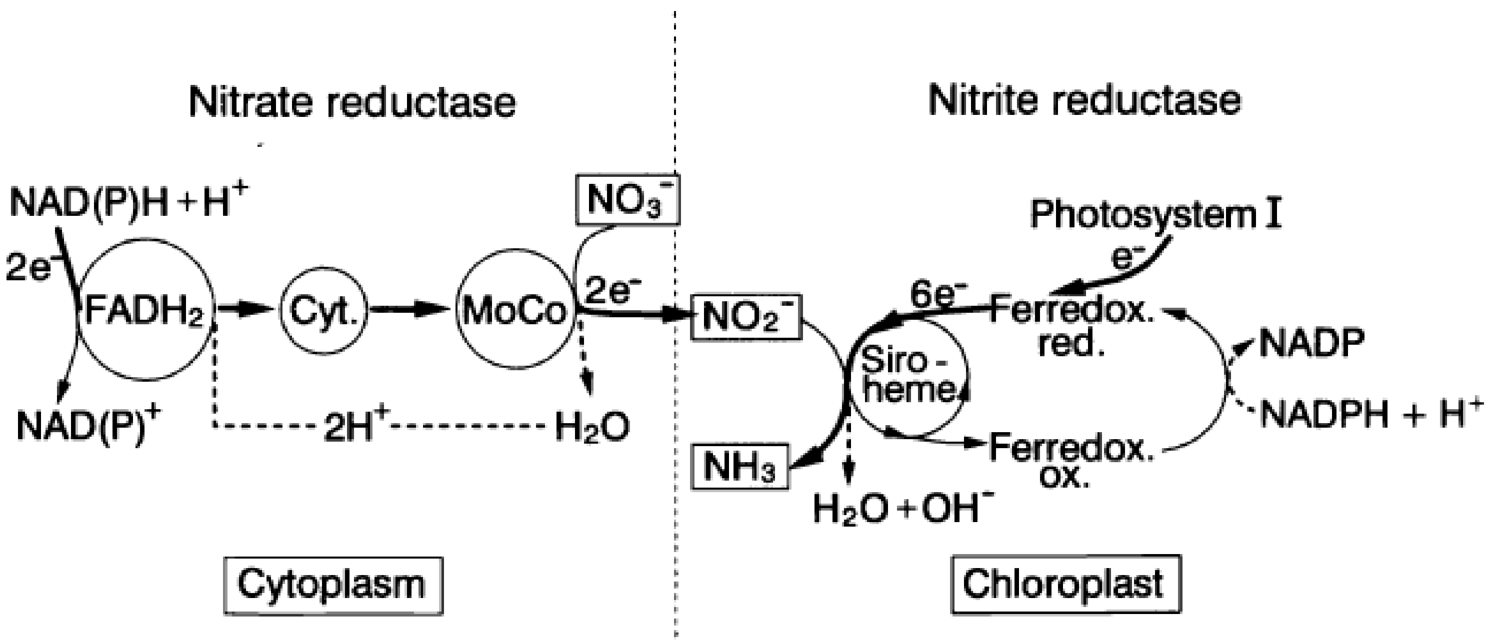
# In the name of God

# Assimilation of Nitrogen

- Nitrate and ammonium are the major sources of inorganic nitrogen taken up by the roots of higher plants.
- Most of the ammonium has to be incorporated into organic compounds in the roots.
- whereas nitrate is readily mobile in the xylem and can also be stored in the vacuoles of roots, shoots, and storage organs.
- The importance of the reduction and assimilation of nitrate for plant life is similar to that of the reduction and assimilation of C02 in photosynthesis.

# *Nitrate Reduction and Assimilation*

$$NO_3^- + 8\,H^+ + 8\,e^- \rightarrow NH_3 + 2\,H_2O + OH^-$$



As would be expected, nitrate reductase activity is very low in molybdenum-deficient plants

Effect of Pretreatment with Molybdenum on Nitrate Reductase Activity in Wheat Leaf Segments[a]

| Molybdenum supply during plant growth ($\mu$g per plant) | Pretreatment of leaf segments ($\mu$g Mo $l^{-1}$) | Nitrate reductase activity ($\mu$mol $NO_2^-$ $g^{-1}$ fresh wt) after | |
|---|---|---|---|
| | | 24 h | 70 h |
| 0.005 | 0 | 0.2 | 0.3 |
| 0.005 | 100 | 2.8 | 4.2 |
| 5.0 | 0 | – | 8.0 |
| 5.0 | 100 | – | 8.2 |

- In $C_4$ plants, mesophyll and bundle sheath cells differ in their functions not only in $C0_2$ assimilation but also in nitrate assimilation. Both, nitrate reductase and nitrite reductase are localized in the mesophyll cells and are absent in the bundle sheath cells .This 'division of labour' in $C_4$ plants,whereby mesophyll cells utilize light energy for nitrate reduction and assimilation and bundle sheath cells for $C0_2$ reduction, is most probably the cause for higher photosynthetic nitrogen use efficiency (NUE) in $C_4$ compared with $C_3$ plants

# Localization in Roots and Shoots

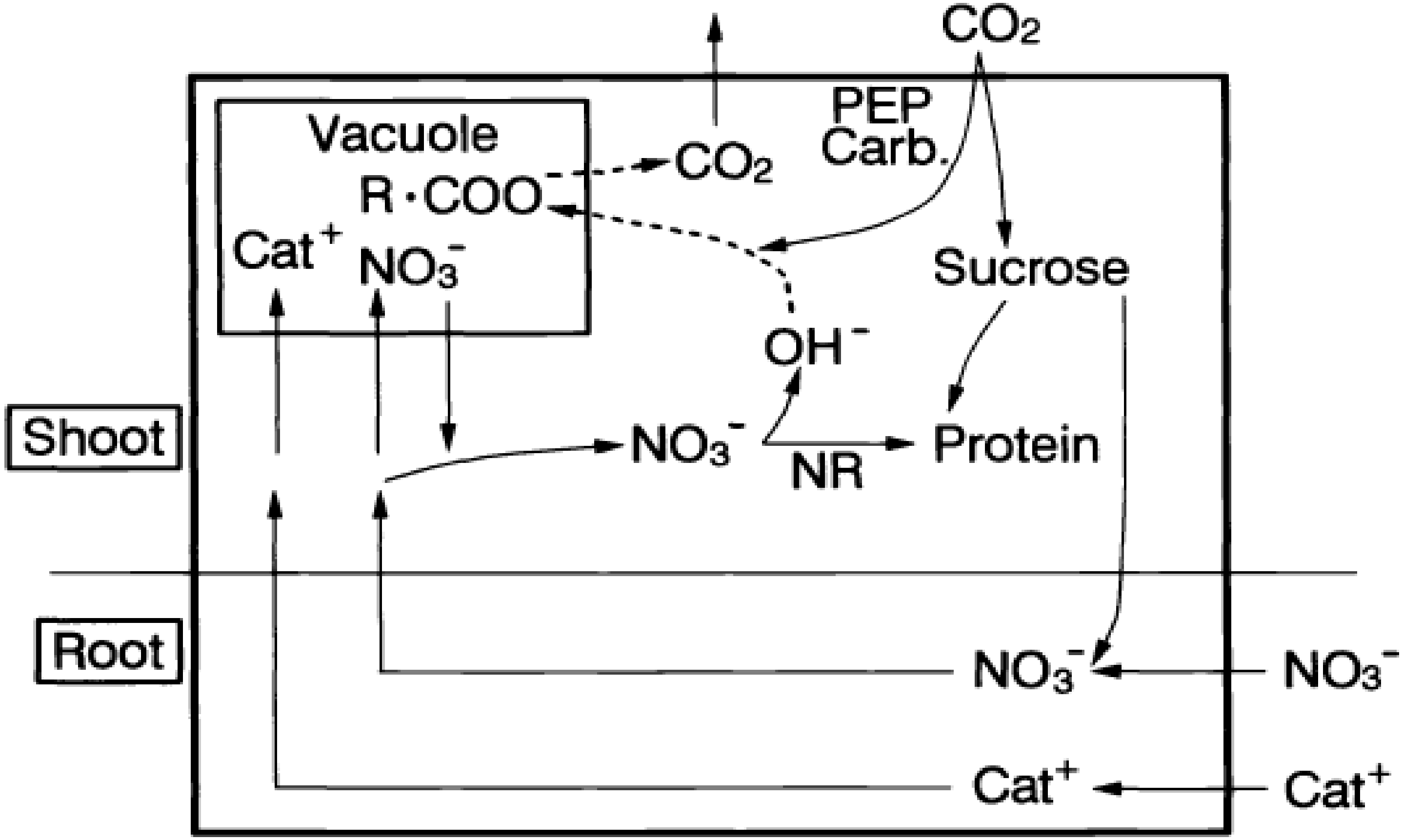
The proportion of reduction carried out in roots and shoots depends on various factors,

- the level of nitrate supply
- the plant species,
- the plant age,
- accompanying cation

- In general, when the external nitrate supply is low, a high proportion of nitrate is
- reduced in the roots. With an increasing supply of nitrate, the capacity for nitrate
- reduction in the roots becomes a limiting factor and an increasing proportion of the total nitrogen is translocated to the shoots in the form of nitrate

- For a given species, the proportion of nitrate reduced in the roots increases with temperature and plant age

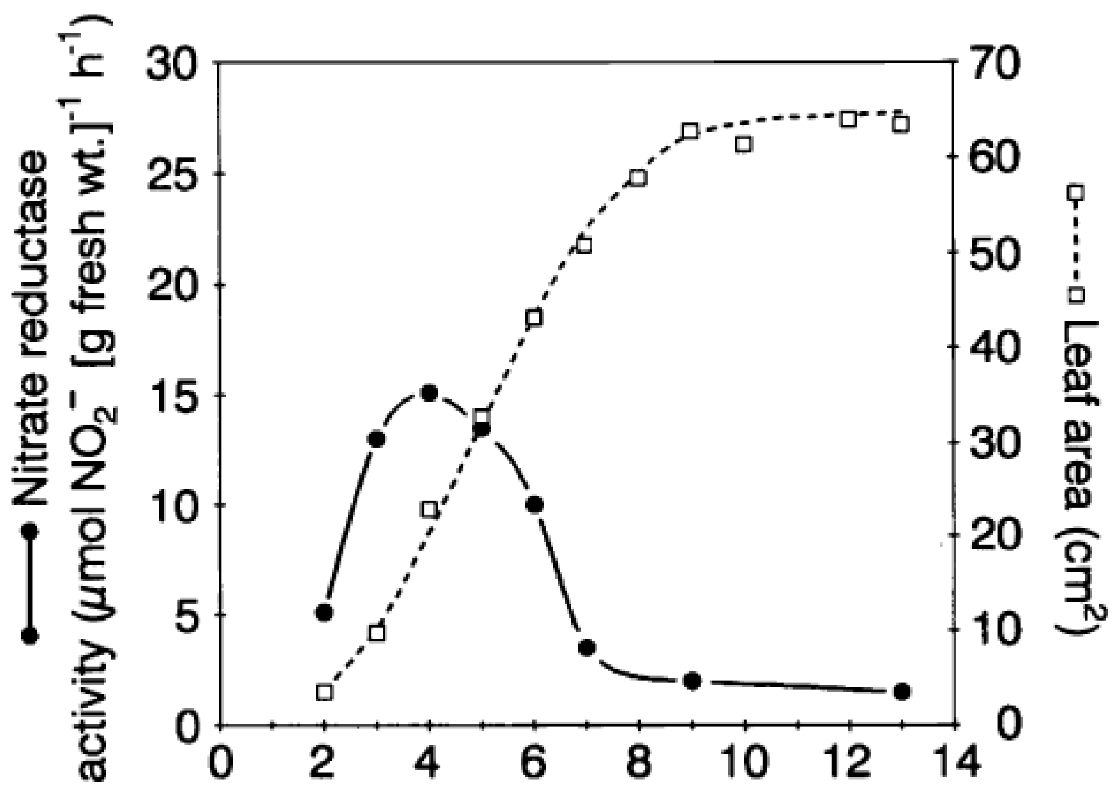
- The uptake rate of the accompanying cation also affects this proportion. With potassium as the accompanying cation, translocation of both potassium and nitrate to the shoots is rapid; correspondingly, nitrate reduction in the roots is relatively low. In contrast, when calcium or sodium is the accompanying cation, nitrate reduction in the roots is considerably higher



$CO_2$
PEP
Carb.
Vacuole
$R \cdot COO^-$
$CO_2$
$Cat^+$
$NO_3^-$
Sucrose
$OH^-$
Shoot
$NO_3^-$
NR
Protein
Root
$NO_3^-$
$NO_3^-$
$Cat^+$
$Cat^+$

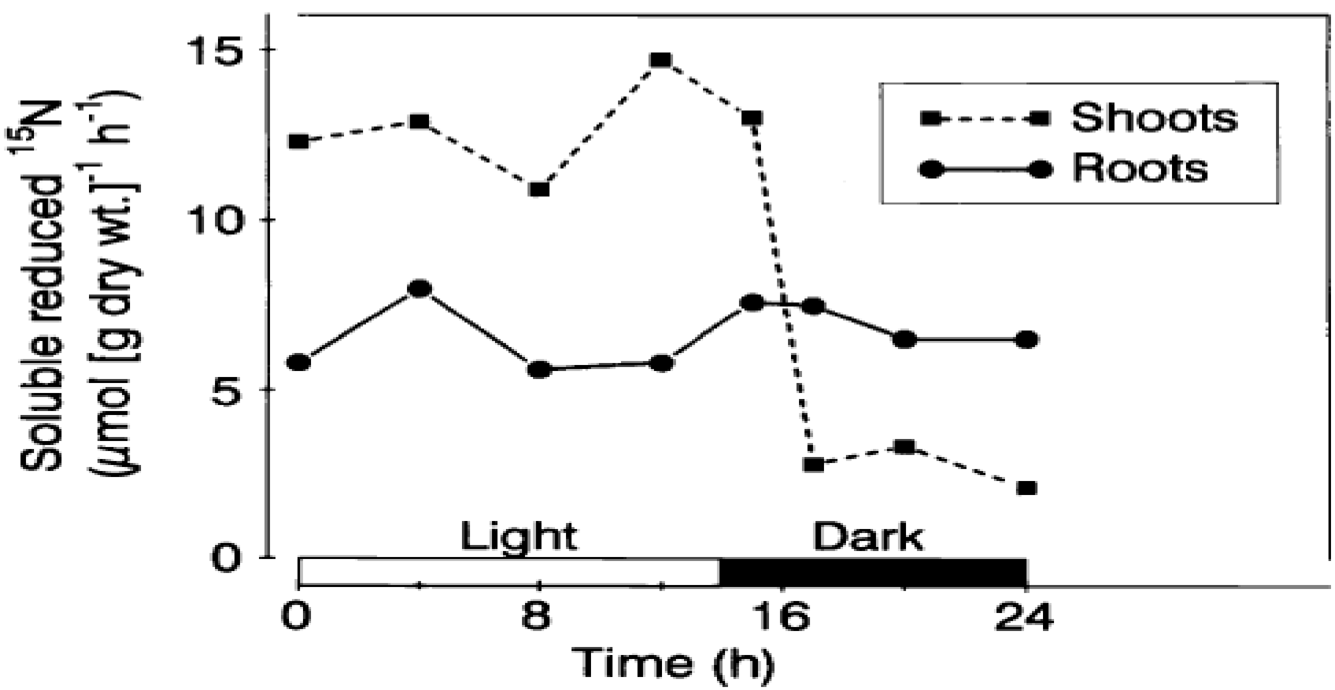
*Leaf Age.*

Maximum activity occurs when the rate of leaf expansion is maximal. Thereafter, the activity declines rapidly



# *Light*

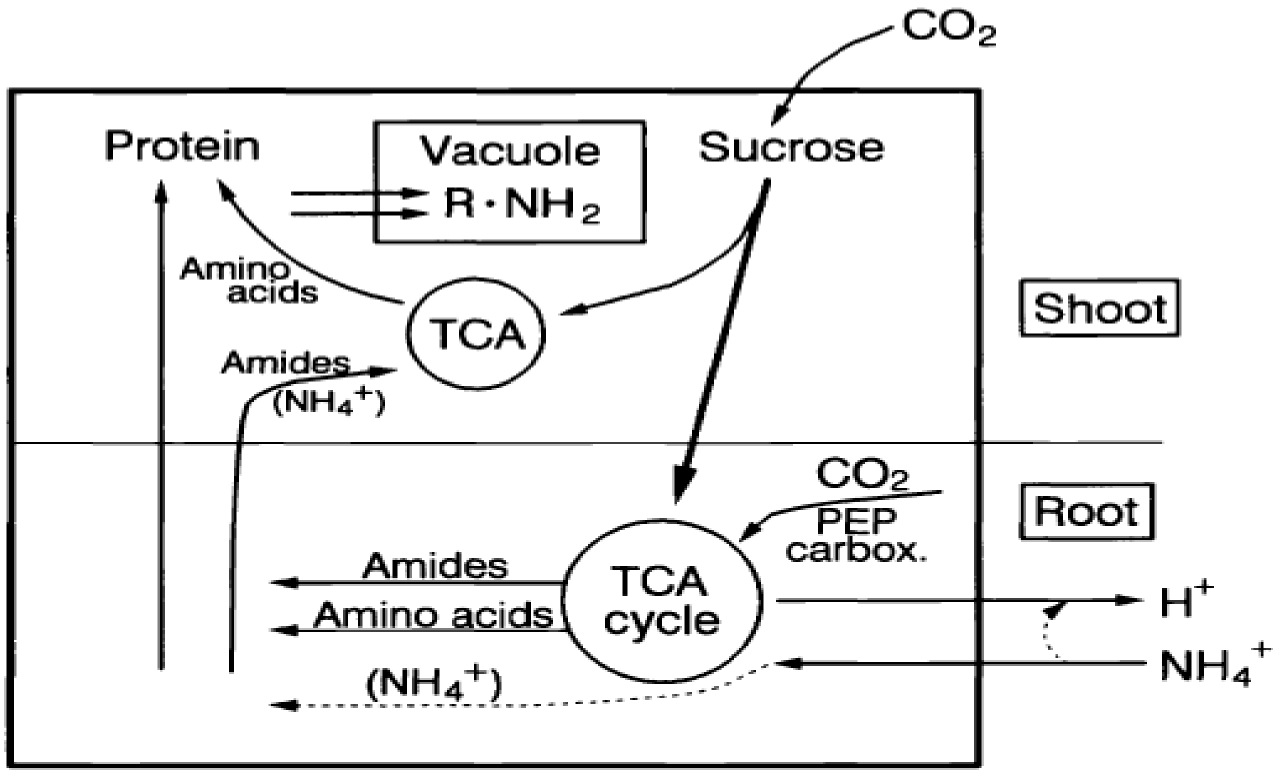
- In green leaves a close correlation exists between light intensity and nitrate reduction. for example, there is a distinct diurnal pattern of reduction in the shoots but not in the roots

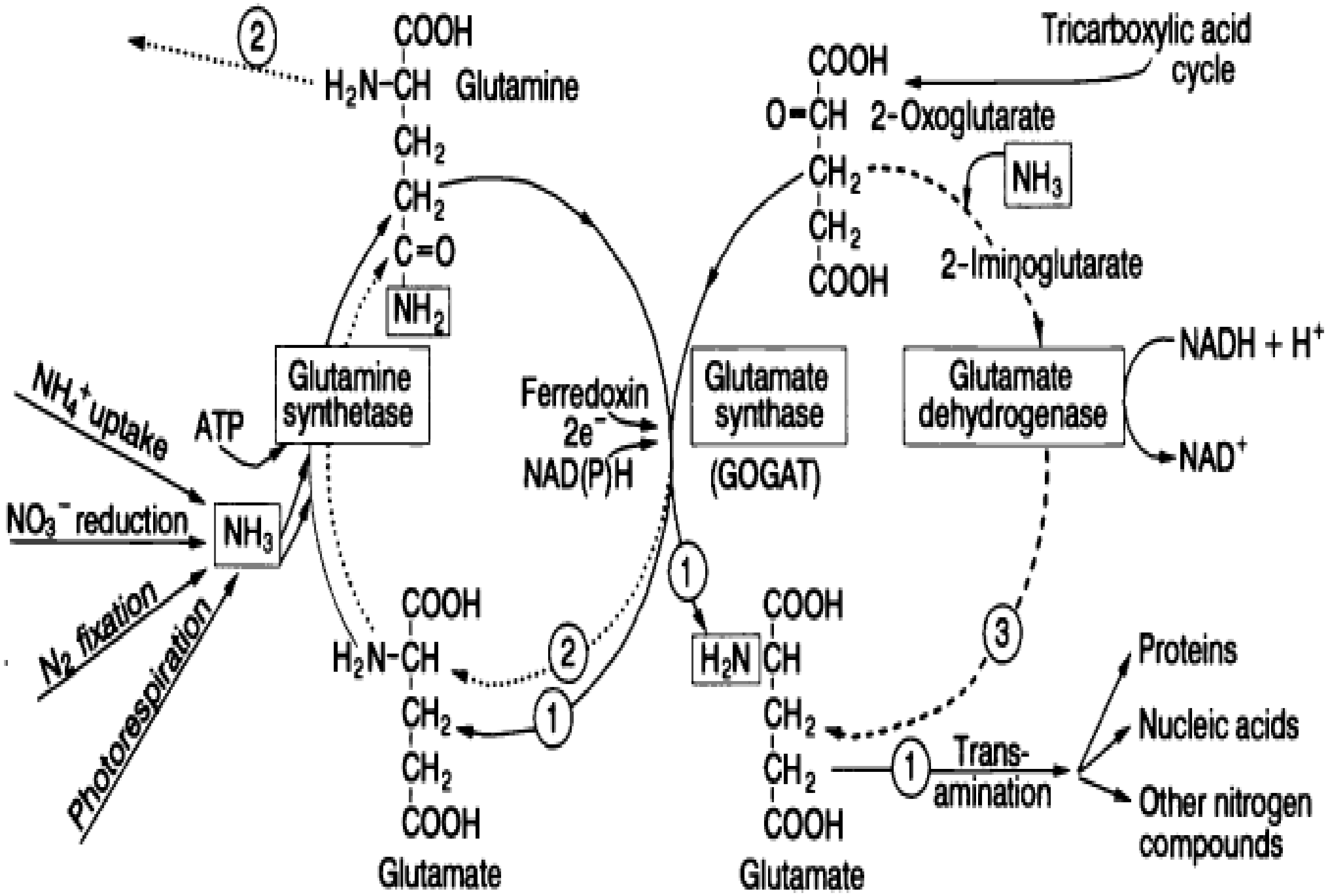


Time Course of Nitrate Content in Spinach Leaves during the Light Period from 9:00 to 18:00[a]

| | Concentration of nitrate N (mg kg$^{-1}$ fresh wt) | |
|---|---|---|
| Time of day | Leaf blade | Petioles |
| 8:30 | 228.2 | 830.2 |
| light 9:30 | 166.6 | 725.1 |
| light 13:30 | 100.8 | 546.0 |
| light 17:30 | 91.0 | 504.0 |
| 18:30 | 106.4 | 578.2 |

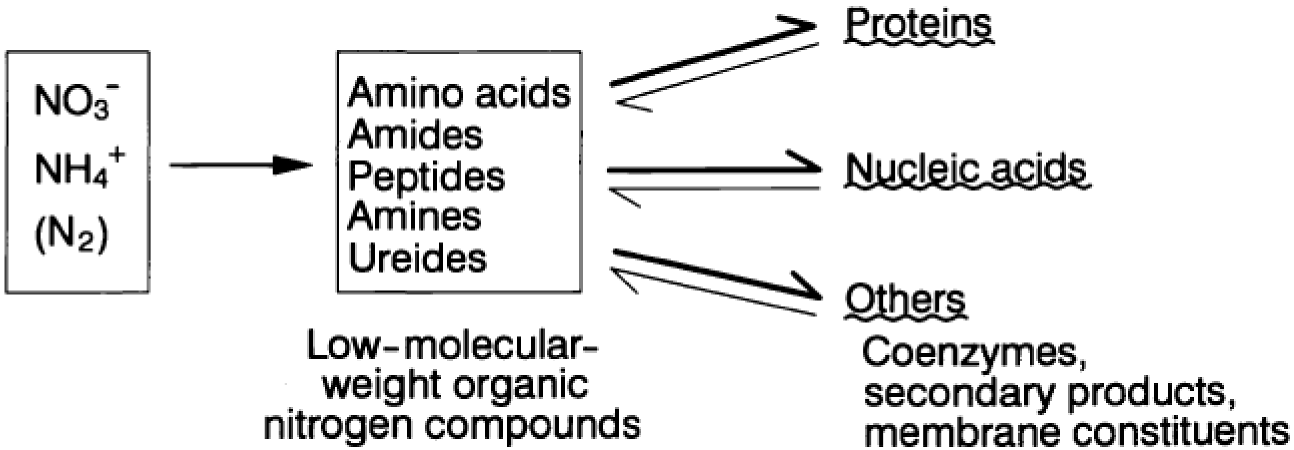
# Assimilation of Ammonium





2
COOH
$H_2N-CH$ Glutamine
$CH_2$
$CH_2$
C=O
$NH_2$
Tricarboxylic acid cycle
COOH
O=CH 2-Oxoglutarate
$CH_2$
$NH_3$
$CH_2$
COOH
2-Iminoglutarate
Glutamine synthetase
Ferredoxin
$2e^-$
NAD(P)H
Glutamate synthase
(GOGAT)
Glutamate dehydrogenase
NADH + $H^+$
$NAD^+$
$NH_4^+$ uptake
ATP
$NO_3^-$ reduction
$NH_3$
$N_2$ fixation
Photorespiration
1
COOH
$H_2N-CH$
2
1
$CH_2$
$CH_2$
COOH
Glutamate
3
COOH
$H_2N$ CH
$CH_2$
$CH_2$
COOH
Glutamate
1
Trans-amination
Proteins
Nucleic acids
Other nitrogen compounds

# Role of Low-Molecular-Weight Organic Nitrogen Compounds



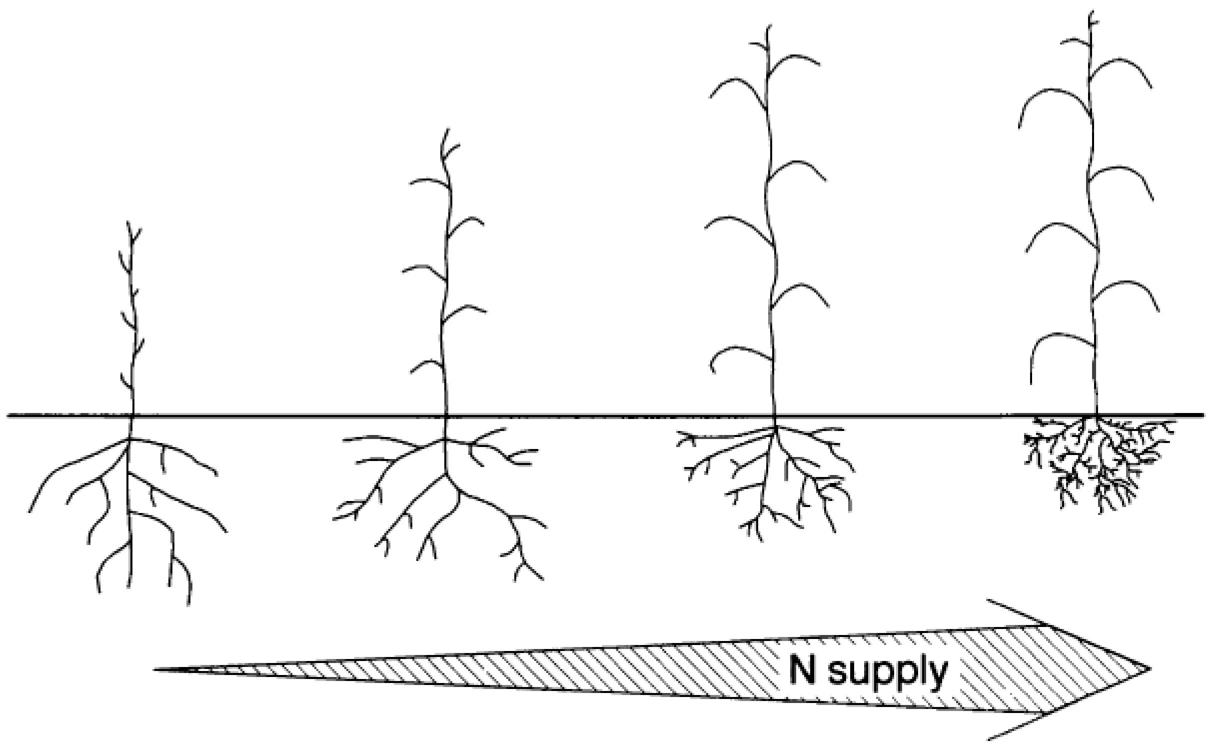
- Peptides had also been considered to be involved in long-distance transport of heavy metals in the xylem. However, most of the heavy metals in the xylem are present either as free cations or complexed with organic acids.

- Another important class of low-molecular-weight organic nitrogen compounds are amines and poly amines. More recently poly amines have attracted attention as secondary messengers.

Poly amines seem to serve many functions in plants, either in free or bound form, for example with various phenolics. They are involved in cell division, embryogenesis, and floral initiation and development.Poly amines are also quite effective in delaying senescence of leaves by inhibiting the activity of acid proteinases Putrescine which is usually the dominant polyamine in plants, may constitute up to 1.2% of the plant dry matter

- Amines are components of the lipid fraction of biomembranes

- Stabilization of cell structures and osmoregulation is betaine (also referred to as glycine betain

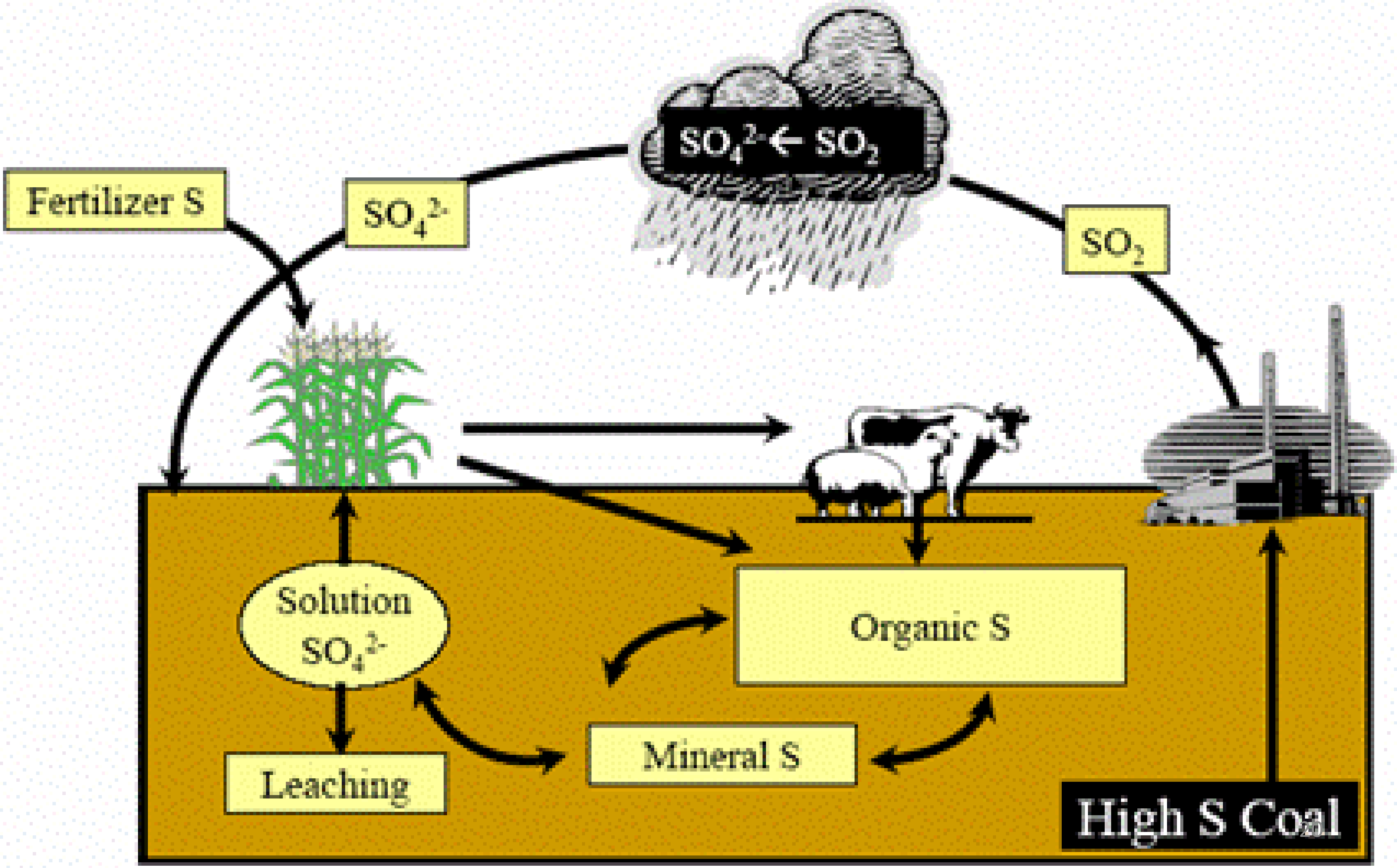

N supply

# Sulfur

- Although atmospheric $So_2$ is taken up and utilized by the aerial parts of higher plants
- ,the most important source of sulfur is sulfate taken up by the roots.

- In the physiological pH range, the anion $SO_4^-$ is taken up by the roots at relatively low rates, and long-distance transport of sulfate occurs mainly in the xylem

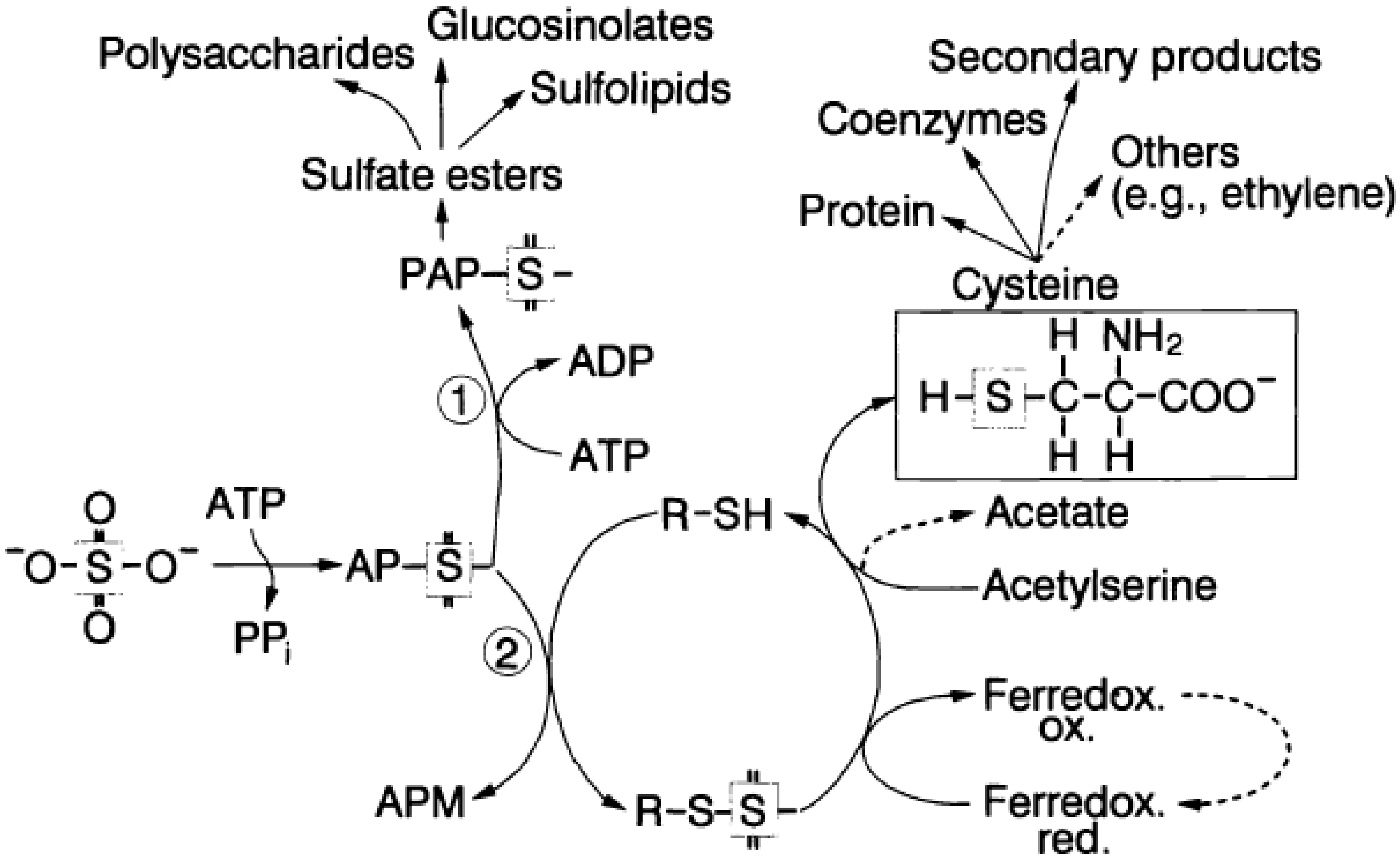
# Sulfur Cycle



- reduction is necessary for the incorporation of sulfur into amino acids, proteins, and coenzymes, and in green leaves ferredoxin is the reductant for sulfate. Unlike nitrate nitrogen, however, sulfate can also be utilized without reduction and incorporated into essential organic structures such as sulfolipids in membranes or polysaccharides such as agar.

- Also in contrast to nitrogen, reduced sulfur can be reoxidized in plants. In this oxidation reaction the reduced sulfur of cysteine is converted into sulfate.

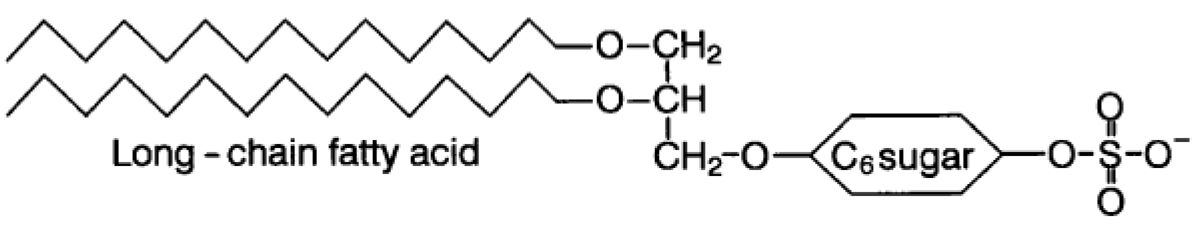
# Sulfate Assimilation and Reduction



# Metabolic Functions of Sulfur

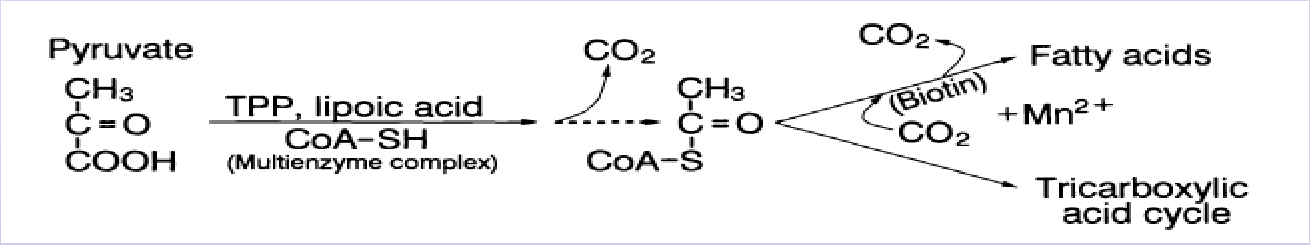
- Sulfur is a constituent of the amino acids cysteine and methionine and hence of proteins. Both of these amino acids are precursors of other sulfur-containing compounds such as coenzymes and secondary plant products. Sulfur is a structural constituent of these compounds (e.g., R1—C—S—C—R2) or acts as a functional group (e.g., R—SH) directly involved in metabolic reactions.

- Sulfur in its nonreduced form, i.e. as sulfate ester, is a component of sulfolipids and is thus a structural constituent of all biological membranes. Sulfolipids are particularly abundant in the thylakoid membranes of chloroplasts,about 5% of the chloroplast lipids are sulfolipids .Sulfolipids may also be involved in the regulation of ion transport across biomembranes. Sulfolipid levels in roots have been shown to be positively correlated with plant salt tolerance, the higher the level the greater the tolerance .



- Reduced sulfur is a structural constituent of several coenzymes and prosthetic groups such as ferredoxin ,biotin, and thiamine pyrophosphate (Vitamin B ).

- The formation of acetyl coenzyme A are catalyzed by a multienzyme complex involving three sulfur-containing coenzymes: thiamine pyrophosphate (TPP), lipoic acid, and the sulfhydryl group of coenzyme A:

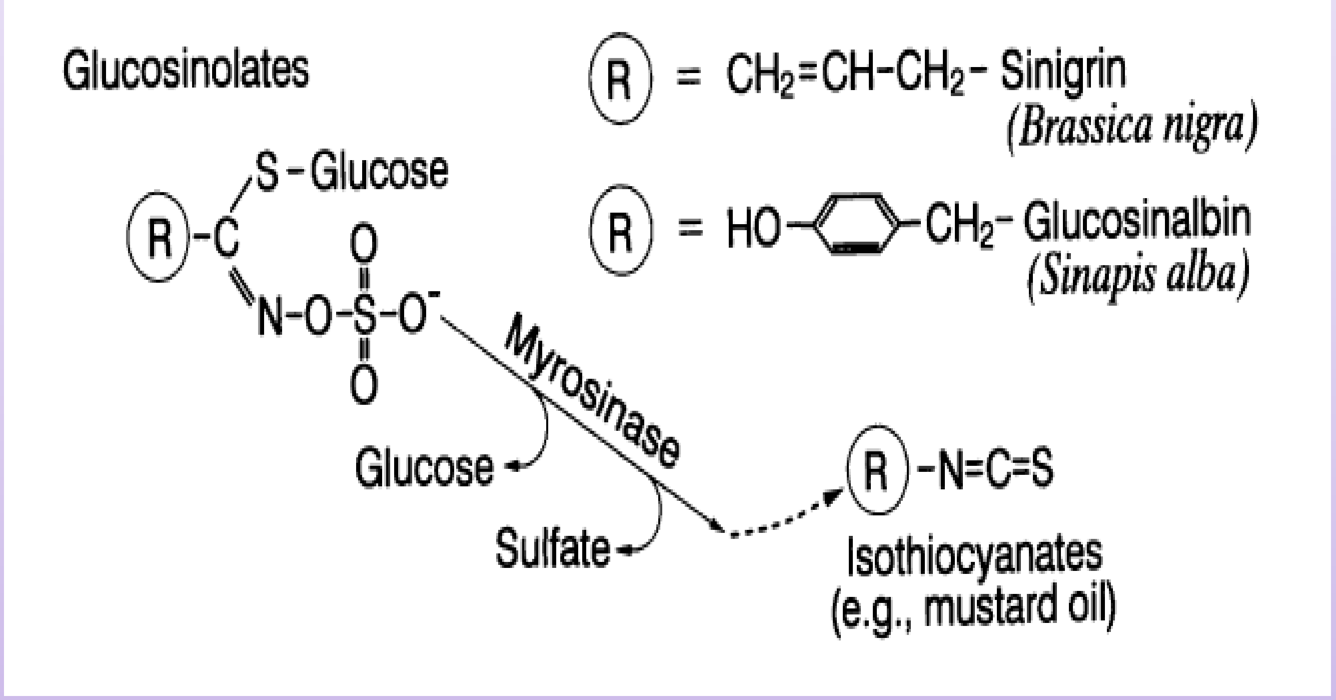



- In many enzymes and coenzymes such as urease, sulfotransferases and coenzyme A, the —SH groups act as functional groups in the enzyme reaction.

The protection of—SH groups in proteins from the formation of disulfide bridges is considered to be of great importance for providing cellular resistance to dehydration (caused by drought and heat) and frost damage.

Cells respond to exposure to high concentrations of heavy metals such as cadmium and zinc, by the synthesis of polypeptides high in cysteine content, termed 'metallothioneins'.

low-molecular-weight proteins: metallothioneins or phytochelatins. Phytochelatins are capable of binding heavy metal cations and thereby detoxifying them

- volatile compounds such as sulfoxide and isothiocyanates in *Brassica*
- 

# Sulfur Supply, Plant Growth, and Plant Composition

- Sulfur requirement for optimal growth varies between 0.2 and 0.5% of the dry weight of plants.
- For the families of crop plants, the requirement increases in the order Gramineae < Leguminosae < Cruciferae and this is also reflected in corresponding differences in the sulfur content.
- 0.18-0.19, 0.25-0.3, and 1.1-1.7, respectively

## Phosphorus

Unlike nitrate and sulfate, phosphate is not reduced in plants but remains in its highest oxidized form. After uptake - at physiological pH mainly as H2PO4

1-either it remains as inorganic phosphate (Pi)

2-or is esterified through a hydroxyl group to a carbon chain (C—O—®) as a simple phosphate ester (e.g., sugar phosphate)

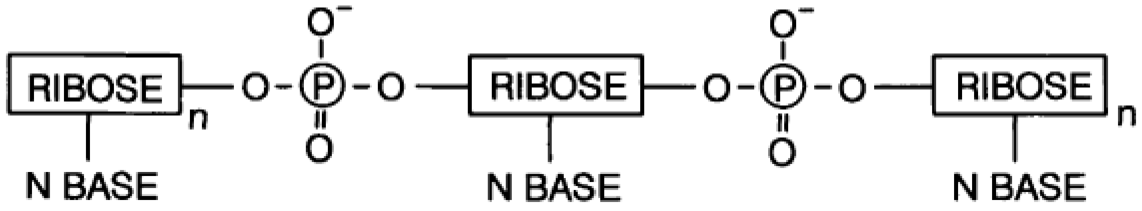
3-or attached to another phosphate by the energy-rich pyrophosphate bond ®~® *(e.g., in ATP)*.

The rates of exchange between Pi and the ® in ester and the pyrophosphate bond are very high. For example, Pi taken up by roots is incorporated within a few minutes into organic ® but thereafter is released again as Pi into the xylem . Another type of phosphate bond is characterized by the relative high stability of its diester state (C—®—C). In this association phosphate forms a bridging group connecting units to more complex or macromolecular structures.

# Phosphorus as a Structural Element

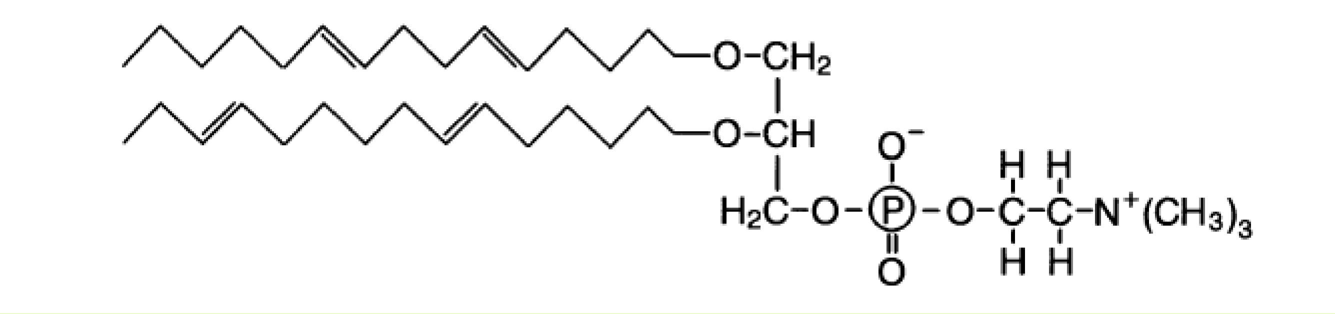
as units of the DNA and RNA molecule, are the carriers of genetic information.

Phosphorus is responsible for the strongly acidic nature of nucleic acids and thus for the exceptionally high cation concentration in DNA and RNA structures.

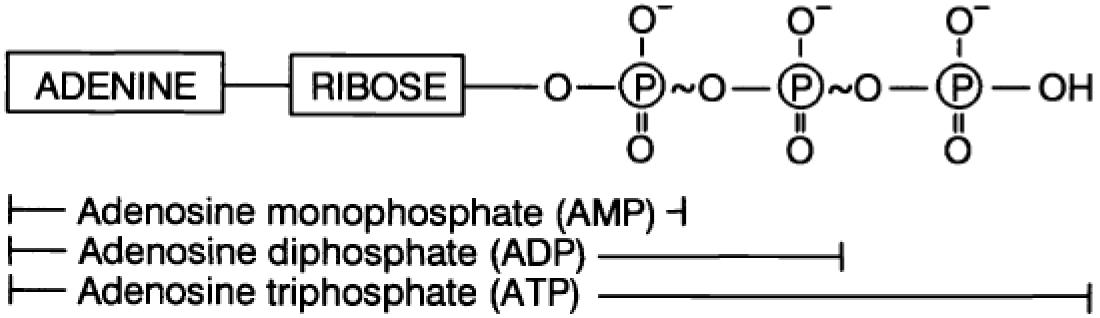



(Section of RNA molecule)

The bridging form of phosphorus diester is also abundant in the phospholipids of biomembranes. There it forms a bridge between a diglyceride and another molecule (amino acid, amine, or alcohol). In biomembranes the amine choline is often the dominant partner, forming phosphatidylcholine.



# Role in Energy Transfer



# Compartmentation and regulatory Role of Inorganic Phosphate

- ✓ In many enzyme reactions, Pi is either a substrate or an end product.
- ✓ ATP -» ADP + Pi
- ✓ Furthermore, Pi controls some key enzyme reactions.
- ✓ Pi released from the vacuoles into the cytoplasm can stimulate phosphofructokinase activity. Delayed fruit ripening in phosphorus-deficient tomato plants may be related to this function of Pi.

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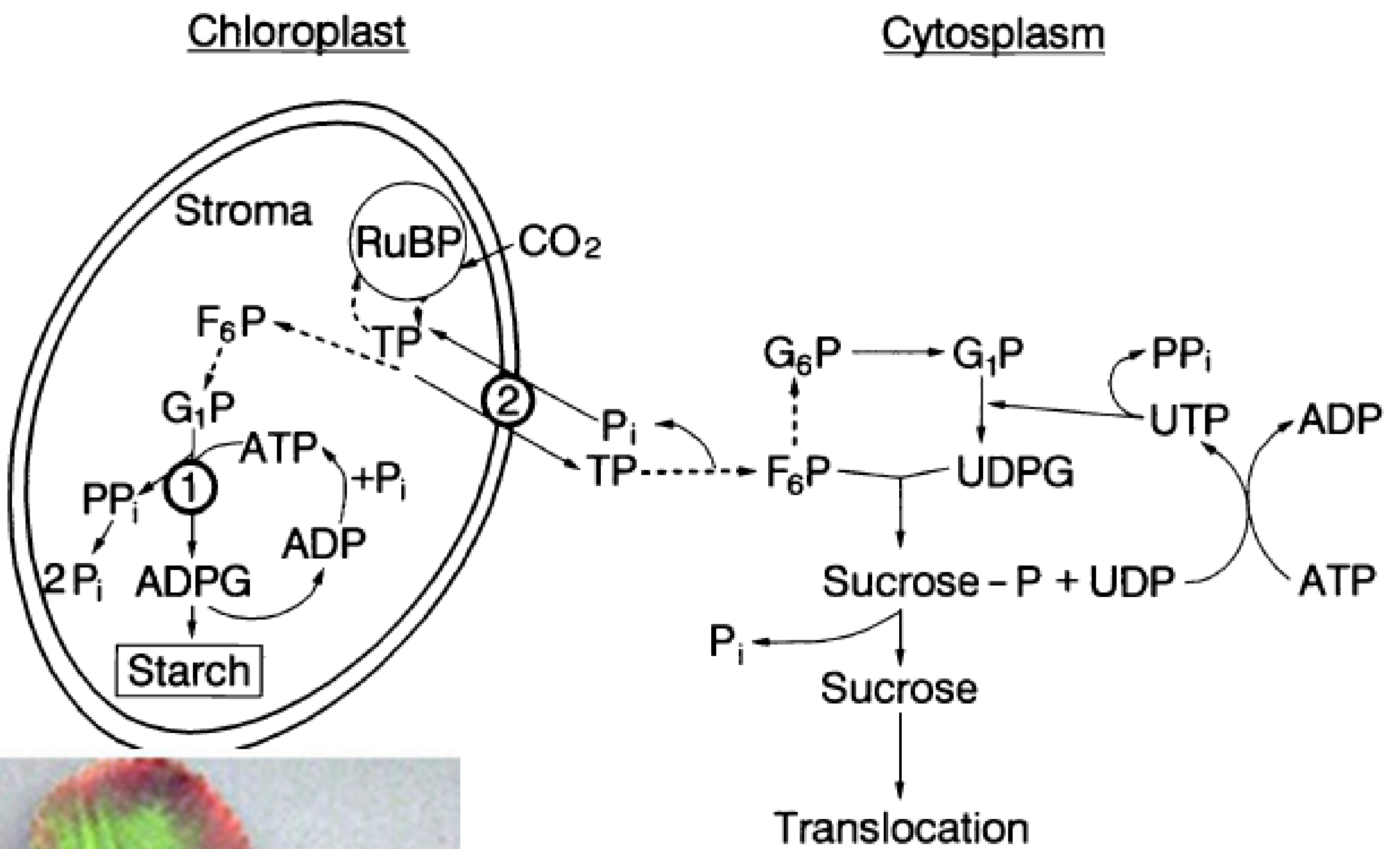



Leaf size
Dark chlorophyll

# Phytate is the typical storage form of phosphorus in grains and seeds

Phytic acid is synthesized from the cyclic alcohol myoinositol by esterification of the hydroxyl groups with phosphate groups

The sparingly soluble calcium-magnesium salt of phytic acid is termed phytin.

In legume seeds and cereal grains the main phytates are the potassium-magnesium salts

Phytate in the form of the potassium-magnesium-calcium salt is also the major form of phosphorus in pollen grains

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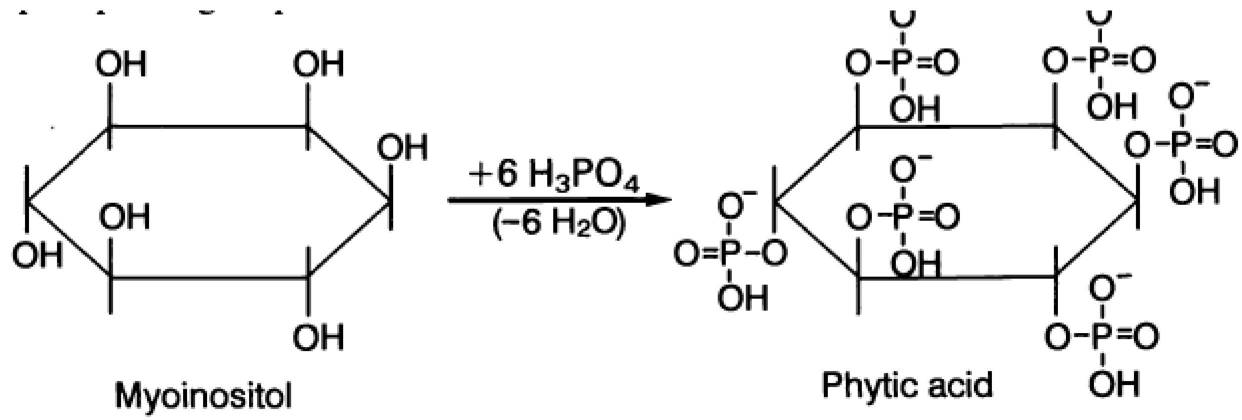
# Role of Phytate

Effect of Phosphorus Supply on Phosphorus Fractions of Tobacco Leaves[a]

| P supply (mg l$^{-1}$) | Leaf dry wt (g per leaf) | Phosphorus fraction (mg P (100 g)$^{-1}$ leaf dry wt) | | | |
|---|---|---|---|---|---|
| | | Lipid | Nucleic acid | Ester | Inorganic |
| 2 | 0.82 | 32 | 74 | 36 | 33 |
| 6 | 1.08 | 83 | 134 | 91 | 83 |
| 8 | 1.10 | 89 | 133 | 104 | 123 |
| 20 | 1.06 | 91 | 142 | 109 | 338 |

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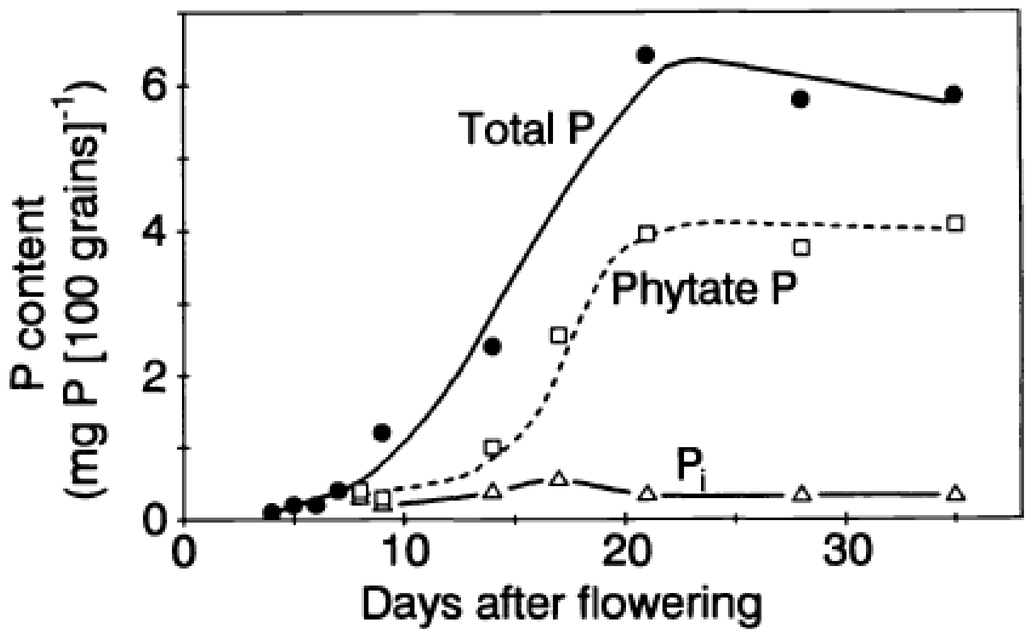
# seed



Total P
Phytate P
P$_i$
P content
(mg P [100 grains]$^{-1}$)
0
2
4
6
0
10
20
30
Days after flowering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Changes in Phosphorus Fractions of Rice Seeds during Germination[a]

| Duration of germination (h) | Phosphorus fraction (mg P $g^{-1}$ dry wt) | | | | |
|---|---|---|---|---|---|
| | Phytate | Lipid | Inorganic | Ester | RNA + DNA |
| 0 | 2.67 | 0.43 | 0.24 | 0.078 | 0.058 |
| 24 | 1.48 | 1.19 | 0.64 | 0.102 | 0.048 |
| 48 | 1.06 | 1.54 | 0.89 | 0.110 | 0.077 |
| 72 | 0.80 | 1.71 | 0.86 | 0.124 | 0.116 |

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- Its rate of uptake can be strongly depressed by
- other cations, such as $K^+$, $NH_4$, $Ca^{2+}$, and $Mn^{2+}$ ,as well as by $H^+$, that is, by low pH.

# Magnesium

Its rate of uptake can be strongly depressed by other cations, such as $K^+$, $NH^{4+}$ , $Ca^{2+}$, and $Mn^{2+}$, as well as by $H^+$, that is, by low pH.

Magnesium deficiency induced by competing cations is thus a fairly widespread phenomenon

# Chlorophyll and Protein Synthesis

In green leaves a major function of magnesium, and certainly its most familiar function, is its role as the central atom of the chlorophyll molecule

Magnesium also has an essential function as a bridging element for the aggregation of ribosome subunits

Magnesium is also required for RNA polymerases and hence for the formation of RNA in the nucleus.

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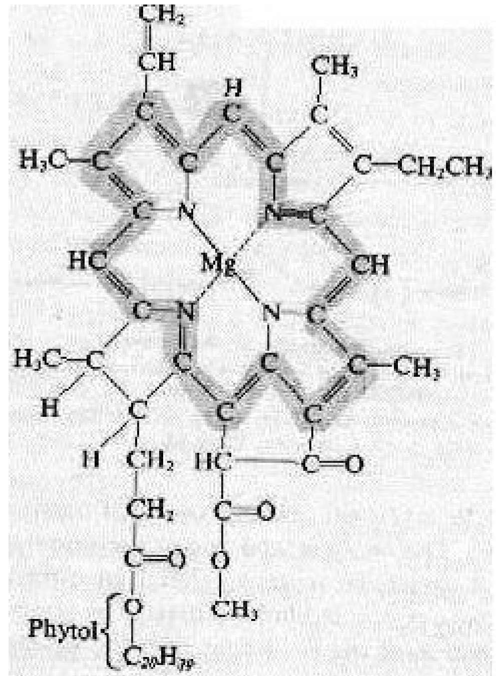
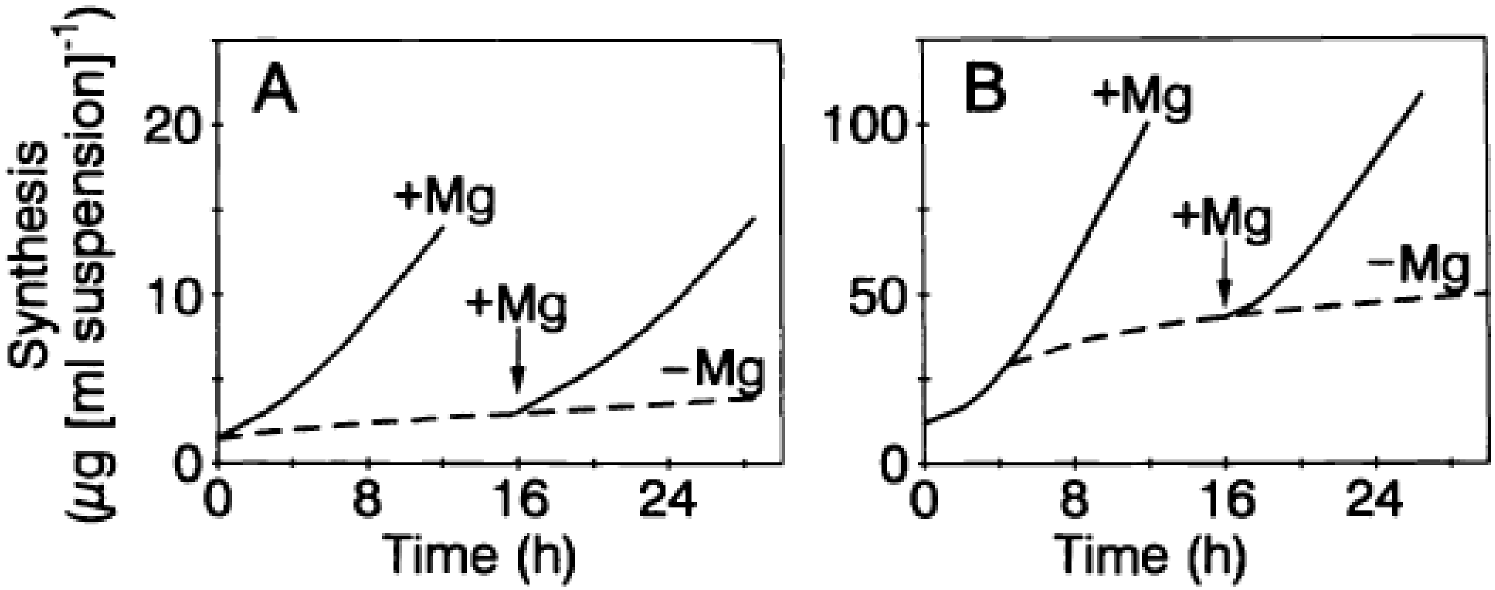

CH2
CH
CH3
H
H3C
C—CH2CH3
HC
Mg
CH
H3C
C—CH3
H
H
CH2
HC
C=O
CH2
C=O
C=O
O
O
CH3
Phytol
O
C20H39




Effect of magnesium supply on (A) RNA and (B) protein synthesis in *Chlorella pyrenoidosa* suspension culture. (Based on Galling, 1963.)

In leaf cells at least 25% of the total protein is localized in chloroplasts.

This explains why a deficiency of magnesium particularly affects the size, structure, and function of chloroplasts, including electron transfer in photosystem II.

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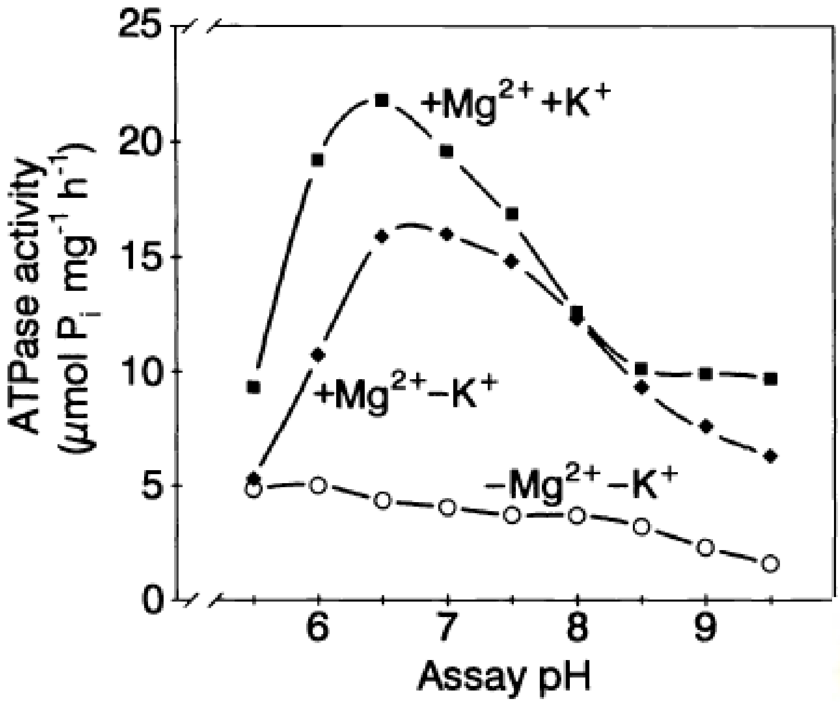
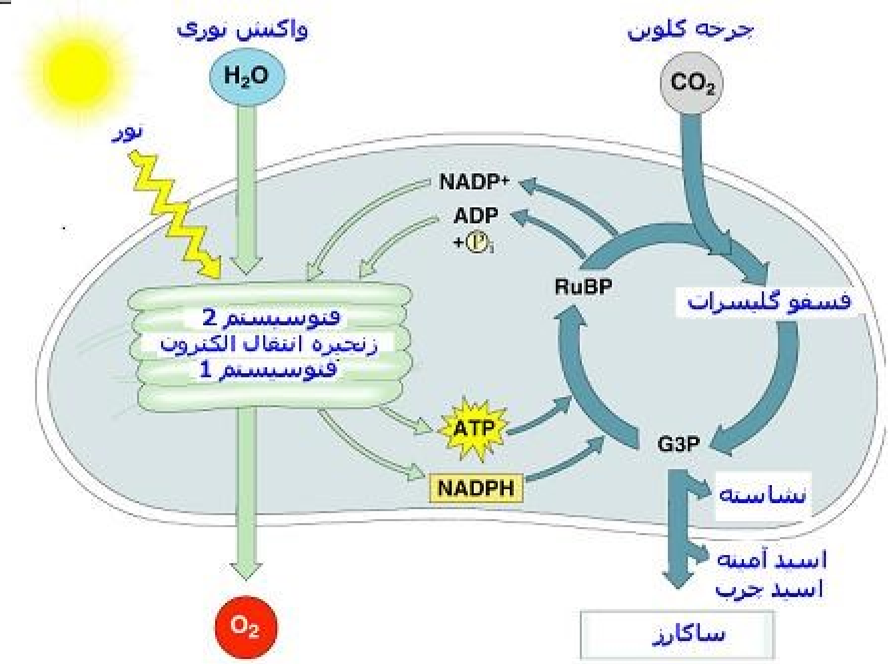
# Enzyme Activation, Phosphorylation, and Photosynthesis

There is a long list of enzymes and enzyme reactions which require or are strongly promoted by magnesium, for example, glutathione synthase or PEP carboxylase.

Also the synthesis of ATP (phosphorylation: ADP + Pi —> *ATP) has an absolute* requirement for magnesium as a bridging component between ADP and the enzyme.

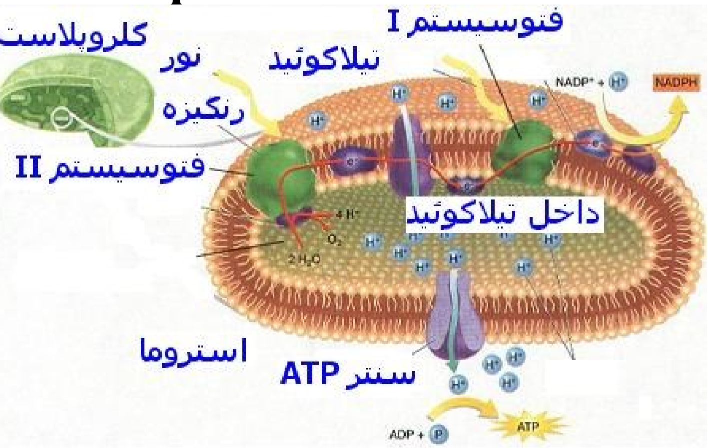


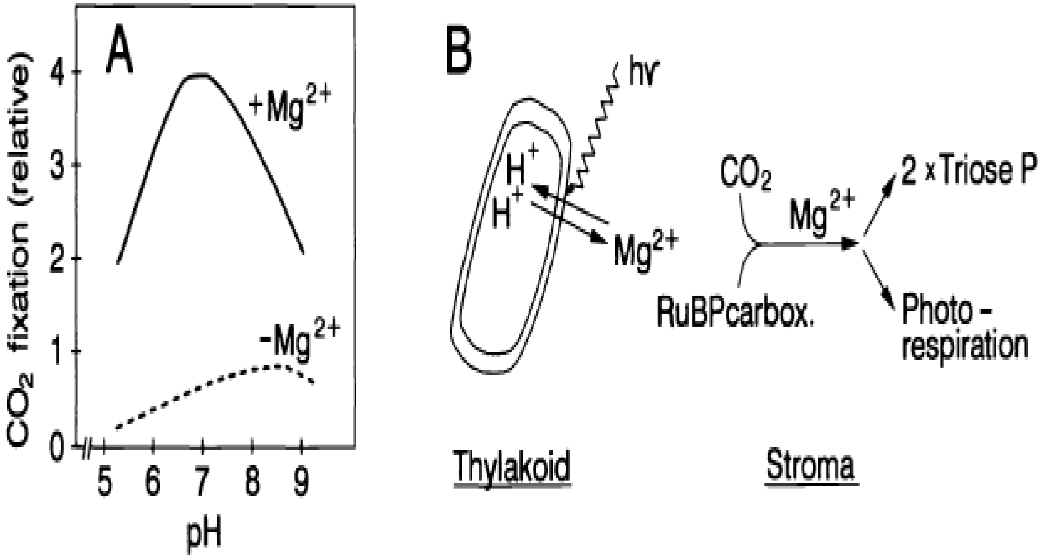
ATPase activity
(μmol P_i mg^-1 h^-1)
25
20
15
10
5
0
6
7
8
9
Assay pH
+Mg2+ +K+
+Mg2+ −K+
−Mg2+ −K+

واکنش نوری
چرخه کلوین
H2O
CO2
نور
NADP+
ADP
+Pi
RuBP
فسفو گلیسرات
فتوسیستم 2
زنجیره انتقال الکترون
فتوسیستم 1
ATP
NADPH
G3P
نشاسته
اسید آمینه
اسید چرب
ساکارز
O2

Another key reaction of magnesium is the modulation of RuBP carboxylase in the stroma of chloroplasts. The activity of this enzyme is highly dependent on both magnesium and pH



One of the key enzymes with a high magnesium requirement and high pH optimum is fructose-l,6-bisphosphatase which, in chloroplasts, regulates assimilate partitioning between starch synthesis and export of triosephosphates

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**Chlorosis of fully expanded leaves is the most obvious visible symptom of magnesium deficiency.**

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# Calcium

In the apoplasm, part of the calcium is firmly bound in structures, another part is exchangeable at the cell walls and at the exterior surface of the plasma membrane. A high proportion of calcium might be sequestered in vacuoles whereas its concentration in the cytosol is extremly low.

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a high proportion of the total calcium in the

plant tissue is often located in the cell walls (apoplast) In the middle lamella it is bound to R · COO~ group of the polygalacturonic acids (pectins) in a more or less readily exchangeable form.

In dicotyledons such as sugar beet,which have a large cation-exchange capacity, and particularly when the level of calcium supply is low, up to 50% of the total calcium can be bound as pectates .In storage tissue of apple fruits, the cell wall-bound fraction of calcium can make up as much as 90% of the total .

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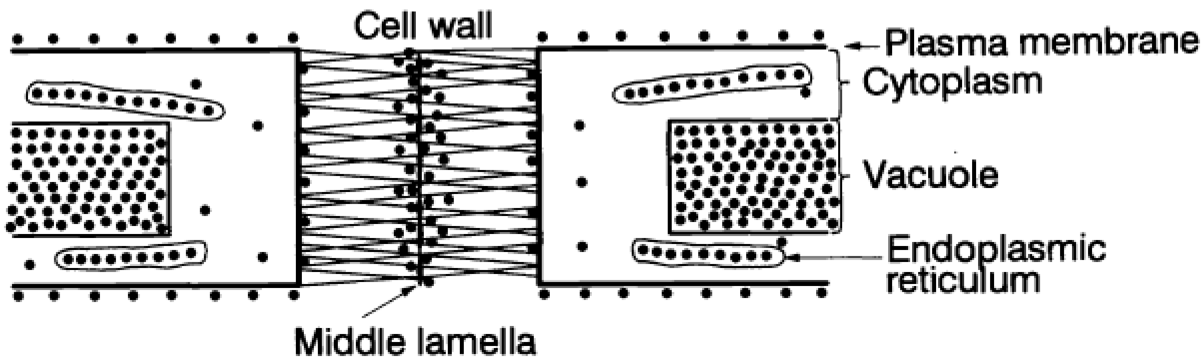


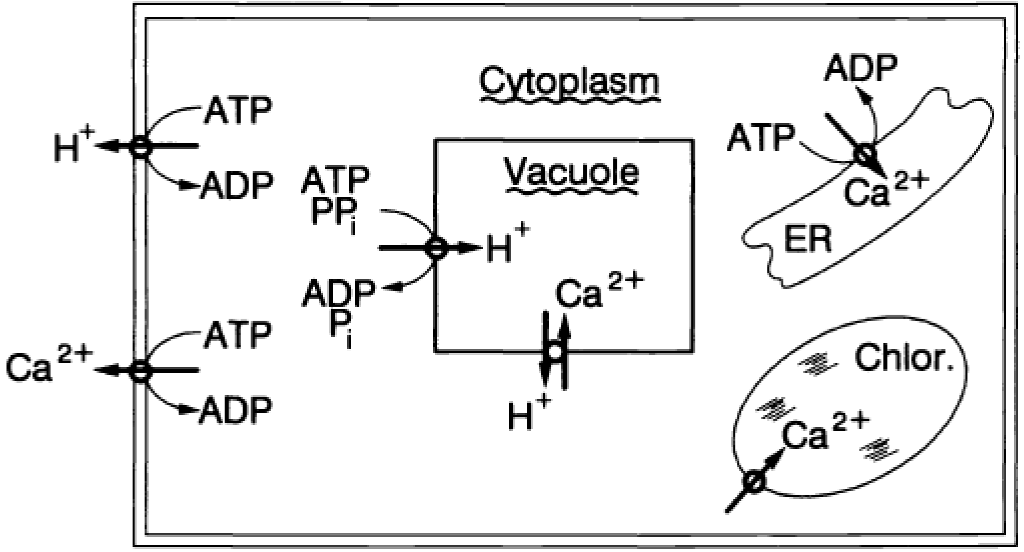


Calcium transport processes in cell membranes for maintenance of low cytosolic free $Ca^{2+}$. (Modified from Evans *et al.*, 1991.)

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# Function

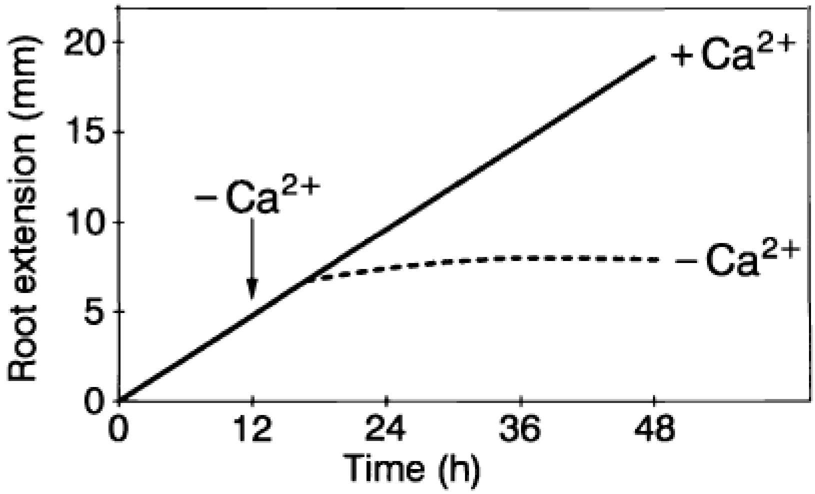
# Cell Wall Stabilization

Calcium bound as pectate in the middle lamella is essential for strengthening of the cell walls and of plant tissues.

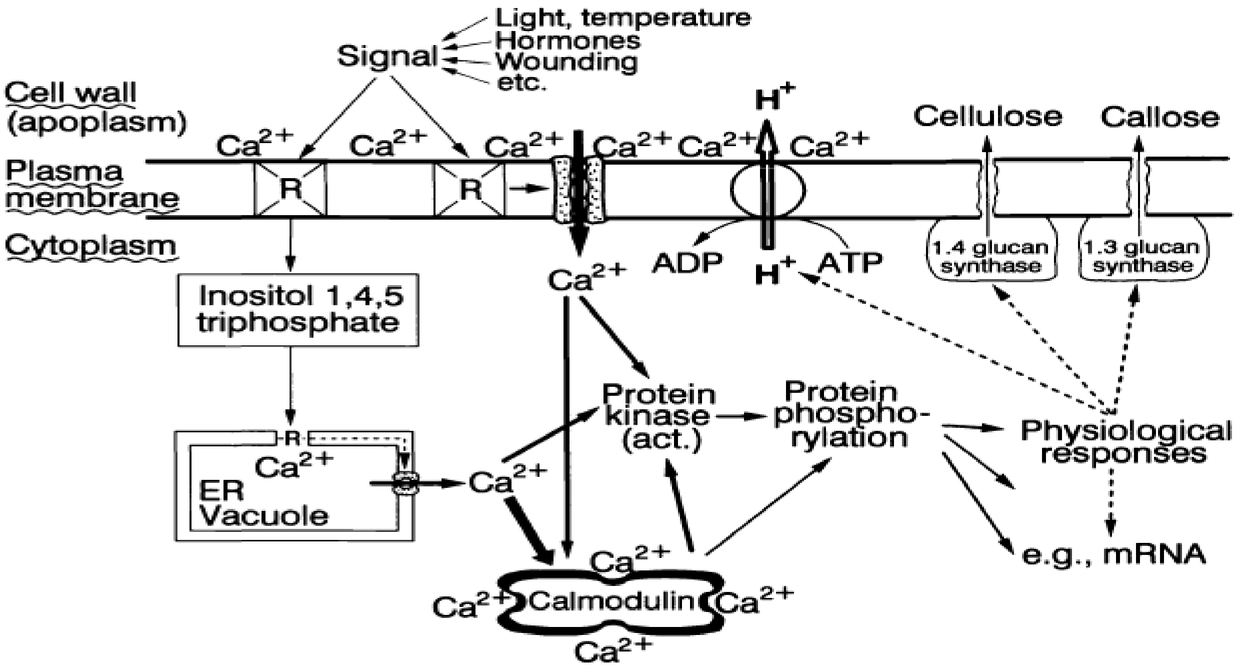
In the middle lamella it is bound to R · COO~ group of the polygalacturonic acids (pectins) in a more or less readily exchangeable form The low cytosolic free $Ca^{2+}$ concentrations are achieved by a generally low constitutive permeability of membranes for calcium, and by the action of membrane transporters removing calcium from the cytosol and expelling it to the apoplasm or accumulating it in intracellular stores such as the endoplasmic reticulum (ER), the chloroplasts, and the vacuole

# Cell Extension

In the absence of an exogenous calcium supply, root extension ceases within a few hours Calcium provides cell wall rigidity by cross-linking the pectic chains of the middle lamella. On the other hand, for extension growth cell wall loosening is required,a process in which auxin-induced acidification of the apoplasm and replacement of calcium from the cross-links of the pectic chain are involved, although this is only one component of the event



Root extension (mm)
20
15
10
5
0
0
12
24
36
48
Time (h)
+ Ca2+
− Ca2+
− Ca2+

Light, temperature
Hormones
Wounding
etc.
Signal
Cell wall
(apoplasm)
Plasma
membrane
Cytoplasm
Ca2+
Ca2+
Ca2+
Ca2+
Ca2+
Ca2+
R
R
H+
ADP
H+
ATP
Cellulose
Callose
1.4 glucan
synthase
1.3 glucan
synthase
Ca2+
Inositol 1,4,5
triphosphate
R
Ca2+
ER
Vacuole
Ca2+
Protein
kinase
(act.)
Protein
phospho-
rylation
Physiological
responses
e.g., mRNA
Ca2+
Ca2+
Calmodulin
Ca2+
Ca2+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# Membrane Stabilization

Calcium stabilizes cell membranes by bridging phosphate and carboxylate groups of phospholipids and proteins, referentially at membrane Surfaces.

There can be an exchange between calcium at these binding sites and other cations (e.g. K+, Na+, or H+).

it regulates the selectivity of ion uptak. and prevents solute leakage from the cytoplasm. The membrane-protecting effect of calcium is most prominent under stress conditions such as low temperature and anaerobiosis . Calcium also alleviates the damage of tissues caused by freezing-thawing stress.

Calcium stimulates a range of membrane-bound enzymes :

particularly ATPases at the plasma membrane of roots of certain plant species

stimulate the activity of phospholipase

Stimulation of á-amylase activity in germinating cereal seeds

PEP carbocsylase

.

# Cation-Anion Balance and Osmoregulation

large proportion of calcium is localized in the vacuoles, where it might contribute to the cation-anion balance by acting as a counterion for inorganic and organic anions.

In mature sugar beet leaves, for example, up to 90% of the total calcium is bound to oxalate.

And thereby activate calcium channels in the plasma membrane.In the cytosol the principal targets of calcium signals are calcium-binding proteins known as *calcium-modulated proteins*,

# Calcium Supply, Plant Growth, and Plant Composition

- The calcium content of plants varies between 0.1 and >5.0% of dry wt depending on the growing conditions, plant species, and plant organ.
- The calcium requirement for optimum growth is much lower in monocotyledons than in dicotyledons
- At low compared to high pH the $Ca^{2+}$ concentration in the external solution has to be several times higher in order to counteract the adverse effect of high $H^{+}$ concentrations on root elongation

.

# Potassium

- Its uptake is highly selective and closely joined to metabolic activity.
- It is characterized by high mobility in plants at all levels – within individual cells, within tissues, and in long-distance transport via the xylem and phloem.
- Potassium is the most abundant cation in the cytoplasm.

# Enzyme Activation

**A large number of enzymes is either completely dependent on or stimulated by K+**

**These changes in carbohydrate metabolism are presumably related to the high K+ requirement of certain regulatory enzymes, particularly pyruvate kinase and phosphofructokinase .**

**the activity of starch synthase is also highly dependent on K+ The enzyme catalyzes the transfer of glucose to starch molecules:**

**ADP-glucose + starch $\longrightarrow$ ADP + glucosyl-starch**

**Another function of K+ is the activation of membrane-bound proton-pumping ATPases**

**Tissues of potassium-deficient plants exhibit a much higher activity of certain hydrolases or oxidases such as polyphenol oxidase than do tissues of normal (sufficient) plants.**

# Protein Synthesis

K is involved in several steps of the translation process, including the binding of tRNA to ribosomes.

It seems that K+ not only activates nitrate reductase but is also required for its synthesis.

# Photosynthesis

- In higher plants potassium affects photosynthesis at various levels. Potassium is the dominant ion to the light-induced H+ flux across the thylakoid membranes and for the establishment of the transmembrane pH gradient necessary for the synthesis of ATP (photophosphorylation).

Relationship between Potassium Content in Leaves, Carbon Dioxide Exchange, and RuBP Carboxylase Activity in Alfalfa[a]

| Leaf potassium (mg $g^{-1}$ dry wt) | Stomatal resistance (s $cm^{-1}$) | Photosynthesis (mg $CO_2$ $dm^{-2}$ $h^{-1}$) | RuBP carboxylase activity ($\mu$mol $CO_2$ $mg^{-1}$ protein $h^{-1}$) | Photorespiration (dpm $dm^{-2}$) | Dark respiration (mg $CO_2$ $dm^{-2}$ $h^{-1}$) |
|---|---|---|---|---|---|
| 12.8 | 9.3 | 11.9 | 1.8 | 4.0 | 7.6 |
| 19.8 | 6.8 | 21.7 | 4.5 | 5.9 | 5.3 |
| 38.4 | 5.9 | 34.0 | 6.1 | 9.0 | 3.1 |

# Osmoregulation

There are two major requirements for cell extension:

an increase in cell wall extensibility, and solute accumulation to create an internal osmotic potential .

the accumulation of k in the cells of $K^+$, which is required for both stabilizing the pH in the cytoplasm and increasing the osmotic potential in the vacuoles.

# *Stomatal Movement*

In most plant species K+, associated with an anion, has the major responsibility for turgor changes in the guard cells during stomatal movement. An increase in the K+ concentration in the guard cells increases their osmotic potential and results in the uptake of water from the adjacent cells and a corresponding increase in turgor in the guard cells and thus stomata opening.

The accumulation of K+ in the guard ,The accumulation of K+ in the vacuoles has to be balanced by ,mainly Cl~ or malate2-, depending on the plant species and concentrations of Cl~ in the guard cells.

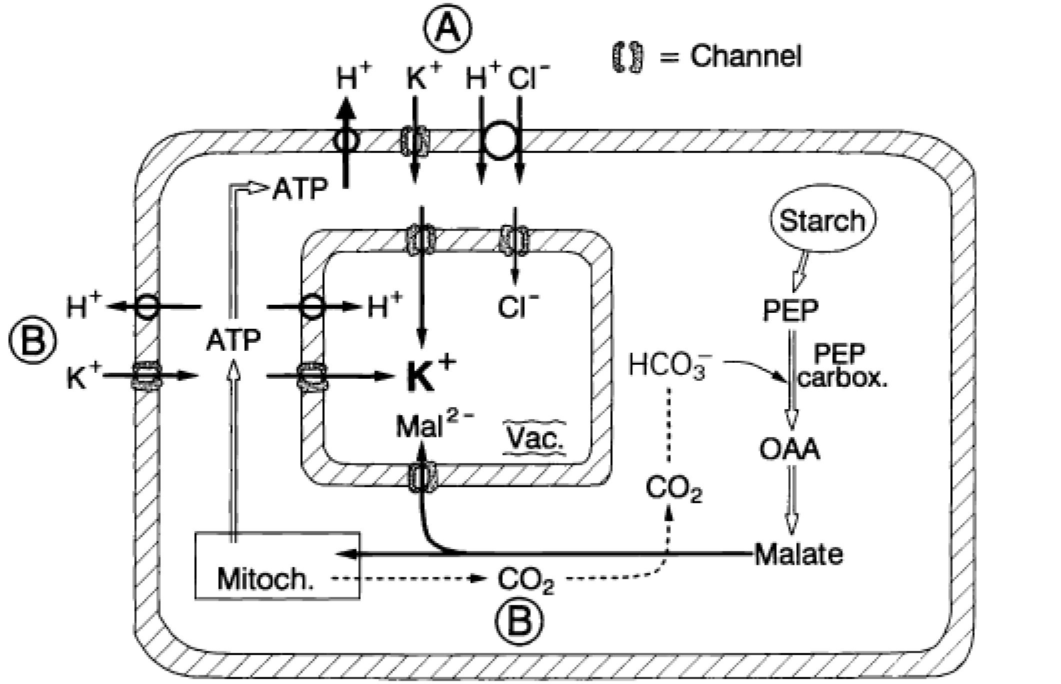
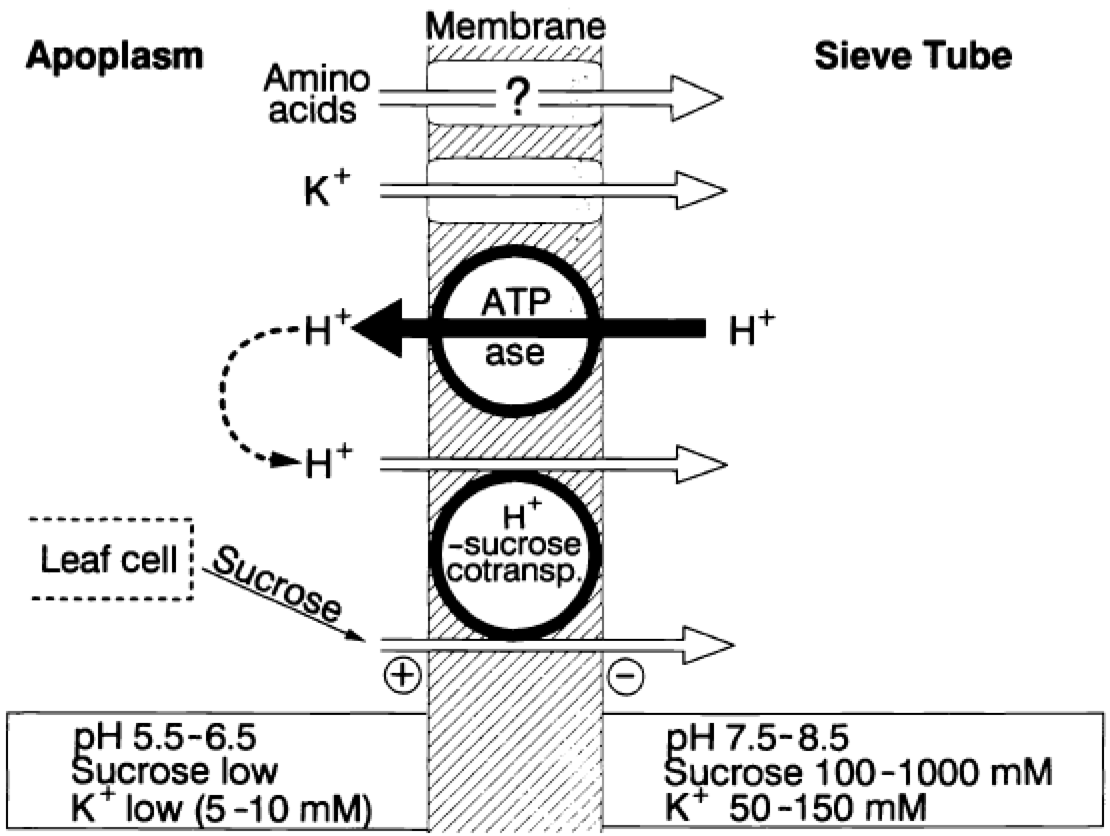



**Fig. 8.34** Model of stomatal opening driven by proton pumps and $K^+ + Cl^-$ transport (A) or $K^+ +$ malate transport (B) into guard cell vacuole. (Modified from Raschke *et al.*, 1988.)

# Phloem Transport

Potassium has important functions in both loading of sucrose, and in the rate of mass flow-driven solute transport in the sieve tubes .function of K+ is related to the necessity to maintain a high pH in the sieve tubes for sucrose loading and the contribution of K+ to the transport rates of photosynthates from source to sink.


Membrane
Apoplasm
Sieve Tube
Amino acids
?
K+
ATP ase
H+
H+
H+
H+ -sucrose cotransp.
Leaf cell
Sucrose
+
−
pH 5.5-6.5
Sucrose low
K+ low (5 -10 mM)
pH 7.5-8.5
Sucrose 100-1000 mM
K+ 50-150 mM

# Cation-Anion Balance

The role of $K^+$ in the cation-anion balance is also reflected in nitrate metabolism, in which $K^+$ is often the dominant counter for NO3 in long-distance transport in the xylem as well as for storage in vacuoles.

# Potassium Supply, Plant Growth and Plant Composition

When the soil water supply is limited, loss of turgor and wilting are typical symptoms of potassium deficiency.

The lower stability of potassium-sufficient plants to drought stress is related to several factors :

(a) the role of K+ in stomatal regulation, which is the major mechanism controlling the water regime of higher plants,

(b) the importance of K+ for the osmotic potential in the vacuoles, maintaining a high tissue water content even under drought conditions.

# iron

Iron as a transition element is characterized by the relative ease by which it may change its oxidation state

$$Fe^{3+} \underset{-e^-}{\overset{+e^-}{\rightleftharpoons}} Fe^{2+}$$

The high affinity of iron for various ligands (e.g., organic acids or inorganic phosphate) makes it very important in short- or long-distance transport in plants.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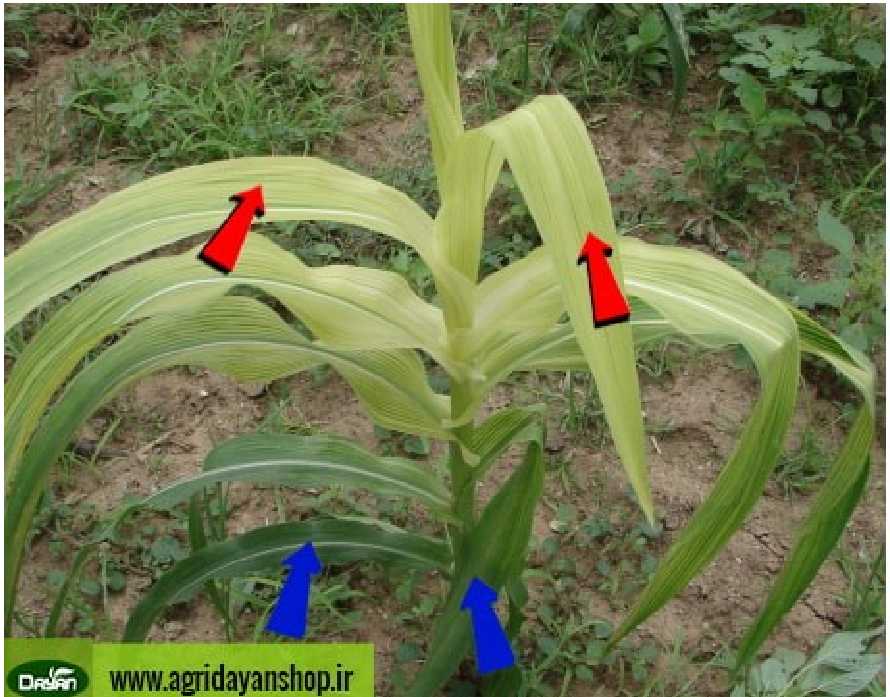
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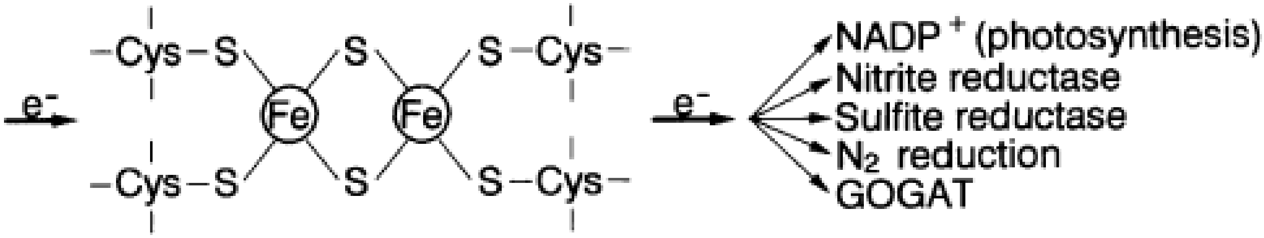
# *Heme Proteins*

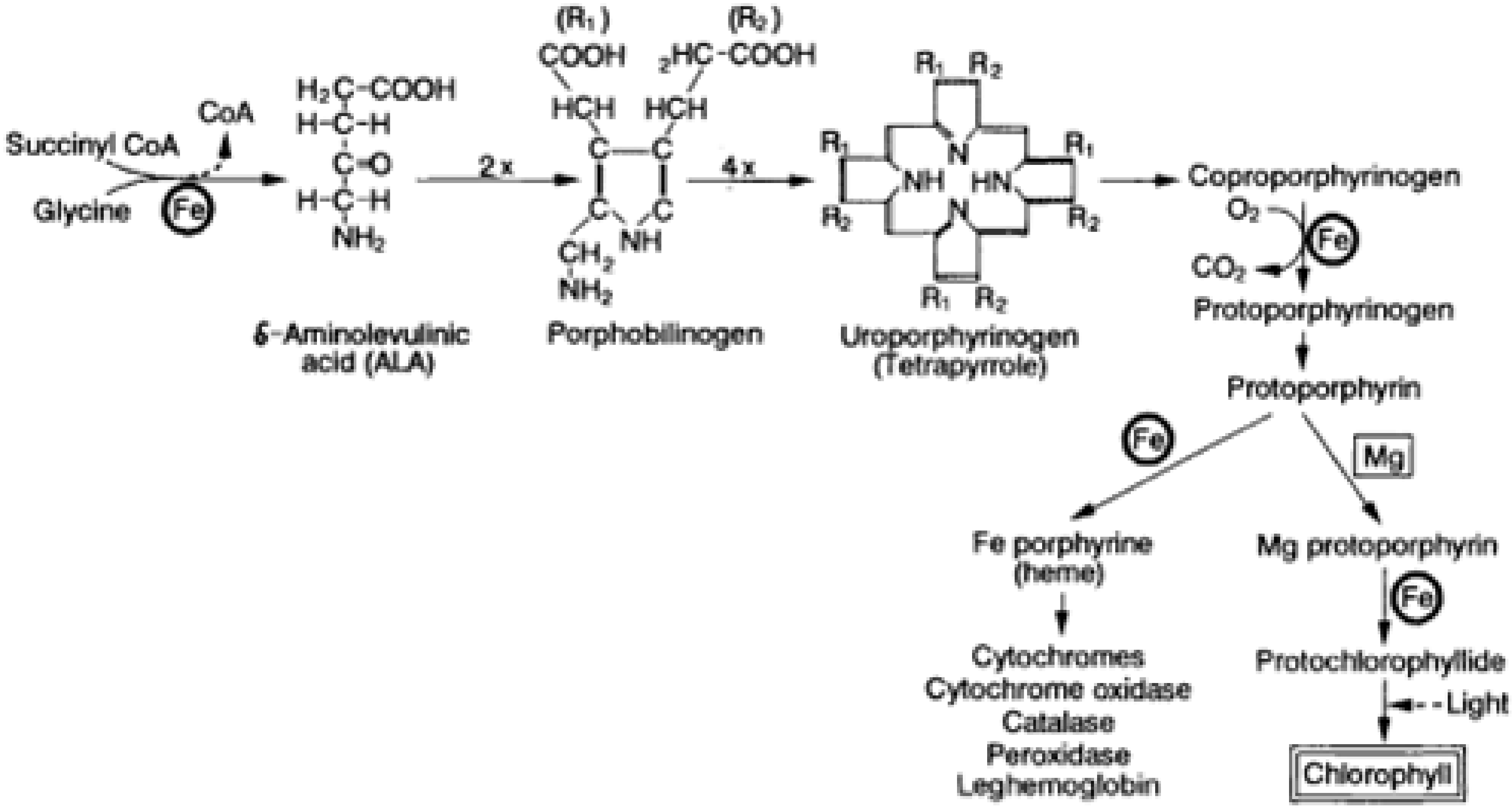
- Cytochromes are constituents of the redox systems in chloroplasts ,in mitochondria, and also a component in the redox chain in nitrate reductase.

- Other heme enzymes are catalase and peroxidases

# Iron-Sulfur Proteins

- In these nonheme proteins iron is coordinated to the thiol group of cysteine or to inorganic sulfur as clusters, or to both. The most well-known one is ferredoxin, which acts as an electron transmitter in a number of basic metabolic processes according to the principle:





Succinyl CoA
Glycine
CoA
Fe
2 x
4 x
δ-Aminolevulinic acid (ALA)
Porphobilinogen
Uroporphyrinogen (Tetrapyrrole)
Coproporphyrinogen
O2
CO2
Protoporphyrinogen
Protoporphyrin
Mg
Fe porphyrine (heme)
Mg protoporphyrin
Cytochromes
Cytochrome oxidase
Catalase
Peroxidase
Leghemoglobin
Protochlorophyllide
Light
Chlorophyll

Aconitase is an iron-sulfur protein *which catalyzes the* isomeration of citrate to isocitrate in the tricarboxylic acid cycle.

Riboflavin also accumulates in most dicotyledenous plant species under iron deficiency,and its release from roots may be enhanced by a factor of 200 in iron deficient plants .

Accumulation of riboflavin is presumably the result of alterations in purine metabolism due to impairment of xanthine oxidase.

Lipoxygenases are enzymes containing one atom iron per molecule (Hildebrand, 1989), and catalyze the peroxidation of linolic and linolenic acid, i.e., of long-chain polyunsaturated fatty acids.

# Chloroplast Development and Photosynthesis

Iron is required for protein synthesis, and the number of ribosomes - the sites of protein synthesis - decrease in iron-deficient leaf cells.

However, under iron deficiency, protein synthesis in chloroplasts is much more impaired than in the cytoplasm

Effect of Iron Deficiency on Chlorophyll Content and Enzyme Activity in Tomato Leaves[a]

| Treatment | Iron in leaves ($\mu g\ g^{-1}$ fresh wt) | Chlorophyll ($mg\ g^{-1}$ fresh wt) | Enzyme activity (relative) | |
|---|---|---|---|---|
| | | | Catalase | Peroxidase |
| +Fe | 18.5 | 3.52 | 100 | 100 |
| −Fe | 11.1 | 0.25 | 20 | 56 |

Effect of Iron Deficiency on Content of Chlorophyll and Ferredoxin and Nitrate Reductase Activity in Citrus Leaves[a]

| Fe content ($\mu g\ g^{-1}$ dry wt) | Chlorophyll ($mg\ g^{-1}$ dry wt) | Ferredoxin ($mg\ g^{-1}$ dry wt) | Nitrate reductase (nmol $NO_2\ g^{-1}$ fresh wt $h^{-1}$) |
|---|---|---|---|
| 96 | 1.80 | 0.82 | 937 |
| 62 | 1.15 | 0.44 | 408 |
| 47 | 0.55 | 0.35 | 310 |
| 47 → 81[b] | — | 0.63 | 943 |

Relationship between Iron Supply, Chlorophyll Content in Leaves, and Organic Acid Content in Roots of Oat[a]

| Treatment | Chlorophyll content (relative) | Organic acid content ($\mu g\ (10\ g)^{-1}$ fresh wt) | | | |
|---|---|---|---|---|---|
| | | Malic | Citric | Other | Total |
| +Fe | 100 | 39 | 11 | 23 | 73 |
| −Fe | 12 | 93 | 67 | 78 | 238 |

Effect of Iron Nutritional Status of Tobacco Leaves on Contents of Chlorophyll and Photosystem I (PS I) Components and Photosynthetic Electron Transport Capacity of PS II and PS I[a]

| | | | PS I components | | | $e^-$-Transport capacity[b] | |
|---|---|---|---|---|---|---|---|
| Fe treatment | Fe ($\mu g\ cm^{-2}$ leaf) | Chlorophyll ($\mu g\ cm^{-2}$ leaf) | P700 | Cytochromes ($pmol\ cm^{-2}$) | Protein ($\mu g\ cm^{-2}$) | PS II | PS I |
| +Fe | 1.44 | 89 | 545 | 599 | 108 | 56 | 840 |
| −Fe | 0.25 | 26 | 220 | 201 | 38 | 30 | 390 |
| −Fe + Fe[c] | 1.16 | 24 | 430 | 474 | 79 | 36 | 764 |

# Localization and Binding State of Iron

- When plants are grown under controlled conditions, about 80% of the iron is localized
- in the chloroplasts
- Under iron deficiency a shift in the distribution of iron occurs only within the chloroplasts, whereby the lamellar iron content increases at the expense of the stromal iron.
- Iron can be stored in plant cells in the stroma of plastids as phytoferritin

# Root Responses to Iron Deficiency

- In both dicots and monocots, with the exception of the grasses (graminaceous species), iron deficiency is associated with inhibition of root elongation, increase in the diameter of apical root zones, and abundant root hair formation

- These morphological changes are often associated with the formation of cells with a distinct wall labyrinth typical of transfer cells (Fig. 9.4). These transfer cells may be induced either in the rhizodermis (Fig. 9.4) or in the hypodermis

# Iron Deficiency and Iron Toxicity

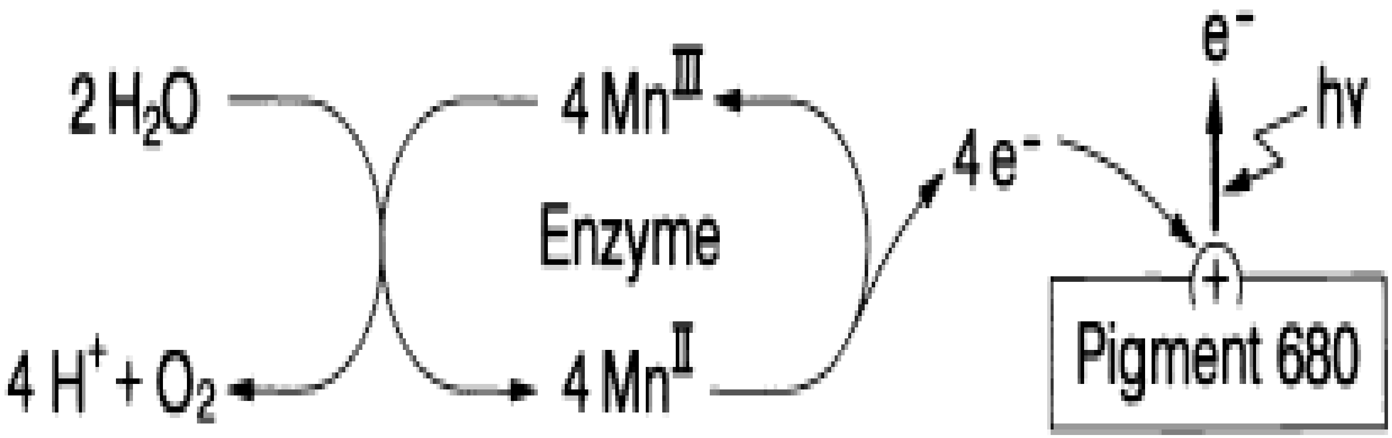
- Iron deficiency is a worldwide problem in crop production on calcareous soils. It is the major factor responsible for so-called lime-induced chlorosis .Iron deficiency might also limit $C0_2$ fixation of the phytoplankton in oceans such as the Pacific.

# manganese

Manganese can exist in the oxidation states 0, II, III, IV, VI and VII

In plants, Mn(II) is by far the dominant form, but it can readily be oxidized to Mn(III) and Mn(IV).

Manganese (II) forms only relatively weak bounds with organic ligands.



2 H2O
4 MnIII
Enzyme
4 H+ + O2
4 MnII
4 e-
e-
hν
+
Pigment 680

# Manganese Containing Enzymes

- Superoxide dismutases (SOD) are present in all aerobic organisms and play an essential role in the survival of these organisms in the presence of oxygen
- The conversion of O is catalyzed by SOD, and the subsequent dismutation of $H_20_2$ into $H_20$ and $0_2$ facilitated by either peroxidases, catalase

- The isoenzymes of SOD differ in their metal component which might be either iron ,manganese (MnSOD) or copper+zinc (Cu-ZnSOD).

$$O_2 + e^- \longrightarrow O_2^{\cdot -} \text{ (Superoxide)}$$

$$O_2^{\cdot -} + O_2^{\cdot -} + 2H^+ \xrightarrow[\text{dismutase (SOD)}]{\text{Superoxide-}} H_2O_2 \text{ (Hydrogen peroxide)} + O_2$$

$$2H_2O_2 \longrightarrow 2H_2O + O_2$$

**Malic enzyme** catalyzing the reaction :

$$\text{Malate} + \text{NADP}^+ \xrightarrow[\text{Mn}^{2+},\ \text{Mg}^{2+}]{} \text{Pyruvate} + \text{NADPH} + \text{H}^+ + \text{CO}_2$$

**Isocitrate dehydrogenase** catalyzing the reaction :

$$\text{Isocitrate} + \text{NADP}^+ \xrightarrow[\text{Mn}^{2+},\ \text{Mg}^{2+}]{} \text{Oxalosuccinate} + \text{NADPH}$$

Mn2+ activates RNA polymerase.

# Proteins, Carbohydrates, and Lipids

The accumulation of soluble nitrogen is a reflection of a shortage in reducing equivalents and carbohydrates for nitrate reduction, as well as a lower demand for reduced nitrogen.

Manganese deficiency has the most severe effect on the content of nonstructural carbohydrates.

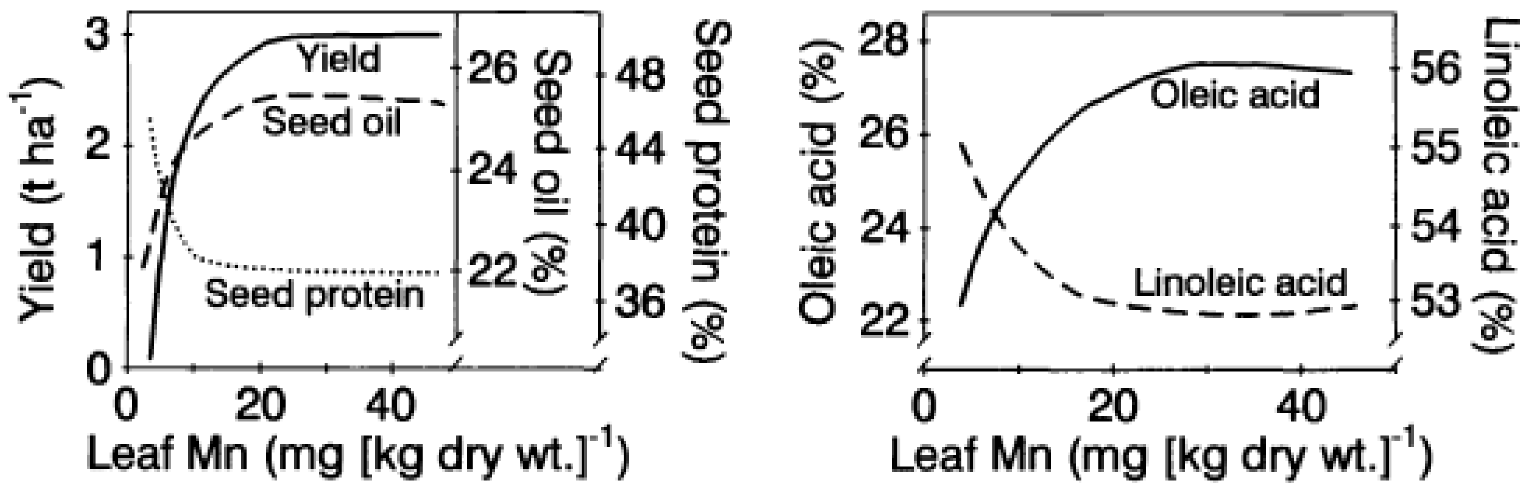
This decrease in carbohydrate content is particularly evident in the roots and most likely a key factor responsible for the depression in root growth of the deficient plants. This depression in lipid content in chloroplasts can be attributed to the role of $Mn^{2+}$ in biosynthesis of fatty acids .

Effect of Manganese Deficiency on the Growth and Composition of Bean Plants[a]

| Parameter | Leaves | | Stems | | Roots | |
|---|---|---|---|---|---|---|
| | +Mn | −Mn | +Mn | −Mn | +Mn | −Mn |
| Dry wt (g per plant) | 0.64 | 0.46 | 0.55 | 0.38 | 0.21 | 0.14 |
| Protein nitrogen (mg $g^{-1}$ dry wt) | 52.7 | 51.2 | 13.0 | 14.4 | 27.0 | 25.6 |
| Soluble nitrogen (mg $g^{-1}$ dry wt) | 6.8 | 11.9 | 10.0 | 16.2 | 17.2 | 21.7 |
| Soluble carbohydrates (mg $g^{-1}$ dry wt) | 17.5 | 4.0 | 35.6 | 14.5 | 7.6 | 0.9 |

The fatty acid composition of the oil is also markedly altered, the content of linoleic acid and certain other fatty acids increasing. This is counteracted by a decrease in oleic acid content.

Lower lignin contents in the manganese-deficient plants are a reflection of the requirement for manganese in various steps of lignin biosynthesis. The decrease is particularly evident in the roots, and an important factor responsible for the lower resistance of manganese deficient plants to root infecting pathogens


Yield
Seed oil
Seed protein
Yield (t ha-1)
Seed oil (%)
Seed protein (%)
0
1
2
3
22
24
26
36
40
44
48
0
20
40
Leaf Mn (mg [kg dry wt.]-1)
Oleic acid
Linoleic acid
Oleic acid (%)
Linoleic acid (%)
22
24
26
28
53
54
55
56
0
20
40
Leaf Mn (mg [kg dry wt.]-1)

# Cell Division and Extension

Inhibition of root growth in manganese-deficient plants is caused by shortage in

carbohydrates as well as by a direct requirement for growth.

The rate of elongation seems to respond more rapidly to manganese deficiency

than does the rate of cell division.