Mineral Nutrients in Soils and Wild Plants

Many inorganic elements are essential for healthy plant growth. These elements are derived from minerals in the soil, from atmospheric dust inputs, or mineralized by decay of organic matter. Mineral nutrients are taken up as ions and stored in the cell sap. The range of concentrations of different elements is extremely large (Table 1) and can vary with soil type and climatic zone as seen when comparing different vegetation types (Table 2 and below). Each element is required in a different concentration and is required for different reasons (Table 3). When an element is deficient, different symptoms show up (Table 8 at end of handout).

Table 1 Average content of mineral elements (in g kg^{-1} dry matter) in the soil and in the phytomass of land plants, together with the average mineral nutrient requirements. (Epstein 1972, 1994; Bowen 1979; data for various plant groups are given by Altman and Dittmer 1972; Baumeister and Ernst 1978; Lieth and Markert 1988

Element	Soil mean	Plants' range	Requirements
Si	330	0.2 − 10	
Al	70	0.04 − 0.5	
Fe	40	0.002 − 0.7	ca. 0.1
Ca	15	0.4 − 15	3 − 15
K	14	1 − 70	5 − 20
Mg	5	0.7 − 9	1 − 3
Na	5	0.02 − 1.5	
N	2	12 − 75	15 − 25
Mn	1	0.003 − 1	0.03 − 0.05
P	0.8	0.1 − 10	1.5 − 3
S	0.7	0.6 − 9	2 − 3
Sr	0.25	0.003 − 0.4	
F	0.2	up to 0.02	
Rb	0.15	up to 0.05	
Cl	<0.1	0.2 − 10	>0.1
Zn	0.09	0.001 − 0.4	0.01 − 0.05
Ni	0.05	up to 0.005	
Cu	0.03	0.004 − 0.02	0.005 − 0.01
Pb	0.03	up to 0.02	
B	0.02	0.008 − 0.2	0.01 − 0.04
Co	0.008	up to 0.005	
Mo	0.003	up to 0.001	<0.0002

Table 2 The mineral contents of different types of vegetation. (After Rodin and Bazilevich 1967)

Type	Ash characteristics	Mineral content	Rate of litter breakdown	Vegetation
Nitro-boreal	N >(K, Mn)	Slight	Slow	Tundra
	N >Ca	Slight	Slow	Boreal coniferous forests
	N >Ca (Si, Mg)	Moderate	Slow	Boreal birch forests
Nitro-arid	N >Ca (Na, Cl)	Moderate	Very rapid	Shrub deserts
Nitro-subtropical	N >Ca (Si, Al, Fe)	Moderate	Rapid	Deciduous forests
Calco-temperate	Ca>N	Moderate	Delayed	Oak-beech forests
Calco-subtropical	Ca>Si (Al, Fe)	Moderate	Very rapid	Subtropical desert vegetation
Silico-semiarid	Si >N	Moderate	Very rapid	Steppes
Silico-arid	Si >N (Na, Cl)	Moderate	Very rapid	Desert annuals, semishrubs
Silico-tropical	Si >N (Fe, Al)	Moderate	Very rapid	Savannas
	Si >N (Al, Fe, Mn, S)	Moderate	Very rapid	Equatorial rainforests
Haline	Cl >Na	High	Very rapid	Halophytic vegetation

Table 3. Occurrence, uptake, distribution, incorporation and function of macronutrients. (Compiled from measurements made by numerous authors, after Finck 1969)

Bio-element	Bound form in soil	Accessible form in soil	Taken up as	Incorporation in plant	Function in plant	Sites of accumulation	Transportability
N	Organically bound, nitrate, ammonium	Supplied by microbial decomposition; NH_4^+ adsorbed on clay minerals and humus; NO_3^- in solution	NO_3^-, NH_4^+	Free as NO_3^- ion (vacuoles), in organic compounds, in protein, nucleic acids, secondary plant substances	Essential component of protoplasm and enzymes	Young shoots, leaves, buds, seeds, storage organs	Good, primarily in organically bound form
P	Organically bound, phosphates of Ca, Fe, Al	As PO_4^{3-}, HPO_4^{2-}, rel. insoluble, adsorbed and in chelated complexes, Microbial release slight	HPO_4^{2-}/ $H_2PO_4^-$	Free as ion, in esteric compounds, nucleotides, phosphatides, phytin	Basal metabolism and synthesis (phosphorylation)	More in reproductive organs than in vegetative (pollen granules)	Good, in organically bound form
S	Organically bound, sulphur-containing minerals, sulphates of Ca, Mg and Na	SO_4^{2-} readily soluble, little adsorbed	SO_4^{2-} from soil (SO_2 from air)	Free as ion, bound as SH- or SS-group and as ester, in protein, coenzymes, secondary plant substances	Component of protoplasm and enzymes	Leaves, seeds	Good in organic form, poor as ion
K	Feldspar, mica, clay minerals	Adsorbed > > dissolved	K^+	Dissolved as ion (primarily in cell sap) and adsorbed	Regulation of hydration (synergists: NH_4^-, Na^+; antagonist: Ca^{2+}), electrochemical effects (membrane potential, osmoregulation), enzyme activation	Meristem, young tissue, bark parenchyma, sites of intense metabolism	Good
Mg	Carbonate (dolomite), silicate (augite, hornblende, olivine), sulfate, chloride	dissolved > > adsorbed; deficient in acid soils, in excess in serpentine soils	Mg^{2+}	As ion dissolved and adsorbed, bound in complexes, organically bound in chlorophyll and pectates, component of enzymes and ribosomes	Regulation of hydration (antagonist to Ca^{2+}), basal metabolism (photosynthesis, phosphate transfer) synergists: Mn^{2+}, Zn^{2+}	Leaves	Good in part
Ca	Carbonate, gypsum, phosphate, silicate, (feldspar, augite)	Adsorbed > > dissolved; deficient in very acid soils	Ca^{2+}	As ion, as salt dissolved, crystallized and incrusted; as chelate; organically bound in pectates	Regulation of hydration (antagonists: K^+, Mg^{2+}); enzyme activator (amylase, ATPase); regulator of growth in length; signal substance (via calmodulin)	Leaves, tree bark	Very poor
Fe	Sulphides, oxides, phosphates, silicates (augite, hornblende, biotite)	Adsorbed > > mobilized; fixed in chalk soils	Fe^{2+}, Fe(III)-chelate	In metal-organic compounds; component of enzymes (heme, cytochrome, ferredoxin, catalase, peroxidase, nitrate reductase)	Basal metabolism (redox reactions), nitrogen metabolism, chlorophyll synthesis	Leaves	Poor

Table 3. Occurrence, uptake, distribution, incorporation and function of trace elements

Bio-element	Bound form in soil	Accessible form in soil	Taken up as	Incorporation in plant	Function in the plant	Site of accumulation	Transportability
Mn	Amorphous oxide (MnO_2), carbonates, in silicates	Adsorbed> >dissolved; better available in acid soils; accumulates under reducing conditions	Mn^{2+} Mn^{-} chelate	In metal-organic compounds and complexes; component of enzymes (pyruvate carboxylase)	Basal metabolism (photosynthesis, phosphate transfer), stabilizes chloroplast structure, nucleic-acid synthesis, synergists: Mg, Zn	Leaves	Poor in part
Zn	Phosphates, carbonates, sulphides, oxides, in silicates	Adsorbed> >soluble; mobilization acid>basic	Zn^{2+} Zn^{-} chelates	Component of enzymes (carbonic anhydrase, alcohol dehydrogenase)	Chlorophyll formation, enzyme activator, basal metabolism, protein breakdown, biosynthesis of growth regulators (IAA)	Roots, shoots	Poor
Cu	Sulphides sulphates, carbonates	Adsorbed, mobilization acid>basic strong fixation of humus	Cu^{2+} and Cu^{-}	Bound as complexes (plastocyanin), component of enzymes (cytochrome oxidase, phenol oxidase)	Basal metabolism, nitrogen metabolism; sec. metabolism	Woody shoots	Poor
Mo	Molybdates, in silicates	Adsorbed, mobilization basic>acid	MoO_4^{2-}	In metal-organic compounds; component of enzymes (nitrate reductase, nitrogenase)	Nitrogen fixation, phosphorus metabolism, iron absorption and translocation		Poor
B	Tourmaline, borates	Adsorbed> >soluble, availability acid>basic	HBO_3^{2-} $H_2BO_3^{-}$	Bound to carbohydrates as complexes; esteric binding	Carbohydrate transport and metabolism; phenol metabolism, activation of growth regulators (growth of pollen tubes)	Leaves, tips of shoots	Poor
Cl	Salt, silicates	Soluble> >adsorbed	Cl^{-}	Free as ion, mostly stored in cell sap	Chemico-colloidal effect (strongly increases hydration); enzyme activation (photosynthesis)	Leaves	Good

I. *Macro- and micro-nutrients*

A. Soil nutrients fall into two categories based upon their relative importance for plant growth. These two categories are Macronutrients and Micronutrients.

B. **Macronutrients** are required in large concentrations; they are present in plants at concentrations ranging from 1,000 - 15,000 ppm. Most macronutrients are more concentrated in the plant tissues than in the soil.

Table 4. Approximate concentration for **macronutrients** (ppm)

	Soil	Plant
Fe	38,000	100
S	700	1,000
P	600	2,000
Mg	5,000	2,000
Ca	13,000	5,000
K	14,000	10,000
N	1,000	15,000

C. **Micronutrients** are essential to plants as enzyme co-factors, and are almost always more abundant in the soil than in the plant.

Table 5. Approximate concentrations for **micronutrients** (ppm)

	Soil	Plant
Mo	2	0.1
Cu	20	6
Zn	50	20
Cl	100	100
Mn	800	50
B	10	20

D. Of particular interest to wild plant investigations are the Macronutrients N and P. N is required in high amounts, and P is essential for many reactions (e.g. as part of ATP) but both can be scarce or in very low concentration in the soil (figures).

(1) Inorganic **P** is the form taken-up by the plant and is relatively well distributed throughout the soil depth profile. However, it is very immobile and P demonstrates a large degree of heterogeneity in soils = "local patches". As such, plants must "seek it out" (below).

(2) Inorganic **N** is concentrated in the uppermost layers of the soil depth profile making it more difficult to obtain for deeper roots.

E. Some unique plants groups require other nutrients not generally required by most plants. For example, **Na** for Chenopodiaceae, **Co** for all Fabales w/symbiotic N-fixers, **Al** for most ferns, **Si** for all diatoms and many Poaceae and grass allies, and **Se** for many planktonic algae and locoweeds!

II. *Soil properties and nutrients available for plants*

Plant nutrients occur in <u>three</u> forms: dissolved (0.2%), bound in organics (98%), and absorbed onto soil colloids (~ 2%).

A. Nutrients in the soil are present as both cations and anions and thus are held between the crystalline lattice sheets, or on broken, exposed and charged, soil particle edges (outer surfaces of the crystalline lattices).

(1) The specific surface are from which plants obtain nutrients is a function of the particle size and exchange properties (figure).

(2) The type of particle can markedly affect a plant's ability to adsorb water and thus nutrients dissolved in that water, for example (water : particle):

CLAYS:	Kaolinite	1:1	non-swelling clay
	Montmorillinite	3 to 7:1	swelling clay
	Illinite	2:1	mild-swelling clay
	Vermiculite	2 to 5:1	partly swelling clay

B. Cation exchange capacity (CEC) is another important property of soils than will effect nutrient availability. CEC = sum total of exchangeable cations that a soil can adsorb (figure).

CEC can be expressed as microequivalents per liter of soil (μeq L^{-1}) or surface are (m^2 g^{-1})

Table 6. CEC of various particle types:

	μeq L^{-1}	**m^2 g^{-1}**
Humus	200	1000+
Montmorillinite	80-100	600-800
Kaolinite	3-15	150-450
Illinite	15-40	280-500
Clay	4-60	180-450
Silty Loam	9-26	250-400
Loam	7-15	175-325
Sand	2-3	50-110

C. Ions are preferentially adsorbed by all types of soils particles and the strength by which they are held is a function of the CEC of that particular particle

(1) General tendency for the adsorption of **CATIONS**

$$Al^{3+} > Ca^{2+} > Mg^{2+} > NH_4^+ > K^+ > Na^+$$

(2) General tendency for the adsorption of **ANIONS**

$$PO_4^{3-} > SO_4^{3-} > NO_3^- > Cl^-$$

(3) Heavy metal ions are adsorbed only in trace amounts, however, this is affected to some extent by their abundance (e.g. soil types like ultramafic soils which are high in Mg, Fe, Ni and low in N, P and K adsorb metal ions five times more than non-ultramafic soils).

D. **Soil pH**: the majority of the world's soils are slightly to very acidic. Why? - bases are removed by leaching, withdrawal from solution by cations, root and microorganism organic acid secretion, and carbonic acid dissociation from respiration/fermentation (figure).

III. Nutrient Availability

A. Nitrogen availability

(1) Nitrogen is added to ecosystems primarily as ammonium, nitrate and organic nitrogen dissolved in precipitation, by gas and aerosol inputs to plant canopies and as ammonia fixed biologically by prokaryotes

(2) Annual inputs in precipitation range from 1 to 5 (10) kg ha^{-1} in unpolluted regions but can be as much as 30-55 (75) kg ha^{-1} in areas with nitric acid rain (NE United States, SE Canada, central China, Poland, other areas in central Europe).

(3) Ecosystems dominated by N-fixing plants may have inputs of up to 90-150 kg ha^{-1}.

(4) The total N content for most ecosystems is between 1,100 and 17,000 kg ha^{-1}, yet uptake

in natural ecosystems is only 20 to 300 kg $ha^{-1} yr^{-1}$.

(5) 98% of this nitrogen is bound in organic detritus and soil humus.
(i) 2-5% of this soil organic nitrogen is released to inorganic forms from microbial oxidation

(ii) 50-99% is taken up by microbes and immobilized but often modified and released where plants can get access to it

(6) Assessing N availability is very difficult and many methods to do so exist. Experiments using stable isotopes of nitrogen (^{15}N) are the most powerful yet expensive and provide little resolution when the label is mixed with (lost to) soil nitrogen pools (figure) - more in the next lecture!

B. Phosphorus availability

(1) Phosphorus is always present as a phosphate anion; it does not undergo oxidation or reduction as does nitrogen. Inputs from the atmosphere are small, 0.1 to 0.5 kg ha^{-1}, but from chemical weathering up to 30 kg $ha^{-1} yr^{-1}$ depending upon the parent rock material and soil moisture.

(2) Annual uptake of P by plants is commonly 2 - 15 kg ha^{-1} and the "seek out " P (figures).

(3) Availability in the soil is very low (e.g. < 5 μeq L-1) and is strongly dependent upon inorganic chemical reaction and soil pH (previous figure).

(4) Between pH 4 to 6 most phosphate in the soil solution is $H_2PO_4^-$ and its availability depends upon the solubility of P salts (figure)

C. Diffusivity and concentration characteristics differ greatly among ions

Table 7.	NO_3^-	K^+	PO_4^{3-}
diffusive conductivity ($cm^2 s^{-1}$)	10^{-5}	10^{-6}	10^{-7}
concentration ($mol\ cm^{-3}$)	10^{-5}	10^{-6}	10^{-6} to 10^{-9}
apparent diffusivity ($cm^2 s^{-1}$)	10^{-5}	10^{-7}	10^{-7} to 10^{-11}

(1) Buffering capacity (BC_p) is the ratio of diffusive conductivity to apparent diffusivity.

(2) The ability of a plant to deplete ions from charged soil particles depends on buffering capacity and the rooting density

i) with low BC_p, low rooting density can deplete up to 90% of the available ion
ii) with high BC_p, high rooting density will only deplete 10-25% of available ion

(3) Ion uptake by a ROOT can occur by:

(i) absorption of nutrient ions from the soil solution
(ii) exchange absorption of "adsorbed" nutrient ions on soil particles
(ii) freeing (at last) bound nutrient stores by excreting H^+ ions into soil

(4) Ion uptake into cell can be either through the symplast or apoplast (figures)

(5) Rooting density and patterns can suggest something about the availability of resources with distances between fine roots suggesting the importance of different resources (figures):

(i)	water	approx. 8 cm between roots
(ii)	NO_3^-	approx. 3-4 cm between roots

(iii) PO_4^{3-} approx. 0.5 cm between roots

(6) Mycorrhizal fungi are common associates with roots and facilitate nutrient uptake - especially with high immobile nutrients, or in nutrient depauperate soils. The fungal hyphae act to increase absorptive root area (figures). Understanding the role of FUNGI is critical to understanding wild plant nutrient relations in pristine and anthropogneically-changed environments (e.g. acidic or polluted environments).

IV. Nutrients as "selective agents"

Terry Chapin (U. of Alaska) and his research group have proposed several schemes for thinking about how soil nutrient availability might influence the "strategy" a plant uses to obtain and then growth/survive in different environments (figure). His thesis states:

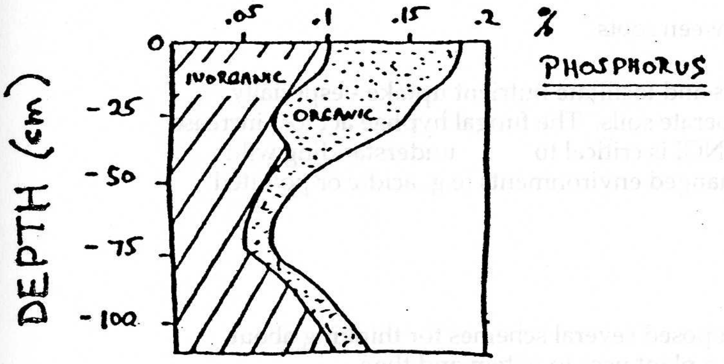
(1) No plant is best at all aspects of nutrient uptake, efficient use, or retention; being good at one thing usually means your not as good at another.

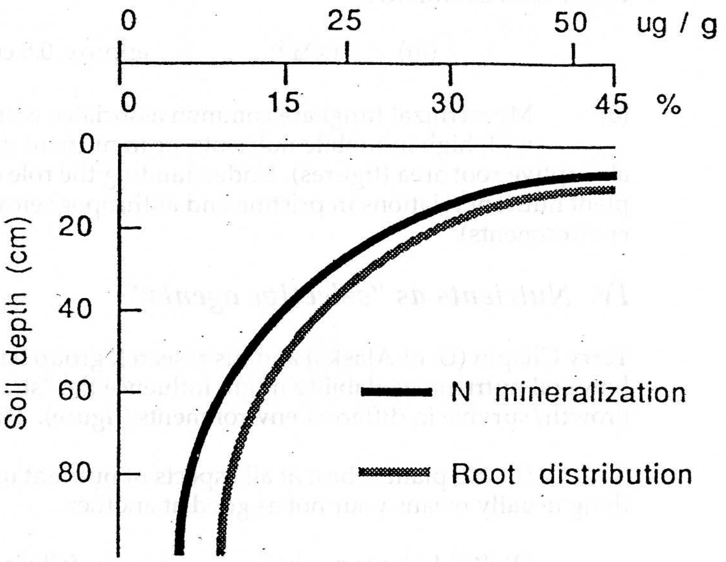
(2) Wild plants might be thought of as falling into one of three groups with respect to nutrients; (a) stress-tolerant, (b) competitive, (c) ruderal (of disturbance-prone habitats) - after Grime, 1979.

(3) Moderate to high fertility habitats favor competitive and ruderal strategies respectively. These tend to be herbaceous, short-lived plants with low carbon reserves, high root respiration and other metabolic rates that are very responsive to increasing nutrient availability (e.g. A vs. N), and relatively rapid turnover/cycling.

(4) Infertile habitats favor stress-tolerators, with low growth rates, low metabolic rates, but high nutrient-use efficiencies, storage, long-lived, nutrient conservation is high, turnover is low.

Question:
What happens when elements in the soil become toxic either naturally (e.g. ultramafic soils) or by pollution in the environment (figure)?

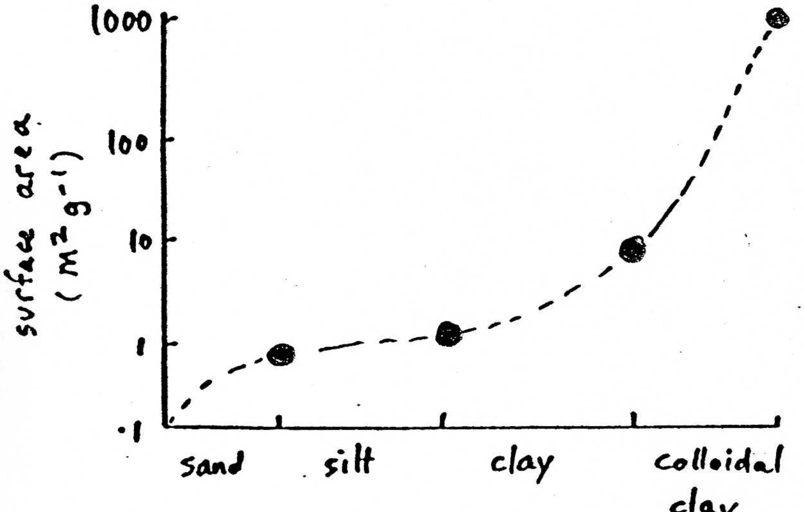


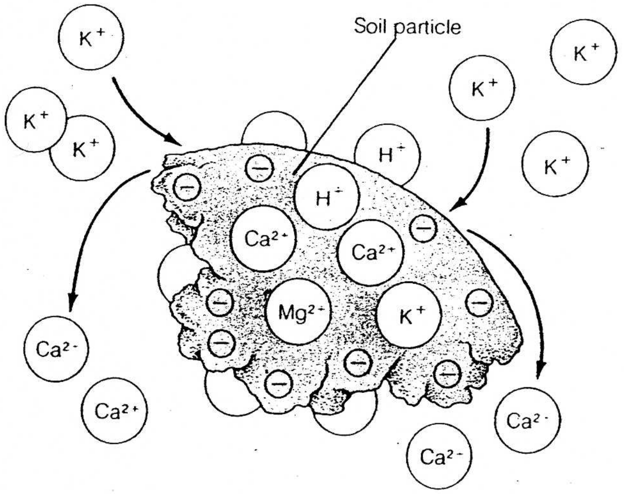


The distribution of fine roots of ponderosa pine parallel the mineralizable N profile (after Powers, 1984).

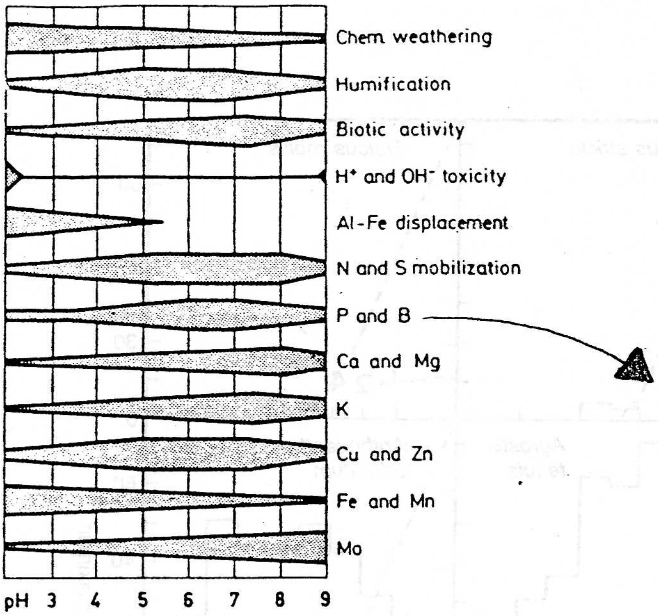
Particle sizes

< 2 μm	clay
2-50 μm	silt
50-2000 μm	Sand
> 2000 μm	gravel

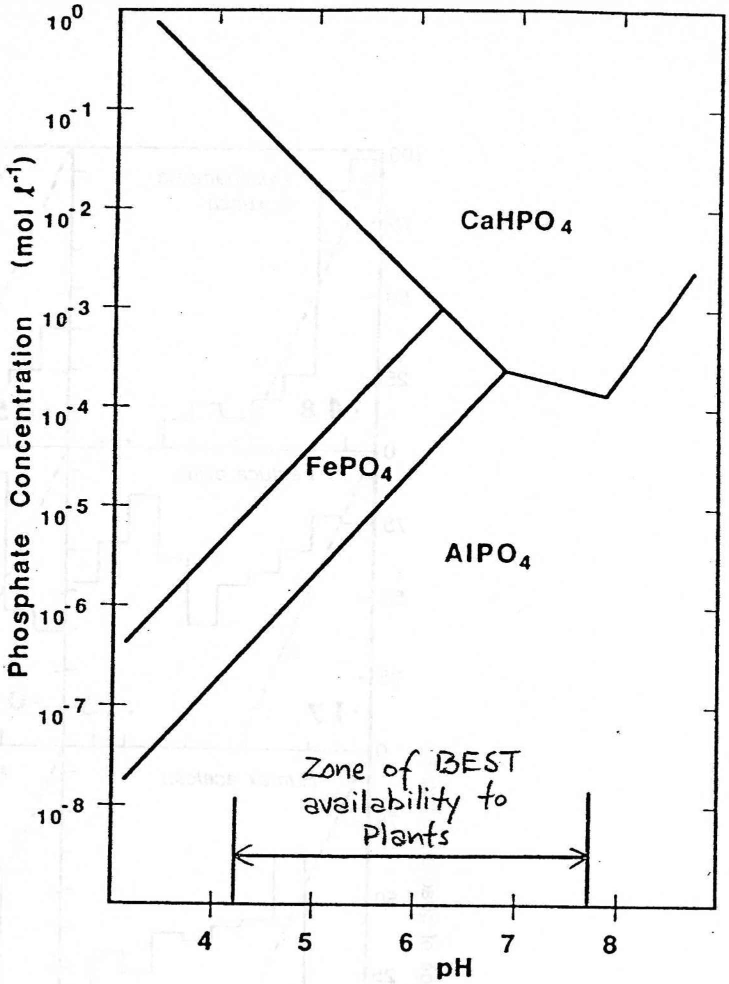




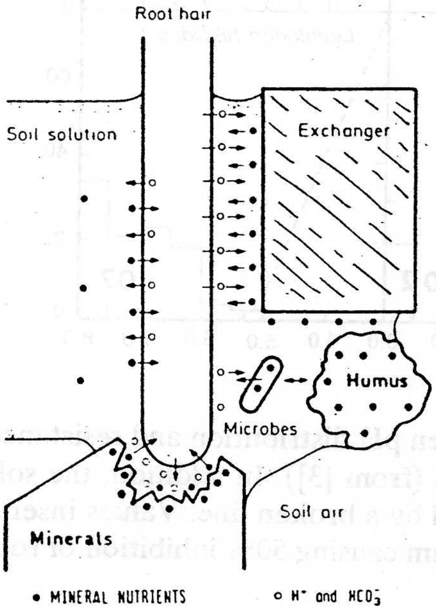
The principle of cation exchange on the surface of a soil particle. Cations are bound to the surface of soil particles because the surface is negatively charged. Addition of a cation such as potassium can displace another cation such as calcium from its binding on the surface of the soil particle and make it available for uptake by the root.



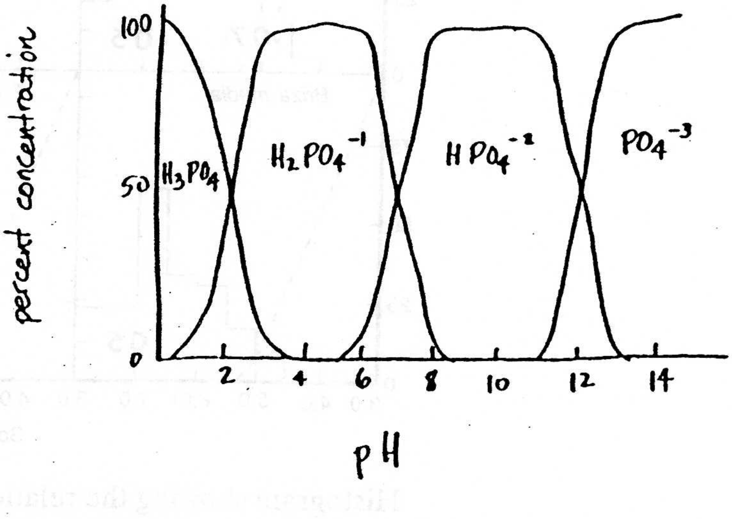
Influence of the soil pH on soil formation, mobilization and availability of mineral nutrients, and the conditions for life in the soil. *The width of the bands* indicates the intensity of the process or the availability of the nutrients. After Truog (1947). For a detailed treatment of the effect of pH on soil properties and plant functions see, e.g., Rorison (1969) and Etherington (1975)

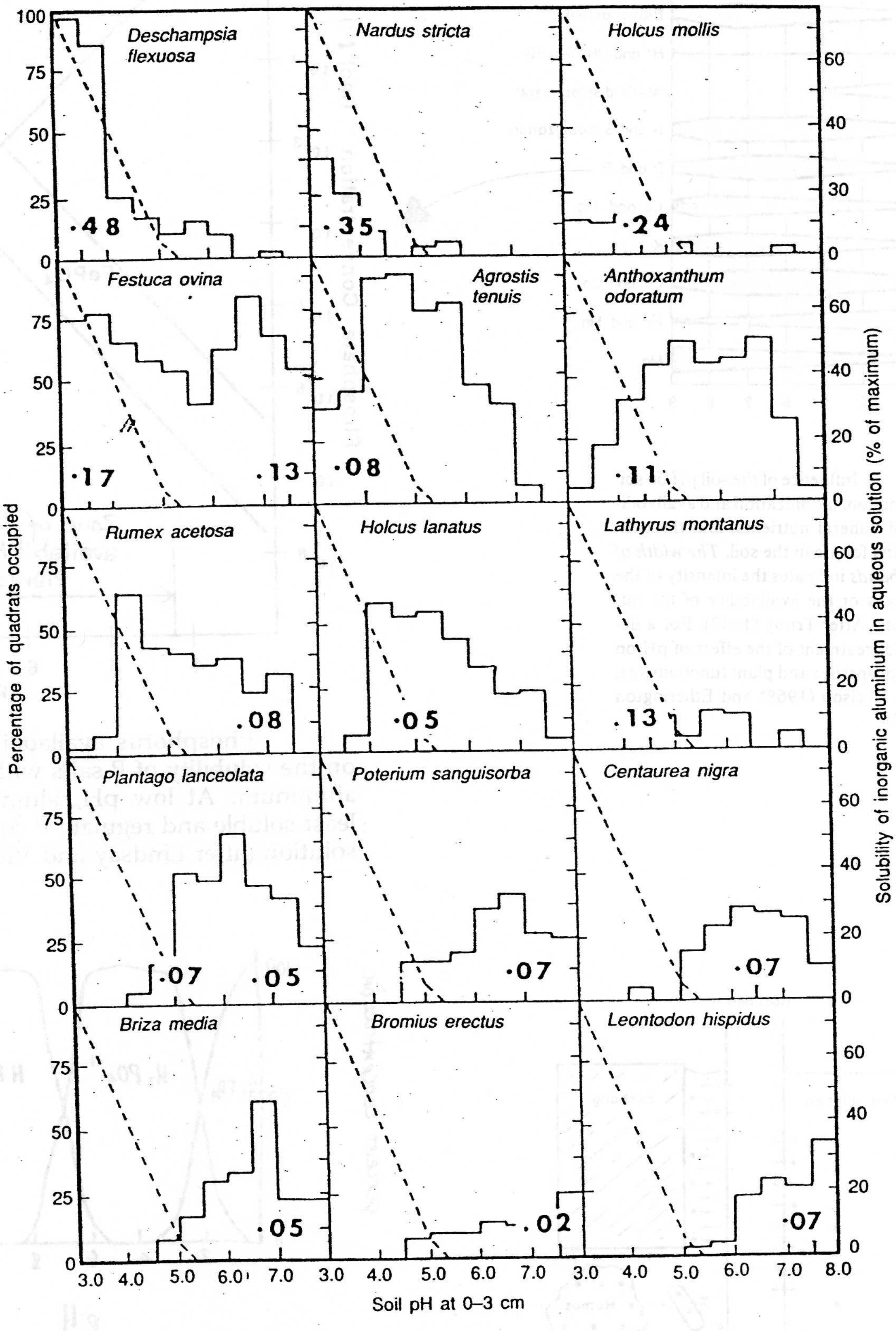


Phosphorus availability depends in part on the solubility of P salts with calcium, iron and aluminum. At low pH, aluminum salts are the least soluble and regulate P concentrations in soil solution (after Lindsay and Vlek, 1977).



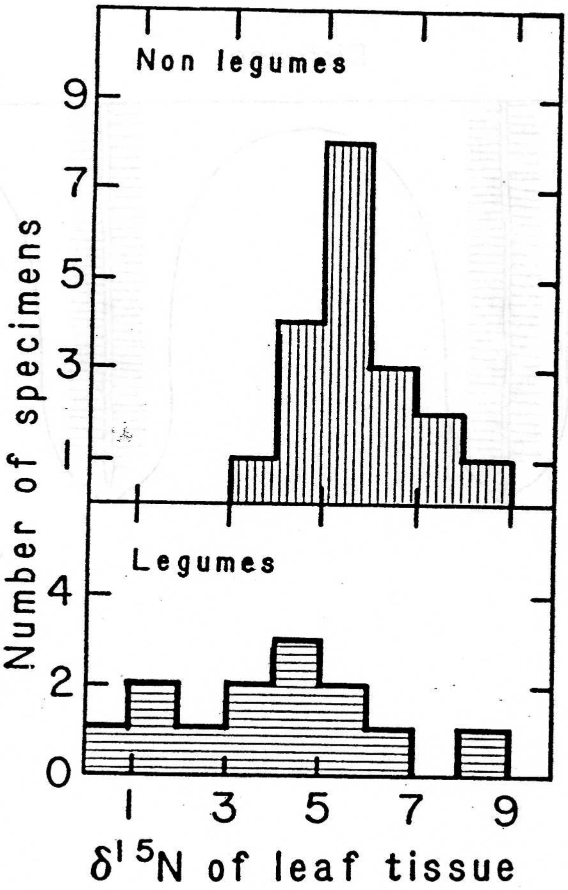
Mobilization of mineral nutrients in the soil and the uptake of mineral substances by the root. After Finck (1969)





Histogram showing the relationship between pH distribution and resistance of see ling roots to aluminium toxicity of 15 grassland species (from [3]). In addition, the solubility Al^{3+} over the pH range (after Magistad [4]) is illustrated by a broken line. Values inserted with the histogram refer to the mM concentration of aluminium causing 50% inhibition of root growt

The potential sources of N used by plants can often possess very different $\delta^{15}N$ ($^{15}N/^{14}N$). The isotope method has been used to look for sources and N dynamics.



Some important considerations about fractionation do need to be included; above 'model' may be too simplistic.

[Next Lecture on N!]

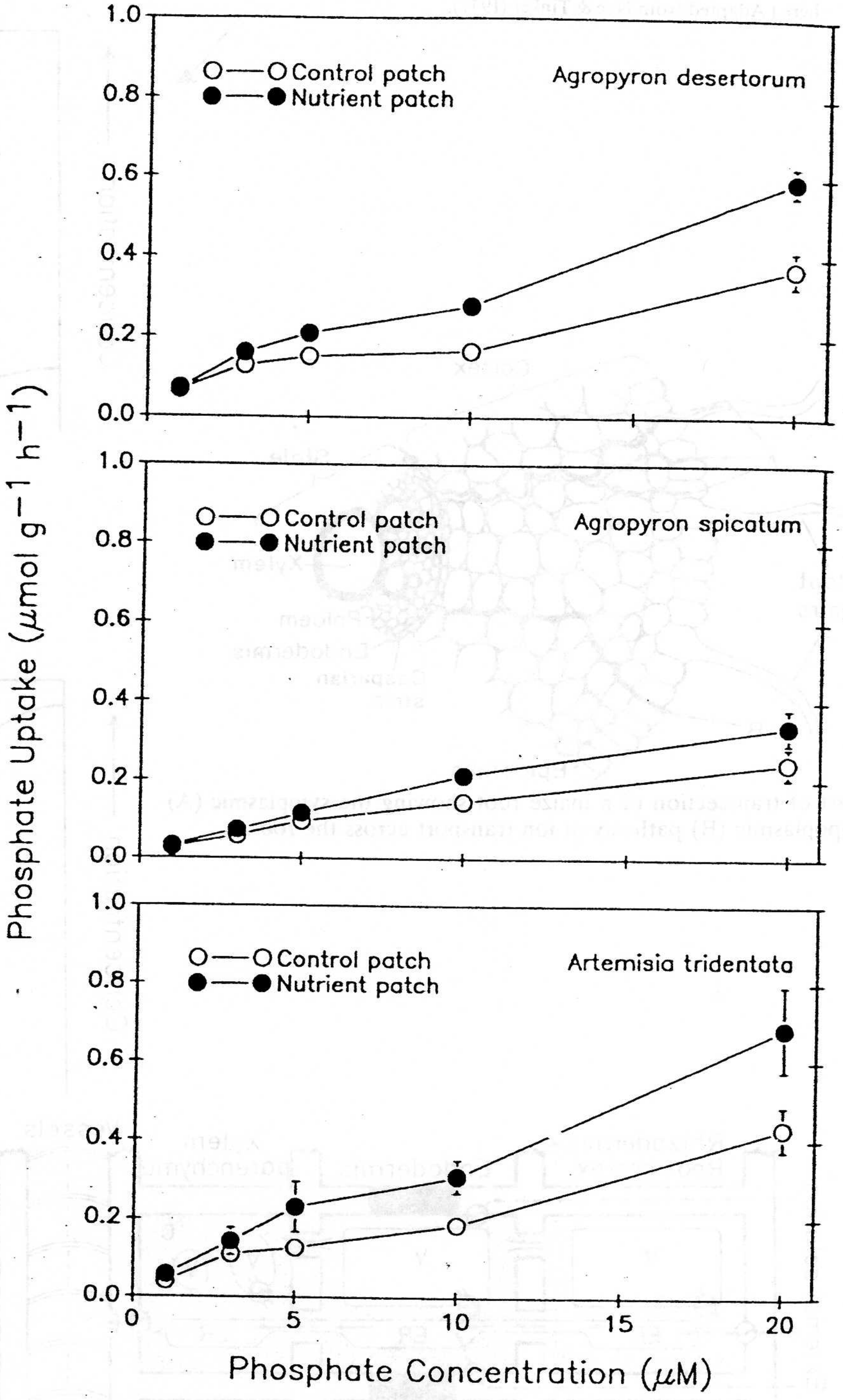
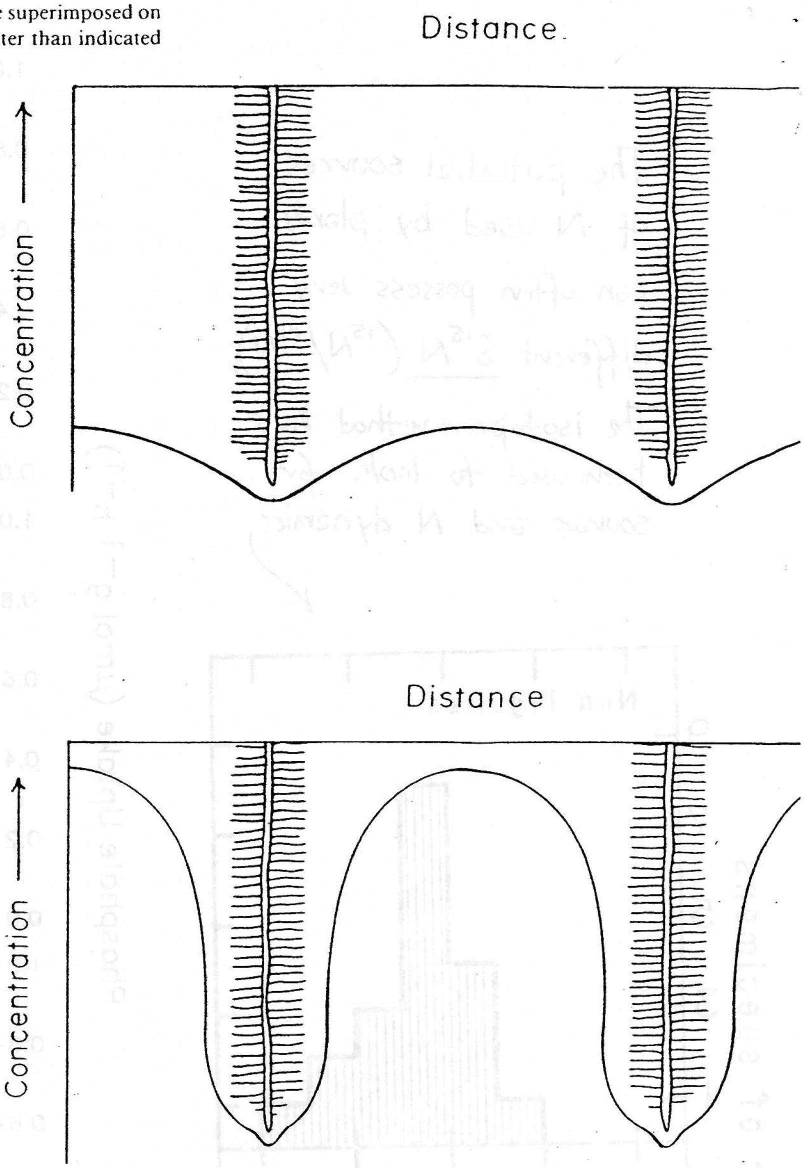
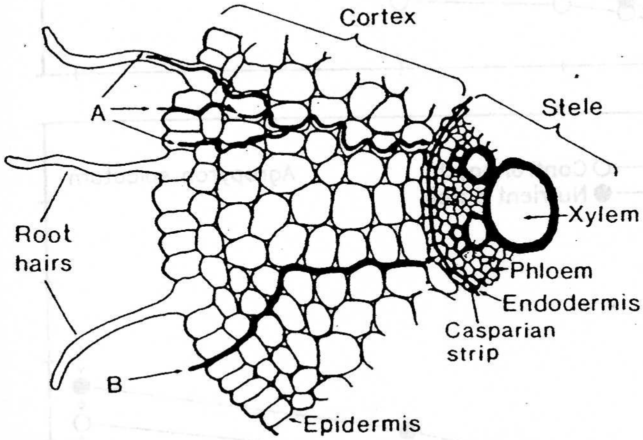


FIG. 1 The rate of phosphate uptake for roots from enriched and control soil patches as a function of the solution phosphate concentration (mean ±s.e.m.; $n=6$ for *Agropyron desertorum*, $n=8$ for *Agropyron spicatum* and *Artemisia tridentata*). Soil patches on opposite sides of plants in monoculture field plots were treated with 750 ml nutrient solution or distilled water. Samples of the soil patches were cored one week after treatment. Roots from each core were subsampled and immersed in radioactive phosphate solutions. The three single-species experiments were conducted at different times and in separate field plots; direct comparison of results among species is therefore inappropriate. The treatment effect was significant at $P<0.05$ for each species (two-factor split-plot analyses of variance set out in blocks).

from: Jackson et al. 1990.
Nature 344: 58-60

Depiction of ion concentration gradients near neighbouring roots with root hairs for relatively mobile (top) and immobile (bottom) ions. Diagrams of the roots are superimposed on the concentration profiles. (Near the root tips concentrations would be greater than indicated here.) Adapted from Nye & Tinker (1977).





Part of transsection of a maize root showing the symplasmic (A) apoplasmic (B) pathway of ion transport across the root.

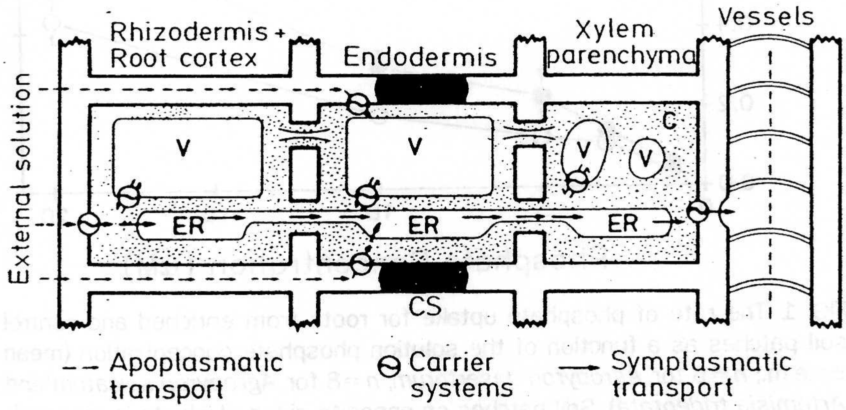
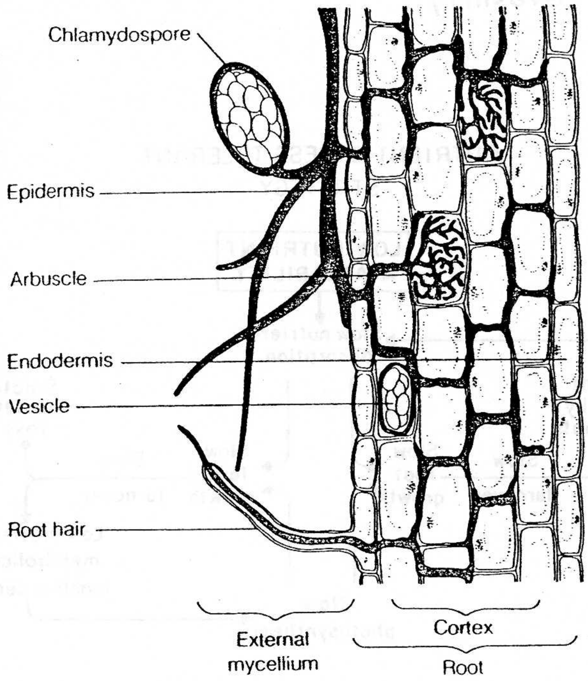


Diagram of ion transport from the *external solution* to the long-distance conducting system in the central cylinder of the root (*vessels*). From the rhizodermis to the endodermis (the Casparian strip, *CS*) ions, together with water, are transported apoplasmatically – that is, in the cell walls and in water-filled intercellular spaces. After they have been taken into the living protoplasts (cytoplasm, *C*) ions are transported symplasmatically, over the endomembrane system (ER) and through plasmodesmas. Vacuoles (*V*) are spaces for the excretion and accumulation of substances; they are not part of the symplast. The pathways for transport in the opposite direction, which is mainly passive, are not shown. Modified from Lüttge (1973) and Läuchli (1976). A schematic diagram of ion transport through the whole plant is given by Weatherley (1969). For active transport processes see Bowling (1976)



The association of vesicular-arbuscular mycorrhizal fungi with a section of a plant root. The external mycelium can bear reproductive chlamydospores and extend out from the root into the surrounding soil. The fungal hyphae grow into the intercellular wall spaces of the cortex and penetrate individual cortical cells. As they extend into the cell, they do not break the plasma membrane or the tonoplast of the host cell. Instead, the hypha is surrounded by these membranes as it occupies intracellular space. In this process, the fungal hyphae may form ovoid structures known as vesicles or branched structures known as arbuscules. The arbuscules participate in nutrient ion exchange between the host plant and the fungus. Arbuscules develop and proliferate following the penetration of the hyphae into the root cortical cells. In later stages, the arbuscules separate from the hyphae and degenerate. (From Mauseth, 1988.)

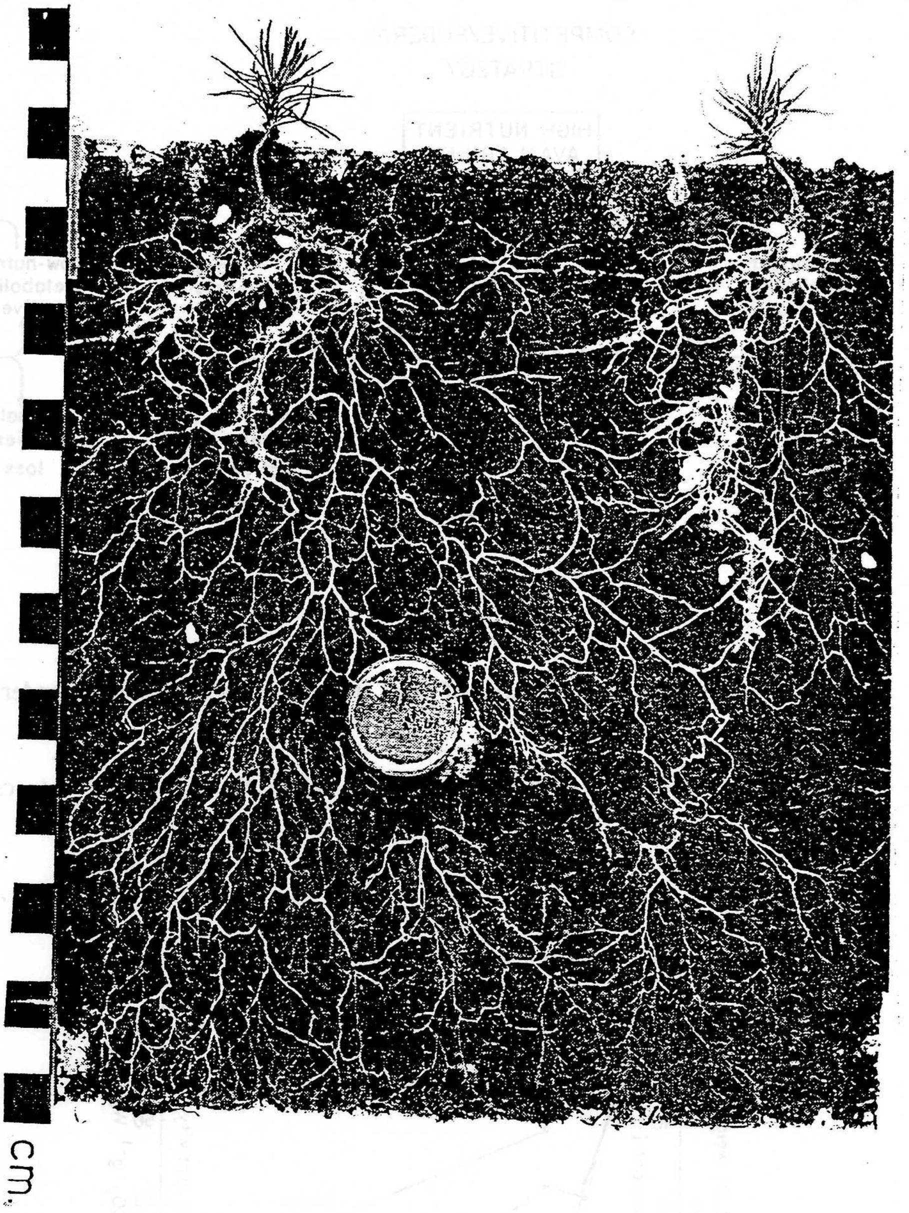
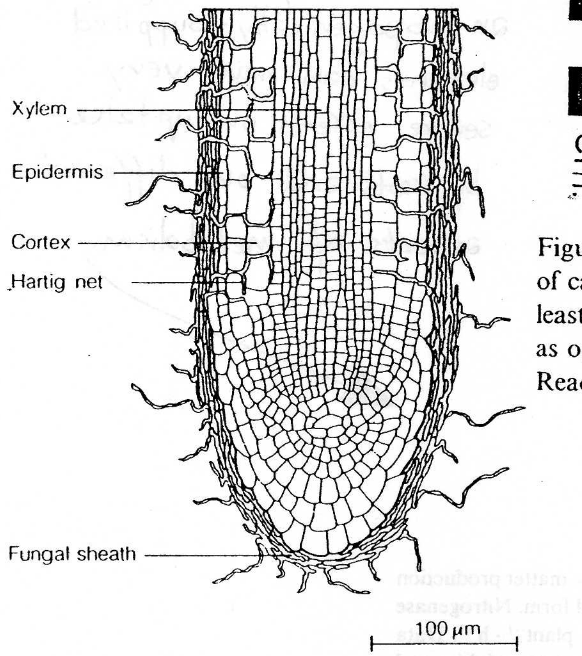


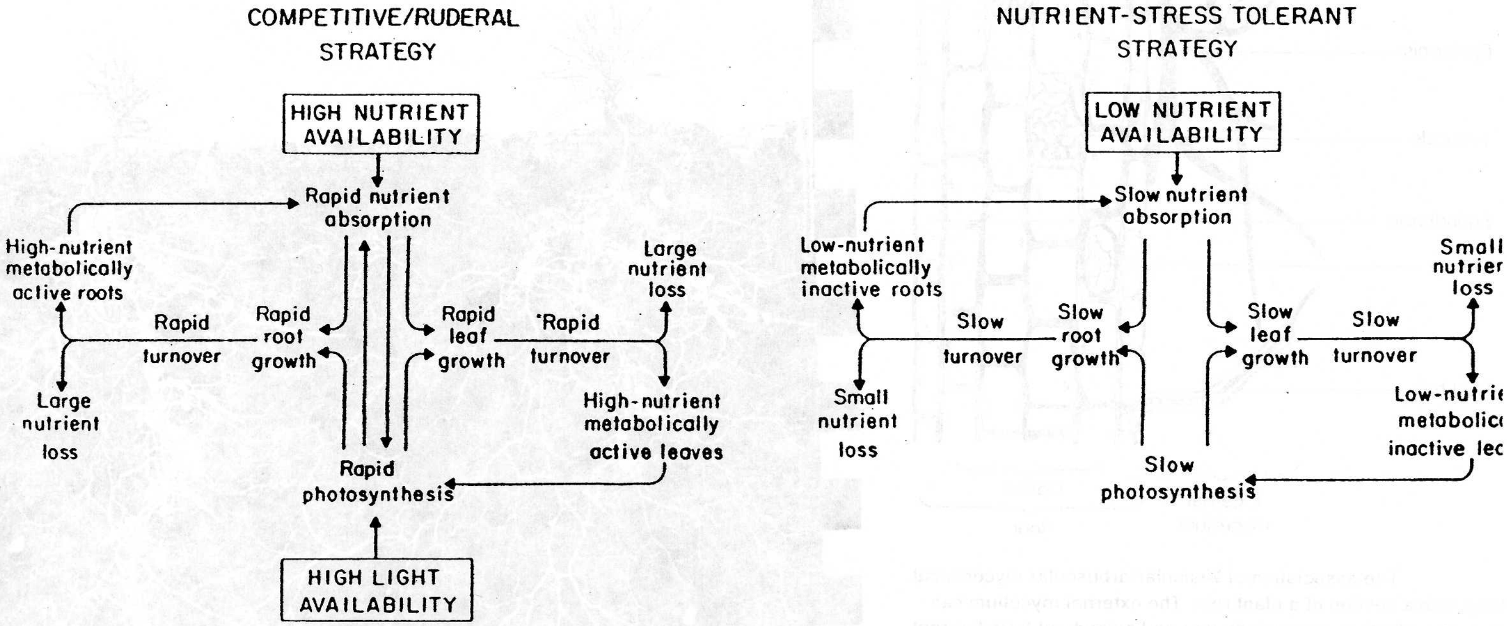
Figure 4.7. Mycorrhizal hyphal bridges connecting plants and the major routes of carbon and nutrient flow. As is shown, the vast majority of carbon from at least most connected plants flows to the fungus maximizing its own energy gain as opposed to connecting only one plant (photograph provided by David Read).



A root infected with ectotrophic mycorrhizal fungi. In the infected root, the fungal hyphae surround the root to produce a dense fungal sheath and penetrate the intercellular spaces of the cortex to form the Hartig net. It is apparent that the total mass of fungal hyphae is comparable to the root mass itself. (From Rovira et al., 1983.)

We'll take up mycorrhizae in two lectures!

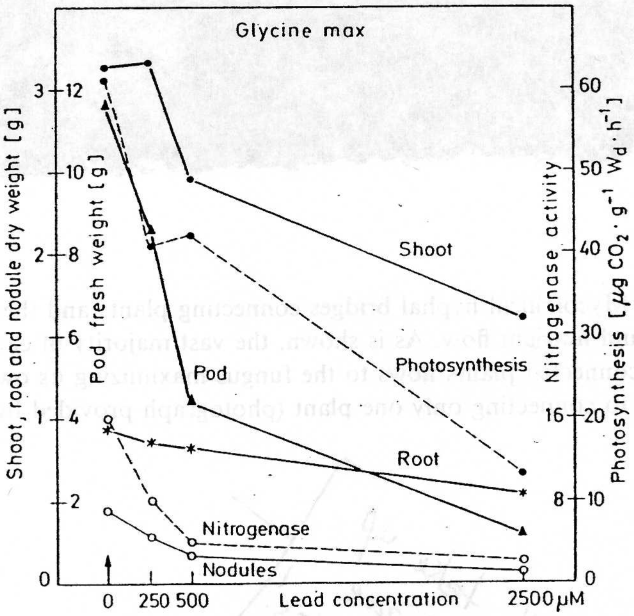
Plant Strategies in relation to soil nutrient avability:



Interacting characteristics of plant strategies that are adaptive under conditions of high or low nutrient availability.

↑ after: Chapin, 1980, Annual Review of Ecol. + Syst. 11: 233-260

Some naturally occuring and anthropogenically-supplied elements can have very severe effects on uptake by roots and on different aspects of metabolism.



The influence of lead on photosynthesis, nitrogen fixation, and dry-matter production by soybean plants. The lead was added to the nutrient solution in dissolved form. Nitrogenase activity was determined via C_2H_4 reduction, and is given as µmol $C_2H_4 \cdot plant^{-1} \cdot h^{-1}$. Data from Huang et al. (1974). For further examples of the effects of lead on enzyme activities and metabolic processes see Bazzaz et al. (1974) and Mathys (1975); on extension growth, Lane et al. (1978)

Table 8 Symptoms of deficiency in crop plants and forest trees. (After Wallace 1951; Bergmann 1983; Mengel 1984; Marschner 1986; Hartmann et al. 1988; Walker and Gessel 1990; Walker 1991)

Deficient element	Herbs and broadleaved woody plants	Conifers
N	Stunting (dwarfism), scleromorphism; shoot/root ratio shifted towards roots; premature yellowing of old leaves	Chlorophyll deficiency, discoloration, less growth (shorter needles and new shoots), premature loss of needles and browning of assimilation shoots
P	Disturbance of reproductive processes (delayed flowering), spindly appearance, dark green or bronze-violet discoloration of leaves and stalks	Reddening of needles and young shoots, necrosis without previous chlorosis
S	Similar to N-deficiency, intercostal chlorosis of young leaves	Chlorosis of young needles and shoots
K	Disturbed water balance (tip drying), curling of edges of older leaves	Tips of needles dry out, needles drop prematurely
Ca	Disturbances in growth by division (small cells), tip drying, leaf deformation, impaired root growth	Drying of buds; young shoots and root tips die off; chlorosis of the tips of fir trees, followed by browning of needles
Mg	Stunted growth, intercostal chlorosis of older leaves	Chlorosis, mainly of older needles and scales, in firs also discoloration of tips of needles (yellow to brown), lower branches become bare
Fe	Straw-yellow intercostal chloroses, in extreme cases young leaves turn white (veins green), apical bud formation suppressed	Young needles yellow to white, older needles green
Mn	Inhibition of growth, chloroses and necroses on young leaves	Young needles chlorotic, tip drying of shoots and tree
Zn	Stunted growth, white-green discoloration of older leaves, disturbances in fructification	Young needles first chlorotic, then necrotic
Cu	Tip drying, leaf curl, spotty chloroses of young leaves	Chlorosis of young needles, dieback of shoots and tree
B	Impaired growth (meristem necroses), diminished branching of roots, phloem necroses, disturbances in fructification	Terminal buds dry out, diminished growth in length, lateral branches dense and bent (nest-like), branch roots die