decrease in the depolarizing inward K+ flux. This depolarization increases the driving force for K+ uptake and also increases the conductance of voltage-gated inward-rectifying channels such as AKT1. Other responses to potassium deficiency include transcriptional changes, modifications in root growth pattern, and remobilization of potassium from older to younger tissues. The strategies of potassium homeostasis extend from single channels to the entire organism and from fractions of seconds to the lifespan of the plant.

**SODIUM TOXICITY, TRANSPORT, AND TOLERANCE (64 – 94)**

**The challenges of soil salinization (65 – 72)**

Soil salinity is a major problem for plants and plant growers. Globally, about 7% of the world’s land and about 30% of irrigated land is saline. Coastal lands acquire salt carried inland from waves, storms and mists, and through intrusion of seawater into coastal groundwater reserves. Inland, many agricultural lands lie over deep salt deposits that can rise towards the surface as a consequence of changing land use patterns. Most crop plants cannot grow in soils with significant levels of salt, and in some regions this is a substantial problem. Plant scientists examine how plants respond to salinity by studying halophytes (salt-tolerant plants) as well as glycophytes (salt-sensitive plants), and can apply this information to breed greater salinity tolerance into crop plants.

**Mechanisms of sodium toxicity and tolerance (73 – 82)**

Sodium toxicity is based on osmotic and ionic effects. Osmotic stress affects water potential and the plant’s ability to move water into and within the plant, and is not a specific effect of NaCl but rather a solute effect. Ionic stress affects the movement of ions and ionic homeostasis. Several lines of evidence indicate that a plant’s ability to tolerate salinity depends on its ability to exclude Na+ from the cytosol. Plants can accomplish this exclusion...
by: 1) not taking it up in the first place, 2) pumping out that which leaks in, 3) sequestering it in the vacuole, or 4) extruding it through salt glands or other structures.

**Ion pumps, channels and transporters contribute to Na⁺ tolerance (76 – 82)**

Sodium is only rarely taken up from the soil by active processes. The negative membrane potential of plant cells, exacerbated by the high external concentration of Na⁺ in saline soils, drives Na⁺ into cells through non-selective cation channels (NCSS) or through incompletely selective K⁺ channels. Much of the active transport of Na⁺ involves its removal from the cytoplasm, into the apoplast or the vacuole, or its removal from the transpirational stream to exclude it from the shoot.

HKT transporters contribute to Na⁺ transport. There is one HKT gene in Arabidopsis but multiple HKT genes in monocots that fall into two types that contribute to the removal of Na⁺ from the transpiration stream or assimilatory Na⁺ uptake under conditions of low K⁺.

A second important Na⁺ transport family encodes the NHXs (sodium / proton exchangers). The Arabidopsis genome encodes eight NHXs that accumulate in various membranes. NHX7 is also known as SOS1, which stands for salt-overly sensitive and was first identified as a loss-of-function mutant that is much more sensitive to NaCl. SOS1 sits in the plasma membrane and exports Na⁺ by exchanging it for H⁺, driven by the movement of protons down their concentration gradient across the plasma membrane.

What can we learn from halophytes and salt-tolerant plants? (83 – 87)

An estimated 1% of terrestrial plants are halophytes, which are often defined as plants that are able to complete their life cycle in >200 mM NaCl. Their presence in numerous families indicates that this ability has arisen independently multiple times. Even plants that are able to grow in the presence of high levels of external NaCl cannot tolerate elevated levels of cytosolic NaCl. Their tolerance lies in their ability to exclude, extrude or compartmentalize Na⁺ very efficiently.

Plants show a continuum of salinity tolerance, from very sensitive [such as chickpea (*Cicer arietinum*), some varieties of which die on 25 mM NaCl], to extreme halophytes such as *Salicornia* spp. that can tolerate 2 M NaCl and accumulate as much as 40% of their dry weight as NaCl. Several halophytes have been studied to uncover their mechanisms of salt tolerance, and others are being studied as possible food, fodder or fuel plants.

**Breeding and engineering for salt tolerance (88 –91)**

*Nax1* and *Nax2* were identified through gene mapping studies of a salt-tolerance trait in wheat, and found to encode HKT transporters that remove sodium from the xylem stream. When introgressed into durum or bread wheat, they confer enhanced salinity tolerance by excluding Na⁺ from the salt-sensitive leaf blade. The candidate gene approach has had some success but has proven to be a bit more difficult than expected. The most intensively pursued genes are those encoding vacuolar NHXs and H⁺-PPases, with the goal of eliminating Na⁺ from the cytoplasm through sequestration into the vacuole. Both types of genes have been shown to confer salinity tolerance in a variety of plant species, but as yet none of the transgenic plants are being grown commercially.

**The intersection of potassium nutrition and sodium toxicity (92 – 94)**

Up to this point, we have considered potassium and sodium as independent entities, but now we address their interactions. Potassium uptake is adversely affected by soil salinity, and salinity tolerance is somewhat mitigated by a plentiful supply of potassium. Na⁺ interferes with K⁺ uptake by depolarizing the plasma membrane (which interferes with K⁺ uptake by lowering the inward driving force, and by inactivating voltage-sensitive inward-rectifying potassium channels), and by activating outward rectifying potassium channels. Although we
have described salinity tolerance as being dependent on the exclusion of Na⁺ from the cytosol, it also can be described in some plants as the maintenance of a high ratio of K⁺ to Na⁺ in the cytosol, so mechanisms that promote K⁺ influx to the cytosol of cells in the shoot are likely to promote salinity tolerance. Whether you are particularly interested in potassium nutrition or sodium toxicity, it is important to remember that the activities of one impact the other, and that their transporters and homeostatic mechanisms cannot function in isolation.

SUMMARY AND ONGOING RESEARCH (95 - 96)
Nutrient uptake is one of the more energetically demanding suites of plant processes, which in plants is supported by proton gradients established by several types of proton pumps. In this lesson we have focused on the role of membrane pumps and transporters as well as the electrochemical gradient and membrane voltage on the uptake of nutrients, specifically examining how these elements affect K⁺ and Na⁺ uptake. Most plants require a high cytosolic ratio of K⁺ to Na⁺ and large amounts of potassium for optimal growth. Changing land use patterns as well as changing water use and rainfall patterns mean that many agricultural lands are becoming more saline with time, and in some cases have had to be abandoned.
<table>
<thead>
<tr>
<th>Slides</th>
<th>Table of contents – concepts</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><strong>Plant Nutrition 1: Membrane energetics and transport, potassium nutrition and sodium toxicity</strong></td>
</tr>
<tr>
<td>2</td>
<td>Outline</td>
</tr>
<tr>
<td>3</td>
<td><strong>Plant Nutrition: Introduction</strong> Plants are made from C, H and O (from carbon dioxide and water) and mineral nutrients: macronutrients (K, N, P, Ca, Mg, S) and micronutrients</td>
</tr>
<tr>
<td>4</td>
<td>Plants assimilate mineral nutrients from their surroundings</td>
</tr>
<tr>
<td>5</td>
<td>Nutrient uptake, assimilation and utilization involve many processes</td>
</tr>
<tr>
<td>6</td>
<td>Nutrients removed from soils can be replenished with fertilizers</td>
</tr>
<tr>
<td>7</td>
<td>Global mineral nutrient resources are unevenly distributed</td>
</tr>
<tr>
<td>8</td>
<td>The global trade in fertilizers is worth billions of dollars annually</td>
</tr>
<tr>
<td>9</td>
<td>How much is the right amount of fertilizer to apply to a field?</td>
</tr>
<tr>
<td>10</td>
<td>Fertilizer use can cause environmental and health problems</td>
</tr>
<tr>
<td>11</td>
<td><strong>Nutrient uptake and transport: Overview</strong></td>
</tr>
<tr>
<td>12</td>
<td>Plants assimilate mineral nutrients mainly as cations or anions</td>
</tr>
<tr>
<td>13</td>
<td>Nutrients are concentrated in the plant relative to the environment</td>
</tr>
<tr>
<td>14</td>
<td>Transport can be down or against an electrochemical gradient</td>
</tr>
<tr>
<td>15 - 17</td>
<td>Solutes cross membranes through different types of transporters: Pumps, channels and carriers / coupled transporters</td>
</tr>
<tr>
<td>18</td>
<td>Pumps, channels and carriers are also involved in nutrient distribution</td>
</tr>
<tr>
<td>19</td>
<td>Cells expend ATP to maintain high internal ([K^+]) and exclude (Na^+)</td>
</tr>
<tr>
<td>20</td>
<td>The membrane as a battery: Mitchell’s big idea</td>
</tr>
<tr>
<td>21</td>
<td>Plant cells have a membrane potential ((E_m)) -100 to -200 mV</td>
</tr>
<tr>
<td>22</td>
<td>The electrochemical gradient is important for ion transport</td>
</tr>
<tr>
<td>23</td>
<td><strong>Energizing the membrane requires energy and selective transporters</strong></td>
</tr>
<tr>
<td>24</td>
<td><strong>Energizing the membrane: Plant H⁺-ATPases and H⁺-PPases</strong></td>
</tr>
<tr>
<td>25</td>
<td>The PM H⁺-ATPase is a “master enzyme” and “powerhouse”</td>
</tr>
<tr>
<td>26</td>
<td>PM H⁺-ATPases were first characterized in fungi</td>
</tr>
<tr>
<td>27</td>
<td>Plant and fungal PM H⁺-ATPases are members of a larger family</td>
</tr>
<tr>
<td>28</td>
<td>Several differentially expressed genes encode plant PM H⁺-ATPases</td>
</tr>
<tr>
<td>29</td>
<td>PM H⁺-ATPase activity also is regulated post-transcriptionally</td>
</tr>
<tr>
<td>30</td>
<td>Plant PM H⁺-ATPase are essential for nutrient uptake and allocation</td>
</tr>
<tr>
<td>31</td>
<td>PM H⁺-ATPases have diverse physiological roles</td>
</tr>
<tr>
<td>32</td>
<td><strong>Vacuolar pumps pump protons into the vacuole and endocompartments</strong></td>
</tr>
<tr>
<td>33</td>
<td>The VH⁺-ATPase is a large multi-subunit enzyme</td>
</tr>
<tr>
<td>34</td>
<td>VH⁺-ATPases contribute to growth, salt tolerance &amp; ion uptake / storage</td>
</tr>
<tr>
<td>35</td>
<td>The VH⁺-ATPases have different roles in different compartments</td>
</tr>
<tr>
<td>36</td>
<td>VH⁺-ATPases have multiple functions in plants and animals</td>
</tr>
<tr>
<td>37</td>
<td>The vacuolar pyrophosphatase (H⁺-PPase) uses PP, as an energy source</td>
</tr>
<tr>
<td>38</td>
<td>Plants have 2 types of H⁺-PPases</td>
</tr>
<tr>
<td>39</td>
<td>Each H⁺-PPase subunit has 16 membrane spanning domains</td>
</tr>
<tr>
<td>40</td>
<td>H⁺-PPases have many physiological roles</td>
</tr>
<tr>
<td>41</td>
<td><strong>Energizing the membrane: Summary</strong></td>
</tr>
<tr>
<td>42</td>
<td>(K^+) and (Na^+) - “The twins”. So alike yet so different</td>
</tr>
</tbody>
</table>
43 **Potassium uptake, transport and homeostasis**

44 Potassium fertilizers are mined from underground reserves as “potash”

45 Potash provides K⁺ for fertilizers, which supplement natural sources

46 Potash prices can be volatile and there are few suppliers

47 **Potassium is an essential plant nutrient**

48 Early studies of potassium uptake in plants: Biphasic uptake

49 More energy must be expended to take up K⁺ when it is scarce

50 There are several types of coupled transporters for K⁺

51 There are 15 genes encoding potassium channels in Arabidopsis

52 Shaker channels form as tetramers that can be heteromers

53 Ion flux through Kv channels is voltage driven and voltage gated

54 Kv channels are voltage gated: Their “openness” is voltage sensitive

55 Current depends on the product of membrane voltage and gating

56 Different Shaker-type channels respond differently to voltage

57 Example: SKOR is open only when Eₘ is > E_K, so K⁺ *only moves out*

58 Guard cells are model systems for the study of K⁺ transport

59 The activity of membrane pumps and channels is coordinated

60 Potassium homeostasis: Responses to low K⁺ availability

61 - 62 K⁺ mobilization is critical for K⁺ homeostasis

63 **Summary: Potassium uptake, transport and homeostasis**

64 **Sodium toxicity, transport and tolerance**

65 Saline soils occur worldwide and are becoming more abundant

66 Coastal and inland soils become saline for different reasons

67 Melting land ice is raising sea levels and threatening agricultural lands

68 The San Francisco Bay and Delta are becoming increasingly salty

69 Inland, many soils lie above ancient deep salt deposits that can move up

70 Irrigation also contributes to soil salinity by mobilizing deep salts

71 How can we address the problems caused by soil salinization?

72 Plant species have a broad range of salinity tolerances

73 Mechanisms of sodium toxicity and tolerance

74 General sodium tolerance strategy: Keep sodium out of cytosol & shoot

75 Na⁺ transport and exclusion is an integral part of Na⁺ tolerance

76 Ion pumps, channels & carriers contribute to Na⁺ tolerance

77 HKTs (High-affinity K⁺ Transport) have essential roles in salt exclusion and salinity tolerance

78 HKT1 expression level and activity is correlated with Na⁺-tolerance

79 Monocots have two types of HKTs with different functions

80 NHX (Sodium / proton exchangers) are part of the Cation / Proton Antiporter (CPA) family

81 Loss of function of SOS1 makes plants “salt overly sensitive”

82 NHXs roles include Na⁺, K⁺ and H⁺ transport and homeostasis

83 **Identification of salt tolerance in halophytes and crop relatives**

84 Salt tolerance has evolved repeatedly and independently

85 Halophytes can be grown on saline soils for food and fodder

86 Quinoa is a facultative halophyte and a popular food grain

87 Models for salt tolerance: *Eutrema spp.* (salt/saltwater cress)
<table>
<thead>
<tr>
<th>Page</th>
<th>Section</th>
</tr>
</thead>
<tbody>
<tr>
<td>88</td>
<td>Breeding and engineering for salt tolerance</td>
</tr>
<tr>
<td>89</td>
<td>Wheat yield on saline soils improved by an ancestral Na⁺ transporter gene</td>
</tr>
<tr>
<td>90</td>
<td>Nax1 and Nax2 exclude Na⁺ from leaf blades by removal from xylem</td>
</tr>
<tr>
<td>91</td>
<td>The candidate gene approach has had some success</td>
</tr>
<tr>
<td>92</td>
<td>The intersection of potassium nutrition and sodium toxicity</td>
</tr>
<tr>
<td>93</td>
<td>As [Na⁺]_{ext} increases and enters the cell, K⁺ is driven out</td>
</tr>
<tr>
<td>94</td>
<td>Interaction between K⁺ nutrition and Na⁺ toxicity</td>
</tr>
<tr>
<td>95-96</td>
<td>Salinity tolerance: Summary, and Ongoing Research</td>
</tr>
</tbody>
</table>