Section D: Nutritional Adaptations: Symbiosis of Plants and Soil Microbes

1. Symbiotic nitrogen fixation results from intricate interactions between roots and bacteria
2. Mycorrhizae are symbiotic associations of roots and fungi that enhance plant nutrition
3. Mycorrhizae and root nodules may have an evolutionary relationship
Introduction

• The roots of plants belong to subterranean communities that include a diversity of other organisms.
  • Among these are certain species of bacteria and fungi that have coevolved with specific plants, forming symbiotic relationships with roots that enhance the nutrition of both partners.
  • The two most important examples are symbiotic nitrogen fixation (roots and bacteria) and the formation of mycorrhizae (roots and fungi).
1. **Symbiotic nitrogen fixation results from intricate interactions between roots and bacteria**

- Many plant families include species that form symbiotic relationships with nitrogen-fixing bacteria.
  - This provides their roots with a built-in source of fixed nitrogen for assimilation into organic compounds.
  - Much of the research on this symbiosis has focused the agriculturally important members of the legume family, including peas, beans, soybeans, peanuts, alfalfa, and clover.
• A legume’s roots have swellings called **nodules**, composed of plant cells that contain nitrogen-fixing bacteria of the genus *Rhizobium*.

• Inside the nodule, *Rhizobium* bacteria assume a form called **bacterioids**, which are contained within vesicles formed by the root cell.
The development of root nodules begins after bacteria enter the root through an infection thread.
(1) Chemical signals from the root attract the Rhizobium bacteria and chemical signals from the bacteria lead to the production of an infection thread.

(2) The bacteria penetrate the root cortex within the infection thread.

(3) Growth in cortex and pericycle cells which are “infected” with bacteria in vesicles continues until the two masses of dividing cells fuse, forming the nodule.

(4) As the nodule continues to grow, vascular tissue connects the nodule to the xylem and phloem of the stele, providing nutrients to the nodule and carrying away nitrogenous compounds for the rest of the plant.
• The symbiotic relationship between a legume and nitrogen-fixing bacteria is mutualistic, with both partners benefiting.
  
  • The bacteria supply the legume with fixed nitrogen.
    
    • Most of the ammonium produced by symbiotic nitrogen fixation is used by the nodules to make amino acids, which are then transported to the shoot and leaves via the xylem.
  
  • The plant provides the bacteria with carbohydrates and other organic compounds.
• The common agricultural practice of crop rotation exploits symbiotic nitrogen fixation.

  • One year a non-legume crop such as corn is planted, and the following year alfalfa or another legume is planted to restore the concentration of fixed soil nitrogen.

  • Often, the legume crop is not harvested but is plowed under to decompose as “green manure”.

  • To ensure the formation of nodules, the legume seeds may be soaked in a culture of the correct *Rhizobium* bacteria or dusted with bacterial spores before sowing.
• Species from many other plant families also benefit from symbiotic nitrogen fixation.

• For example, alders and certain tropical grasses host nitrogen-fixing bacteria of the actinomycete group.

• Rice benefits indirectly from symbiotic nitrogen fixation because it is often cultivated in paddies with a water fern *Azolla* which has symbiotic nitrogen-fixing cyanobacteria.

• This increases the fertility of the rice paddy through the activity of the cyanobacteria and through decomposition of water fern after the growing rice eventually shades and kills the *Azolla*.

• This adds more nitrogenous compounds to the paddy.
• The specific recognition between legume and bacteria and the development of the nodule is the result of a chemical dialogue between the bacteria and the root.

• Each partner responds to the chemical signals of the other by expressing certain genes whose products contribute to nodule formation.

• The plant initiates the communication when its roots secrete molecules called flavonoids, which enter *Rhizobium* cells living in the vicinity of the roots.

• Each particular legume species secretes a type of flavonoid that only certain *Rhizobium* species will detect and absorb.
(1) A specific flavonoid signal travels from the root to the plant’s *Rhizobium* partner.

(2) The flavonoid activates a gene regulator, named Nod D.

(3) Nod D, a transcription factor, binds to the Nod box, activating transcription of the *nod* genes.

(4) The products of the *nod* genes are metabolic enzymes.

(5) These enzymes produce a chitinlike substance, called Nod factor.

(6) The Nod factor travels to the root, triggering development of the infection thread and nodule.
Fig. 37.13

Activation of early nodulin genes, leading to formation of infection thread and proliferation of cortical cells
• The molecular structures of Nod factors are very similar to chitins, the main substances in the cell walls of fungi and the exoskeletons of arthropods.
  • However, plants also produce chitinlike substances that appear to function as growth regulators.
  • It is possible that the Nod factors mimic certain plant growth regulators in stimulating the roots to grow new organs - nodules, in this case.
  • It may be possible in the future to induce *Rhizobium* uptake and nodule formation in crop plants that do not normally form such nitrogen-fixing symbioses.
  • In the short term, research is focused on improving the efficiency of nitrogen fixation and protein production.
2. Mycorrhizae are symbiotic associations of roots and fungi that enhance plant nutrition

- **Mycorrhizae** ("fungus roots") are modified roots, consisting of symbiotic associations of fungi and roots.

- The symbiosis is mutualistic.
  - The fungus benefits from a hospitable environment and a steady supply of sugar donated by the host plant.
• The fungi provide several potential benefits to the host plants.
  • First, the fungus increases the surface area for water uptake and selectively absorbs phosphate and other minerals in the soil and supplies them to the plant.
  • The fungi also secrete growth factors that stimulate roots to grow and branch.
  • The fungi produce antibiotics that may help protect the plant from pathogenic bacteria and pathogenic fungi in the soil.
Almost all plant species produce mycorrhizae.

This plant-fungus symbiosis may have been one of the evolutionary adaptations that made it possible for plants to colonize land in the first place.

Fossilized roots from some of the earliest land plants include mycorrhizae.

Mycorrhizal fungi are more efficient at absorbing minerals than roots, which may have helped nourish pioneering plants, especially in the nutrient poor soils present when terrestrial ecosystems were young.

Today, the first plants to become established on nutrient-poor soils are usually well endowed with mycorrhizae.
• Mycorrhizae take two major forms: ectomycorrhizae, and endomycorrhizae.

• In **ectomycorrhizae**, the mycelium forms a dense sheath over the surface of the root and some hyphae grow into the cortex in extracellular spaces between root cells.

• In **endomycorrhizae**, the fungus makes extensive contact with the plant through branching of hyphae (arbuscles) that form invaginations in the host cells, increasing surface area for exchange of nutrients.
• The mycelium of ectomycorrhizae extends from the mantle surrounding the root into the soil, greatly increasing the surface area for water and mineral absorption.

• Hyphae do not penetrate root cells but form a network in the extracellular spaces that facilitates nutrient exchange.

• Compared with “uninfected” roots, ectomycorrhizae are generally thicker, shorter, more branched, and lack root hairs.

• Ectomycorrhizae are especially common in woody plants, including trees of the pine, spruce, oak, walnut, birch, willow, and eucalyptus families.
• Endomycorrhizae have fine fungal hyphae that extend from the root into the soil.
  
• Within the root, the hyphae digest small patches of root cell walls and form tubes by invagination of the root cell’s membrane.
  
• Some fungal hyphae within these invaginations may form dense knotlike structures called arbuscules that are important sites of nutrient transfer.
  
• Roots with endomycorrhizae look like “normal” roots with root hairs, but the symbiotic connects are very important, albeit microscopic.
  
• Endomycorrhizae are found in over 90% of plant species, including important crop plants.
• Roots can be transformed into mycorrhizae only if they are exposed to the appropriate fungal species.
  • In most natural systems, these fungi are present in the soil, and seedlings develop mycorrhizae.
  • However, seeds planted in foreign soil may develop into plants that show signs of malnutrition because of the absence of the plant’s mycorrhizal partners.
  • Researchers observe similar results in experiments in which soil fungi are poisoned.
  • Farmers and foresters are already applying the lessons learned from this research by inoculating plants with the spores from the appropriate fungal partner to ensure development of mycorrhizae.
3. Mycorrhizae and root nodules may have an evolutionary relationship

- There is growing evidence that the molecular biology of root nodule formation is closely related to mechanisms that first evolved in mycorrhizae.
  - The nodulin genes activated in the plant during the early stages of root nodule formation are the very same genes activated during the early development of endomycorrhizae.
  - Mutations in these genes block development of both root nodules and mycorrhizae.
  - The signal transduction pathways of both systems share some components.
• Experimental application of plant hormones called cytokinins to root cells of legumes activates expression of early nodulin genes even in the absence of bacterial or fungal symbionts.

• “Infection” by either symbiont causes cytokinin concentrations to increase naturally.

• Cytokinins may be one of the links between the “I’m here” announcement of the microbes and the changes in gene expression in the plant that lead to structural modifications of the roots.
Further evidence comes from the similarities in the chemical cues used by both microbes.

- The Nod factors secreted by *Rhizobium* bacteria are related to chitins, the same compounds that make up the cells wall of fungi.

- A reasonable hypothesis is that root cells have a family of closely related receptors that detect their particular bacterial and fungal symbionts.
• Mycorrhizae evolved very early, probably over 400 million years ago in the earliest vascular plants.

• In contrast, the root nodules in legumes originated only 65-150 million years ago, during the early evolution of angiosperms.

• The common molecular mechanism in the root’s two major symbiotic relationships suggests that root nodule development was at least partly adapted from a signaling pathway that was already in place in mycorrhizae.