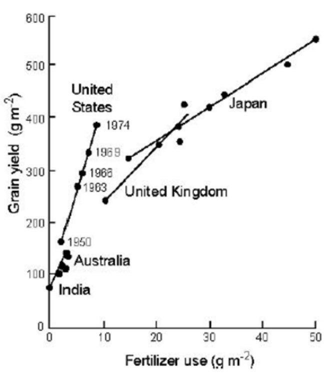
Plants acquire nutrients via roots and microbes

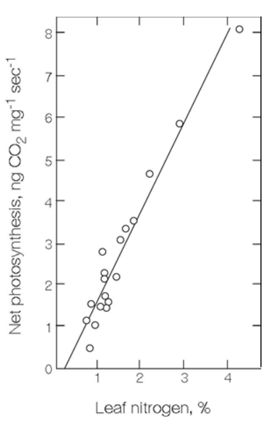
Nutrients matter!!



(Evans, 1980, *American Scientist*)

More fertilizer = More food

Nutrients matter!!



Photosynthetic machinery accounts for more than half of the nitrogen in leaves.

Changes in leaf nitrogen content reflect changes in protein content, particularly changes in the amount of Rubisco (photosynthetic enzyme).

Photosynthesis is down-regulated under conditions of nitrogen limitation.

Similar relationship between phosphorus and photosynthesis.

Element	Principal form absorbed	Usual concentration in healthy plants (% or ppm of Dry Weight)	Important Functions
Macronutrients			
Carbon (C)	CO_2	~44%	Component of organic compounds
Oxygen (O)	H_2O or O_2	~44%	Component of organic compounds
Hydrogen (H)	H_2O	~6%	Component of organic compounds
Nitrogen (N)	NO_3^- or NH_4^+	1-4%	Component of amino acids, proteins, nucleotides, nucleic acids, chlorophylls, and coenzymes
Potassium (K)	K^+	0.5-6%	Involved in osmosis and ionic balance and in opening and closing of stomata; activator of many enzymes
Calcium (Ca)	Ca^{2+}	0.2-3.5%	Component of cell walls; enzyme cofactor; involved in cellular membrane permeability; component of calmodulin, a regulator of membrane and enzyme activities
Phosphorus (P)	$H_2PO_4^-$ or HPO_4^{2-}	0.1-0.8%	Component of energy-carrying phosphate compounds (ATP and ADP), nucleic acids, several essential coenzymes, phospholipids
Magnesium (Mg)	Mg^{2+}	0.1-0.8%	Part of the chlorophyll molecule; activator of many enzymes
Sulfur (S)	SO_4^{2-}	0.05-1%	Component of some amino acids and proteins and of coenzyme A

(Raven et al. 1992, *Biology of Plants*)

Element	Principal form absorbed	Usual concentration in healthy plants (% or ppm of Dry Weight)	Important Functions
Micronutrients			
Iron (Fe)	Fe^{2+} or Fe^{3+}	25-300 ppm	Required for chlorophyll synthesis; component of cytochromes and nitrogenase
Chlorine (Cl)	Cl^-	100-10,000 ppm	Involved in osmosis and ionic balance; probably essential in photosynthetic reactions that produce oxygen
Copper (Cu)	Cu^{2+}	4-30 ppm	Activator or component of some enzymes
Manganese (Mn)	Mn^{2+}	15-800 ppm	Activator of some enzymes; required for integrity of chlorplast membrane and for oxygen release in photosynthesis
Zinc (Zn)	Zn^{2+}	15-100 ppm	Activator or component of many enzymes
Molybdenum (Mo)	MoO_4^{2-}	0.1-5.0 ppm	Required for nitrogen fixation and nitrate reduction
Boron (B)	$B(OH)_3$ or $B(OH)_4^-$	5-75 ppm	Influences Ca^{2+} utilization, nucleic acid synthesis, and membrane integrity

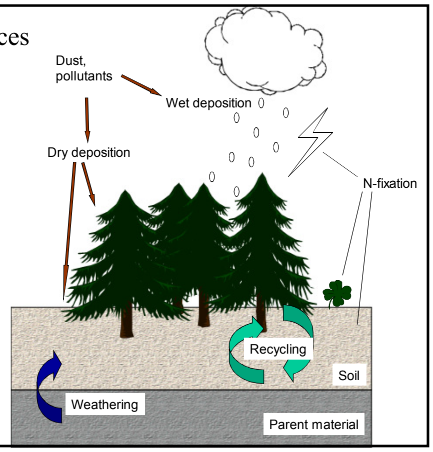
C HOPKNS CaFe Mg Mn B Cl CuZn Mo

(Raven et al. 1992, *Biology of Plants*)

Element	Amount in Dry Plant Tissue [%]	
Carbon (C)	45	**Source**: air and water.
Oxygen (O)	45	
Hydrogen (H)	6.0	
Nitrogen (N)	1.5	
Potassium (K)	1.0	**Source**: mainly parent material.
Calcium (Ca)	0.5	
Magnesium (Mg)	0.2	
Phosphorus (P)	0.2	
Sulfur (S)	0.1	
Chlorine (Cl)	0.01	
Iron (Fe)	0.01	
Manganese (Mn)	0.005	
Boron (B)	0.002	
Zinc (Zn)	0.002	
Copper (Cu)	0.0006	
Molybdenum (Mo)	0.00001	

(Salisbury and Ross, 1992, *Plant Physiology*)

Nutrient sources to terrestrial ecosystems



Weathering of parent material to produce soil occurs over geological time scales

- **Weathering** = f(parent material, climate, organisms, topography, time)

- **Parent material**: underlying rock, water- or wind-transported sediment (chemical composition, structure, texture).
- **Climate**: temperature, precipitation (freeze-thaw cycles, chemical reactions, biological activities).
- **Organisms**: microbes, vegetation, animals (microbial decomposition, root action, soil mixing, pH effects because of excreted organic acids).
- **Topography**: slope, aspect (erosion, movement of nutrients, influence on climate).
- **Time**: time-dependent processes; nutrient depletion.

Atmospheric sources of nutrients

- Rain, clouds, and fog (wet deposition):
  - Aerosols and gases are dissolved by rain.

- Dry deposition (sedimentation):
  - Gravitational deposition of particles (dust, soil).
  - Lake bed salts can provide important ion sources (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, SO_4^{2-}, Cl^{-}).

- Largest reservoir of nitrogen is N_2 gas in atmosphere:
  - N_2 fixed to NH_4^+ by lightening (< 20 Tg yr^{-1}).
  - Biological N-fixation (140 Tg yr^{-1}).
  - Anthropogenic fixation (200 Tg yr^{-1}) and increasing.

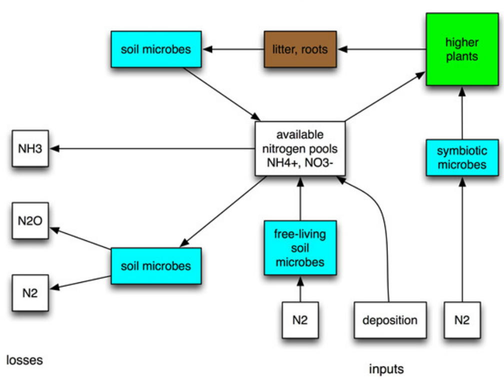
Nutrient recycling

Table 1. Major sources of available nutrients that enter the soil.

Nutrient	Source of plant nutrient (% of total)		
	Atmosphere	Weathering	Recycling
Temperate forest			
N	7	0	93
P	1	<10?	>89
K	2	10	88
Ca	4	31	65
Arctic tundra			
N	4	0	96
P	4	<1	96

Source: Chapin 1991.

Generalized nitrogen cycle



How do nutrients get to plant root surfaces?

- **Diffusion in water:**
  - Decomposition and weathering makes nutrients available (mineralization).
  - Soluble ions diffuse in water, diffusion rates differ among ions.
  - Nutrient concentration at root surface is less than concentration in soil.
  - Typically the most important process.
- **Mass flow in water**:
  - Largely associated with water movement in soil due to plant uptake.
  - Infiltration of precipitation can also have an influence.
  - Replenishes zones depleted of nutrients.
  - Typically transport rates are too low for growth limiting nutrients.
- **Interception by roots**:
  - Roots grow into new areas in the soil.
  - Typically not a major source of direct nutrient acquisition; enhances diffusion.
- **Symbioses**:
  - Mycorrhizae: Significantly increases surface area in contact with soil.
  - N-fixers: Direct source of nitrogen.

How do nutrients get into plant roots?

- Nutrient concentration is greater in roots than in soil; concentration gradient does not favor ion diffusion into root.
- Energy is required to transport nutrients against the concentration gradient; 30-50 % of photosynthates (carbon energy) transported to root is used for nutrient uptake, significant component of root respiration.
- Cations diffuse along electrochemical potential gradient:
  - Proton pumping ATP-ase pumps H^+ out of cell, charge gradient.
  - Ions diffuse into cell through specific channels.
- Anions must be actively transported against the electrochemical potential gradient:
  - Ion-specific carriers.

Soil type matters: ion exchange complex

- Clay particles and soil organic matter have electrically-charged surfaces, which attract and bind ions (adsorption).
- Tendency for adsorption varies:
- Cations: $Al^{3+} > H^+ > Ca^{2+} > Mg^{2+} > K^+ \approx NH_4^+ > Na^+$
- Anions: $PO_4^{3-} > SO_4^{2-} > Cl^- > NO_3^-$

Immobile (PO_4^{3-}) — Mobile (NO_3^-, Na^+)

Plants can influence rhizosphere chemistry

- Excretion of H^+ or organic acids reduces pH:
  - Increases availability of Fe, Mn, B, Zn, Cu.
- Excretion of chelating agents:
  - Releases PO_4^{3-} bound in insoluble forms; aids uptake of Fe, Zn, and Cu.
- Excretion of phosphatases:
  - Cleave organic bonds to release PO_4^{3-}.
- Priming of rhizosphere mineralization:
  - Excretion of organic acids, carbohydrates, and amino acids stimulates microbial activity and decomposition (recycling).

Rate of nutrient uptake

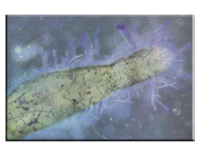
- Nutrient uptake rates depend on:
  - Quantity of root surface area (root length).
  - Nutrient concentration at root surface → dependent on diffusion.
  - Capacity of plant to take up nutrient (resource allocated to ion transport).
  - Demand by plant → growth rate.
- Diffusion is typically the limiting process in nutrient acquisition:
  - Especially true for nutrients like PO_4^{3-} that have low solubility in water and low diffusion coefficients (three orders of magnitude lower than Cl^-, NO^{3-}, and SO_4^{2-}).
- Solutions (increase root length or get help):
  - Increase root mass ratio (RMR, fraction of roots); large investment.
  - Increase number of root hairs (high surface area to volume ratio); moderate investment.
  - Symbiotic associations with fungi and nitrogen fixing bacteria; moderate to large investment.

What kind of root to grow and where to place it in the soil is dependent on tradeoffs: Water uptake versus nutrient uptake

Water has a high diffusion rate.
Nutrient ions have lower diffusion rates.

Mycorrhizal associations

- Occur in most plant species; low host specificity.
- Plant host provides carbon energy to fungus (4-20 % of fixed carbon).
- Fungus substantially increase (1-2 orders of magnitude) the effective absorptive surface for nutrient uptake.
- Particularly important in P and immobile nutrient uptake; can also supply N and water.

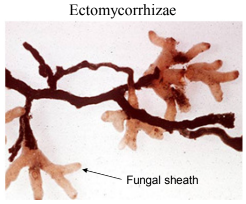


mycorrhiza with hyphae

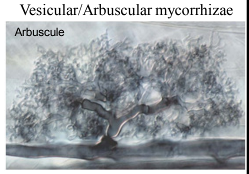
Three types of mycorrhizae (root-fungus symbiosis)

- **Ectomycorrhizae**:
  - Fungus does not penetrate cortical cells; characterized by fungal sheath surrounding root.
  - Primarily association between trees and basidio- or ascomycetes.
- **Vesicular/Arbuscular mycorrhizae** :
  - Fungus grows arbuscules (exchange organs) and vesicles (storage organs) in root cortical cells.
  - Most frequently occur on herbaceous species, but also some trees.
- **Ericoid mycorrhizae**:
  - Similar to V/AM.
  - Tundra ecosystems.

Ectomycorrhizae

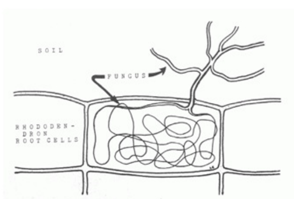


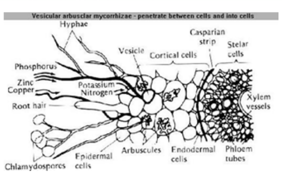
Vesicular/Arbuscular mycorrhizae



http://www.ffp.csiro.au/research/mycorrhiza/arb.html

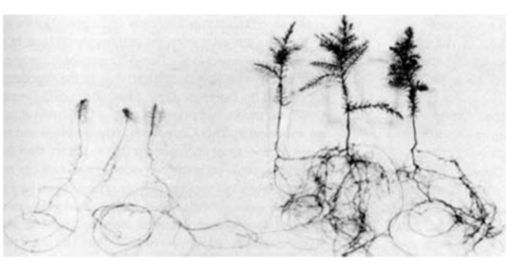
Hyphal network increases root surface area by 10-100 times





(D. Read, 1997, Nature)

Absence of mycorrhizae can have a major impact on photosynthesis



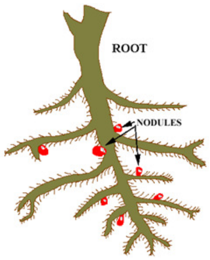
(Salisbury and Ross, 1992, *Plant Physiology*)

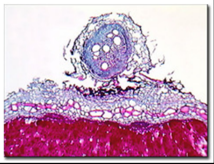
Symbiotic N-fixation

- Restricted to more limited group of plants (legumes); high host specificity.
- Plant host provides carbon energy (25 % of fixed carbon) to N-fixing bacteria.
- N-fixer provides NH_4^+ (or amino acid) to plant.
- Primary N input to natural ecosystems.

Symbiotic N-fixation

- Atmospheric N_2 is converted (fixed) to NH_4^+; reaction is catalyzed by nitrogenase.
- N_2 is triple bonded; requires lots of energy to break bonds.
- N-fixers (bacteria and cyanobacteria) may be free-living organisms or symbiotic with plants.
- Requires anaerobic environment; leghemoglobin (protein) is used to bind O_2.
- Often occurs in root nodules (specialized environments that house N-fixing bacteria).

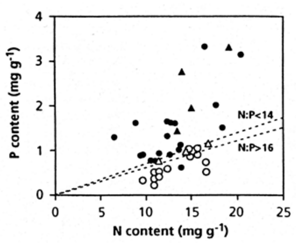




Nutrient limitation of plant growth is usually by N or P

- N limitation:
  - Most non-tropical terrestrial ecosystems; primary succession.
- P limitation:
  - Highly weathered soils, including many tropical soils; calcareous soils (lots of calcium carbonate).
- Different species within a community may be limited by different nutrients.
- Nutrient limitation usually demonstrated by response to fertilization.

N:P < 14 N limitation
14 < N:P < 16 Co-limitation
N:P > 16 P limitation



(Aerts and Chapin, 2000, Adv. Ecol. Res.)

Plant response to Nutrient Deficiency

- When nutrient supply decreases relative to nutrient demand:
  - Specific nutrients are removed from storage; decrease in cellular storage.
  - Reduced rates of leaf growth and photosynthesis.
  - Senescence of older leaves.
  - Relocation of resource reserves from leaves to roots; increased RMR.
  - Dormancy (significantly reduced photosynthesis and nutrient uptake).
  - Death of meristems (growth tissues).

Photosynthesis in most plants/ecosystems increases as a result of nutrient additions.

If the ability of plant roots to take up nutrients was the limiting factor, an increase in photosynthesis probably wouldn't occur.

Thus, nutrient availability in soil appears to control nutrient uptake by plants and subsequent growth ⟶ nutrients absorbed by plants are used primarily for production of new tissues.