

# Laboratoř růstových regulátorů

*Miroslav Strnad*

## Asimilace minerálních živin[kap 12]



- Univerzita Palackého & Ústav experimentální botaniky AV CR



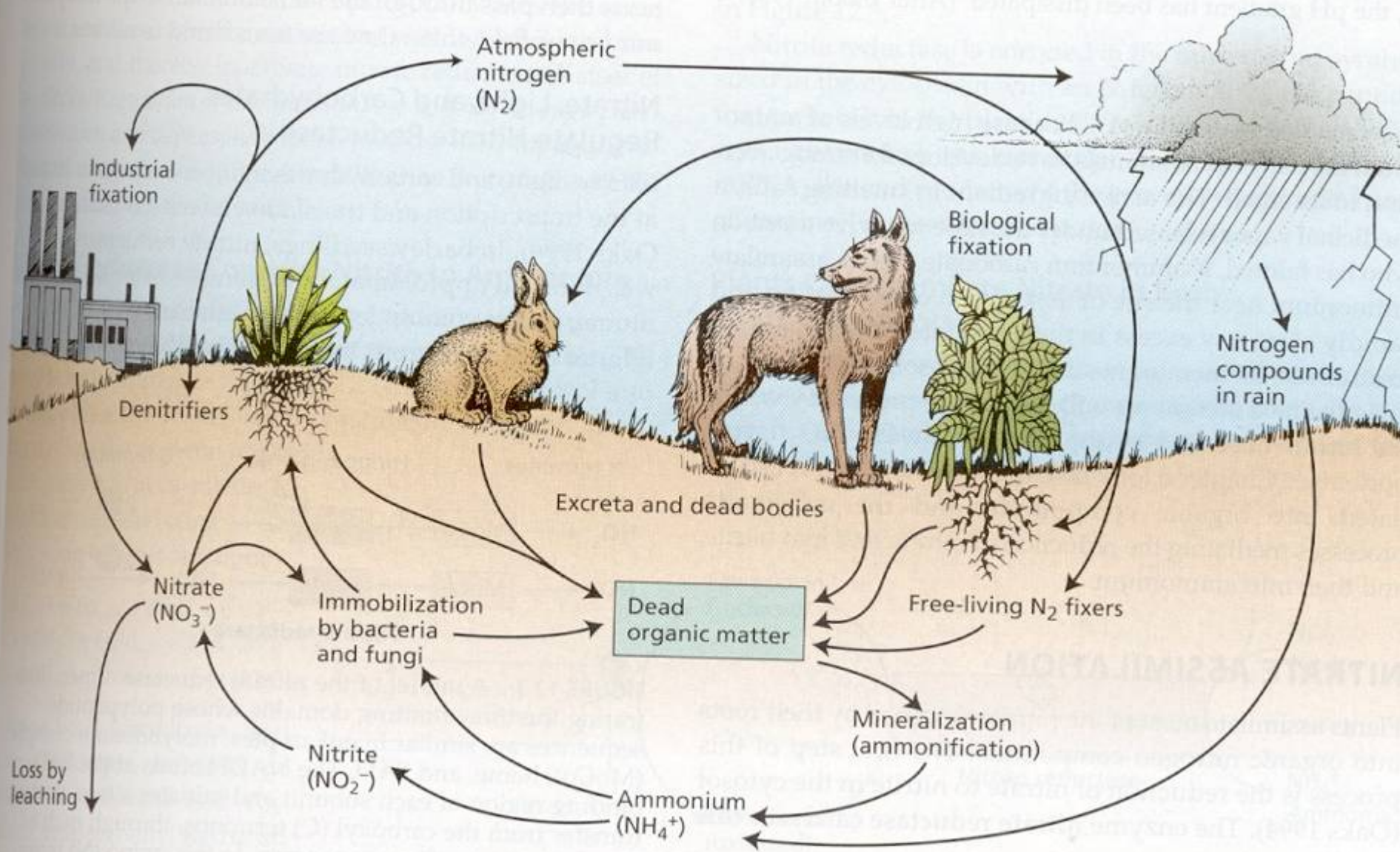


FIGURE 12.1 Nitrogen cycles through the atmosphere as it changes from a gaseous form to reduced ions before being incorporated into organic compounds in living organisms. Some of the steps involved in the nitrogen cycle are shown.



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

Process	Definition	Rate ( $10^{12}$ g yr <sup>-1</sup> )
Industrial fixation	Industrial conversion of molecular nitrogen to ammonia	80
Atmospheric fixation	Lightning and photochemical conversion of molecular nitrogen to nitrate	19
Biological fixation	Prokaryotic conversion of molecular nitrogen to ammonia	170
Plant acquisition	Plant absorption and assimilation of ammonium or nitrate	1200
Immobilization	Microbial absorption and assimilation of ammonium or nitrate	N/C
Ammonification	Bacterial and fungal catabolism of soil organic matter to ammonium	N/C
Nitrification	Bacterial ( <i>Nitrosomonas</i> sp.) oxidation of ammonium to nitrite and subsequent bacterial ( <i>Nitrobacter</i> sp.) oxidation of nitrite to nitrate	N/C
Mineralization	Bacterial and fungal catabolism of soil organic matter to mineral nitrogen through ammonification or nitrification	N/C
Volatilization	Physical loss of gaseous ammonia to the atmosphere	100
Ammonium fixation	Physical embedding of ammonium into soil particles	10
Denitrification	Bacterial conversion of nitrate to nitrous oxide and molecular nitrogen	210
Nitrate leaching	Physical flow of nitrate dissolved in groundwater out of the topsoil and eventually into the oceans	36

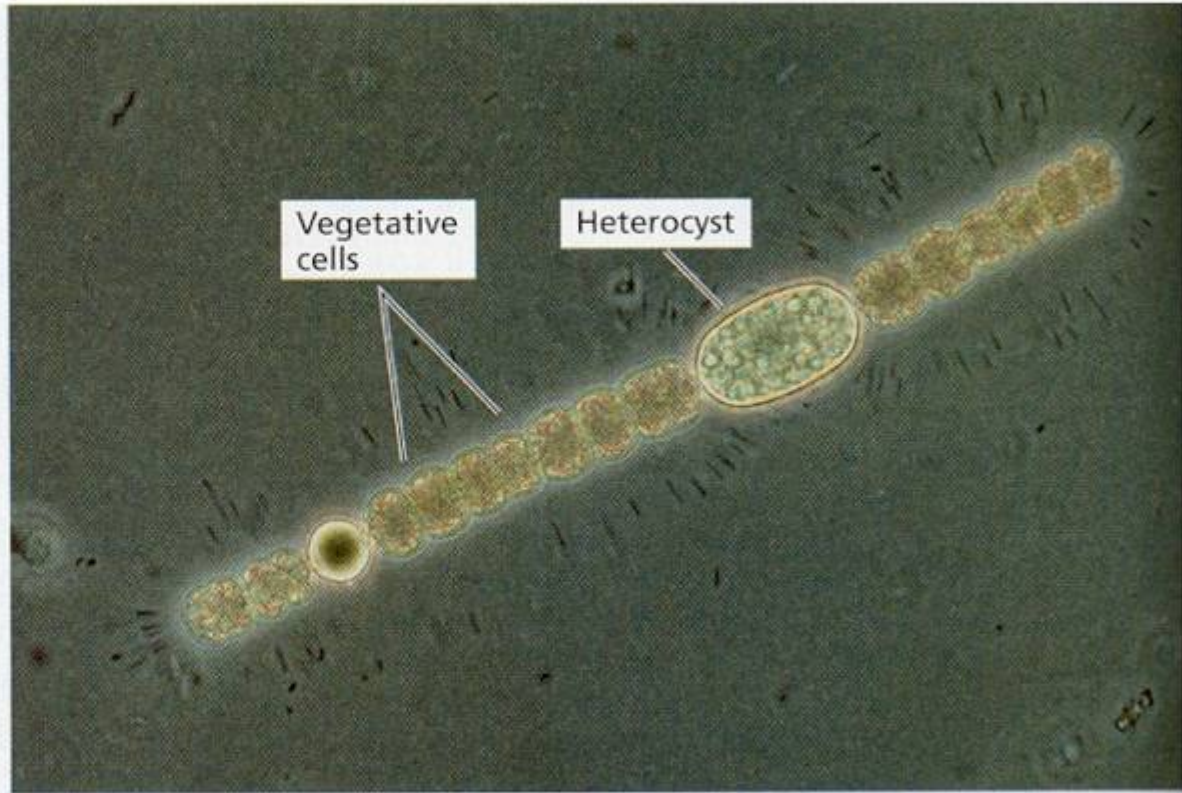
Note: Terrestrial organisms, the soil, and the oceans contain about  $5.2 \times 10^{15}$  g,  $95 \times 10^{15}$  g, and  $6.5 \times 10^{15}$  g, respectively, of organic nitrogen that is active in the cycle. Assuming that the amount of atmospheric  $N_2$  remains constant (inputs = outputs), the mean residence time (the average time that a nitrogen molecule remains in organic forms) is about 370 years [(pool size)/(fixation input) =  $(5.2 \times 10^{15}$  g +  $95 \times 10^{15}$  g)/( $80 \times 10^{12}$  g yr<sup>-1</sup> +  $19 \times 10^{12}$  g yr<sup>-1</sup> +  $170 \times 10^{12}$  g yr<sup>-1</sup>)] (Schlesinger 1997).

**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>Dexia</i>
Facultative	<i>Bacillus</i> , <i>Klebsiella</i>
Anaerobic	
Nonphotosynthetic	<i>Clostridium</i> , <i>Methanococcus</i> (archaebacterium)
Photosynthetic	<i>Chromatium</i> , <i>Rhodospirillum</i>



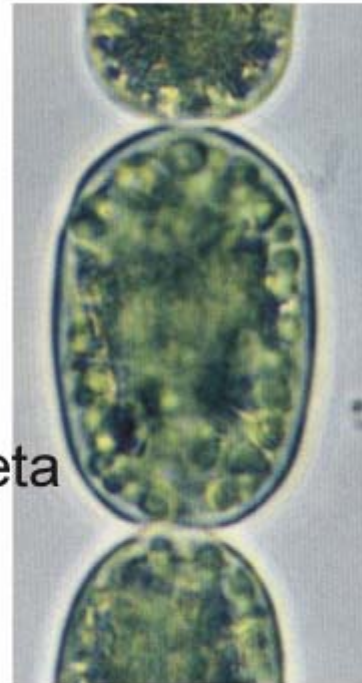
**FIGURE 12.9** A heterocyst in a filament of the nitrogen-fixing cyanobacterium *Anabaena*. The thick-walled heterocysts, interspaced among vegetative cells, have an anaerobic inner environment that allows cyanobacteria to fix nitrogen in aerobic conditions. (© Paul W. Johnson/Biological Photo Service.)



## Heterocyt a akineta u Anabeny

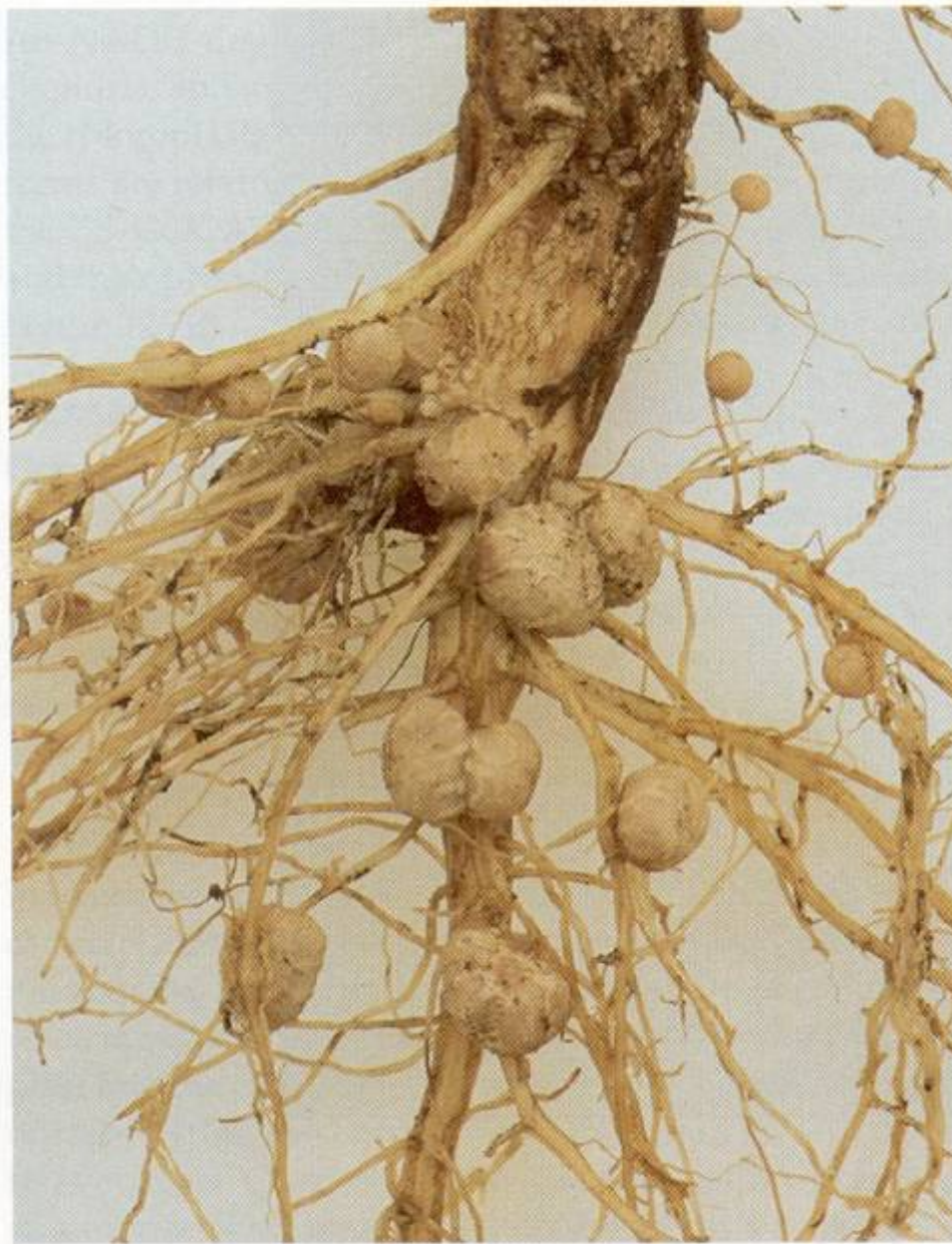


heterocyt

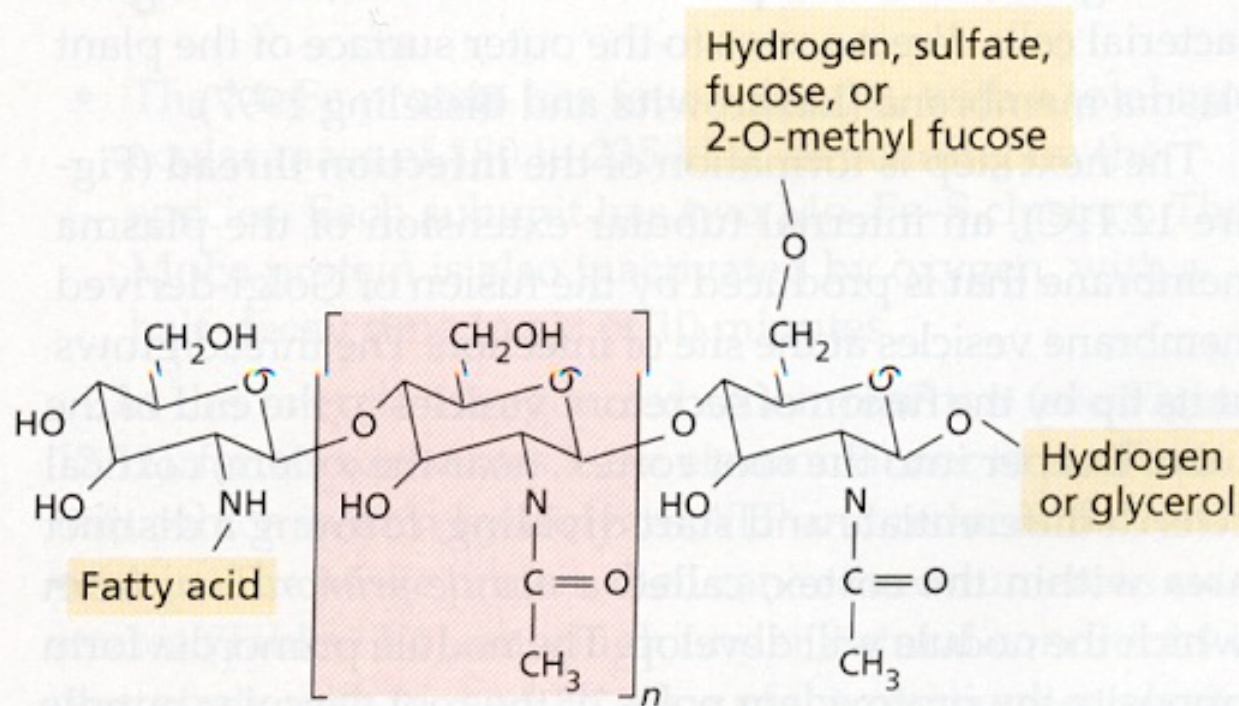


akineta





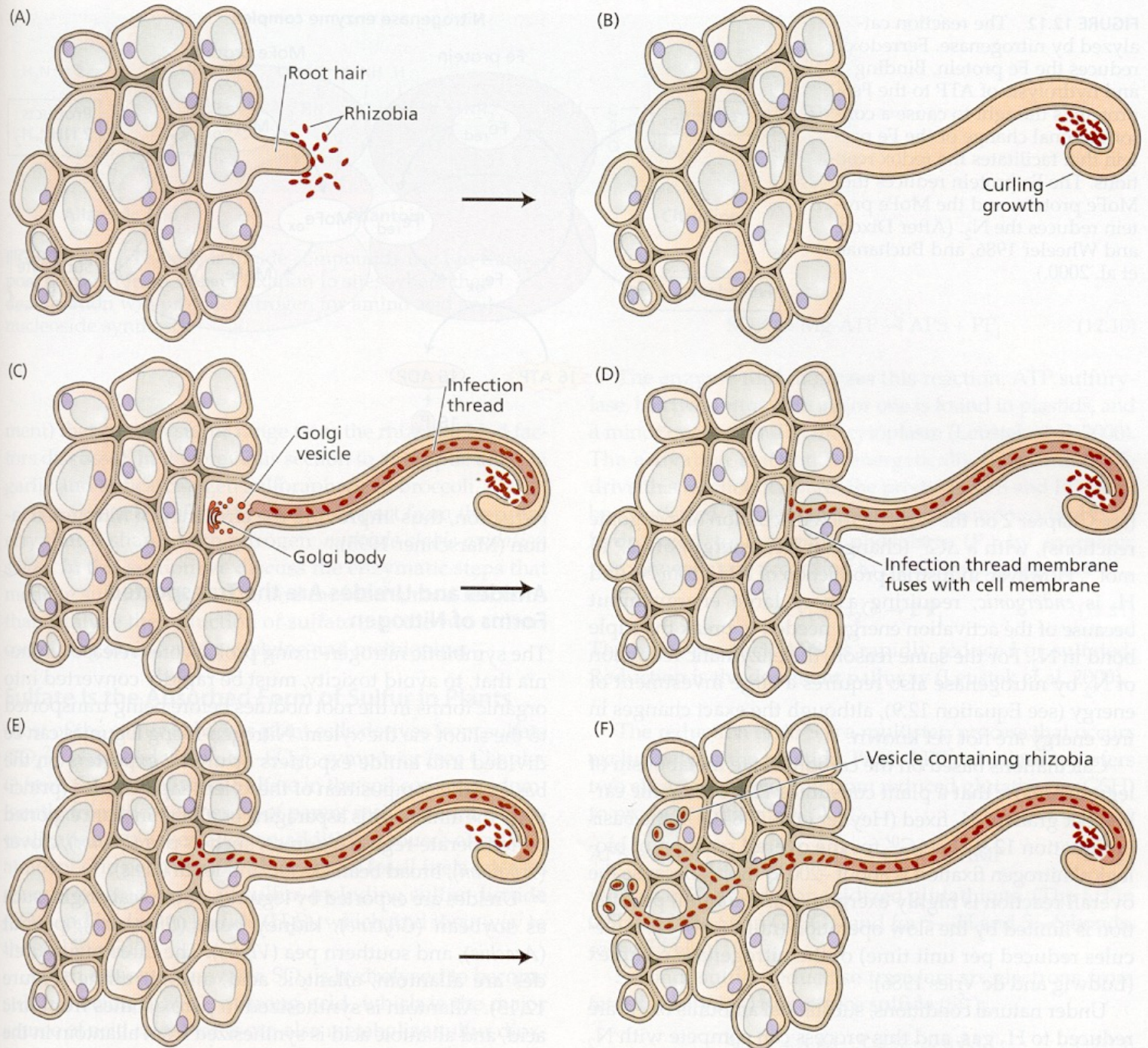
**FIGURE 12.8** Root nodules on soybean. The nodules are a result of infection by *Rhizobium japonicum*. (© Wally Eberhart/Visuals Unlimited.)



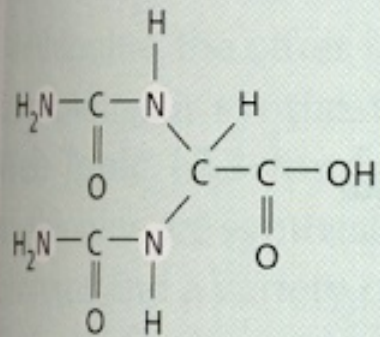
**FIGURE 12.10** Nod factors are lipochitin oligosaccharides. The fatty acid chain typically has 16 to 18 carbons. The number of repeated middle sections ( $n$ ) is usually 2 to 3. (After Stokkermans et al. 1995.)



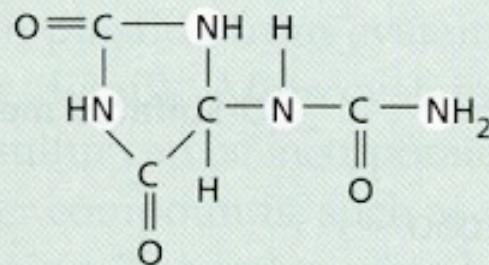
Fig. [12.11]



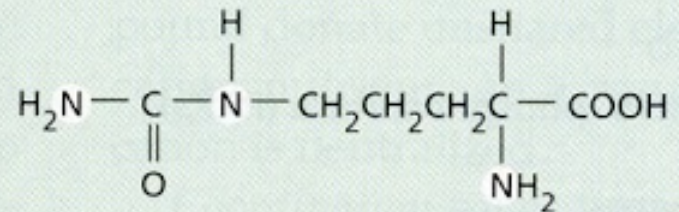




Allantoic acid

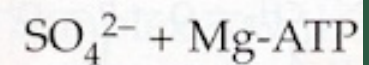


Allantoin



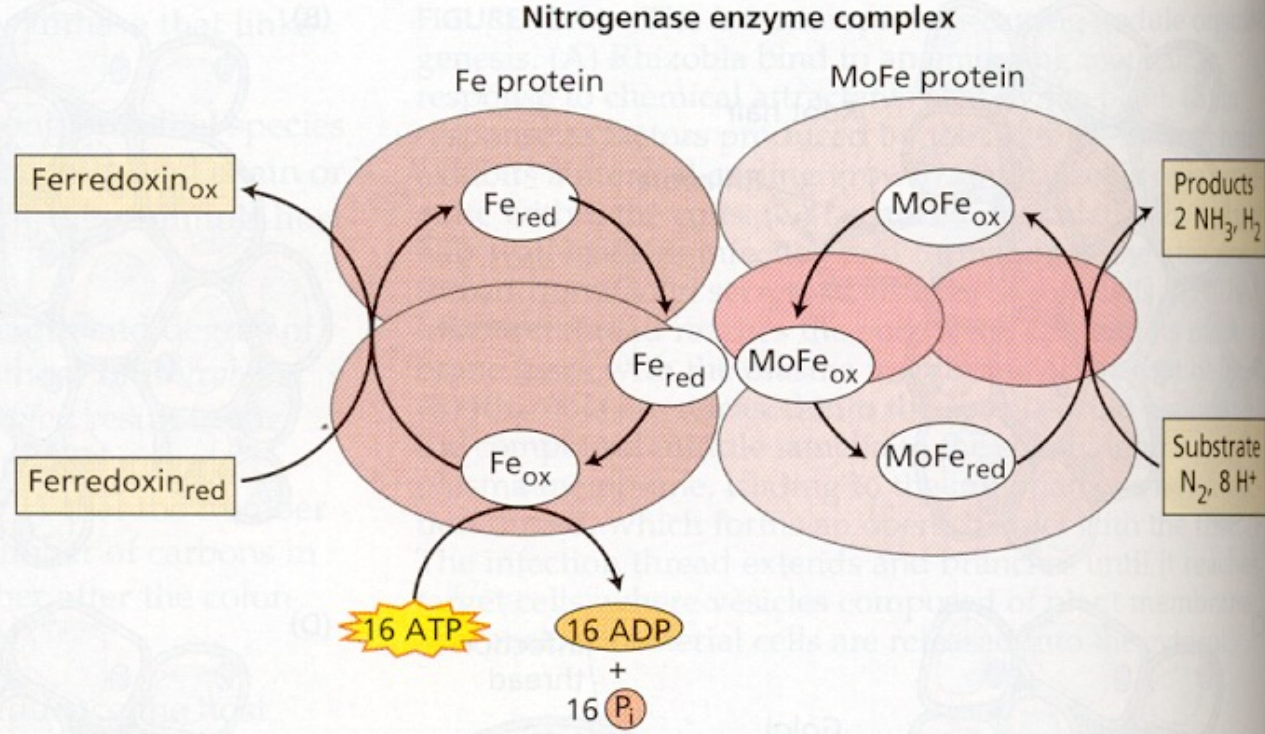
Citrulline

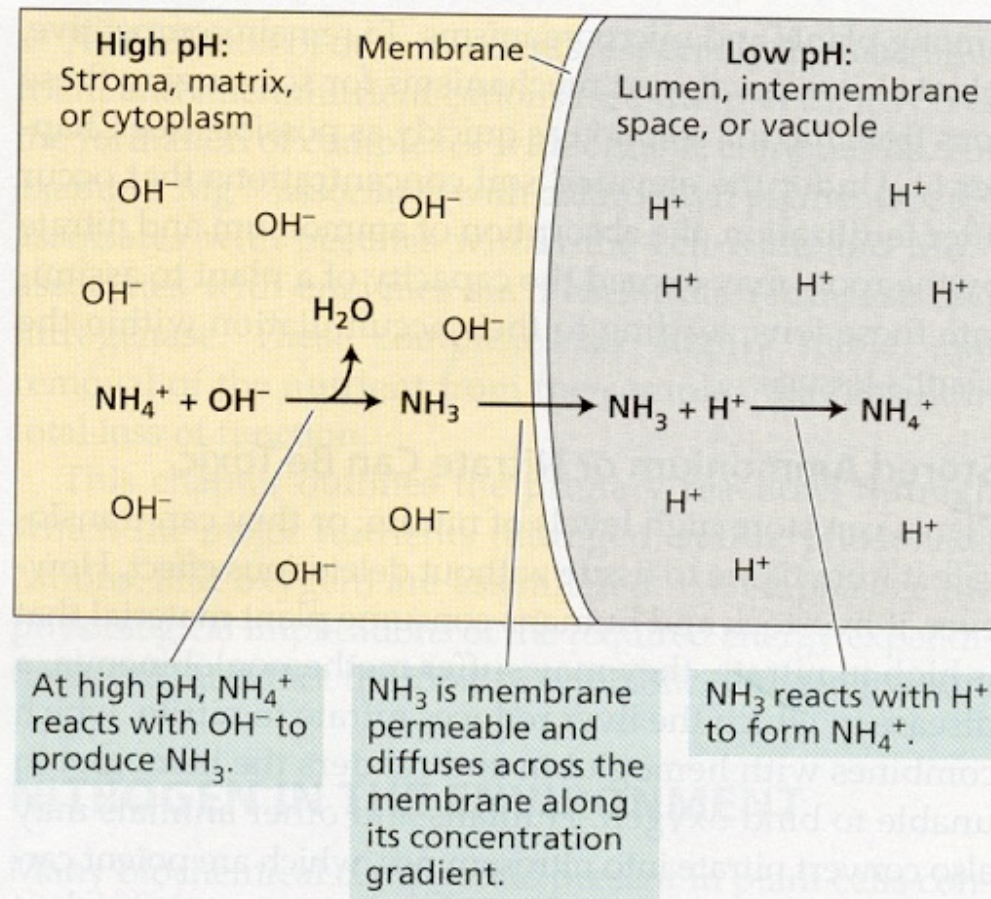
FIGURE 12.13 The major ureide compounds used to transport nitrogen from sites of fixation to sites where their deamination will provide nitrogen for amino acid and nucleoside synthesis.





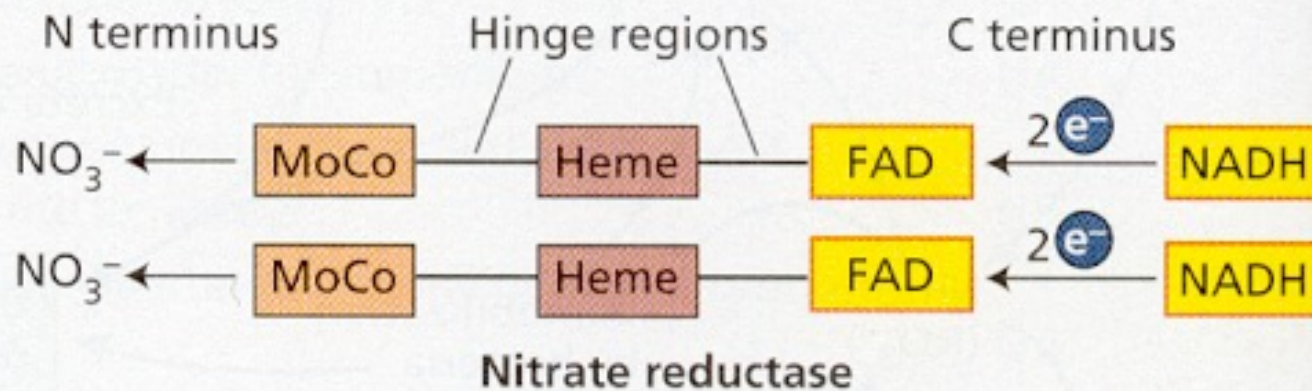
**FIGURE 12.12** The reaction catalyzed by nitrogenase. Ferredoxin reduces the Fe protein. Binding and hydrolysis of ATP to the Fe protein is thought to cause a conformational change of the Fe protein that facilitates the redox reactions. The Fe protein reduces the MoFe protein, and the MoFe protein reduces the  $N_2$ . (After Dixon and Wheeler 1986, and Buchanan et al. 2000.)





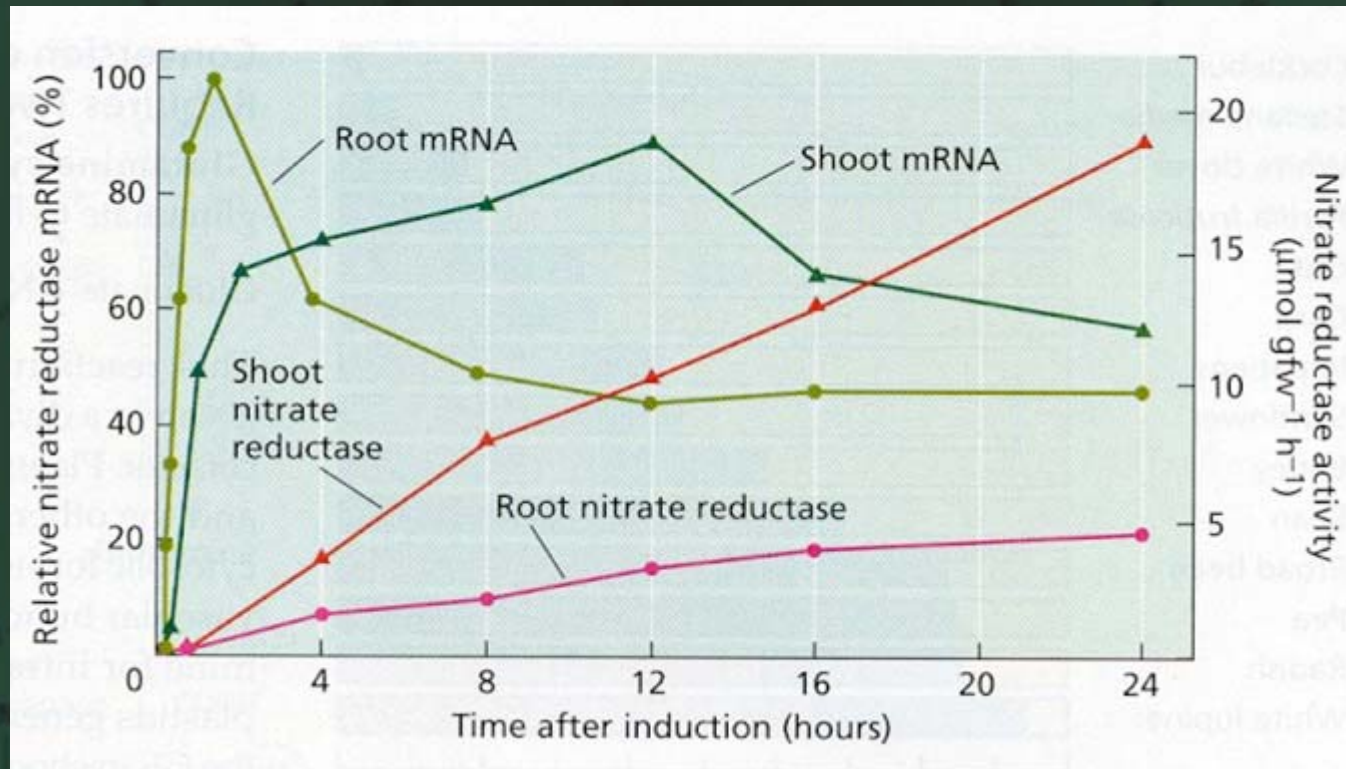
**FIGURE 12.2**  $\text{NH}_4^+$  toxicity can dissipate pH gradients. The left side represents the stroma, matrix, or cytoplasm, where the pH is high; the right side represents the lumen, intermembrane space, or vacuole, where the pH is low; and the membrane represents the thylakoid, inner mitochondrial, or tonoplast membrane for a chloroplast, mitochondrion, or root cell, respectively. The net result of the reaction shown is that both the  $\text{OH}^-$  concentration on the left side and the  $\text{H}^+$  concentration on the right side have been diminished; that is, the pH gradient has been dissipated. (After Bloom 1997.)



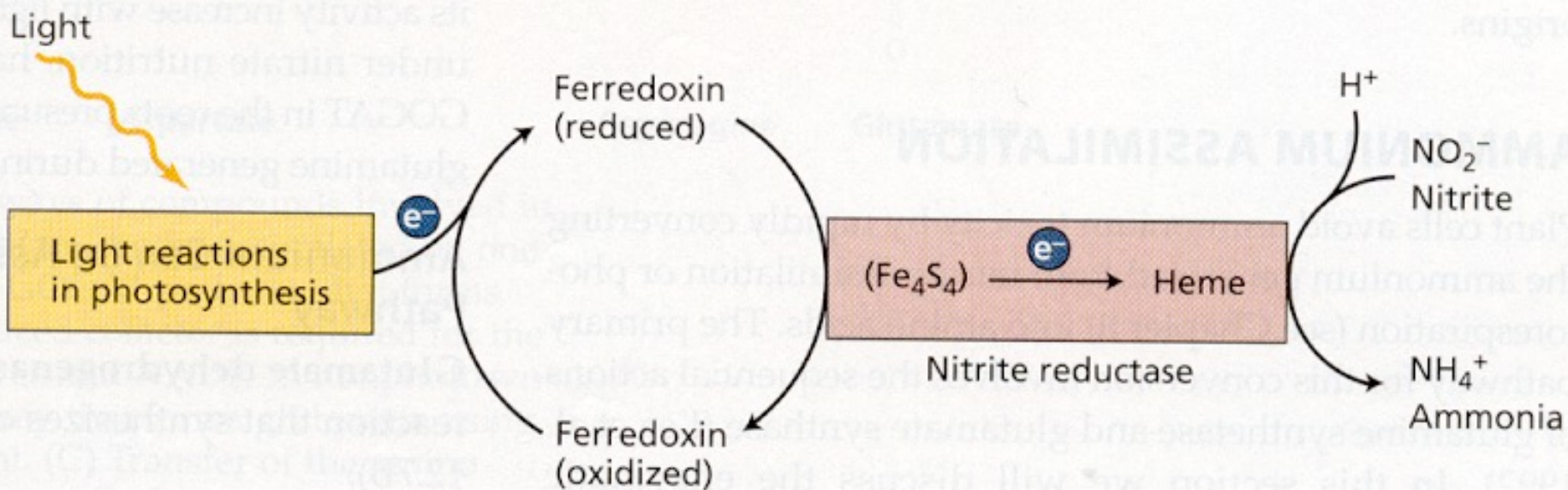


**FIGURE 12.3** A model of the nitrate reductase dimer, illustrating the three binding domains whose polypeptide sequences are similar in eukaryotes: molybdenum complex (MoCo), heme, and FAD. The NADH binds at the FAD-binding region of each subunit and initiates a two-electron transfer from the carboxyl (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.

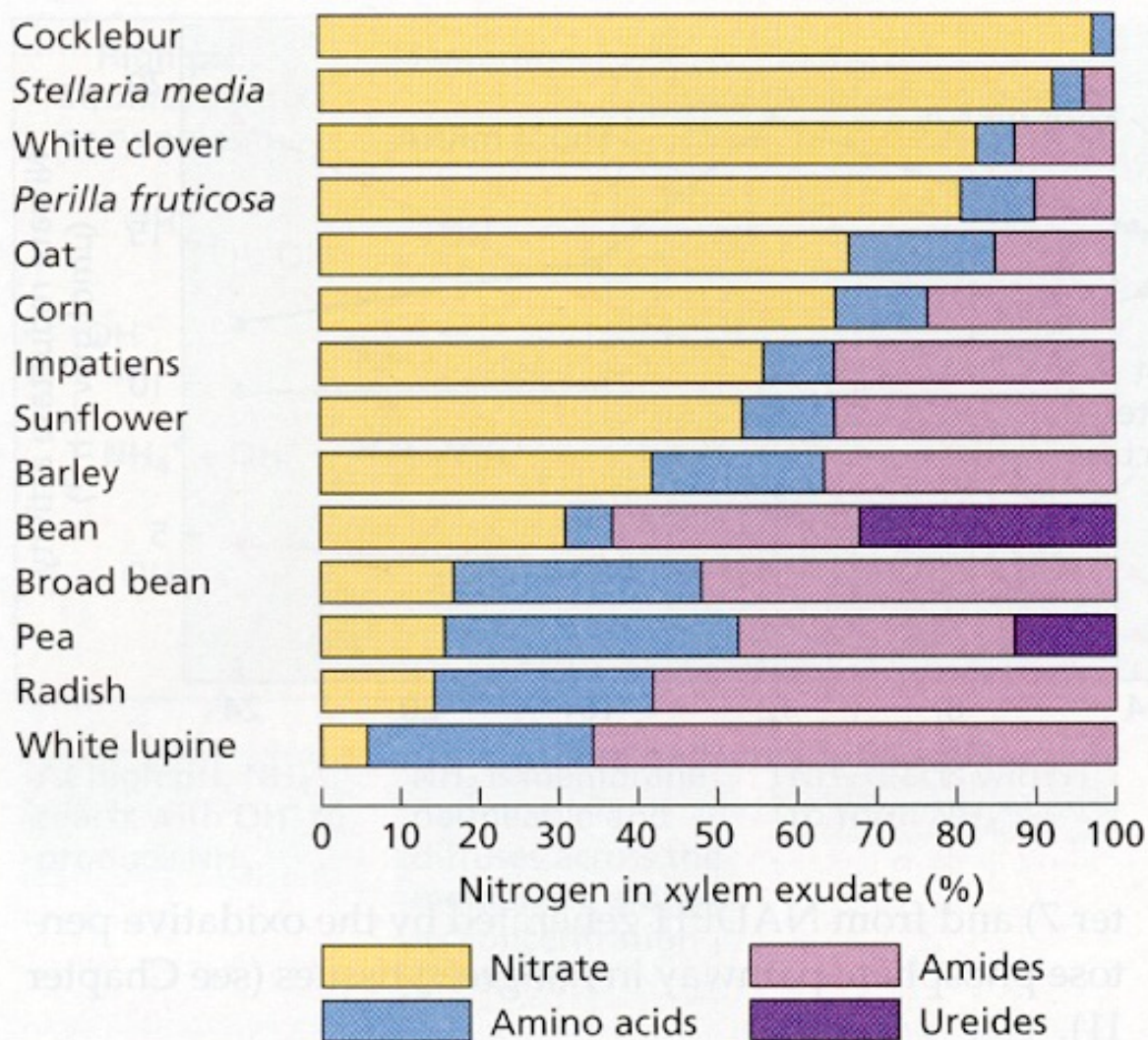
# Stimulation of nitrate reductase activity follows the induction of nitrate reductase mRNA in shoots and roots of barley [12.4]





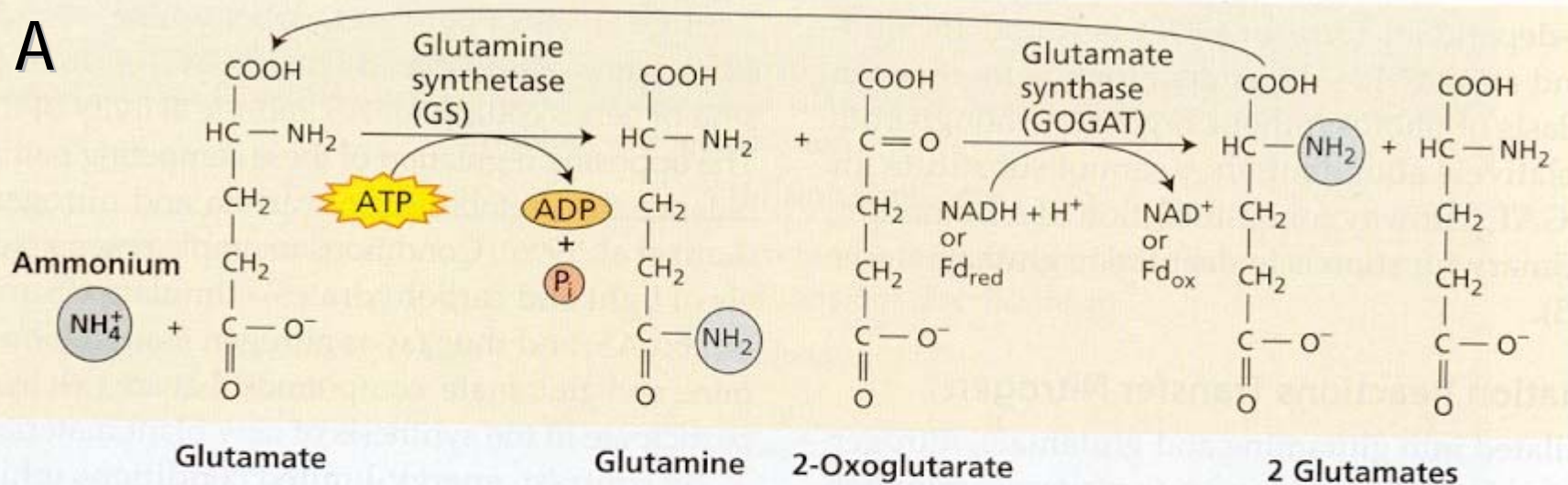
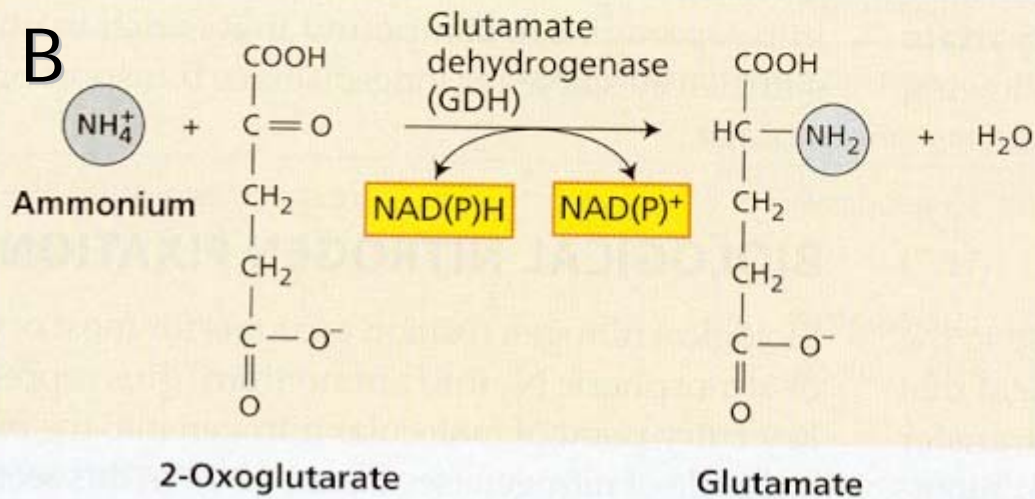


**FIGURE 12.5** Model for coupling of photosynthetic electron flow, via ferredoxin, to the reduction of nitrite by nitrite reductase. The enzyme contains two prosthetic groups, Fe<sub>4</sub>S<sub>4</sub> and heme, which participate in the reduction of nitrite to ammonium.

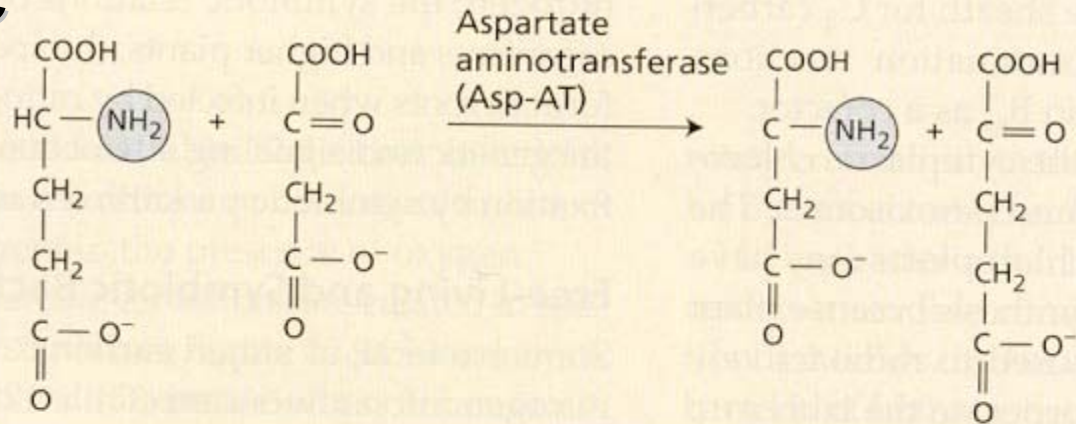


**FIGURE 12.6** Relative amounts of nitrate and other nitrogen compounds in the xylem exudate of various plant species. The plants were grown with their roots exposed to nitrate solutions, and xylem sap was collected by severing of the stem. Note the presence of ureides, specialized nitrogen compounds, in bean and pea (which will be discussed later in the text). (After Pate 1983.)



**A****B**

C



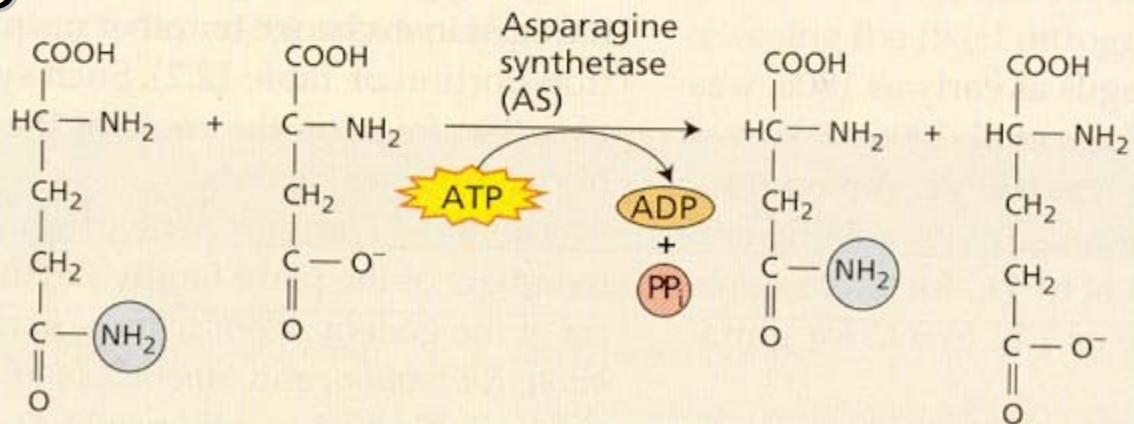
Glutamate

Oxaloacetate

Aspartate

2-Oxoglutarate

D



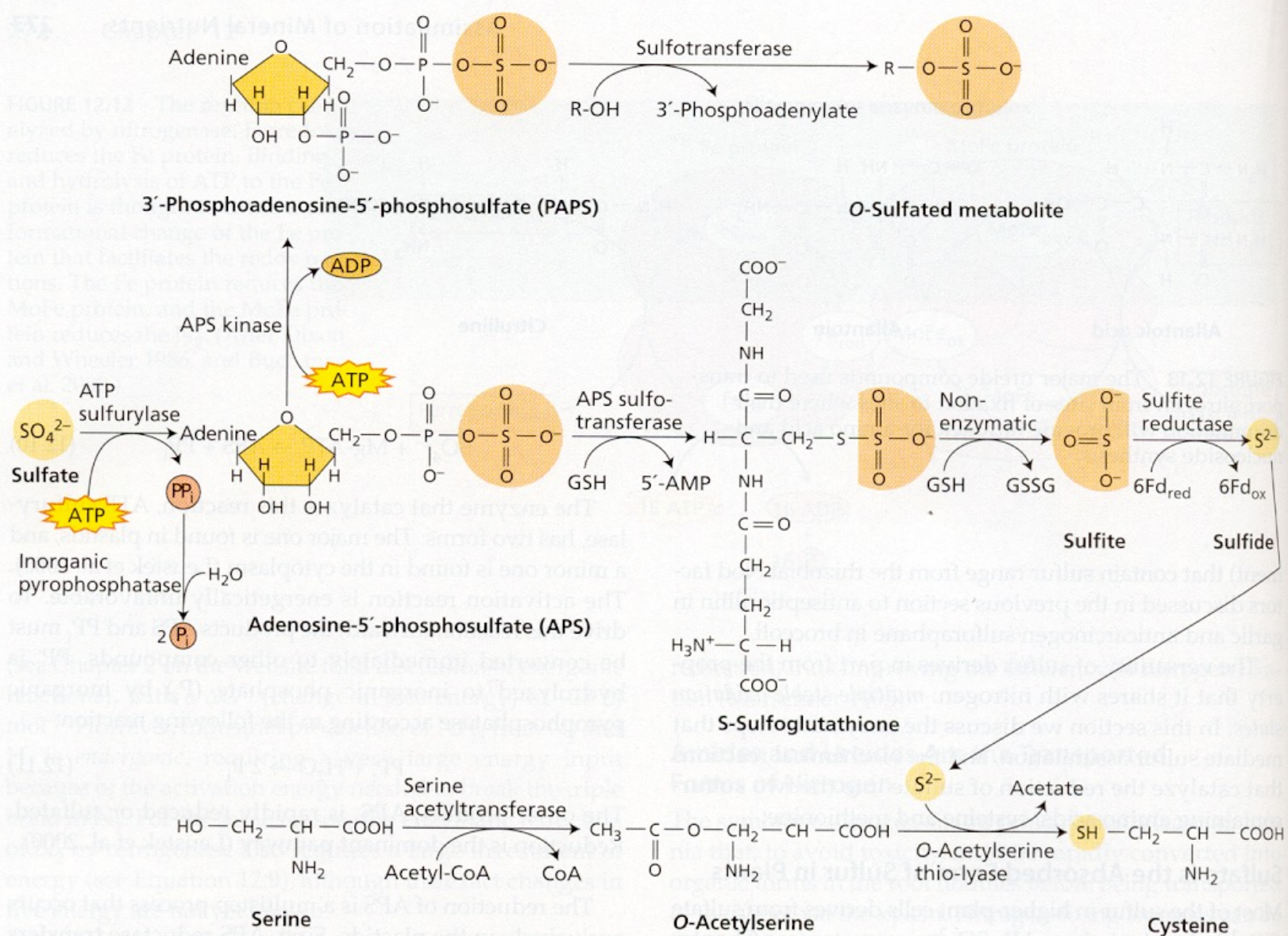
Glutamine

Aspartate

Asparagine

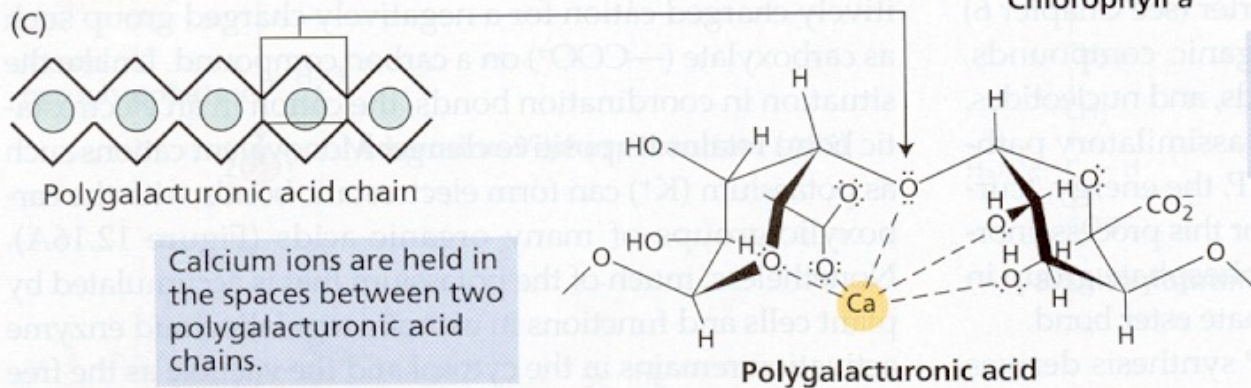
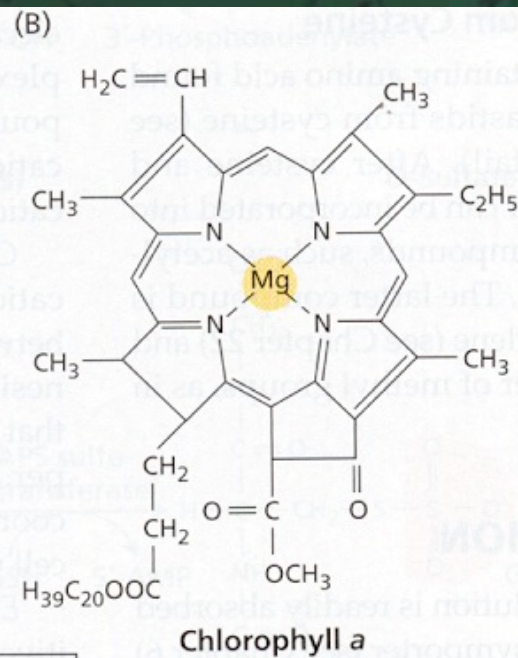
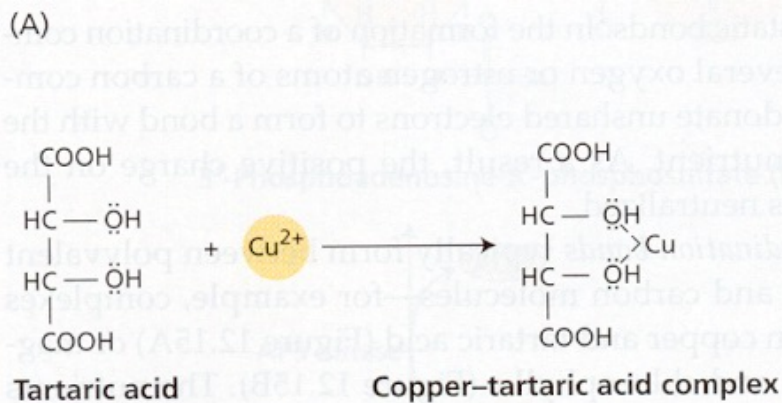
Glutamate





**FIGURE 12.14** Structure and pathways of compounds involved in sulfur assimilation. The enzyme ATP sulfurylase cleaves pyrophosphate from ATP and replaces it with sulfate. Sulfide is produced from APS through reactions involving reduction by glutathione and ferredoxin. The sulfide or thiosulfide reacts with O-acetylserine to form cysteine. Fd, ferredoxin; GSH, glutathione, reduced; GSSG, glutathione, oxidized.





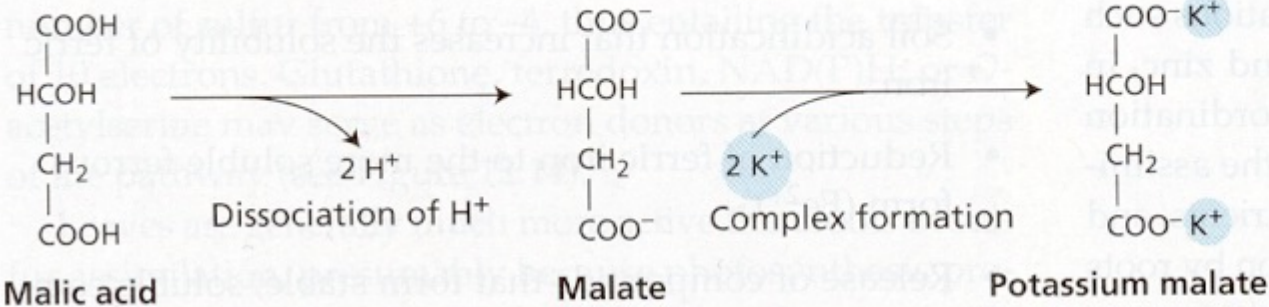
Much of the calcium in the cell wall is thought to be bound in this fashion.

**FIGURE 12.15** Examples of coordination complexes. Coordination complexes form when oxygen or nitrogen atoms of a carbon compound donate unshared electron pairs (represented by dots) to form a bond with a cation. (A) Copper ions share electrons with the hydroxyl oxygens of tartaric acid. (B) Magnesium ions share electrons with nitrogen atoms in chlorophyll *a*. Dashed lines represent a

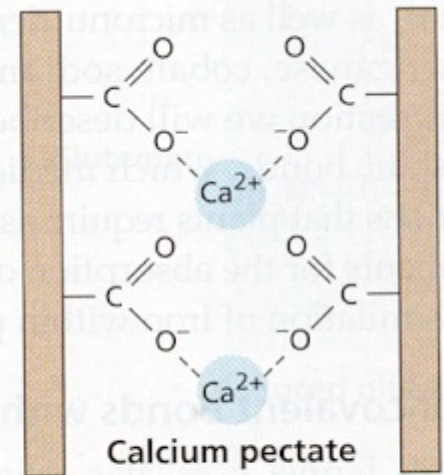
coordination bond between unshared electrons from the nitrogen atoms and the magnesium cation. (C) The “egg box” model of the interaction of polygalacturonic acid, a major constituent of pectins in cell walls, and calcium ions. At right is an enlargement of a single calcium ion forming a coordination complex with the hydroxyl oxygens of the galacturonic acid residues. (After Rees 1977.)



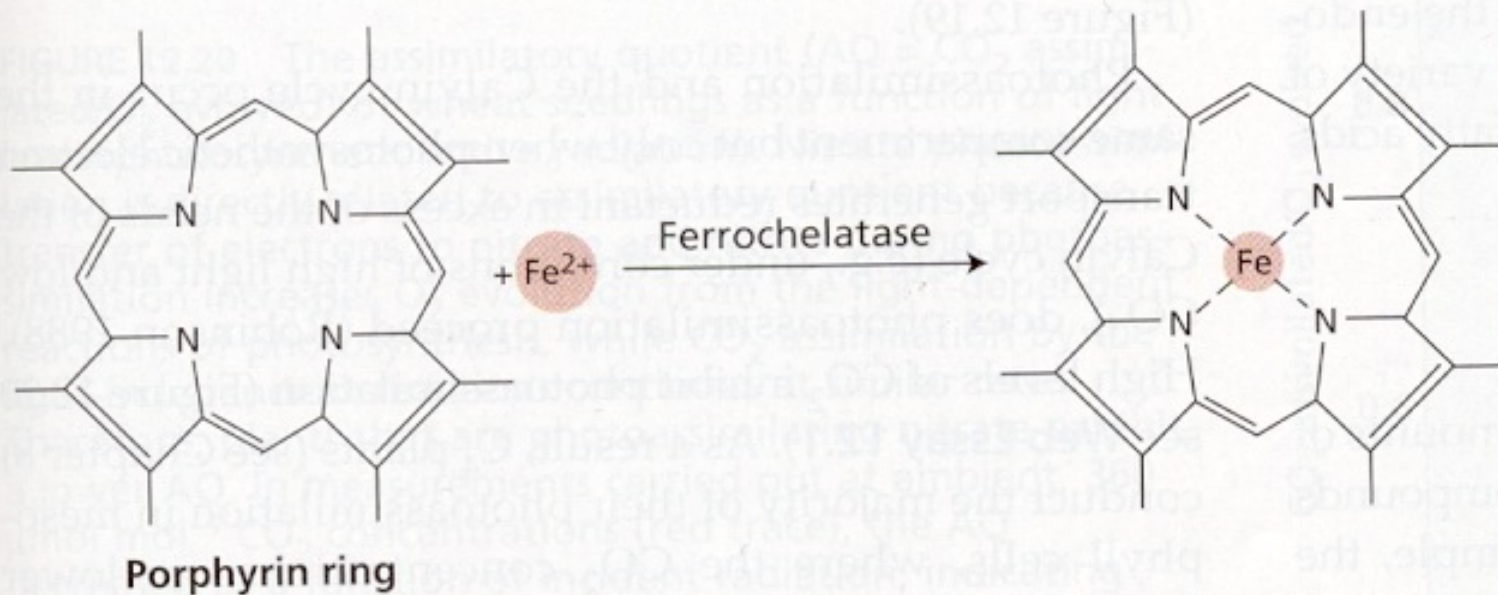
(A) Monovalent cation



(B) Divalent cation



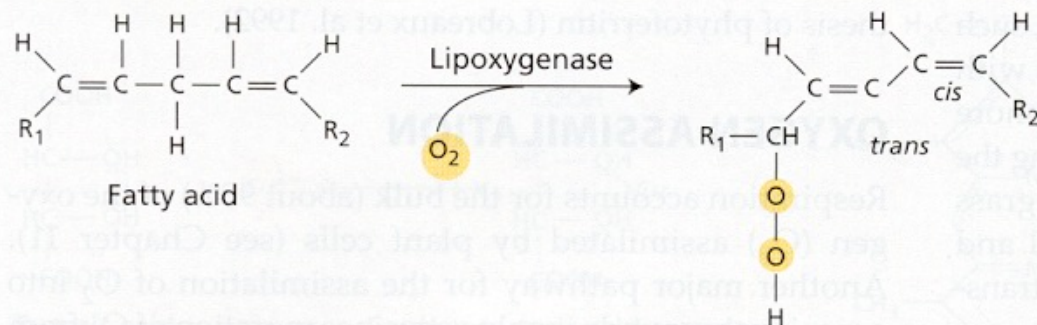
**FIGURE 12.16** Examples of electrostatic (ionic) complexes. (A) The monovalent cation  $K^+$  and malate form the complex potassium malate. (B) The divalent cation  $Ca^{2+}$  and pectate form the complex calcium pectate. Divalent cations can form cross-links between parallel strands that contain negatively charged carboxyl groups. Calcium cross-links play a structural role in the cell walls.



**FIGURE 12.17** The ferrochelatase reaction. The enzyme ferrochelatase catalyzes the insertion of iron into the porphyrin ring to form a coordination complex. See Figure 7.37 for illustration of the biosynthesis of the porphyrin ring.

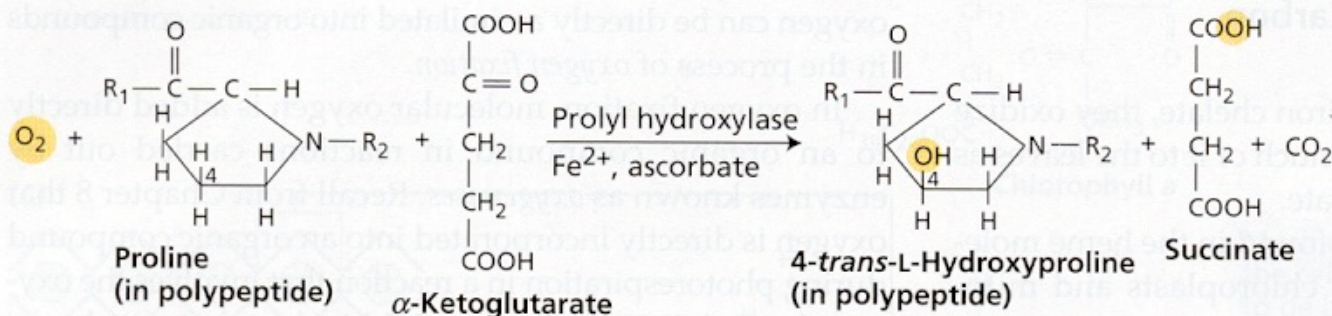


(A) Dioxygenase reaction



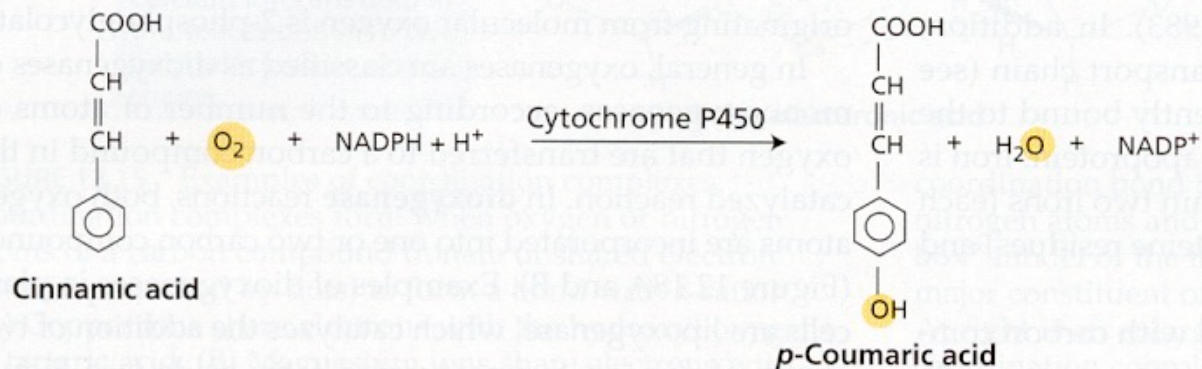
The dioxygenase lipoxygenase catalyzes the addition of two atoms of oxygen to the conjugated fatty acid to form a hydroperoxide with a pair of **cis-trans** conjugated double bonds. The hydroxy peroxy fatty acid may then be enzymatically converted to hydroxy fatty acids and other metabolites.

(B) Dioxygenase reaction



The dioxygenase prolyl hydroxylase catalyzes the addition of one oxygen from  $O_2$  to proline in a polypeptide chain to produce hydroxyproline, and the addition of one oxygen to  $\alpha$ -ketoglutarate to produce succinate and  $CO_2$ .

(C) Monooxygenase reaction



The monooxygenase cytochrome P450 uses one oxygen from  $O_2$  to hydroxylate cinnamic acid (and other substrates) and the other oxygen to produce water.  $NAD(P)H$  serves as the electron donor for monooxygenase reactions.

FIGURE 12.18 Examples of the two types of oxygenase reactions in cells of higher plants.