

# Assimilation of Mineral Nutrients

Chapter 12

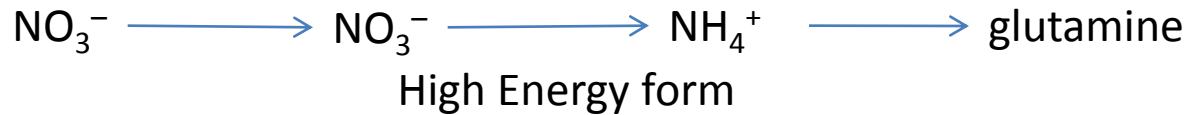
OrR

HIGHER PLANTS ARE AUTOTROPHIC ORGANISMS that can synthesize their organic molecular components out of inorganic nutrients obtained from their surroundings.

This incorporation of mineral nutrients into organic substances such as pigments, enzyme cofactors, lipids, nucleic acids, and amino acids is termed **nutrient assimilation**.

Assimilation of some nutrients—particularly nitrogen and sulfur—requires a complex series of biochemical reactions that are among the most energy-requiring reactions in living organisms:

### 1. Nitrate ( $\text{NO}_3^-$ ) assimilation:



This process consumes the equivalent of 12 ATPs per nitrogen

### 2. Biological Nitrogen fixation :



consumes about 16 ATPs per nitrogen

**3. The assimilation of sulfate** ( $\text{SO}_4^{2-}$ ) into the amino acid cysteine via the two pathways found in plants consumes about 14 ATPs.

in reverse—say, from  $\text{NH}_4\text{NO}_3$  (ammonium nitrate) to  $\text{N}_2$ —they become explosive, liberating vast amounts of energy as motion, heat, and light.

Nearly all explosives are based on the rapid oxidation of nitrogen or sulfur compounds.

**Assimilation of other nutrients, especially the macronutrient and micronutrient cations, involves the formation of complexes with organic compounds.**

**Mg<sup>2+</sup> associates with chlorophyll pigments,**

**Ca<sup>2+</sup> associates with pectates within the cell wall, and**

**Mo<sup>6+</sup> associates with enzymes such as nitrate reductase and nitrogenase.**

# NITROGEN IN THE ENVIRONMENT

Nitrogen is present in many forms in the biosphere.

The atmosphere contains vast quantities (about 78% by volume) of molecular nitrogen ( $N_2$ )

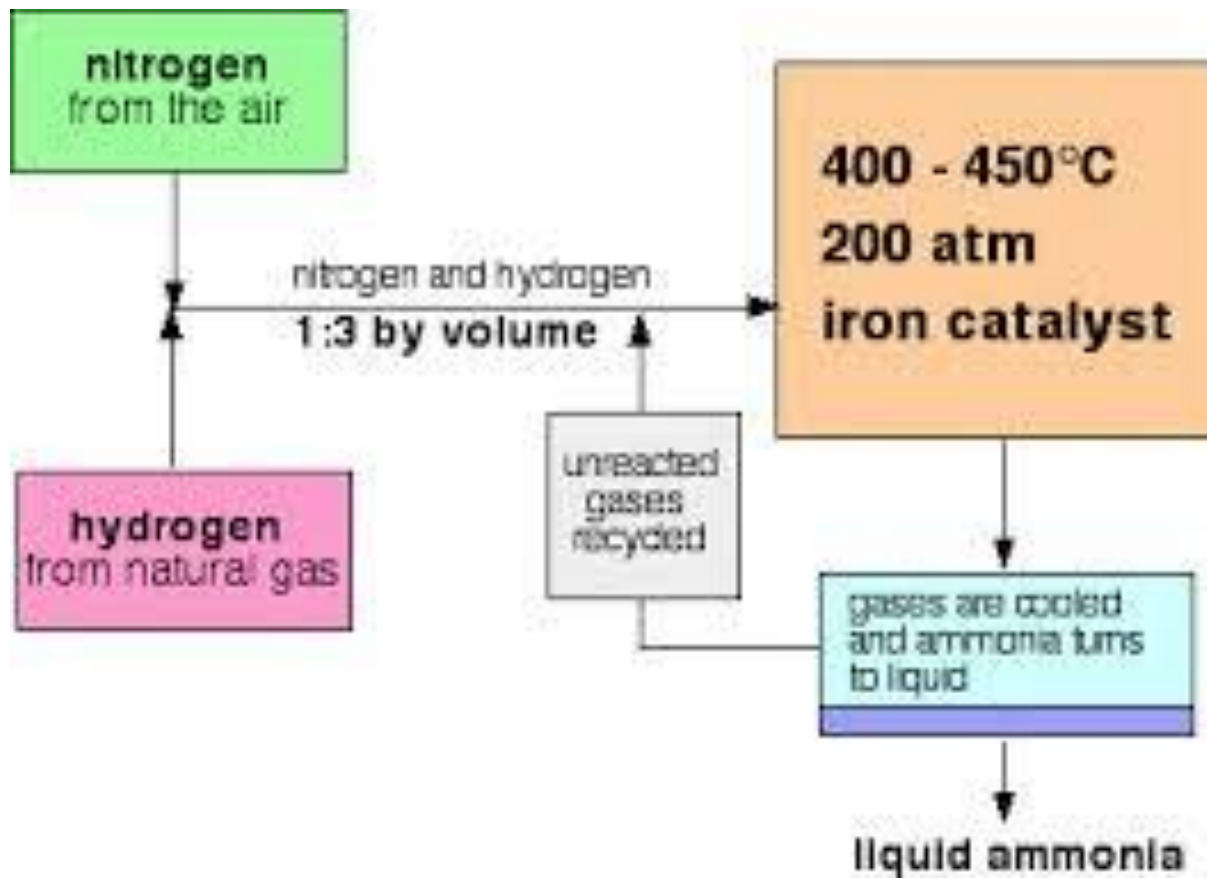
For the most part, this large reservoir of nitrogen is not directly available to living organisms

**Nitrogen fixation** : the breaking of an exceptionally stable triple covalent bond between two nitrogen atoms to produce ammonia ( $NH_3$ ) or nitrate ( $NO_3^-$ ).

can be accomplished by both:

- **industrial processes**
- **natural processes**

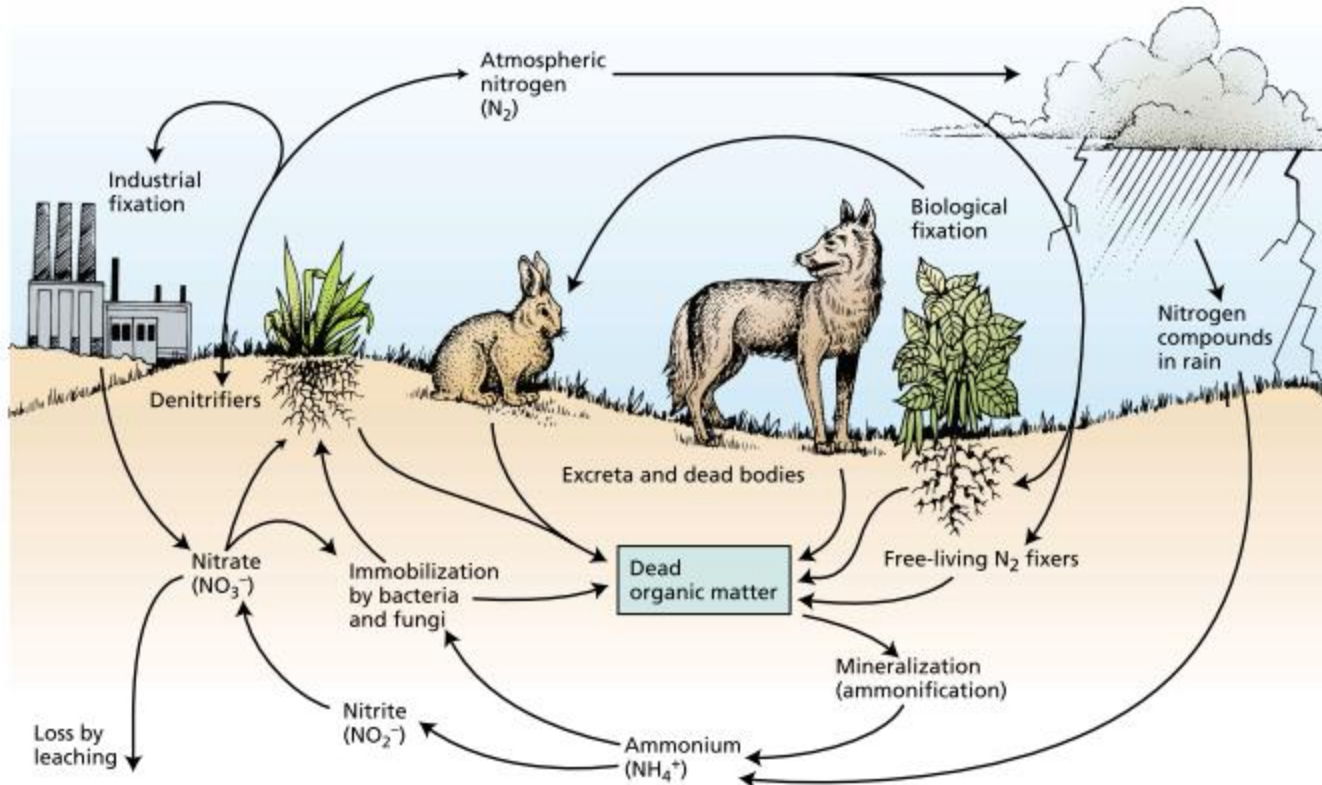
## Haber-Bosch process



## Natural processes

- 1. Lightning.** Lightning is responsible for about 8% of the nitrogen fixed. Lightning converts water vapor and oxygen into highly reactive hydroxyl free radicals, free hydrogen atoms, and free oxygen atoms that attack molecular nitrogen to form nitric acid. This nitric acid subsequently falls to Earth with rain.
- 2. Photochemical reactions.** Approximately 2% of the nitrogen fixed derives from photochemical reactions between gaseous nitric oxide (NO) and ozone (O<sub>3</sub>) that produce nitric acid.
- 3. Biological nitrogen fixation.** The remaining 90% results from biological nitrogen fixation, in which bacteria or blue-green algae (cyanobacteria) fix N<sub>2</sub> into ammonium

Once fixed in ammonium or nitrate, nitrogen enters a **biogeochemical cycle** and passes through several organic or inorganic forms before it eventually returns to molecular nitrogen





**TABLE 12.1**  
**The major processes of the biogeochemical nitrogen cycle**

Process	Definition
Industrial fixation	Industrial conversion of molecular nitrogen to ammonia
Atmospheric fixation	Lightning and photochemical conversion of molecular nitrogen to nitrate
Biological fixation	Prokaryotic conversion of molecular nitrogen to ammonia
Plant acquisition	Plant absorption and assimilation of ammonium or nitrate
Immobilization	Microbial absorption and assimilation of ammonium or nitrate
Ammonification	Bacterial and fungal catabolism of soil organic matter to ammonium
Nitrification	Bacterial ( <i>Nitrosomonas</i> sp.) oxidation of ammonium to nitrite and subsequent bacterial ( <i>Nitrobacter</i> sp.) oxidation of nitrite to nitrate
Mineralization	Bacterial and fungal catabolism of soil organic matter to mineral nitrogen through ammonification or nitrification
Volatilization	Physical loss of gaseous ammonia to the atmosphere
Ammonium fixation	Physical embedding of ammonium into soil particles
Denitrification	Bacterial conversion of nitrate to nitrous oxide and molecular nitrogen
Nitrate leaching	Physical flow of nitrate dissolved in groundwater out of the topsoil and eventually into the oceans

## Stored Ammonium or Nitrate Can Be Toxic

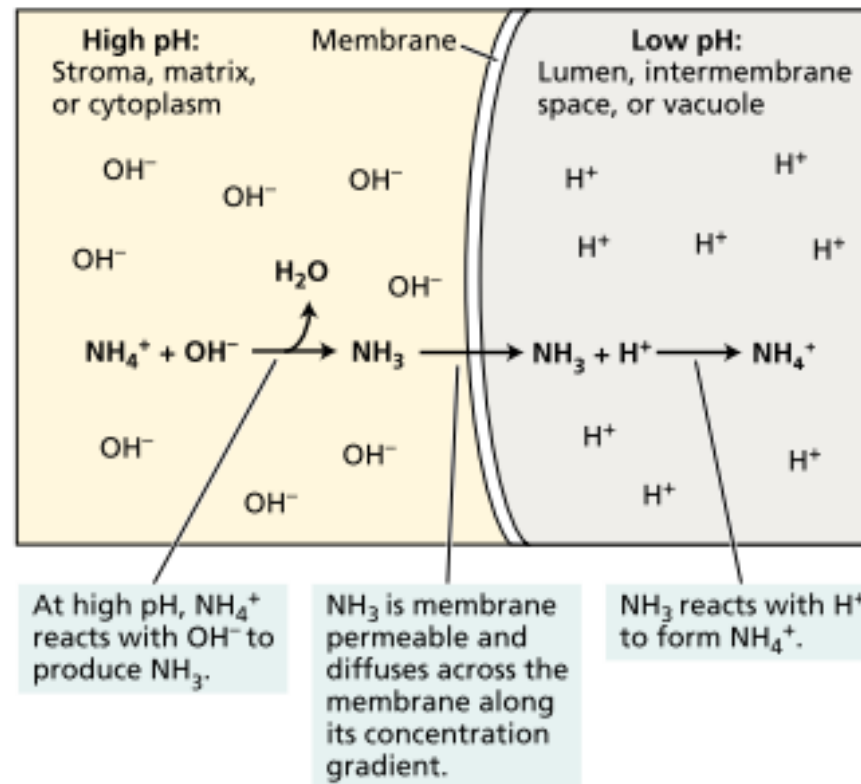
Plants can store high levels of nitrate, or they can translocate it from tissue to tissue without deleterious effect.

If livestock and humans consume plant material that is high in nitrate, they may suffer **methemoglobinemia**, a disease in which the liver reduces nitrate to nitrite, which combines with hemoglobin and renders the hemoglobin unable to bind oxygen.

Humans and other animals may also convert nitrate into nitrosamines, which are potent carcinogens.

## High levels of ammonium are toxic to both plants and animals. How plants deal with it?

Ammonium dissipates transmembrane proton gradients that are required for both photosynthetic and respiratory electron transport and for sequestering metabolites in the **vacuole**.



$\text{NH}_4^+$  toxicity can dissipate/dissolve pH gradients.

# NITRATE ASSIMILATION

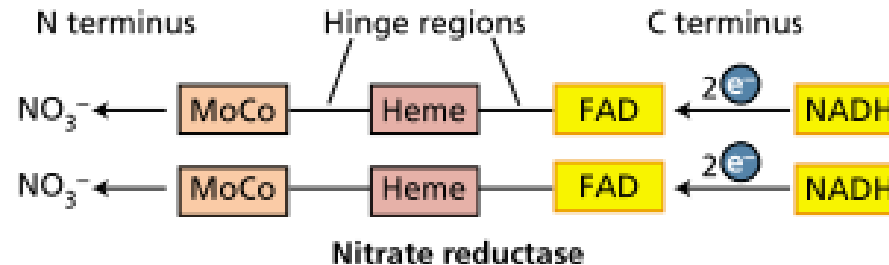
Plants assimilate most of the nitrate absorbed by their roots into organic nitrogen compounds.

nitrate reductase



The most common form of nitrate reductase uses only NADH as an electron donor; another form of the enzyme that is found predominantly in nongreen tissues such as roots can use either NADH or NADPH

## Nitrate reductase



The nitrate reductases of higher plants are composed of two identical subunits, each containing three prosthetic groups: molybdenum complex (MoCo), heme, and FAD.

The NADH binds at the FAD-binding region of each subunit and initiates a two-electron transfer from the **carboxyl (C) terminus**, through each of the electron transfer components, to the **amino (N) terminus**.

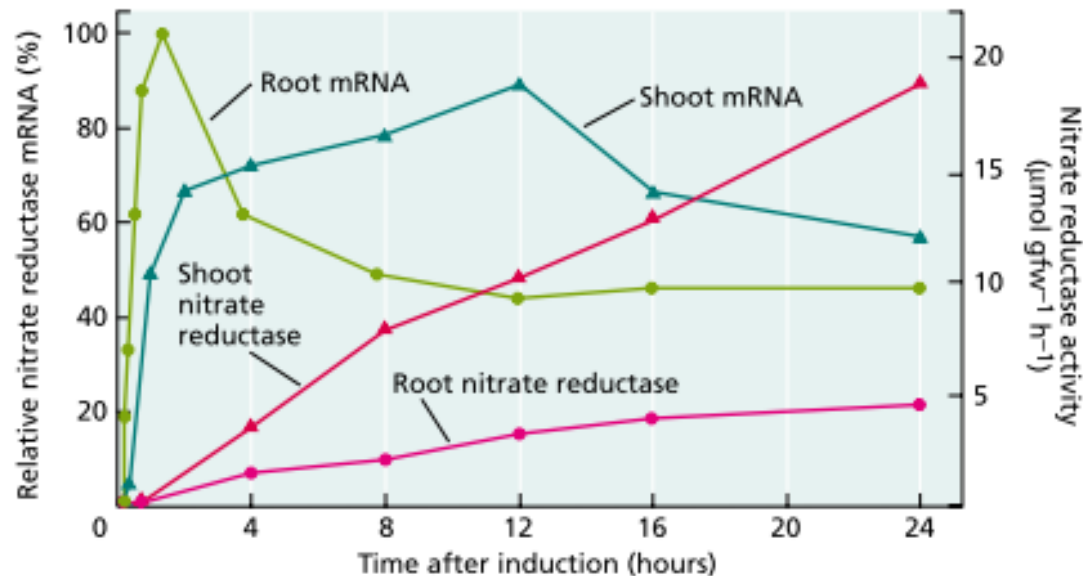
Nitrate is reduced at the molybdenum complex near the amino terminus.

The polypeptide sequences of the hinge regions are highly variable among species.

# Regulation of Nitrate Reductase

Nitrate, light, and carbohydrates influence nitrate reductase at the transcription and translation levels

In barley seedlings, nitrate reductase mRNA was detected approximately 40 minutes after addition of **nitrate**, and maximum levels were attained within 3 hours there was a gradual linear increase in nitrate reductase activity, reflecting the slower synthesis of the protein.



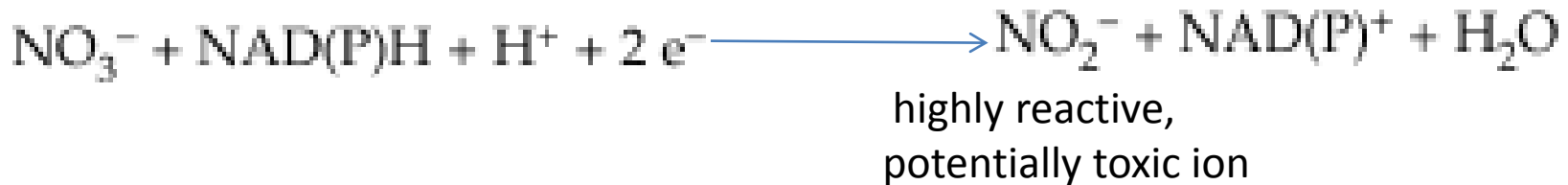
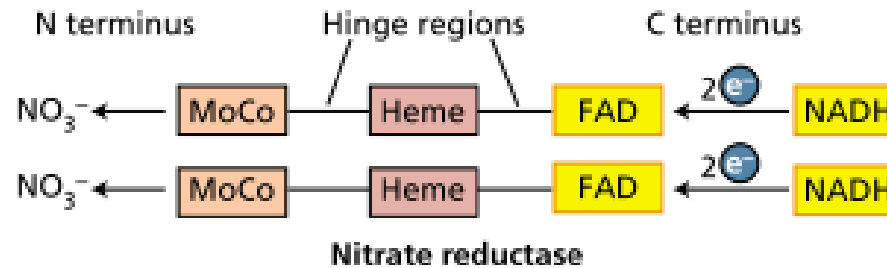
**Light, carbohydrate levels, and other environmental factors** stimulate a protein phosphatase that dephosphorylates several serine residues on the nitrate reductase protein and thereby **activates the enzyme**.

# Regulation of Nitrate Reductase

Operating in the reverse direction, **darkness and Mg<sup>2+</sup>** stimulate a protein kinase that phosphorylates the same serine residues, which then interact with a **14-3-3 inhibitor protein**, and thereby inactivate nitrate reductase

*Regulation of nitrate reductase activity through phosphorylation and dephosphorylation provides more rapid control than can be achieved through synthesis or degradation of the enzyme (minutes versus hours).*

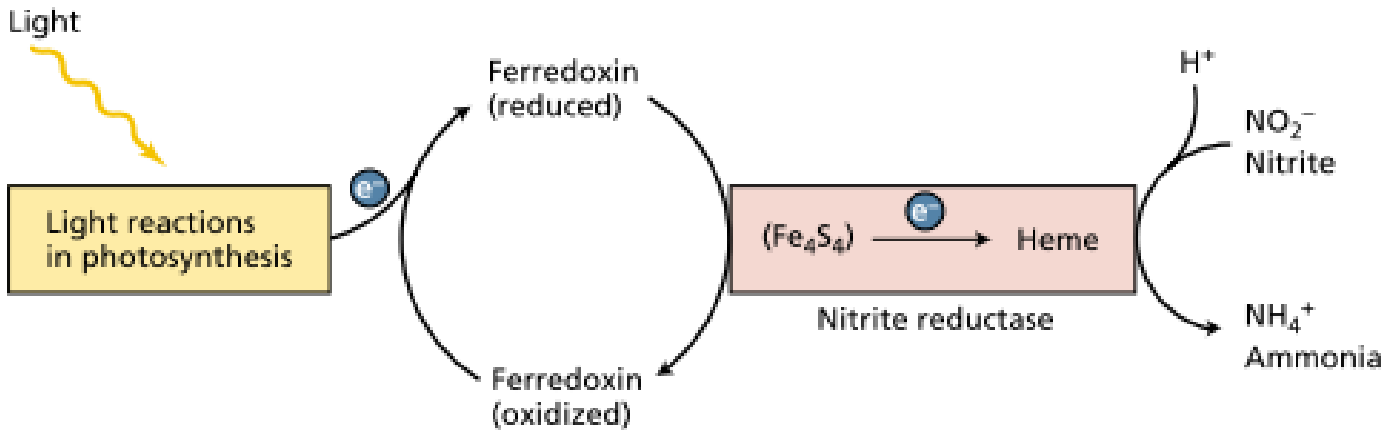
## Nitrite Reductase Converts Nitrite to Ammonium



Reduced ferredoxin derives from photosynthetic electron transport in the chloroplasts and from NADPH generated by the oxidative pentose phosphate pathway in nongreen tissues



## Nitrite reductase



Chloroplasts and root plastids contain different forms of the enzyme, but both forms consist of a single polypeptide containing two prosthetic groups: an iron–sulfur cluster ( $Fe_4S_4$ ) and a specialized heme.

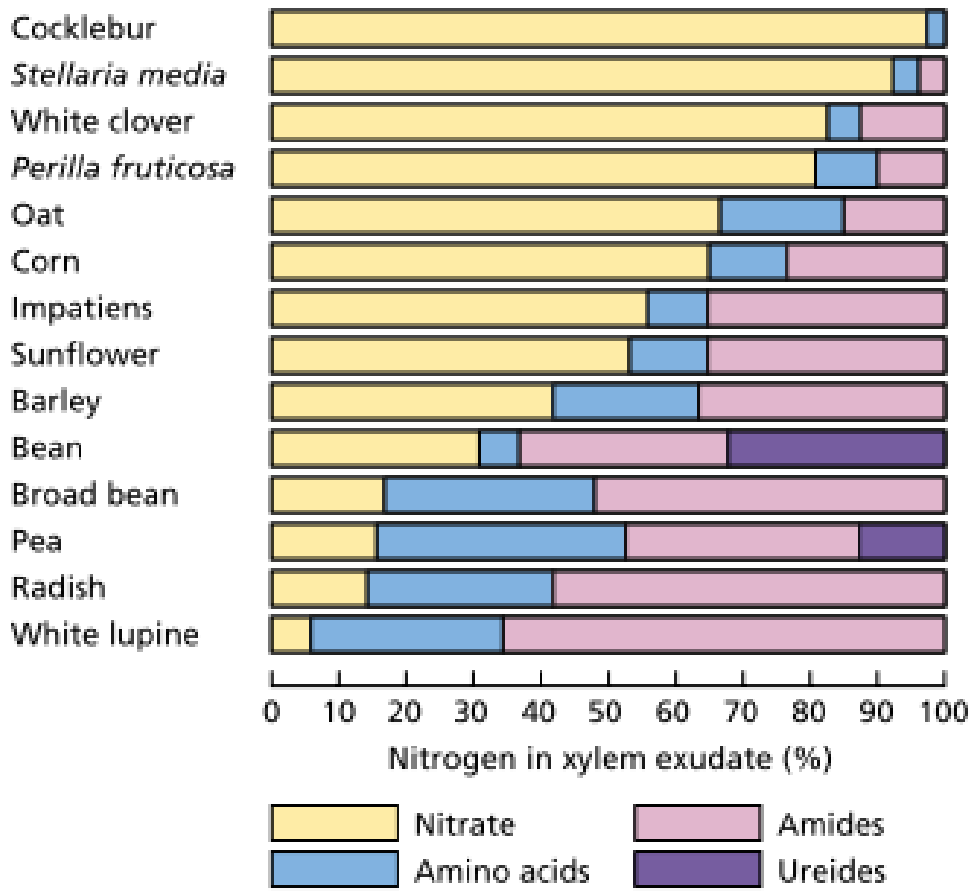
These groups acting together bind nitrite and reduce it directly to ammonium, without accumulation of nitrogen compounds of intermediate redox states.

Nitrite reductase is encoded in the nucleus and synthesized in the cytoplasm with an N-terminal transit peptide that targets it to the plastids

Whereas  $NO_3^-$  and light induce the transcription of nitrite reductase mRNA, the end products of the process—asparagine and glutamine—repress this induction.

# Plants Can Assimilate Nitrate in Both Roots and Shoots

- In many plants, when the roots receive small amounts of nitrate, nitrate is reduced primarily in the roots.
- As the supply of nitrate increases, a greater proportion of the absorbed nitrate is translocated to the shoot and assimilated there.
- Even under similar conditions of nitrate supply, the balance between root and shoot nitrate metabolism—as indicated by the proportion of nitrate reductase activity in each of the two organs or by the relative concentrations of nitrate and reduced nitrogen in the xylem sap—varies from species to species.



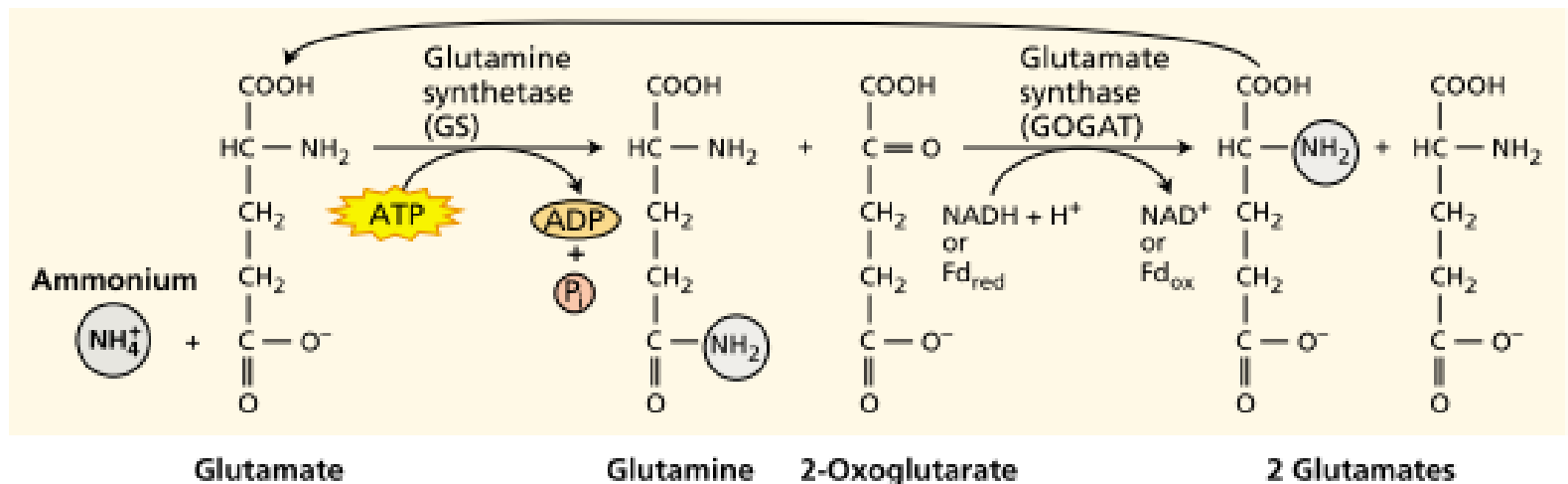
Generally, species native to temperate regions rely more heavily on nitrate assimilation by the roots than do species of tropical or subtropical origins.

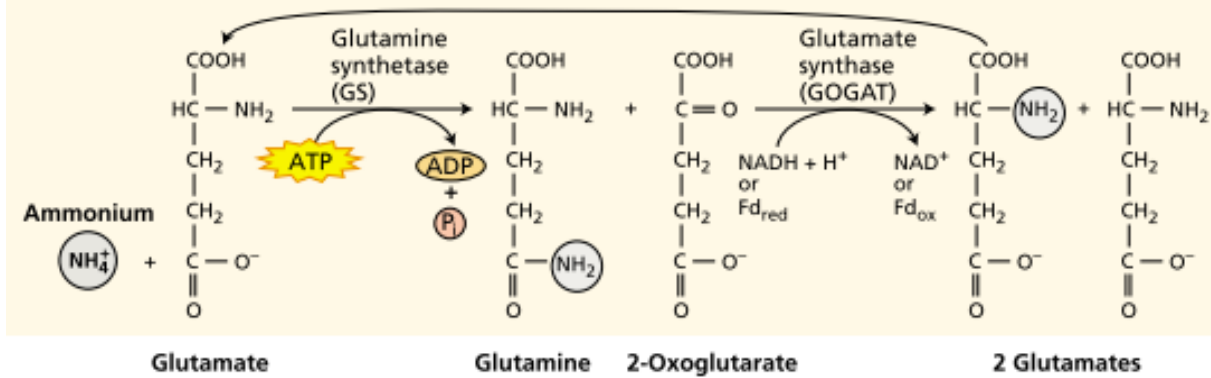
# AMMONIUM ASSIMILATION

Plant cells avoid ammonium toxicity by rapidly converting the ammonium generated from nitrate assimilation or photorespiration into amino acids.

Conversion of Ammonium to Amino Acids Requires Two Enzymes:

1. Glutamine synthetase (GS)
2. Glutamate synthase (also known as glutamine:2-oxo-glutarate aminotransferase, or GOGAT).





## Glutamine synthetase (GS)

This reaction requires the hydrolysis of one ATP and involves a divalent cation such as  $\text{Mg}^{2+}$ ,  $\text{Mn}^{2+}$ , or  $\text{Co}^{2+}$  as a cofactor.

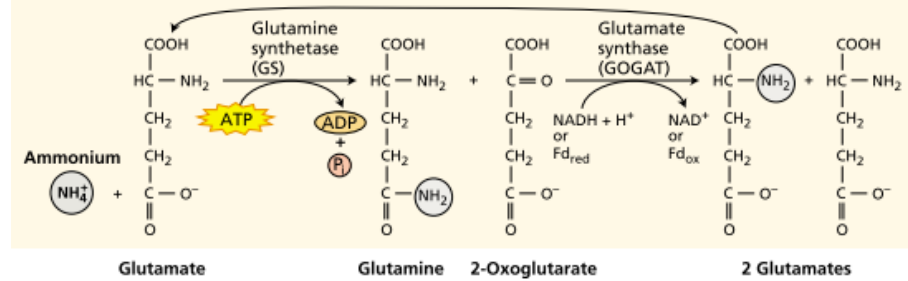
Plants contain two classes of GS, one in the cytosol and the other in root plastids or shoot chloroplasts.

The cytosolic forms are expressed in germinating seeds or in the vascular bundles of roots and shoots and produce glutamine for intracellular nitrogen transport.

The GS in root plastids generates amide nitrogen for local consumption; the GS in shoot chloroplasts reassimilates photorespiratory  $\text{NH}_4^+$

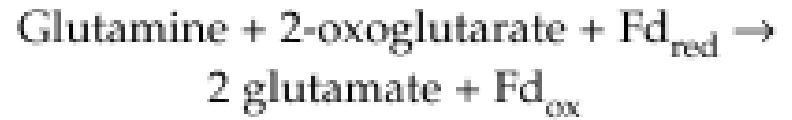
Light and carbohydrate levels alter the expression of the plastid forms of the enzyme, but they have little effect on the cytosolic forms.

## glutamate synthase / glutamine:2-oxoglutarate aminotransferase, or GOGAT)



Plants contain two types of GOGAT:

- One accepts electrons from NADH;
- the other accepts electrons from ferredoxin (Fd):



The NADH type of the enzyme (NADH-GOGAT) is located in plastids of nonphotosynthetic tissues such as roots or vascular bundles of developing leaves.

In roots, NADH-GOGAT is involved in the assimilation of NH<sub>4</sub><sup>+</sup> absorbed from the rhizosphere

in vascular bundles of developing leaves,  
NADH-GOGAT assimilates glutamine translocated from roots or senescing leaves.

The ferredoxin-dependent type of glutamate synthase (Fd-GOGAT) is found in chloroplasts and serves in photorespiratory nitrogen metabolism.

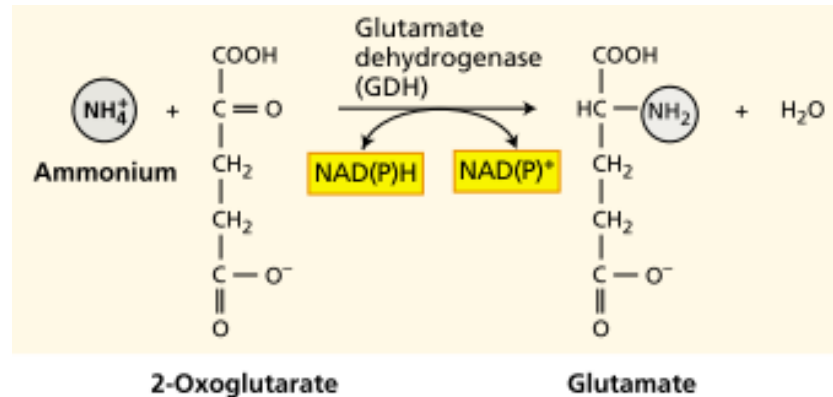
Both the amount of protein and its activity increase with light levels.

Roots, particularly those under nitrate nutrition, have Fd-GOGAT in plastids.

Fd-GOGAT in the roots presumably functions to incorporate the glutamine generated during nitrate assimilation.

## Ammonium Can Be Assimilated via an Alternative Pathway

**Glutamate dehydrogenase (GDH)** catalyzes a reversible reaction that synthesizes or deaminates glutamate

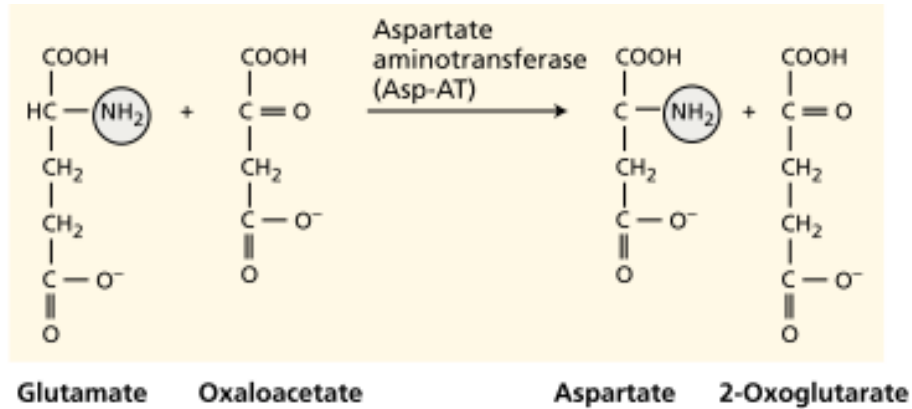


An NADH-dependent form of GDH is found in mitochondria, and an NADPH-dependent form is localized in the chloroplasts of photosynthetic organs.

Although both forms are relatively abundant, they cannot substitute for the GS–GOGAT pathway for assimilation of ammonium, and their primary function is to deaminate glutamate

## Transamination Reactions Transfer Nitrogen

The enzymes that catalyze these reactions are known as aminotransferases.



All transamination reactions require pyridoxal phosphate (vitamin B6) as a cofactor.

Aminotransferases are found in the cytoplasm, chloroplasts, mitochondria, glyoxysomes, and peroxisomes.

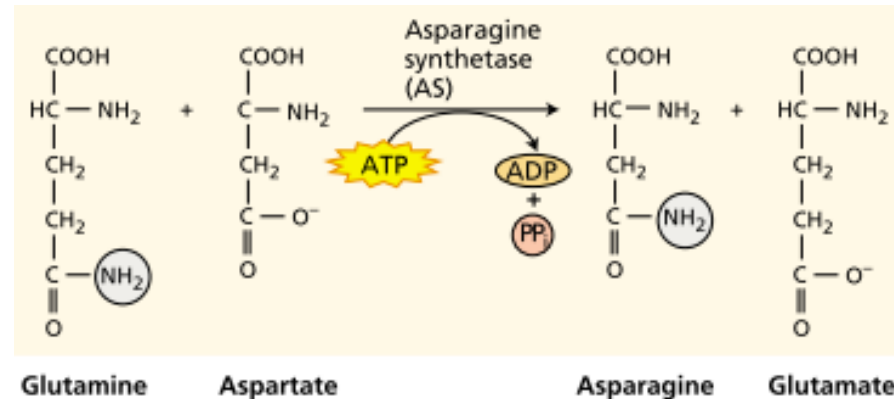
The aminotransferases localized in the chloroplasts may have a significant role in amino acid biosynthesis because plant leaves or isolated chloroplasts exposed to radioactively labeled carbon dioxide rapidly incorporate the label into glutamate, aspartate, alanine, serine, and glycine.

# Asparagine and Glutamine Link Carbon and Nitrogen Metabolism

**Asparagine** serves not only as a protein precursor, but as a key compound for nitrogen transport and storage because of its stability and high nitrogen-to-carbon ratio :

- 2 N to 4 C for asparagine
- 2 N to 5 C for glutamine
- 1 N to 5 C for glutamate

The major pathway for asparagine synthesis involves the transfer of the amide nitrogen from glutamine to asparagine



Asparagine synthetase (AS), the enzyme that catalyzes this reaction, is found in the cytosol of leaves and roots and in nitrogen-fixing nodules



## **Asparagine synthetase (AS)**

High levels of light and carbohydrate—conditions that stimulate plastid GS and Fd-GOGAT—inhibit the expression of genes coding for AS and the activity of the enzyme.

By contrast, energy-limited conditions inhibit GS and GOGAT, stimulate AS, and thus favor nitrogen assimilation into asparagine, a compound that is rich in nitrogen and sufficiently stable for long-distance transport or long-term storage.

# BIOLOGICAL NITROGEN FIXATION

## Free-Living and Symbiotic Bacteria Fix Nitrogen

**TABLE 12.2**

Examples of organisms that can carry out nitrogen fixation

Symbiotic nitrogen fixation	
Host plant	N-fixing symbionts
Leguminous: legumes, <i>Parasponia</i>	<i>Azorhizobium</i> , <i>Bradyrhizobium</i> , <i>Photorhizobium</i> , <i>Rhizobium</i> , <i>Sinorhizobium</i>
Actinorhizal: alder (tree), <i>Ceanothus</i> (shrub), <i>Casuarina</i> (tree), <i>Datisca</i> (shrub)	<i>Frankia</i>
<i>Gunnera</i>	<i>Nostoc</i>
<i>Azolla</i> (water fern)	<i>Anabaena</i>
Sugarcane	<i>Acetobacter</i>
Free-living nitrogen fixation	
Type	N-fixing genera
Cyanobacteria (blue-green algae)	<i>Anabaena</i> , <i>Calothrix</i> , <i>Nostoc</i>
Other bacteria	
Aerobic	<i>Azospirillum</i> , <i>Azotobacter</i> , <i>Beijerinckia</i> , <i>Derxia</i>
Facultative	<i>Bacillus</i> , <i>Klebsiella</i>
Anaerobic	
Nonphotosynthetic	<i>Clostridium</i> , <i>Methanococcus</i> (archaeobacterium)
Photosynthetic	<i>Chromatium</i> , <i>Rhodospirillum</i>

## Nitrogen Fixation Requires Anaerobic Conditions

**Nitrogenase** enzymes involved in nitrogen fixation.

The enzyme irreversibly inactivates by oxygen, therefore the nitrogen fixed under anaerobic condition.

Therefore nitrogen fixing organism can do it in two ways:

1. Anaerobic condition
2. Creating an internal anaerobic environment in the presence of oxygen

A heterocyst in a filament of the nitrogen-fixing cyanobacterium *Anabaena*.

The thick-walled heterocysts, interspaced among vegetative cells, have an anaerobic inner environment that allows cyanobacteria to fix nitrogen in aerobic conditions.



Free-living bacteria that are capable of fixing nitrogen are aerobic, facultative, or anaerobic

- Aerobic nitrogen-fixing bacteria such as *Azotobacter* are thought to maintain reduced oxygen conditions (microaerobic conditions) through their high levels of respiration. Others, such as *Gloeotheca*, evolve O<sub>2</sub> photosynthetically during the day and fix nitrogen during the night.
- Facultative organisms, which are able to grow under both aerobic and anaerobic conditions, generally fix nitrogen only under anaerobic conditions.
- For anaerobic nitrogen-fixing bacteria, oxygen does not pose a problem, because it is absent in their habitat. These anaerobic organisms can be either photosynthetic (e.g., *Rhodospirillum*), or nonphotosynthetic (e.g., *Clostridium*).

## Symbiotic Nitrogen Fixation Occurs in Specialized Structures

Symbiotic nitrogen-fixing prokaryotes dwell within **nodules**, the special organs of the plant host that enclose the nitrogen-fixing bacteria

**Grasses can also develop symbiotic** relationships with nitrogen-fixing organisms, but in these associations root nodules are not produced. Instead, the nitrogen-fixing bacteria seem to colonize plant tissues or anchor to the root surfaces, mainly around the elongation zone and the root hairs

Nodules contain an oxygen-binding heme protein called leghemoglobin.

Leghemoglobin is present in the cytoplasm of infected nodule cells at high concentrations (700  $\mu\text{M}$  in soybean nodules) and gives the nodules a pink color.

The host plant produces the globin portion of leghemoglobin in response to infection by the bacteria ; the bacterial symbiont produces the heme portion.

Leghemoglobin has a high affinity for oxygen (a  $K_m$  of about 0.01  $\mu\text{M}$ ), about ten times higher than the  $\beta$  chain of human hemoglobin.



**FIGURE 12.8** Root nodules on soybean. The nodules are a result of infection by *Rhizobium japonicum*. (© Wally Eberhart/Visuals Unlimited.)

## **Establishing Symbiosis Requires an Exchange of Signals**

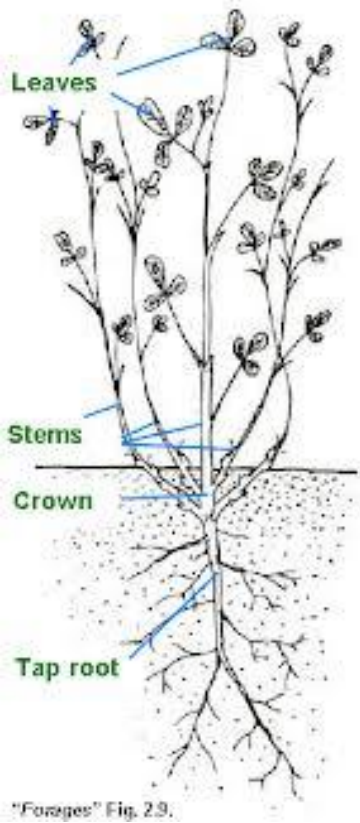
The symbiosis between legumes and rhizobia is not obligatory.

Legume seedlings germinate without any association with rhizobia, and they may remain unassociated throughout their life cycle.

Rhizobia also occur as free-living organisms in the soil.

**When and how symbiosis occur between legume plants and rhizobia?**

# When and how symbiosis occur between legume plants and rhizobia?



nodulin (Nod)  
Genes activate

migration of the bacteria toward the roots of the host plant.

This migration is a chemotactic response mediated by chemical attractants, especially (iso)flavonoids and betaines, secreted by the roots.



activated  
nodulation (nod)  
genes



FIGURE 12.8 Root nodules on soybean. The nodules are a result of infection by *Rhizobium japonicum*. (© Wally Eberhart/Visuals Unlimited.)

nitrogen-limited conditions

Plant genes specific to nodules are called nodulin (*Nod*) genes; rhizobial genes that participate in nodule formation are called nodulation (*nod*) genes

The *nod* genes are classified as common *nod* genes or host-specific *nod* genes.

The common nod genes—*nodA*, *nodB*, and *nodC*—are found in all rhizobial strains;

The host-specific nod genes—such as *nodP*, *nodQ*, and *nodH*; or *nodF*, *nodE*, and *nodL*—differ among rhizobial species and determine the host range.

Only one of the nod genes, the regulatory *nodD*, is constitutively expressed, its protein product (NodD) regulates the transcription of the other *nod* genes.

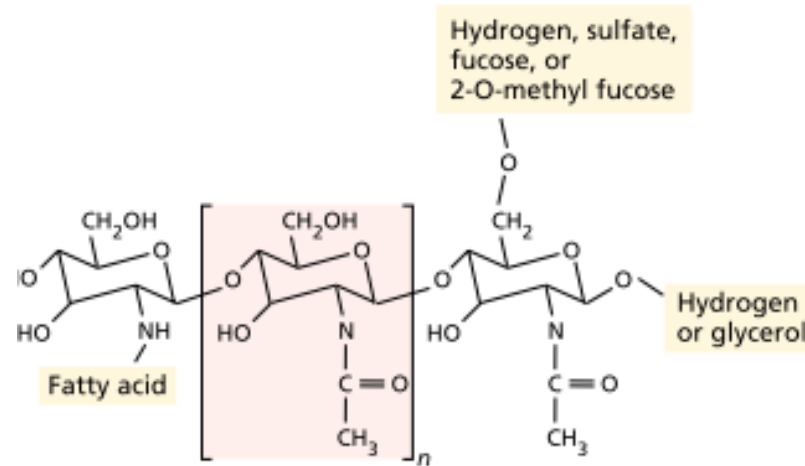
The promoter region of all nod operons, except that of *nodD*, contains a highly conserved sequence called the nod box.

Binding of the activated NodD to the nod box induces transcription of the other nod genes.



The nod genes activated by NodD code for nodulation proteins, most of which are involved in the biosynthesis of Nod factors

Nod factors are lipochitin oligosaccharide signal molecules, all of which have a chitin  $\beta$ -1 $\rightarrow$ 4-linked N-acetyl-D-glucosamine backbone (varying in length from three to six sugar units) and a fatty acyl chain on the C-2 position of the nonreducing sugar



Three of the nod genes (nodA, nodB, and nodC) encode enzymes (NodA, NodB, and NodC, respectively) that are required for synthesizing this basic structure

1. NodA is an N-acyltransferase that catalyzes the addition of a fatty acyl chain.
2. NodB is a chitin-oligosaccharide deacetylase that removes the acetyl group from the terminal nonreducing sugar.
3. NodC is a chitin-oligosaccharide synthase that links N-acetyl-D-glucosamine monomers.

**Host-specific nod genes that vary among rhizobial species are involved in the modification of the fatty acyl chain or the addition of groups important in determining host specificity**

**NodE and NodF** determine the length and degree of saturation of the fatty acyl chain.

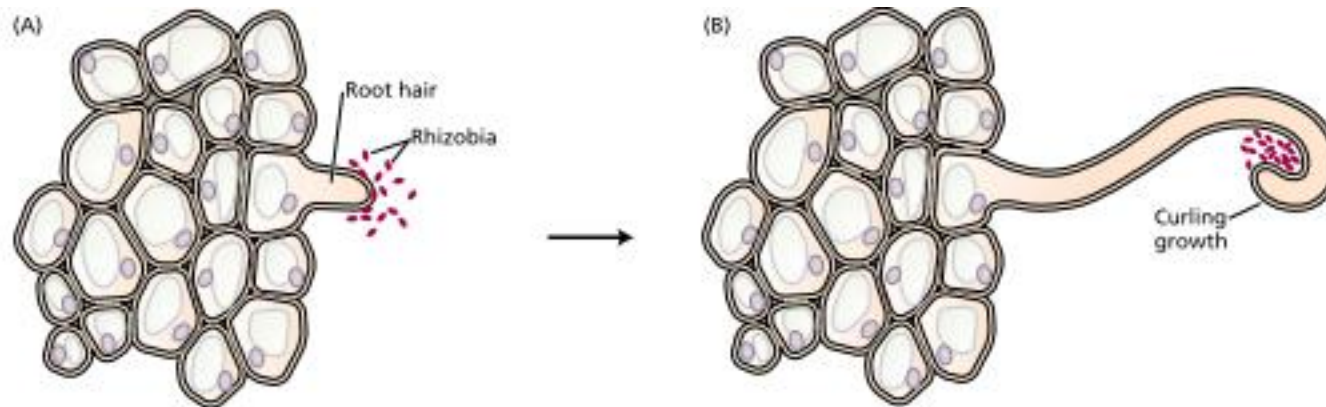
Other enzymes, such as **NodL**, influence the host specificity of Nod factors through the addition of specific substitutions at the reducing or nonreducing sugar moieties of the chitin backbone.

# Nodule Formation Involves Several Phytohormones

Two processes:

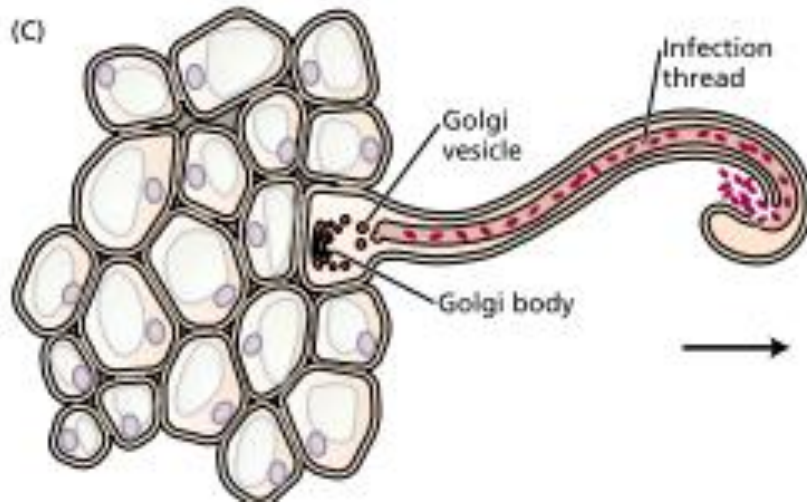
- infection and nodule organogenesis
- occur simultaneously during root nodule formation.

During the infection process, rhizobia that are attached to the root hairs release Nod factors that induce a pronounced curling of the root hair cells

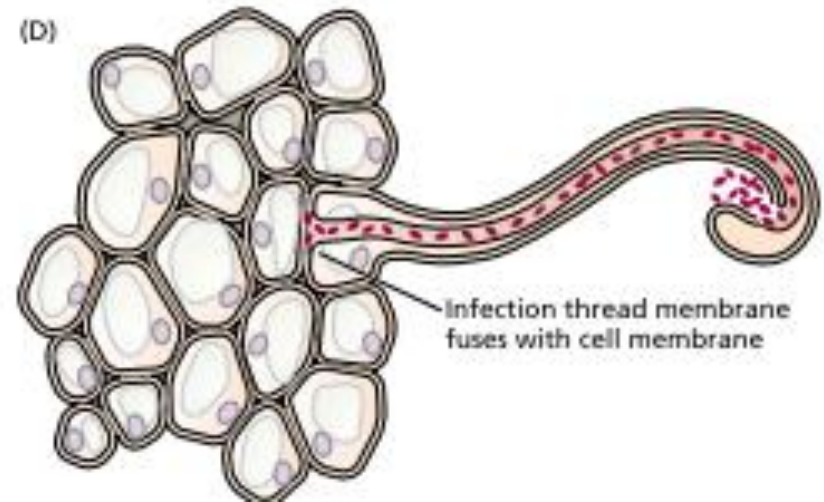


Rhizobia bind to an emerging root hair in response to chemical attractants sent by the plant.

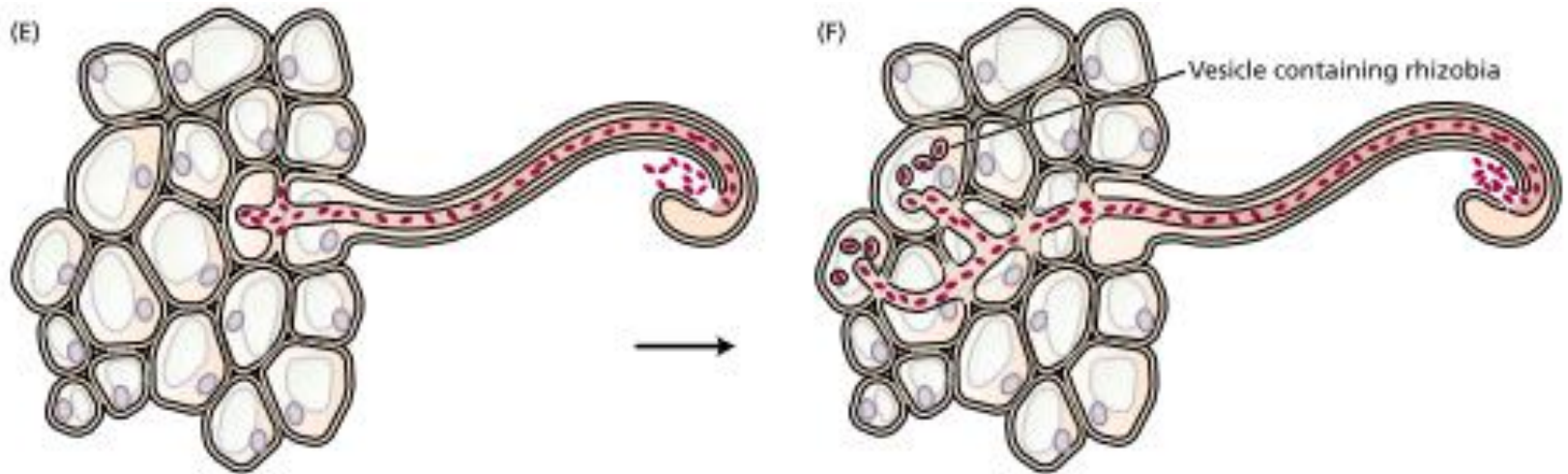
In response to factors produced by the bacteria, the root hair exhibits abnormal curling growth, and rhizobia cells proliferate within the coils.



Localized degradation of the root hair wall leads to infection and formation of the **infection thread** from Golgi secretory vesicles of root cells.



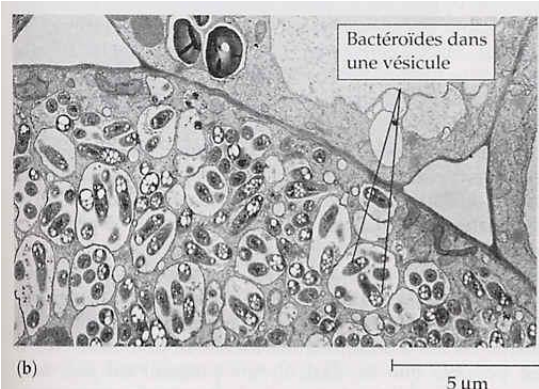
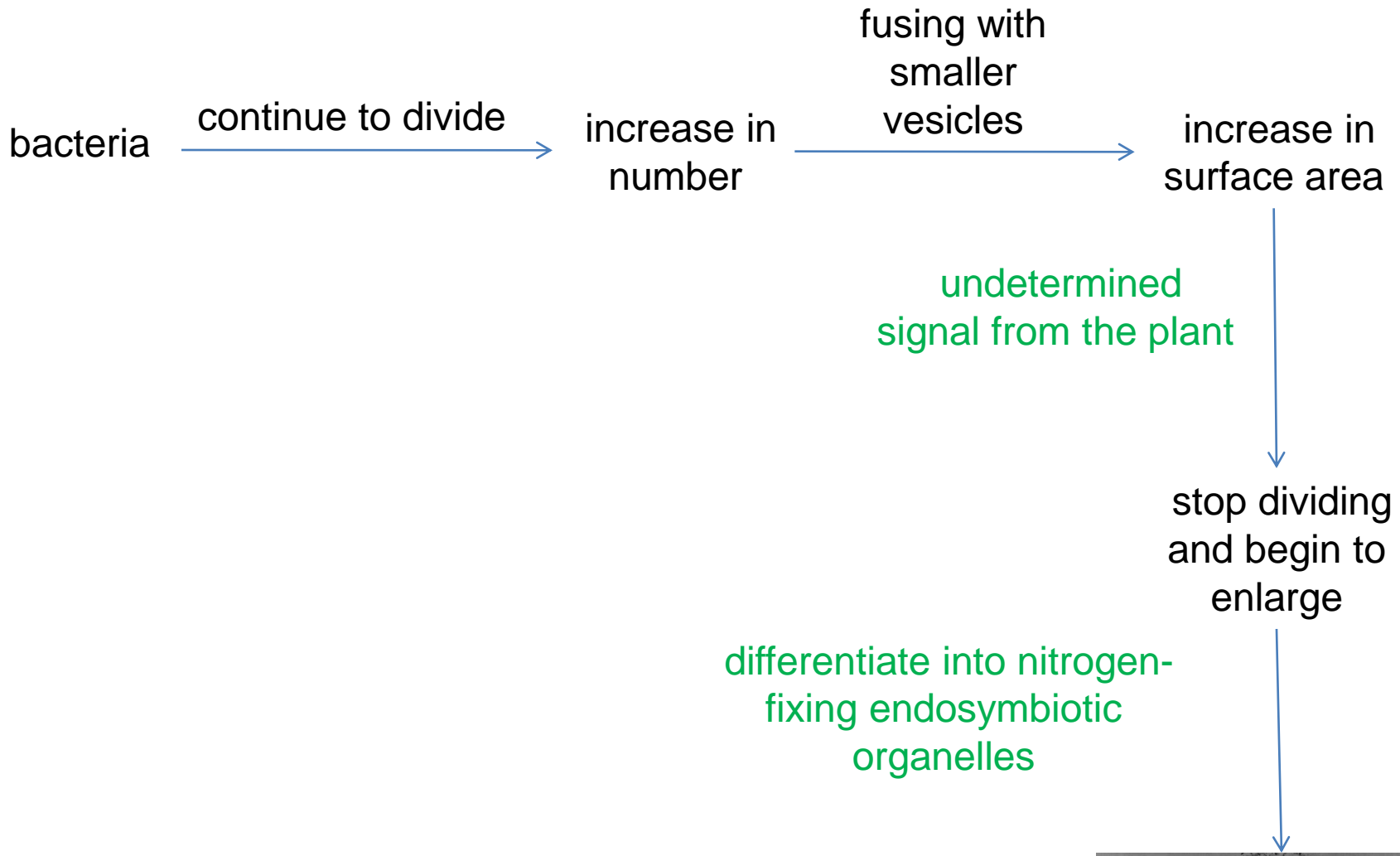
The infection thread reaches the end of the cell, and its membrane fuses with the plasma membrane of the root hair cell.



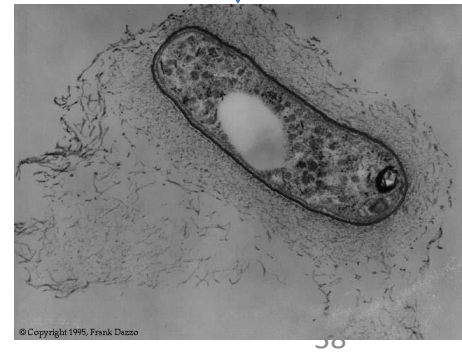
Rhizobia are released into the apoplast and penetrate the compound middle lamella to the subepidermal cell plasma membrane, leading to the initiation of a new infection thread, which forms an open channel with the first.

The infection thread extends and branches until it reaches target cells, where vesicles composed of plant membrane that enclose bacterial cells are released into the cytosol.

*Branching of the infection thread inside the nodule enables the bacteria to infect many cells*



The membrane surrounding the bacteroids is called the peribacteroid membrane.



## The Nitrogenase Enzyme Complex Fixes N<sub>2</sub>

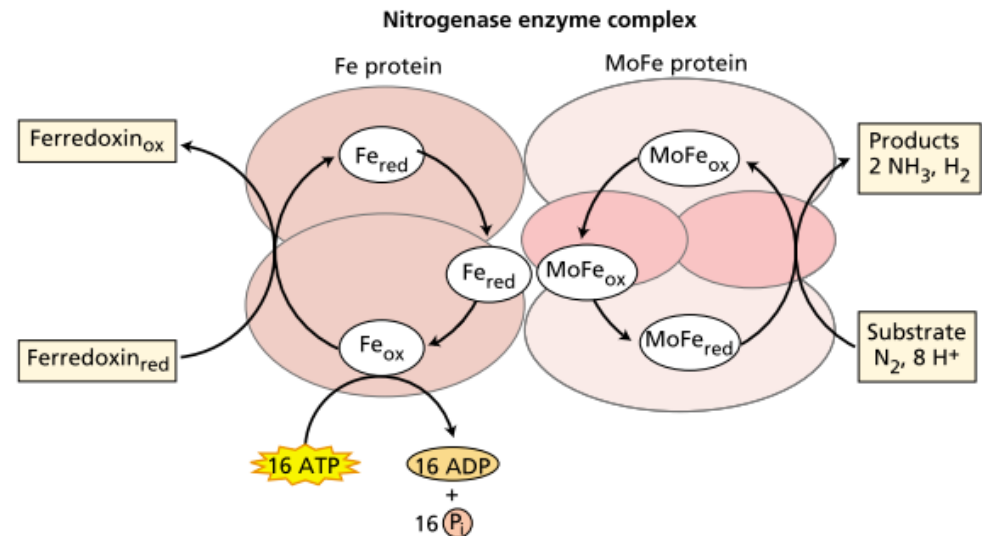
Biological nitrogen fixation, like industrial nitrogen fixation, produces ammonia from molecular nitrogen.



The **nitrogenase enzyme** complex catalyzes this reaction.

## Nitrogenase enzyme

The nitrogenase enzyme complex can be separated into two components—the Fe protein and the MoFe protein—neither of which has catalytic activity by itself



Ferredoxin reduces the Fe protein. Binding and hydrolysis of ATP to the Fe protein is thought to cause a conformational change of the Fe protein that facilitates the redox reactions.

The Fe protein reduces the MoFe protein, and the MoFe protein reduces the N<sub>2</sub>.



# SULFUR ASSIMILATION

## Why sulfur is important in plants?

Sulfur is among the most versatile elements in living organisms.

Disulfide bridges in proteins play structural and regulatory roles

Sulfur participates in electron transport through iron–sulfur clusters.

The catalytic sites for several enzymes and coenzymes, such as urease and coenzyme A, contain sulfur.

Secondary metabolites (compounds that are not involved in primary pathways of growth and development) that contain sulfur range from the rhizobial Nod factors to antiseptic alliin in garlic and anticarcinogen sulforaphane in broccoli.

## Sulfate Is the Absorbed Form of Sulfur in Plants

Most of the sulfur in higher-plant cells derives from sulfate ( $\text{SO}_4^{2-}$ ) absorbed via an  $\text{H}^+-\text{SO}_4^{2-}$  symporter from the soil solution.

Sulfate in the soil comes predominantly from the weathering of parent rock material.

Industrialization, however, adds an additional source of sulfate: atmospheric pollution. The burning of fossil fuels releases several gaseous forms of sulfur, including sulfur dioxide and hydrogen sulfide which find their way to the soil in rain.

When dissolved in water,  $\text{SO}_2$  is hydrolyzed to become sulfuric acid, a strong acid, which is the major source of acid rain.

Plants can also metabolize sulfur dioxide taken up in the gaseous form through their stomata.

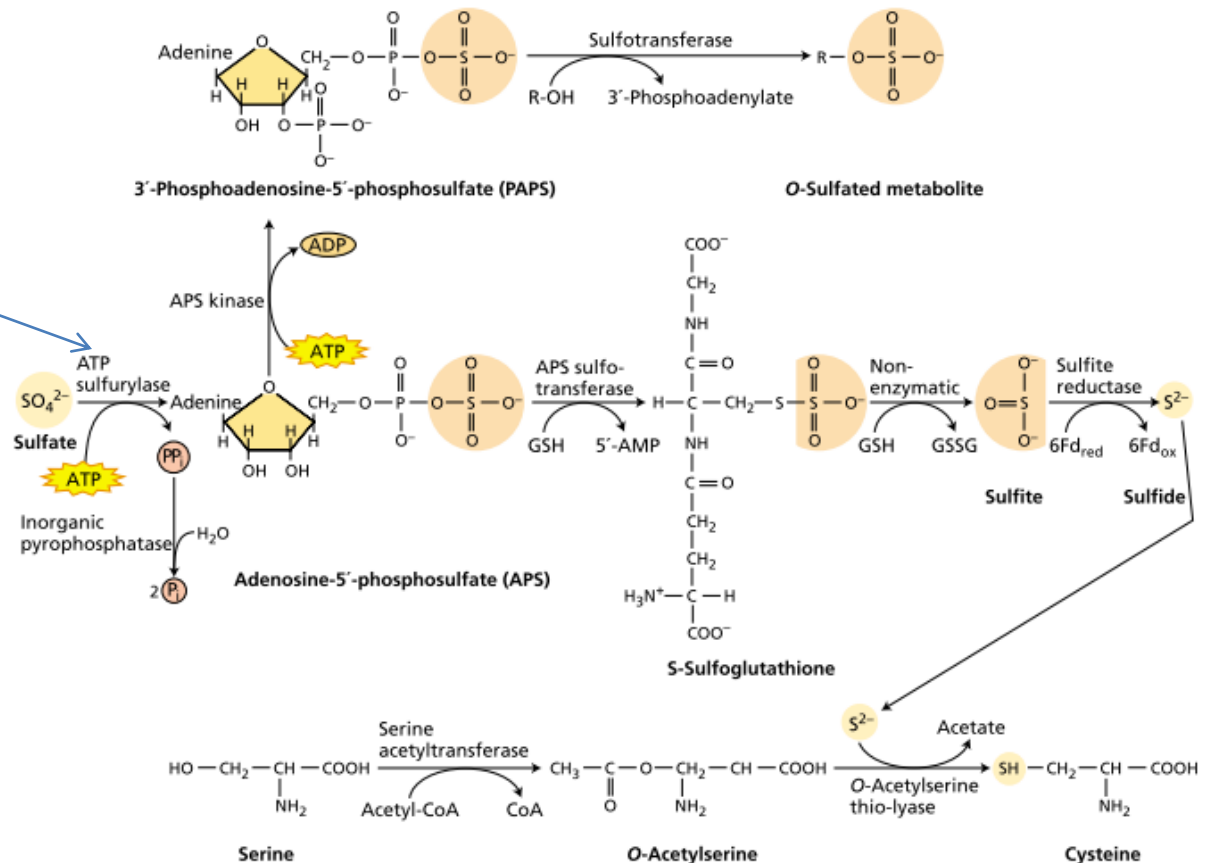
*Nonetheless, prolonged exposure (more than 8 hours) to high atmospheric concentrations (greater than 0.3 ppm) of  $\text{SO}_2$  causes extensive tissue damage because of the formation of sulfuric acid.*

# Sulfate Assimilation

The first step in the synthesis of sulfur-containing organic compounds is the reduction of sulfate to the amino acid cysteine

Sulfate is very stable and thus needs to be activated before any subsequent reactions may proceed.

Activation begins with the reaction between sulfate and ATP to form 5'-adenylylsulfate





The enzyme that catalyzes this reaction, **ATP sulfurylase**, has two forms: The major one is found in plastids, and a minor one is found in the cytoplasm

The activation reaction is energetically unfavorable.

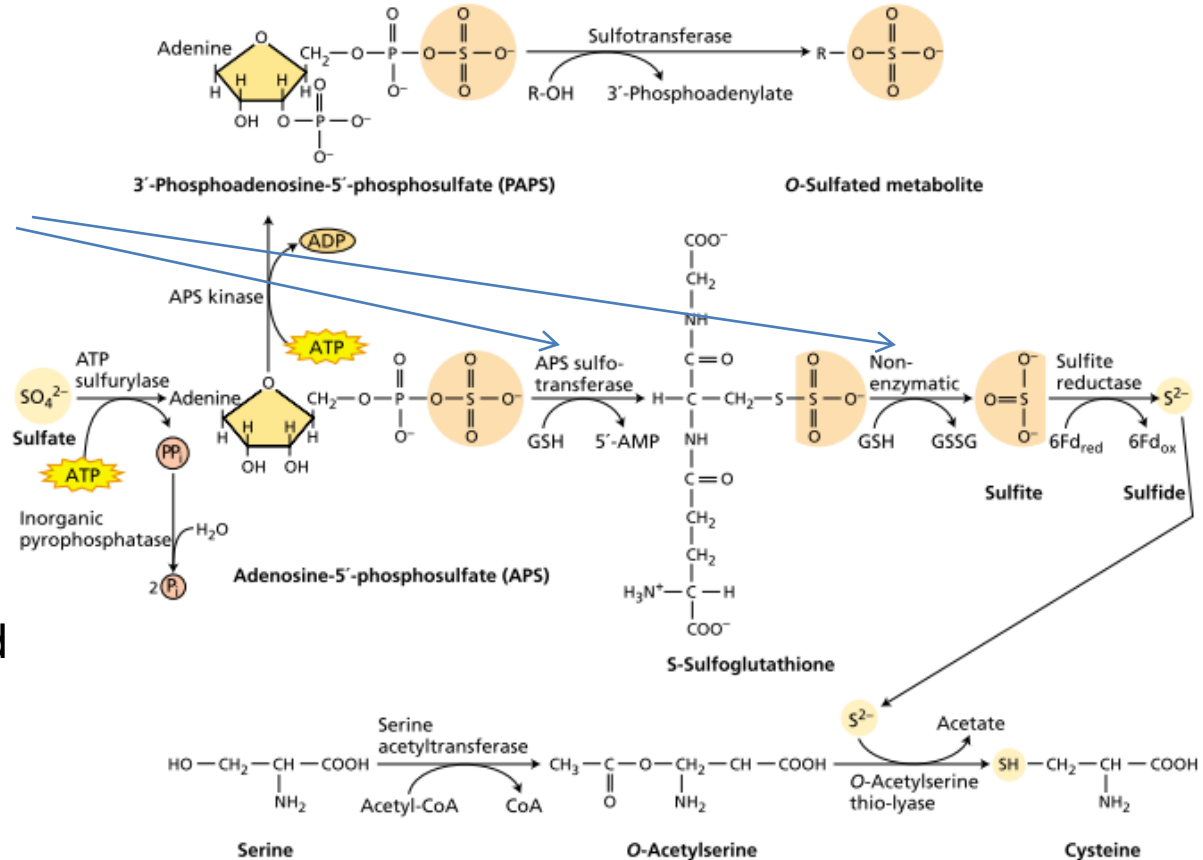
pyrophosphatase



# Sulfate Assimilation

The reduction of APS is a multistep process that occurs exclusively in the plastids.

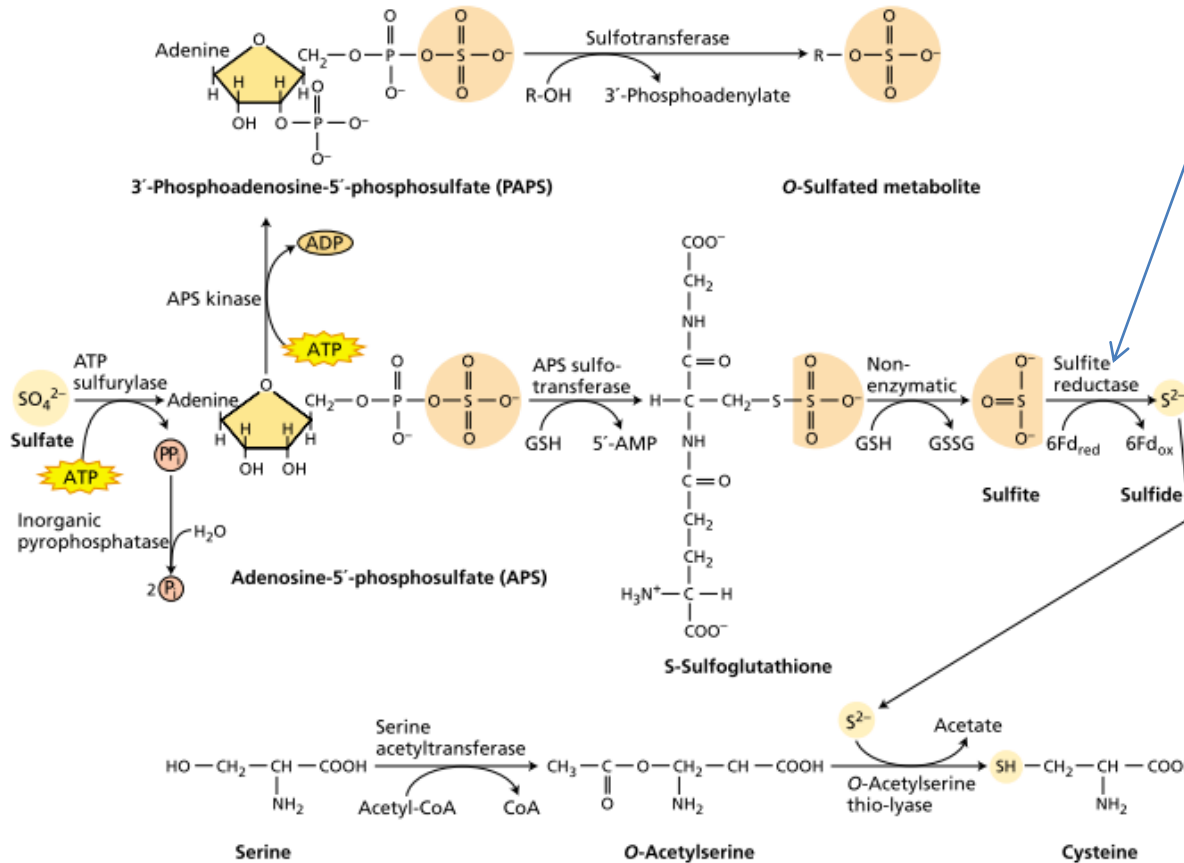
First, APS reductase transfers two electrons apparently from reduced glutathione (GSH) to produce sulfite



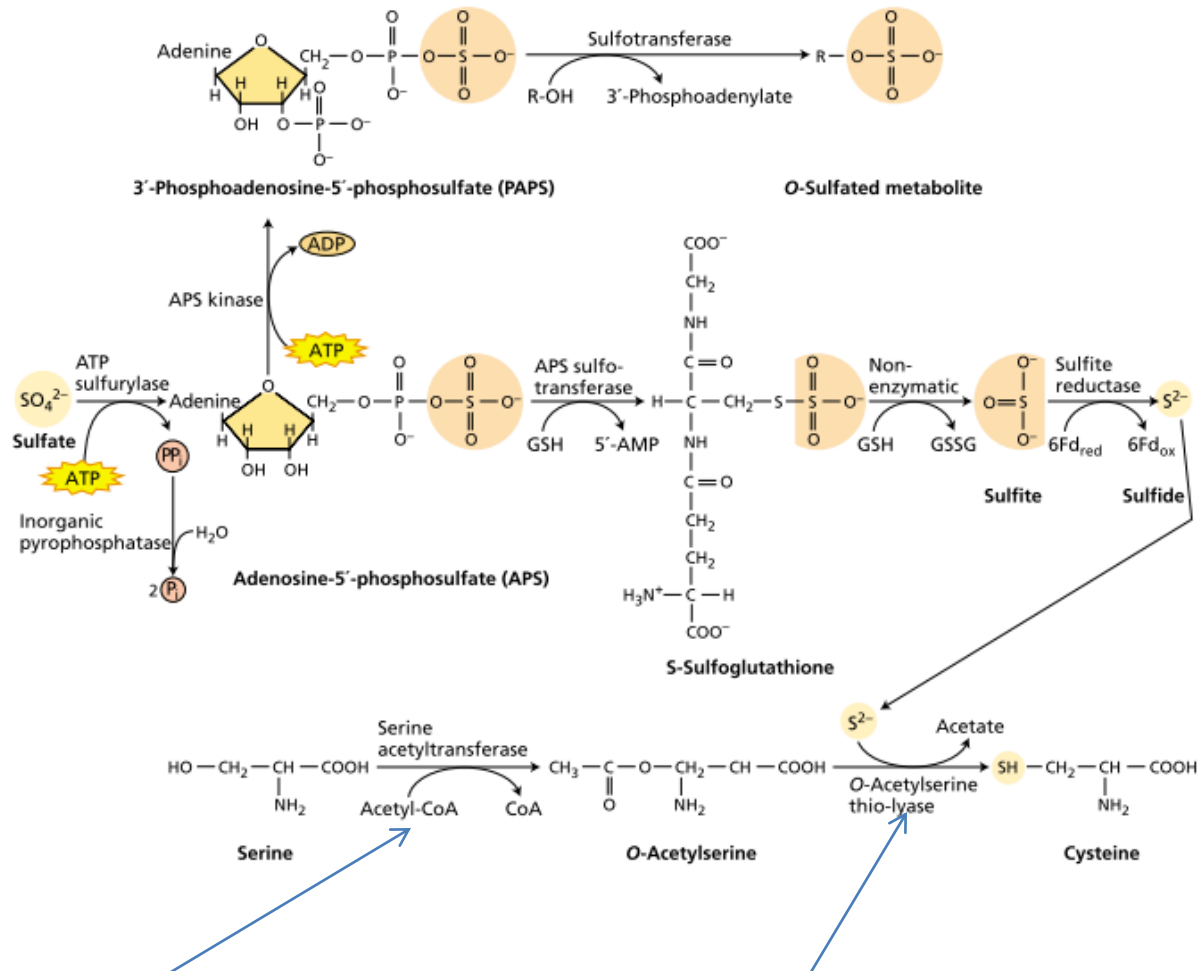
GSSG stands for oxidized glutathione.

# Sulfate Assimilation

Second, sulfite reductase transfers six electrons from ferredoxin ( $Fd_{red}$ ) to produce sulfide



# Sulfate Assimilation



The O-acetylserine (OAS) that reacts with  $\text{S}^{2-}$  is formed in a reaction catalyzed by serine acetyltransferase

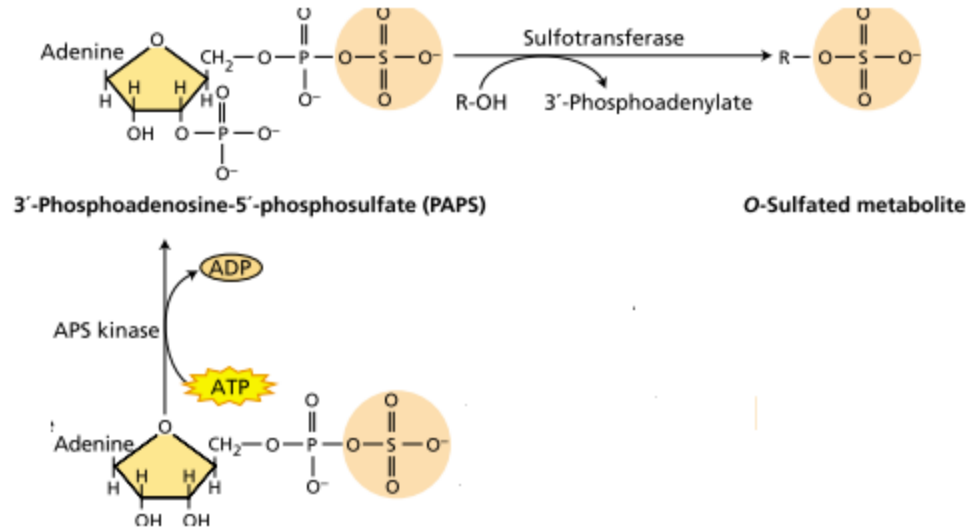
The resultant sulfide then reacts with O-acetylserine (OAS) to form cysteine and acetate.



## Sulfate Assimilation

The sulfation of APS, localized in the cytosol, is the alternative pathway.

First, APS kinase catalyzes a reaction of APS with ATP to form 3'-phosphoadenosine-5'-phosphosulfate (PAPS).



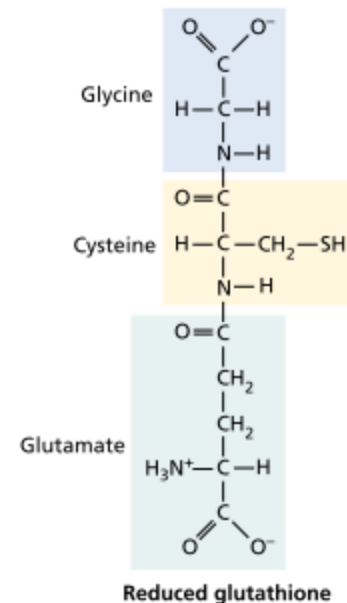
Sulfotransferases then may transfer the sulfate group from PAPS to various compounds, including choline, brassinosteroids, flavonol, gallic acid glucoside, glucosinolates, peptides, and polysaccharides

## Sulfate Assimilation Occurs Mostly in Leaves

Leaves are generally much more active than roots in sulfur assimilation, presumably because photosynthesis provides reduced ferredoxin and photorespiration generates serine that may stimulate the production of O-acetylserine.

Sulfur assimilated in leaves is exported via the phloem to sites of protein synthesis (shoot and root apices, and fruits) mainly as glutathione

Glutathione also acts as a signal that coordinates the absorption of sulfate by the roots and the assimilation of sulfate by the shoot.



## Methionine Is Synthesized from Cysteine

Methionine, the other sulfur-containing amino acid found in proteins, is synthesized in plastids from cysteine.

After cysteine and methionine are synthesized, sulfur can be incorporated into proteins and a variety of other compounds, such as acetyl-CoA and S-adenosylmethionine.

The latter compound, S-adenosylmethionine is important in the synthesis of ethylene and in reactions involving the transfer of methyl groups, as in lignin synthesis

# PHOSPHATE ASSIMILATION

Self study

END