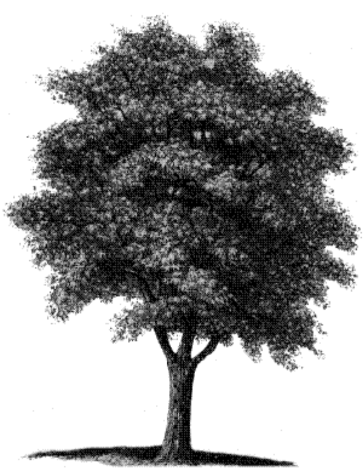
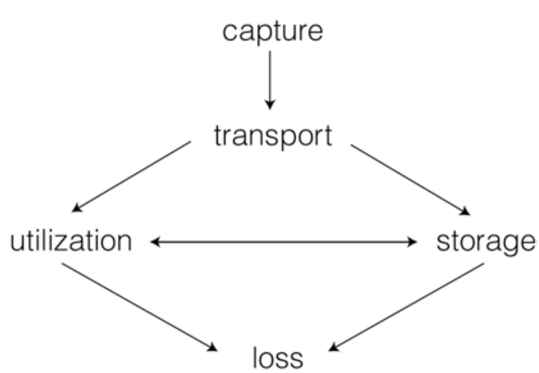
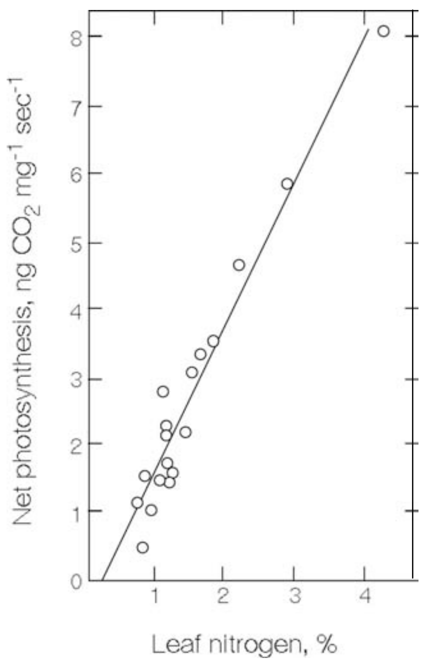
Plants acquire nutrients via roots and microbes

Consideration of whole plant as an integrated system: how are resources used, since photosynthesis is only part of the story





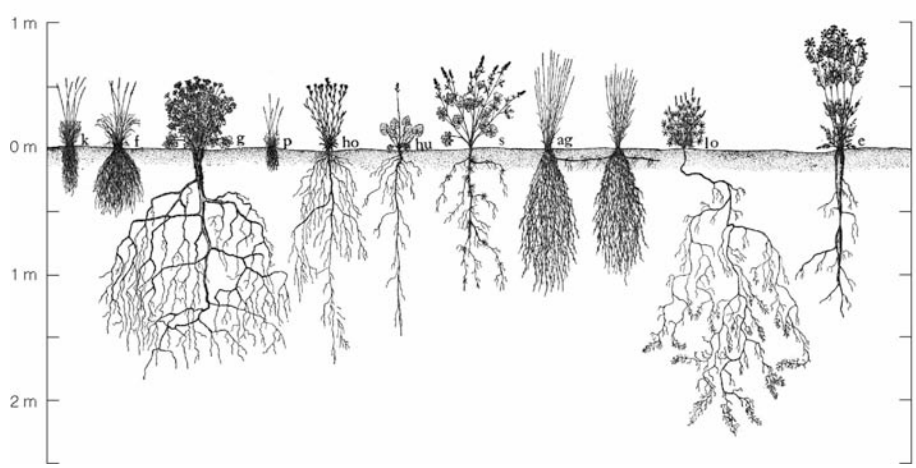


Nutrients matter !

The maximum photosynthetic rate is often linearly proportional to the leaf nitrogen content (N)

The changes in leaf nitrogen content reflect changes in protein content, particularly changes in the amount of Rubisco

What kind of root to build and where to place it in the soil?
What are the tradeoffs? Water uptake versus nutrient uptake



How to acquire the nutrients needed for growth?

- Nutrient sources
  - weathering, atmospheric deposition, N-fixation, recycling within the soil (within ecosystem)
- Plant uptake
  - movement of nutrients, acquisition strategies
- Symbioses with microorganisms
  - mycorrhizae, symbiotic N-fixation

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

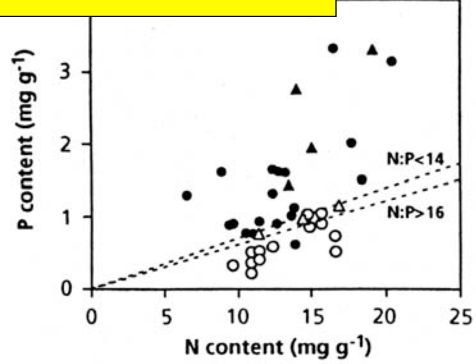
C HOPKINS CaFe Mg B Mn CuZn Mo

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

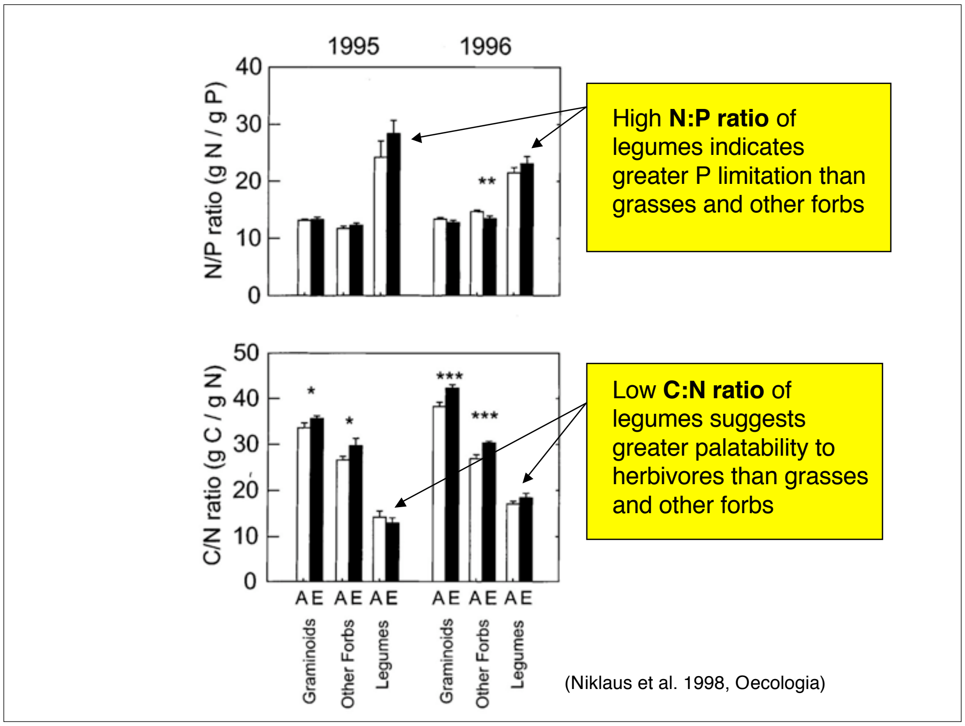
Nutrient limitation of plant growth

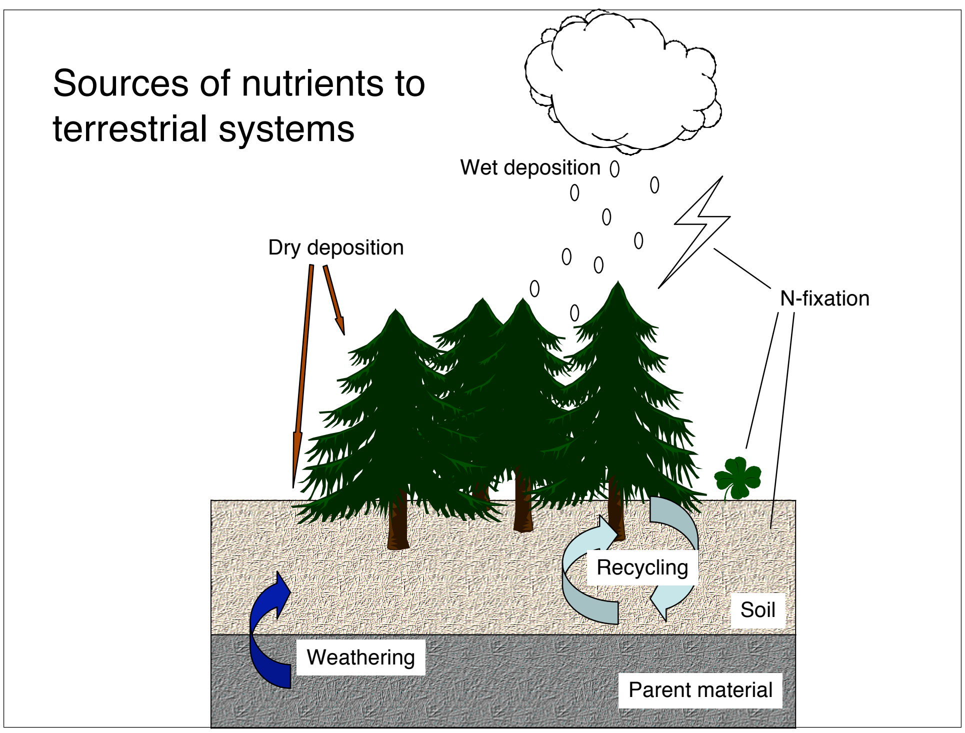
- N limitation
  - most non-tropical terrestrial ecosystems; early 1° succession
- P limitation
  - highly weathered soils, including many tropical soils; calcareous soils
- • Different species within a community may be limited by different nutrients
- • Nutrient limitation usually demonstrated by response to fertilization

N:P < 14   N limitation
14 < N:P < 16   co-limitation
N:P > 16   P limitation
N:P = 10   optimal growth



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


1995
1996
N/P ratio (g N / g P)
40
30
20
10
0
**
High **N:P ratio** of legumes indicates greater P limitation than grasses and other forbs
C/N ratio (g C / g N)
50
40
30
20
10
0
*
*
***
***
Low **C:N ratio** of legumes suggests greater palatability to herbivores than grasses and other forbs
AE AE AE AE AE AE
Graminoids
Other Forbs
Legumes
Graminoids
Other Forbs
Legumes
(Niklaus et al. 1998, Oecologia)


Sources of nutrients to terrestrial systems
Wet deposition
Dry deposition
N-fixation
Recycling
Soil
Weathering
Parent material

Atmospheric sources of nutrients

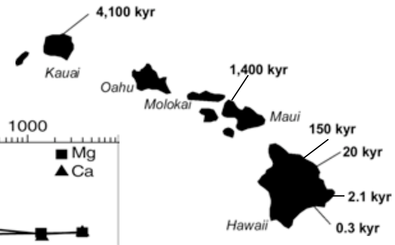
- Rain, clouds, and fog (wet deposition)
  - Aerosols and gases are dissolved by rain or fog
- Dry deposition (sedimentation)
  - Gravitational deposition of particles; dust, soil and sea salts can provide important source of cations (Ca^{2+}, Na^{+}, K^{+}, Mg^{2+}, P)
- Largest reservoir of N as N_2 gas
  - N_2 fixed to NH_4^+ by lightening (< 20 Tg yr^{-1}), biological N-fixation (140 Tg yr^{-1}), anthropogenic fixation (140 Tg yr^{-1})

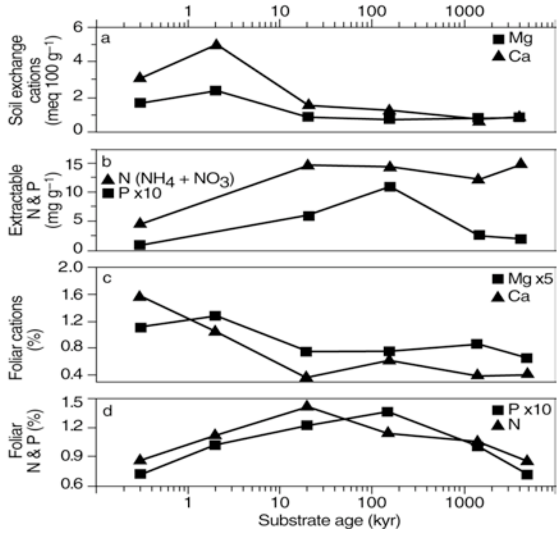
Weathering of parent material

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

- Parent material - chemical composition, texture
- Climate - temperature, precipitation; freeze-thaw
- Vegetation - root action; effects on pH
- Topography - erosion, movement of nutrients
- Time - time-dependant processes; nutrient depletion

Nutrient availability and substrate age

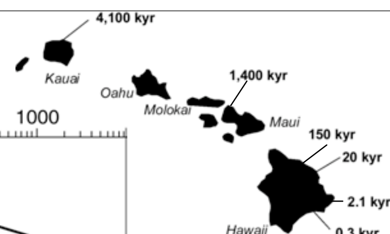


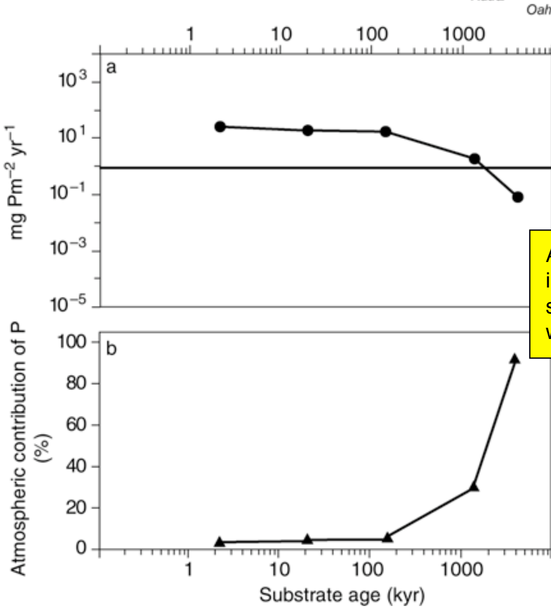


Foliar nutrient concentrations reflect soil nutrient availability

(O.A. Chadwick et al. 1999, Nature)

Nutrient sources and substrate age





Atmospheric P deposition increases in importance as substrate becomes highly weathered

(O.A. Chadwick et al. 1999, Nature)

Controls on litter decomposition

- Three major controls on decomposition:
  - climate > litter chemistry > soil organisms

- Climate most important determinant on global scale
  - microbial activity increases with temperature
  - intermediate moisture conditions maximize activity
- Within climate zone, litter chemistry strongest control
  - faster decomposition with higher nutrient content
  - litter chemistry correlated with site fertility

Cation exchange complex

- Clay particles and humic substances in soil have electrically-charged surfaces, which attract and bind ions (adsorption)
- Net negative charge = more sites for cations than anions

- Tendency for adsorption varies:
- cations: $Al^{3+} > Ca^{2+} > Mg^{2+} > NH_4^+ > K^+ > Na^+$
- anions: $PO_4^{3-} > SO_4^{3-} > NO_3^- > Cl^-$

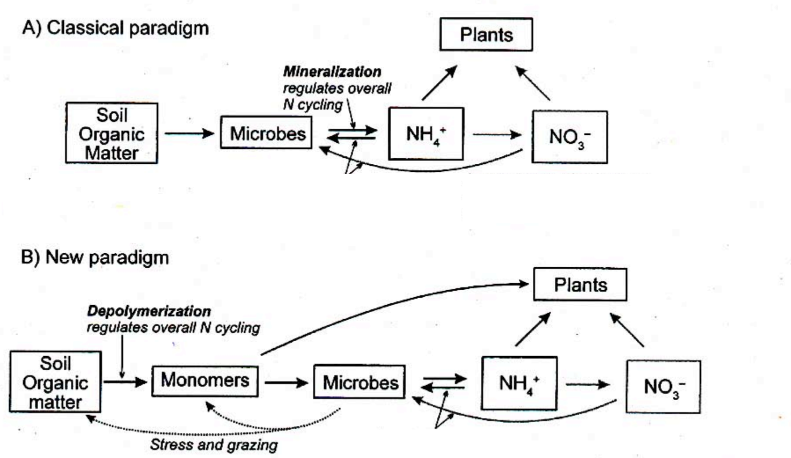
Nutrient pools vs. rate of supply

Nitrogen dynamics in California annual grassland

	Soil pool (mg m^{-2})	Plant uptake (mg m^{-2} d^{-1})	Microbial uptake (mg m^{-2} d^{-1})	Total uptake (mg m^{-2} d^{-1})
February				
NO_3^-	10	41	81	122
NH_4^+	640	81	426	507
April				
NO_3^-	51	83	146	229
NH_4^+	800	110	639	749

(Jackson et al. 1989. Soil Biology & Biochemistry)

Nutrient supply – N mineralization



Ion movement by mass flow

- Transpiration stream
  - Rate of supply depends on transpiration rate/soil moisture and ion concentration in soil solution
- Wetting fronts
  - Highest nutrient concentrations at soil surface; infiltration of rain water can move nutrients to deeper soil
- Lateral movement in wet systems
  - Arctic tundra - permafrost causes lateral movement of water

Nutrient supply – water availability

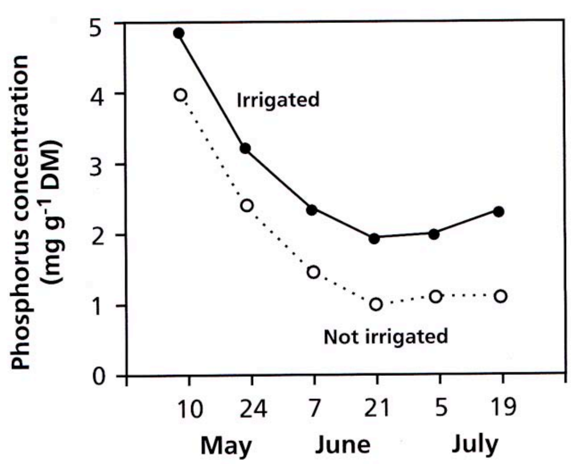


FIGURE 4. Phosphorus concentration in the shoots of *Hordeum vulgare* (barley) grown with or without irrigation (Chapin 1991). Copyright Academic Press.

Ion movement by diffusion

- $D = D_l \times \theta \times f \times 1/b$

- where D_l = diffusion coefficient in free solution
- θ = volumetric water content of soil
- f = an impedance factor
- b = soil buffer capacity
- f is the length of the diffusion pathway, which is a function of soil moisture and soil compaction
- Soil buffer capacity is determined by the supply of ions adsorbed on the Cation Exchange Complex (CEC)

D_l for some soil solution ions ($m^2\ s^{-1}$):

NO_3^- 110 x 10^{-10}; K^+ 1-2810 x 10^{-12}; $H2PO_4^-$ 0.3 – 3.310 x 10^{-13}

Ion uptake

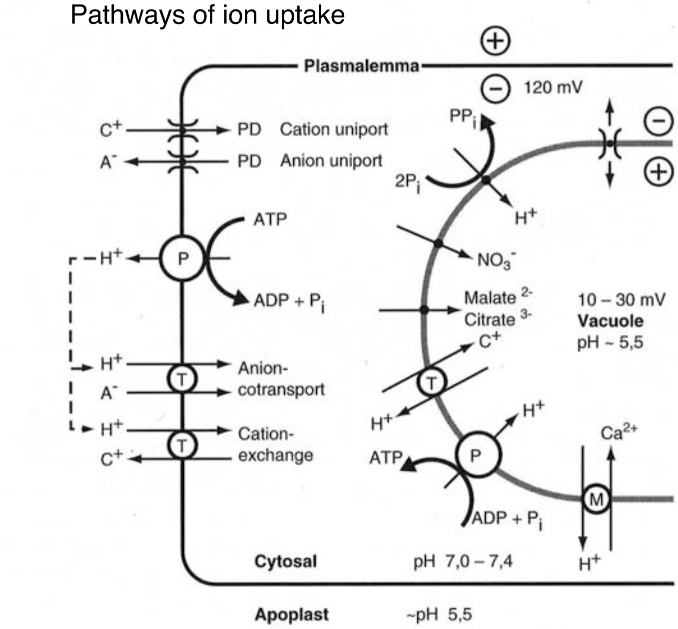
•Concentration gradient across root surface does not favor ion diffusion into the root

•Cations diffuse along electrochemical potential gradient

–Proton-pumping ATP-ase pumps H^+ out of cell

•Anions must be actively transported against the electrochemical potential gradient

Pathways of ion uptake



(Larcher 1995, *Physiological Plant Ecology*)

Acclimation/adaptation to nutrient availability

- Uptake kinetics
- Root allocation and morphology
- Rhizosphere chemistry
- Growth strategies
- Symbioses

Uptake kinetics

- Response to low nutrient supply
  - increase I_{max} (maximum inflow rate; function of the abundance or specific activity of transport proteins)
  - induction of high-affinity transport system (carrier-mediated; has low I_{max})
  - requires investment of energy and proteins

Root allocation and morphology

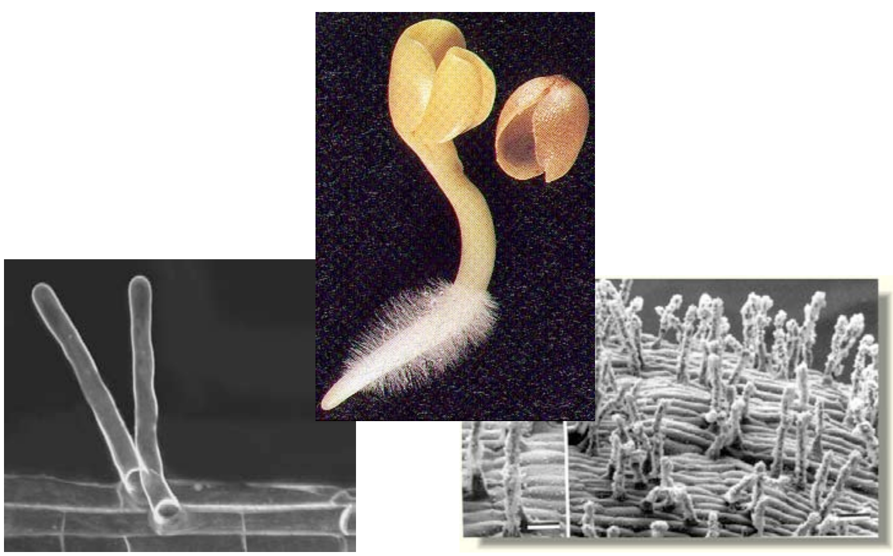
- Root mass ratio (% roots)
  - high RMR increases absorbing surface; largest investment
- Root hairs
  - greatly increase absorbing surface (high surface area to volume ratio); moderate invesment
- Cluster roots
  - proteoid roots; associated with high rates of organic acid excretion

Root mass ratio

N supply (mg/L)	Shoot (g/plant)	Root (g/plant)	S:R ratio	Root length (m)
0	0.24	0.38	0.63	4.7
21	0.75	0.84	0.89	6.2
42	1.34	1.30	1.03	6.8
105	2.40	1.97	1.25	8.1
210	4.49	2.89	1.55	10.2

(Corn – from Marschner 1986)

Root hairs – increase absorptive surface (P)



Non-mycorrhizal (Proteaceae) Cluster roots – P uptake

Roots and spatial heterogeneity

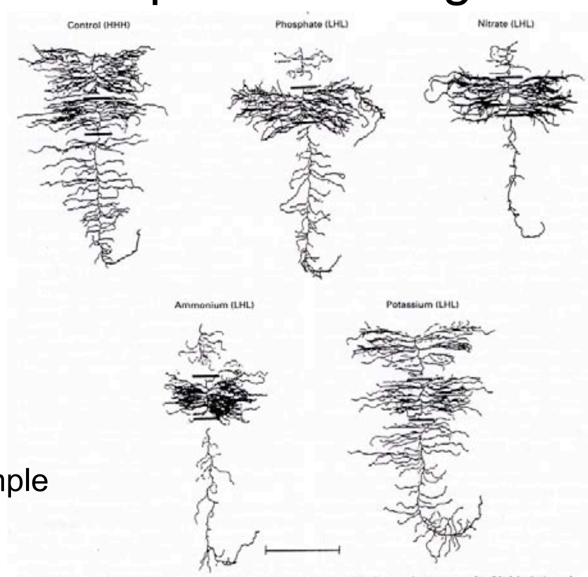


Figure 1. Single first-order axes of the seminal root system of *Hordeum vulgare* grown for 21 d in irrigated sand. All parts of the root systems of control plants were uniformly supplied with a concentrated nutrient solution (HHH treatment). In localized supply treatments (LHL), only the middle zones received the complete solution, the top and bottom zones being supplied with a solution deficient in either P, NO_3^-,

Extreme example
-Barley-

Roots and spatial heterogeneity

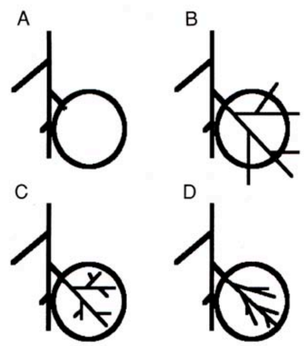
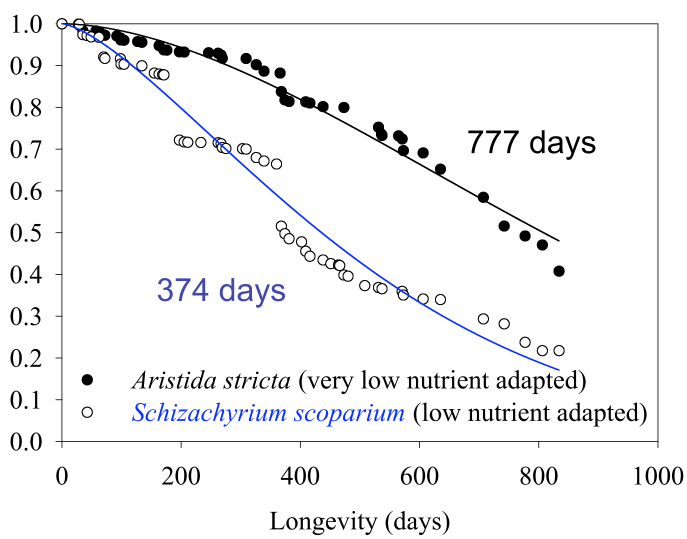


Figure 6 Topological diagrams of model root systems to indicate the distinction between biomass allocation and architectural plasticity. An initial root system (A) may respond to a patch, indicated by a circle, by increased allocation of biomass with no change in architecture (B) or a change in architecture (C and D). Architectural changes may, for example, be a change in topology, leading to a less herringbone system, with no increase in allocation (C), or a change in geometry, such as shorter link lengths and narrower branching angles (D). Biomass allocation plasticity alone (B) is ineffective at localizing new growth within the patch.

Root lifespan

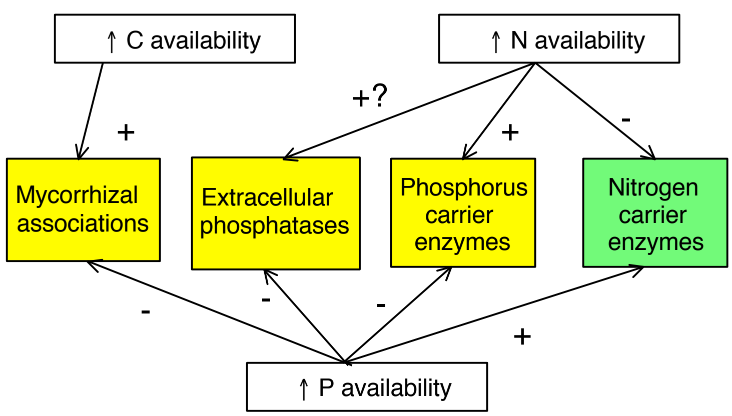


(West et al. 2004)

Rhizosphere chemistry

- Exretion of H^+ or organic acids reduces pH
  - increases availability of Zn, Mn, B, Mn, Fe
- Excretion of chelating agents
  - aids uptake of Fe and Zn; releases PO_4^{2-} bound in insoluble forms
- Excretion of phosphatases
  - cleave organic bonds to release PO_4^{2-}
- Priming of rhizosphere mineralization
  - excretion of organic acids, carbohydrates, and amino acids stimulates microbial activity

Resource availability and acquisition strategies



(Treseder & Vitousek 2000, Ecology)

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.

Plant growth strategies

- Characteristics of plants from low-nutrient environments
  - slow growth
  - low nutrient demand
  - long-lived tissues; C-based defenses
  - low tissue nutrient content; slow decomposition
- Characteristics of plants from high-nutrient environments
  - rapid growth
  - high nutrient demand
  - short-lived tissues; mobile N-based defenses
  - high tissue nutrient content; rapid decomposition

Root allocation and morphology

- Root mass ratio (% roots)
  - high RMR increases absorbing surface
  - large investment
- Root hairs
  - greatly increases absorbing surface (high surface area to volume ratio)
  - moderate investment
- Get help!
  - mycorrhizae
  - nitrogen fixers

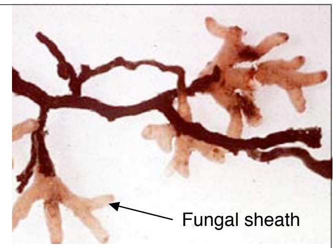
Nutrient availability

- NO_3^-
  - highly mobile
  - leachable
- NH_4^+
  - less mobile
  - binds to SOM
- PO_4^{-3}
  - highly immobile
  - low solubility

Mycorrhizal associations

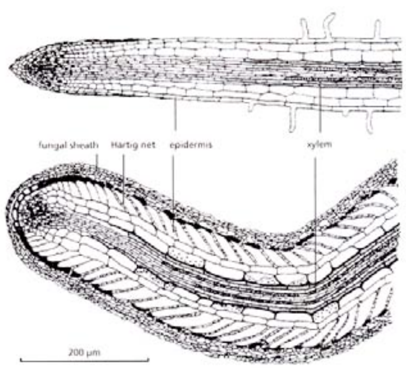
- occur in most plant species; low host specificity
- plant host provides C energy to fungus
- fungus increases effective absorptive surface
- particularly important in P nutrition; may also supply N and water

Types of mycorrhizae

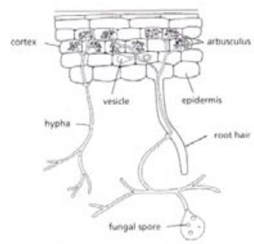


- •Ectomycorrhizae
  - – fungus does not penetrate cortical cells
  - – characterized by fungal sheath
  - – primarily association between trees and basidio- or ascomycetes
- •Vesicular/Arbuscular Mycorrhizae
  - – fungus penetrates root cortical cells
  - – characterized by vesicles (storage), arbuscles (exchange)
  - – most frequently occur on herbaceous species, but also some trees
- •Ericoid mycorrhizae
  - – similar to V/AM
  - – heath and tundra ecosystems

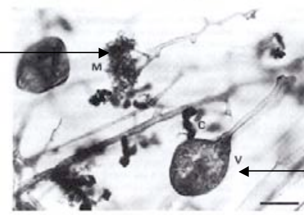
Ecto-



Arbuscular



Arbuscule

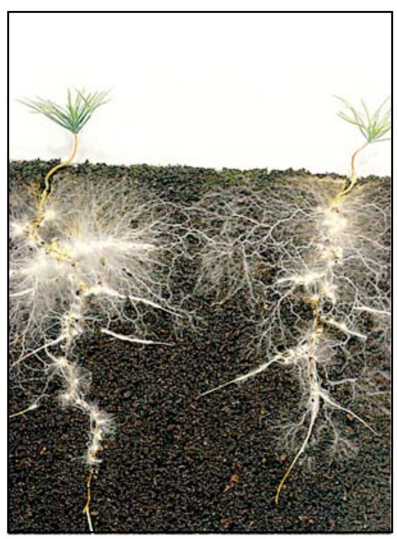


Vesicle

Arbuscule

Resource transfer via hyphal network

- Plant roots linked by fungal hyphae
  - –interspecific and intraspecific
  - –transfer of nutrients and carbon
  - –net transfer appears to follow source-sink relationship
  - –importance of transfer to plant nutrition not clear
  - –transferred carbon may not be available to plant (retained in fungal storage structures)



(D. Read 1997, Nature)

Plant benefits – surface area

TABLE 1. The length of mycorrhizal hyphae per unit colonized root length as measured for a number of plant species, infected with different mycorrhiza-forming fungal species.

Fungus	Host	Hyphal length ($m\,cm^{-1}$ root)
Glomus mosseae	onion	0.79–2.5
Glomus mosseae	onion	0.71
Glomus macrocarpum	onion	0.71
Glomus microcarpum	onion	0.71
Glomus sp.	clover	1.29
Glomus sp.	rye grass	1.36
Glomus fasciculatum	clover	2.50
Glomus tenue	clover	14.20
Gigaspora calospora	onion	0.71
Gigaspora calospora	clover	12.30
Acaulospora laevis	clover	10.55

Various authors, as cited in Smith & Gianinazzi-Pearson 1988.

Symbiotic N-fixation

– reduction of N_2 to NH_3 catalyzed by the **nitrogenase** enzyme
– requires low O_2 environment; **leghemoglobin** controls nodule O_2
– Nitrogenase consists of 2 proteins
    - Fe-S protein accepts e^-, binds ATP
    - Fe-Mo protein binds N_2
– energetically expensive means of acquiring N

Symbiotic N-fixation

- restricted to more limited group of plants (legumes); high host specificity
- plant host provides C energy to bacterial N-fixer
- N-fixer provides available NH_4 to plant