Potassium: Potash, from the ashes in the pot

Potassium is an essential macronutrient

- Enhances fertility
- Promotes stress tolerance
- Regulates enzyme activities
- Strengthens cell walls
- Stimulates photosynthate translocation
- Maintains turgor and reduces wilting
- Regulates stomatal conductance, photosynthesis and transpiration
- Maintains ionic balance
- Stimulates photosynthate translocation
- Promotes stress tolerance
- Regulates enzyme activities
- Strengthens cell walls
- Maintains turgor and reduces wilting
- Regulates stomatal conductance, photosynthesis and transpiration
- Maintains ionic balance
- [K⁺] in soil = ~0.1 – 1 mM
- [K⁺] in plant cell cytoplasm = ~100 mM

Potassium fertilizers are mined from underground reserves as “potash”

Potash is a term that encompasses many forms of potassium:
• KCl (potassium chloride, aka sylvite)
• K₂SO₄ (potassium sulfate)
• K₂CO₃ (potassium carbonate)
• K₂Ca₂Mg(SO₄)₄·2H₂O (polyhalite)
• etc.

Almost half of the world’s reserved of potash are found in Saskatchewan, Canada

For historical reasons, potash is measured in units of K₂O equivalents, even though it is rarely found in the form of K₂O
Potash provides K for fertilizers, which supplement natural sources.

- Underground reserves
- Water pumped underground
- Water with dissolved K+ salts returned to surface
- Salts recovered by evaporation
- 90 – 98% insoluble minerals
- 1 – 3% exchangeable salts
- 0.1 – 0.2% soil solution K+
- Terrestrial cycle: Plant / Animal / Soil
- Potash fertilizer application
- Manure decomposition

Adapted from International Potash Institute
Potash prices can be volatile and there are few suppliers.

Canada is #1 in production (11.2 Mt) and reserves (4,400 Mt).

Russia is #2 in production (7.4 Mt) and reserves (3,300 Mt).

Adapted from International Potash Institute.
Potassium is an essential plant nutrient

- K⁺ uptake involves high and low affinity transporters
- K⁺ is a counter ion for negatively charged molecules including DNA and proteins
- K⁺ moves in and out of the vacuole through specific transporters
- As the major cation in the vacuole, K⁺ contributes to cell expansion and movement, including that of guard cells
- K⁺ is a cofactor for some enzymes


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Early studies of potassium uptake in plants: Biphasic uptake


K+ mobilization is critical for K+ use efficiency

Supraoptimal K+ can be stored in the vacuole

As K+ becomes limiting, it becomes preferentially allocated to the cytosol

K⁺ mobilization is critical for K⁺ use efficiency

As K⁺ becomes limiting, it becomes preferentially allocated to the cytosol

K⁺ can be remobilized from less essential tissues into prioritized tissues such as growing and photosynthetic tissues

Summary: Potassium uptake, transport and regulation

• Potassium is an essential macronutrient required in large amounts
• Potassium uptake involves low and high affinity transporters
• $K^+$ uptake, transport and remobilization are regulated extensively to ensure that the plant’s critical tissues are preferentially supported
Sulfur: Clean air can lead to deficient plants

Until recently, sulfur dioxide emission from fossil fuel combustion led to acid rain and extensive damage to vulnerable plants.

Eliminating S from air pollution uncovered crop plant deficiencies, particularly in oilseed rape and wheat.

Sulfur can be found in many inorganic forms

<table>
<thead>
<tr>
<th>Species</th>
<th>Name</th>
<th>Oxidation State</th>
</tr>
</thead>
<tbody>
<tr>
<td>S(^2)(^-), H(_2)S, R-SH</td>
<td>Sulfide</td>
<td>-2</td>
</tr>
<tr>
<td>S(^0), S(_8)</td>
<td>Sulfur</td>
<td>0</td>
</tr>
<tr>
<td>SO(_2)</td>
<td>Sulfur dioxide (toxic gas)</td>
<td>+4</td>
</tr>
<tr>
<td>SO(_3)(^-)</td>
<td>Sulfite</td>
<td>+4</td>
</tr>
<tr>
<td>SO(_4)(^2)(-)</td>
<td>Sulfate</td>
<td>+6</td>
</tr>
</tbody>
</table>

Plants take up sulfur from soil as SO\(_4\)\(^2\)\(-\) and to a lesser extent from the atmosphere as SO\(_2\) or H\(_2\)S.
Plants are an important part of the global sulfur cycle

Atmospheric pool of sulfur – mostly SO₂ (sulfur dioxide)

Volcanic activity

Combustion of fossil fuels

Acid rain*

*Since the 1980s, SO₂ emissions and SO₄²⁻ precipitation have been declining

Prokaryotic oxidation

Prokaryotic reduction

Sulfur is an essential macronutrient in amino acids & other compounds

Cysteine (Cys)

H₂N-CH₂-SH

HS-CH₂-CH-COOH

NH₂

Methionine (Met)

H₃C-S-CH₂-CH₂-CH-COOH

NH₂

Glutathione

\[ \text{Glutathione is an amino acid derivative involved in Redox reactions} \]

\[ \text{Domain 1 of wheat } E_c (2162) \text{ Zn}_{2}\text{Cys}_6 \]

Amino acids

Flavor or odor

\[ \text{Allicin (garlic flavor)} \]

\[ \text{Alllyl-isothiocyanate (horseradish flavor)} \]

Oxidation/reduction, metal transport and detox

Glutathione

\[ \text{Glutathione is an amino acid derivative involved in Redox reactions} \]

\[ \text{Domain 1 of wheat } E_c (2162) \text{ Zn}_{2}\text{Cys}_6 \]

Defense

\[ \text{Camalexin is a defense compound induced by pathogens} \]

\[ \text{Glucosinolates are anti-herbivores} \]

Sulfate uptake occurs primarily through SULTR transporters

In *Arabidopsis*, 12 genes encode SULTR transporters that fall into four groups.

Most are 12-membrane spanning $\text{SO}_4^{2-}/\text{H}^+$ co-transporters.

Primary assimilation in roots occurs mainly through SULTR1;1 and SULTR1;2.

**References:**

In higher plants, SULTR transporters effect inter-organelle movement

S transporters coordinate long-distance transport too.

Primary sulfur metabolism (overview)

Uptake

- Sulfite
  - APS
    - Adenosine 5'-phosphosulfate
    - PAPS
      - 5'-Phosphoadenosine 3'-phosphosulfate

- Primary sulfur metabolism (overview)
  - Sulfate
    - Adenosine 5'-phosphosulfate
  - Sulfate
    - Serine
    - O-acetylserine
      - O-acetyldeserine
        - Sulfide
          - Sulfide
            - Cysteine
              - Cystathionine
              - Methionine
                - S-adenosylmethionine
                - Lipoic acid
                  - Thiamine
                  - MoCo
                  - Biotin
                  - Fe/S
                  - CoA
                  - Glutathione

Sulfate is assimilated by ATP sulfurylase into APS

This reaction occurs in the cytosol and plastid

APS can enter two pathways for primary or secondary reactions

Adenosine 5'-phosphosulfate (APS)

Located exclusively in plastids

Sulfate

Sulfite reductase

Sulfite

Sulfide

Sulfated compounds, glucosinolates

Cysteine

Sulfide is assimilated into cysteine by the cysteine synthase complex

Adenosine 5’-phosphosulfate (APS)

[Chemical reactions and structures shown]

O-acetylserine (OAS) indicates cellular S status: when S is low, OAS accumulates

Cysteine synthase is a complex of SAT and OAS-TL, and is present in the cytosol, plastid and mitochondria
Model for regulation of cysteine synthesis by the CS complex

When $\text{SO}_4^{2-}$ is available, free OAS-TL dimers produce cysteine

OAS is synthesized by SAT within the cysteine synthase (CS) complex


Model for regulation of cysteine synthesis by the CS complex

When $\text{SO}_4^{2-}$ is unavailable, OAS accumulates, causing the CS complex to dissociate, and decreasing the activity of SAT. Thus, the rate of production of OAS decreases.

Free SAT is deactivated.

Sulfur uptake and assimilation rates are metabolically regulated

SLIM (EIL3) coordinates many transcriptional responses to S

Thioglucosidase activity (increased by S-deficiency) liberates S for recycling

SLIM = Sulfur Limitation
Red, pink = up-regulated by S-deficiency
Blue = down-regulated by S-deficiency
Addressing S deficiency in plants

With stricter laws on S emissions, less S enters soils and plants are more prone to S deficiency.

Soil can be augmented with elemental sulfur, ammonium sulfate or other fertilizers.

Summary: Sulfur uptake and metabolism

- Found in many redox forms and can be assimilated from atmosphere
- Deficiency more common with cleaner air
- SULTR transporter family primarily involved in uptake and transport
- Uptake and assimilation into organic forms subject to positive and negative regulation
Magnesium: The “forgotten element”

Mg in solution is a divalent cation $\text{Mg}^{2+}$

Soil magnesium is a result of rock weathering and $\text{Mg}^{2+}$ from seawater

The Dolomite Mountains are named for the mineral dolomite $\text{MgCO}_3 \cdot \text{CaCO}_3$

Serpentine
$3\text{MgO} \cdot 2\text{SiO}_2 \cdot 2\text{H}_2\text{O}$

Magnesite
$\text{MgCO}_3$

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Didier Descouens; Ra’ike; chensiyuan; James St. John
Magnesium is a cofactor for many enzymes and central to chlorophyll.

**Mg\(^{2+}\) is an essential activator for many enzymes including Rubisco.**

**Mg\(^{2+}\) stabilizes ribosome 3D structure.**

**Mg\(^{2+}\) is central to chlorophyll.**

Mg deficiency interferes with photosynthesis & C transport

Effects of Mg deficiency

-one symptom of Mg deficiency is high-light induced chlorosis

Magnesium transporters move Mg$^{2+}$ across membranes

There are two known classes of Mg transporters:
- MRS/MGT
- MHX (Mg/H$^+$ exchanger)

Mg transporters are different from other cation transporters but conserved across life domains.

Magnesium uptake is mediated by the MRS / MGT family


$MGT6$ is induced in roots by low Mg and required for efficient Mg uptake.
Aluminum toxicity is minimized by increased Mg uptake

Mg deficiency in plants contributes to Mg deficiency in animals

Rapidly growing spring grass can be low in Mg, so grass-fed cattle can experience hypomagnesemia, a sometimes fatal condition called grass tetany.

To ensure adequate dietary Mg\(^{2+}\), human diets should include nuts, legumes, leaves and whole grains.
Summary: Magnesium

- Rarely limiting for plant growth
- Mg\(^{2+}\) transporters are different from other cation transporters, but conserved across life domains
- Elevated Mg\(^{2+}\) uptake can mitigate Al\(^{3+}\) toxicity
- Humans and animals can suffer Mg deficiency if dietary sources are deficient
Calcium: Low free cytosolic levels & functions in apoplast / vacuole

Calcium stabilizes pectin in middle lamella of cell walls

Cytosolic Ca$^{2+}$ oscillations are second messengers in diverse responses


90% of the plant’s calcium can be in the form of calcium oxalate crystals

- The crystals are formed by specialized cells called idioblasts
- Calcium oxalate crystals can function in defense
- Calcium oxalate crystals also can sequester excess calcium

Idioblasts are specialized cells that form calcium oxalate crystals and are illuminated by polarized light (RI = raphide idioblast, DI = druse idioplast)

Plants maintain very low levels of free cytosolic Ca²⁺

The concentration of free Ca²⁺ is ~ 10,000 fold lower in the cytosol than the apoplast.

The challenge at the plasma membrane is to maintain low free internal Ca²⁺ (in contrast to the situation for most other nutrients).

Ca\textsuperscript{2+} transport systems include channels, pumps and antiporters.

Calcium deficiency causes cell wall defects and sometimes cell death

Calcium is translocated in the xylem (apoplast) but not the phloem (symplast), meaning that it cannot be remobilized when external supplies are limited.

Ca\(^{2+}\) deficiency in growing tissues causes weakness and death, leading to blossom end rot (left), tip burn (right) and bitter pit (bottom). Ca\(^{2+}\) deficiency also can result from a low rate of transpiration.

Calcium contributes to pectin crosslinking and stabilization

Pectin is a galacturonic acid polymer. Calcium stabilizes the pectin and causes it to “gel”

Ca\(^{2+}\) interacting with pectin at tip of pollen tube

Molecular gastronomists react calcium with pectin-like polymers to produce interesting foods

Pectin is found in the middle lamella and the cell wall of a growing pollen tube

Calcium oscillations are mediated by ion channels, pumps and carriers

Calcium oscillations contribute to guard cell functions

How $\text{Ca}^{2+}$ oscillations are decoded remains incompletely resolved

A model of the ionic fluxes that result in calcium oscillations around the nucleus during symbiotic interactions

Summary: Calcium

• Much of a plant’s calcium may be in the form of calcium oxalate crystals
• Free Ca\(^{2+}\) ion is mainly stored outside cytosol, in apoplast and vacuole
• Calcium has a structural role in cell walls, particularly pectin gelling
• Calcium has a signaling role conferred by transient spikes in cytosol
Macronutrients: Summary

- Macronutrients (N, P, K, S, Mg, Ca) are essential elements that must be acquired from the environment.
- Soil microbes affect nutrient availability and uptake.
- Nutrient-specific transporters control uptake, translocation and remobilization of mineral nutrients.
- Some macronutrients are assimilated into organic compounds.
- Uptake and assimilation reactions are coordinated by nutrient availability and demand.
- Replenishment of soil nutrients is essential for high-yielding agricultural systems.
The ecological impacts of agriculture are huge and growing – most of these hypoxic regions arose since 1950 and are attributed to human activities.

Macronutrients - Summary

WORLD POPULATION PROJECTION

We must find innovative solutions to the challenge of feeding the plants that feed us.

Demand for food will not slow down during this century.

- 7.2 billion (2012)
- 9.6 billion (2050)
- 10.9 billion (2100)

Ongoing research: Learn how plants integrate different nutrient needs

How do roots optimize growth when two or more nutrients are limiting?

How can understanding this integration support breeding efforts?

Interactive effects of nutrients and daylength on root growth

Cluster analysis of root traits that enhance acquisition of various nutrients


Ongoing research: Use best practices for nutrient management

Manage nutrients properly, using the “4Rs”

- **Right Source**: NH₄NO₃ or Urea?
- **Right Rate**: How much?
- **Right Time**: Before planting? During vegetative growth phase?
- **Right Place**: Between rows? On surface or deep?

Continue to develop technologies to ensure optimal fertilizer use, and make them affordable.

International Plant Nutrition Institute; See also American Society of Agronomy; Video link Plant Nutrition Institute