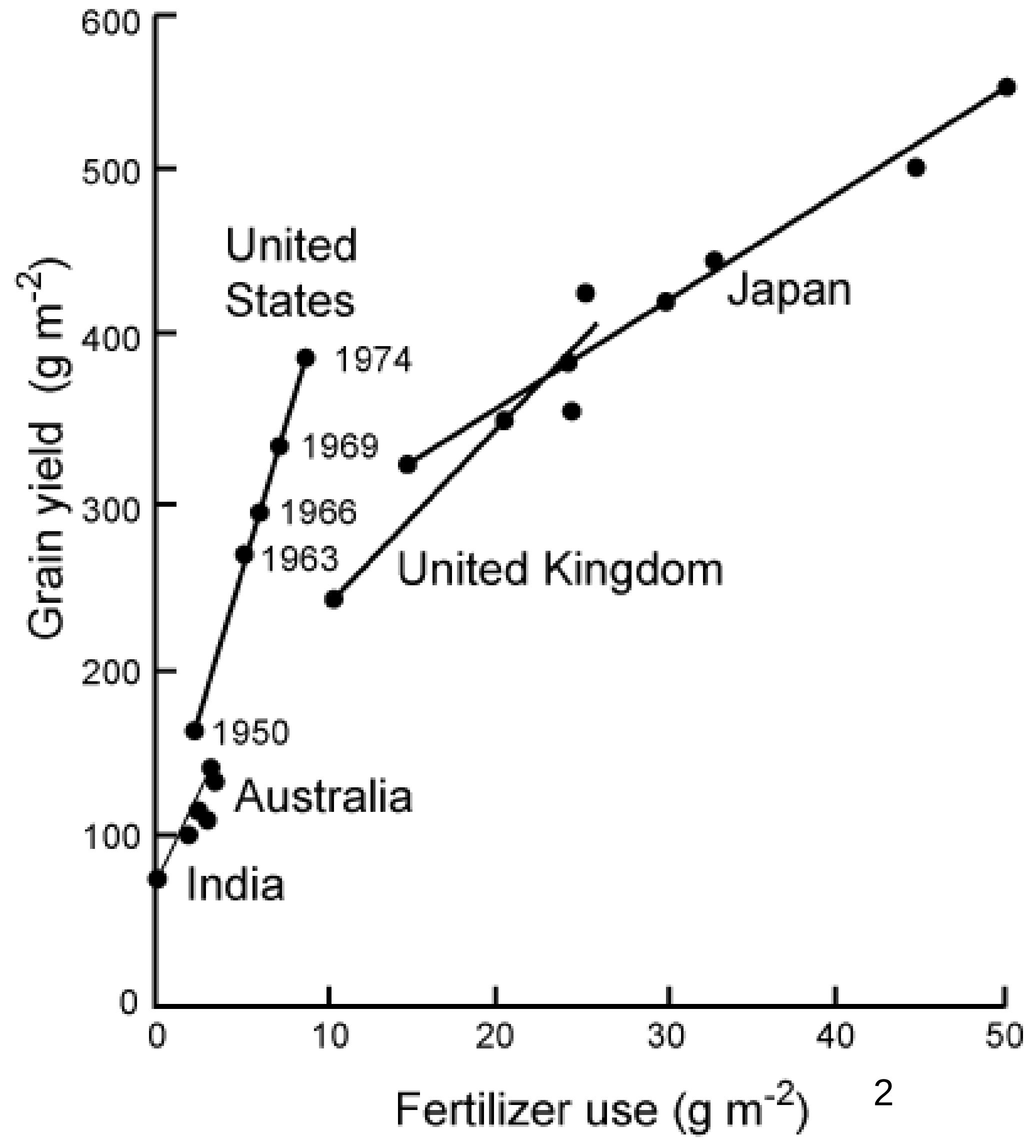
Plant Nutrient Uptake & Use

- Objectives
  - Plant nutrient acquisition, use, and loss
    - Key step in nutrient cycling in terrestrial ecosystems
  - Plant-soil-microbe exchanges of nutrients

Plant Nutrient Uptake & Use

- Nutrient (along with light & H_2O) supply is a dominant control over ecosystem processes (GPP, NPP, etc.)



Plant Nutrient Uptake & Use

- Nutrient cycling dominated by internal transfers
- Belowground resource supply largely controls most ecosystem processes (GPP, NPP, decomp., etc)
    - Belowground resource supply controlled by the 5 state factors
- What controls plant acquisition (i.e., uptake or absorption) of belowground resources?
    - Dynamic balance between supply and demand (i.e., requirements to support growth)

Plant Nutrient Uptake & Use

- Macro- and micronutrients
- Essential nutrients
- Beneficial nutrients
- Toxic nutrients
- Nutrient ratios (i.e., stoichiometry) similar in all plants

Table 8.1 Nutrients required by plants and their major functions

Nutrient	Role in plants
Macronutrients	Required by all plants in large quantities
Primary	Usually most limiting because used in largest amounts
Nitrogen (N)	Component of proteins, enzymes, phospholipids, and nucleic acids
Phosphorus (P)	Component of proteins, coenzymes, nucleic acids, oils, phospholipids, sugars, starches
	Critical in energy transfer (ATP)
Potassium (K)	Component of proteins
	Role in disease protection, photosynthesis, ion transport, osmotic regulation, enzyme catalyst
Secondary	Major nutrients but less often limiting
Calcium (Ca)	Component of cell walls
	Regulates structure and permeability of membranes, root growth
	Enzyme catalyst
Magnesium (Mg)	Component of chlorophyll
	Activates enzymes
Sulfur (S)	Component of proteins and most enzymes
	Role in enzyme activation, cold resistance
Micronutrients	Required by all plants in small quantities
Boron (B)	Role in sugar translocation and carbohydrate metabolism
Chloride (Cl)	Role in photosynthetic reactions, osmotic regulation
Copper (Cu)	Component of some enzymes, role as a catalyst
Iron (Fe)	Role in chlorophyll synthesis, enzymes, oxygen transfer
Manganese (Mn)	Activates enzymes, role as a catalyst
Molybdenum (Mo)	Role in N fixation, NO_3 enzymes, Fe absorption, and translocation
Zinc (Zn)	Activates enzymes, regulates sugar consumption
Beneficial nutrients	Required by certain plants or by plants under specific environmental conditions
Aluminum (Al)	
Cobalt (Co)	
Iodine (I)	
Nickel (Ni)	
Selenium (Se)	
Silicon (Si)	
Sodium (Na)	
Vanadium (V)	

Reprinted from Chapin and Eviner (2004)

Plant Nutrient Uptake & Use

- How do nutrients get to roots?
  - Roots absorb only dissolved nutrients in direct contact with live cells
    - Roots comprise <1% of the belowground volume
    - Nutrients have to move from bulk soil to root surface

1. Diffusion (most important for limiting macronutrients)
2. Mass flow (most imp. for macronutrients in high concentrations, & for micronutrients)
3. Root interception

Plant Nutrient Uptake & Use

- Diffusion
  - Driving forces (sink vs. source) create nutrient concentration gradients
    - Nutrient uptake (sink)
    - ***Mineralization (source of N, P, base cations)
      - CEC (slow source of base cations; “buffering capacity”)
      - Charge density slows diffusion
      - Soil physical properties → length of diffusion path
  - Consequence
    - Diffusion shell = Zone of nutrient depletion around each root
      - Large for mobile ions like NO_3^-
      - Small for slowly diffusing ions like PO_4^{3-}

Plant Nutrient Uptake & Use

- Mass Flow
  – Movement of dissolved nutrients in flowing soil water
    - Transpirational water uptake
    - Gravitational water movement (saturated flow)
  – Insufficient for growth-limiting nutrients but can supply adequate macronutrients (when in high concentration) & micronutrients
    - Can create diffusion gradient away from root
  – ***Replenishes diffusion shells

Plant Nutrient Uptake & Use

- Root Interception
  - Nutrient quantity in soil solution is typically lower than that required to build root tissue
    - So interception is <u>not</u> generally important for increasing nutrient uptake *per se*
  - Root growth is critical because:
    - Explores new soil volume
    - ***Creates new surface area for diffusion and mass flow

Plant Nutrient Uptake & Use

Table 8.3 Mechanisms by which nutrients move to the root surface

Nutrient	Quantity absorbed by the plant ($g\ m^{-2}$)	Mechanism of nutrient supply (% of total absorbed)		
		Root interception	Mass flow	Diffusion
Sedge tundra (Natural ecosystem)				
Nitrogen	2.2	–	0.5	99.5
Phosphorus	0.14	–	0.7	99.3
Potassium	1.0	–	6	94
Calcium[a]	2.1	–	250	0
Magnesium	4.7	–	83	17
Corn crop (Agricultural ecosystem)				
Nitrogen	19	1	79	20
Phosphorus	4	2	4	94
Potassium	20	2	18	80
Calcium[a]	4	150	413	0
Magnesium[a]	4.5	33	244	0
Sulfur	2.2	5	95	0
Iron	0.2	–	53	–
Manganese[a]	0.03	–	133	0
Zinc	0.03	–	33	–
Boron[a]	0.02	–	350	0
Copper[a]	0.01	–	400	0
Molybdenum[a]	0.001	–	200	0

Plant Nutrient Uptake & Use

- Nutrient absorption by vegetation is governed by:
  1. Soil nutrient supply rate
  2. Root length
  3. Root activity per unit root

  – #1 is *the* major factor accounting for nutrient absorption rates → Evidence?

  – #2 important primarily: (a) in situations where supply exceeds demand; and (b) where plants have access to otherwise inaccessible pools (e.g., deep soil layers)

Plant Nutrient Uptake & Use

- Within a biome, root elongation is main way plants can increase nutrient uptake
  - Explores new soil & ↑ S.A. for diffusion & mass flow
- Increased root:shoot ratio
  - Increased investment in roots (allocation to belowground)
  - Root length (SRL) more important than biomass
- Root proliferation in nutrient hot spots
  - Root growth occurs where it does the most good
- Root hairs (elongated epidermal cells) greatly increase surface area for absorption

Plant Nutrient Uptake & Use

- Mycorrhizae increase effective root length by 2-3 orders of magnitude
  - Increases soil volume explored
- Trade carbohydrates for nutrients
  - Symbiosis
    - “Balanced parasitism”
  - 1-21% of NPP may go to mycorrhizae (Hobbie 2006)
- Most advantageous for ‘immobile’ nutrients
  - e.g., Phosphate
  - Phosphatase enzymes “cleave” P from organic matter

Plant Nutrient Uptake & Use

- C allocation to mycorrhizae directly correlated with BNPP
- In line with C allocation theory

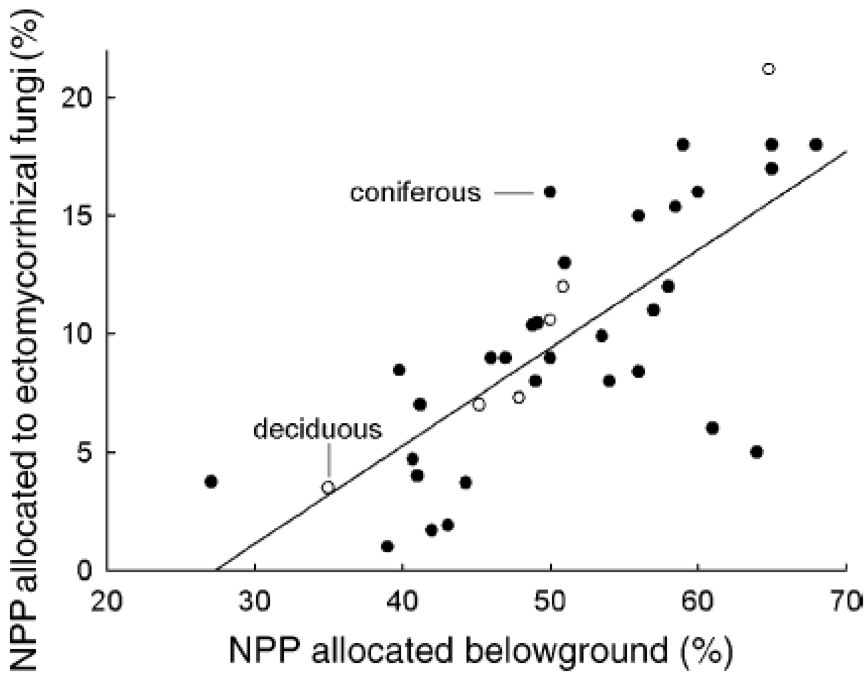
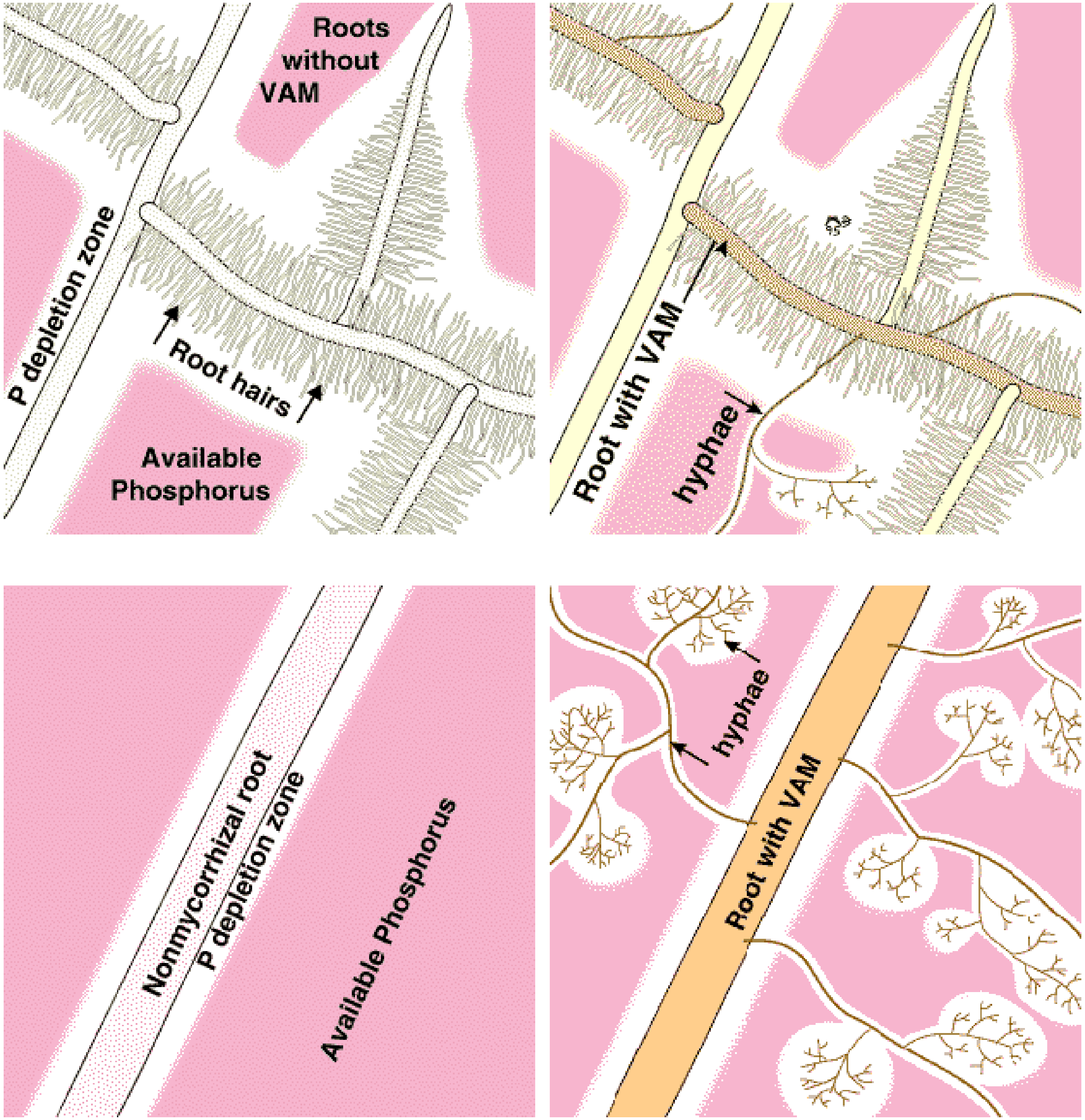


FIG. 1. Net primary production (NPP) allocated to ectomycorrhizal fungi correlates with relative belowground allocation in culture studies ($n = 37$, $r^2 = 0.55$, $P < 0.001$). Deciduous host trees are represented by open circles, and evergreen conifers are represented by solid circles. Studies and study conditions are listed in the Appendix.

(Hobbie 2006)

Plant Nutrient Uptake & Use

- Ectomycorrhizae (ECM)
  - Form sheath around root
  - Common in woody plants
  - Important for N and P uptake
- Vesicular arbuscular mycorrhizae (VAM)
  - Proliferate around root; within cortical cells
  - Common in grasses, herbs, and tropical trees
  - A.k.a. “endomycorrhizae”
  - Particularly effective at P acquisition
    - Can lead to N limitation



Mycorrhizae are more important to some roots than others…

Small diameter of hyphae (0.01 mm) allows plant to explore larger volume of soil

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

Plant Nutrient Uptake & Use

- Mechanisms of nutrient uptake:

1. Active transport most important
   - Across cell membranes against conc. gradient
   - Requires energy (30-50% of root C budget)
     - R_{ion}
   - Nutrients "leak out" of plants via diffusion
     - ~Root exudation; ~1/3 of P uptake

- Abundant nutrients may enter by diffusion or mass flow
  - Still have to be absorbed via active transport

Plant Nutrient Uptake & Use

- N comes in different forms:
  - Amino acids (DON) must be transported thru plant
    - Used for protein synthesis
    - Minimal cost
  - NH_4^+ must be assimilated
    - Attached to a carbon skeleton
    - More costly
  - NO_3^- must be reduced to NH_4^+
    - NO_3^- reduction energetically expensive
    - Most costly
      - But can occur in leaves with excess energy from light harvesting reaction (esp. for plants adapted to NO_3^- uptake)

Plant Nutrient Uptake & Use

- Plants typically "prefer" 1 or more forms of N
  - Species from organic-rich ecosystems (boreal) often prefer amino acids (glycine)
  - NO_3^- is commonly taken up in ag ecosystems
  - NH_4^+ is often preferred
    - Ultimately depends on form of N that is most abundant in ecosystem to which they are adapted; & how limiting N is

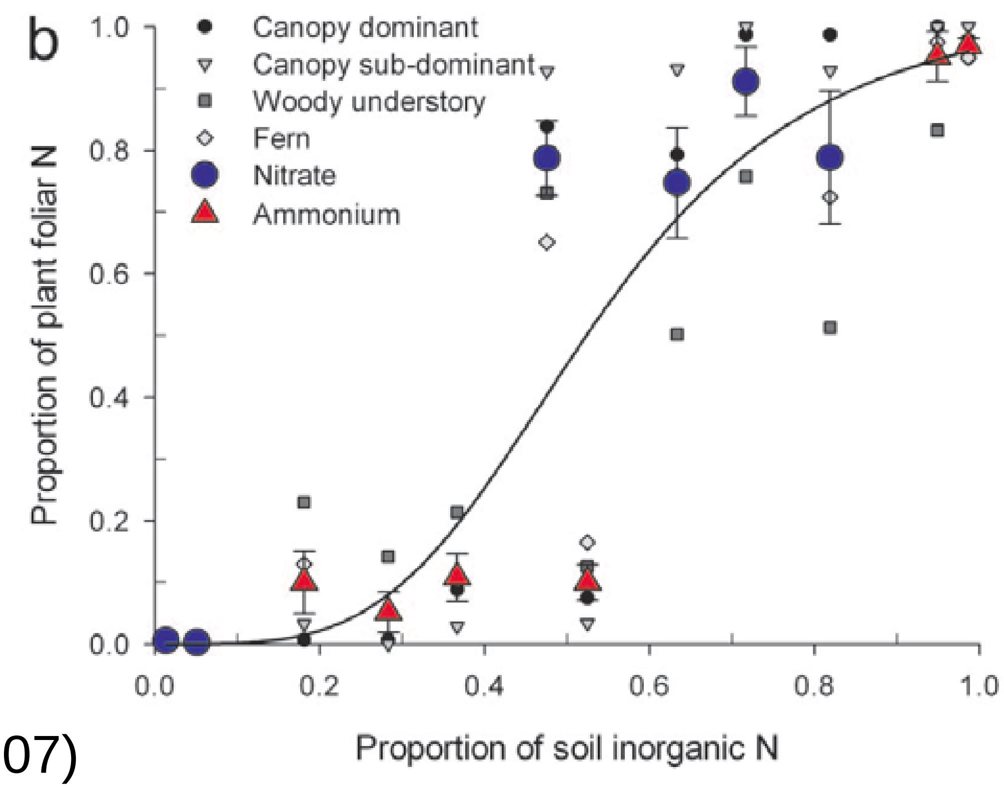
Table 8.4 Preference ratios for plant absorption of different forms of nitrogen, when all forms are equally available

Species	NH_4^+:NO_3^- preference[a]	Glycine:NH_4^+ preference[a]	References
Arctic vascular plants	1.1	2.1 ± 0.6 (12)	Chapin et al. 1993, Kielland 1994
Arctic nonvascular plants	–	5.0 ± 1.5 (2)	Kielland 1997
Boreal trees	19.3 ± 5.8 (4)	1.3	Chapin et al. 1986a, Kronzucker et al. 1997, Näsholm et al. 1998
Alpine sedges	3.9 ± 1.3 (12)	1.5 ± 0.4 (11)	Raab et al. 1999
Temperate heath	–	1.0	Read and Bajwa 1985
Salt marsh	1.3	–	Morris 1980
Mediterranean shrub	1.2	–	Stock and Lewis 1984
Barley	2.5 (2)	0.5	Chapin et al. 1993, Bloom and Chapin 1981
Tomato	0.6	–	Smart and Bloom 1988

[a] A preference ratio > 1 indicates that the first form of nitrogen is absorbed preferentially over the second. Numbers in parenthesis are the number of species or varieties studied. These studies show that many plants preferentially absorb glycine (a highly mobile amino acid) over ammonium and preferentially absorb ammonium over nitrate, when all forms are equally available

Plant Nutrient Uptake & Use

- Plants typically "prefer" 1 or more forms of N
  - Same species can shift uptake to follow availability of NO_3^- vs. NH_4^+



(Houlton et al. 2007)

Plant Nutrient Uptake & Use

- “Tapping” Phosphorus
  - Phosphatase enzymes released by mycorrhizae (and roots of some plants)
    - Cleave P from SOM
  - Siderophores released by some plants
    - Chelating agents which solubilize iron phosphates by binding Fe (releases PO_4^{3-})

Plant Nutrient Uptake & Use

- Roots adjust uptake in response to nutrient limitation

Table 8.5 Effect of environmental stresses on rate of nutrient absorption by barley

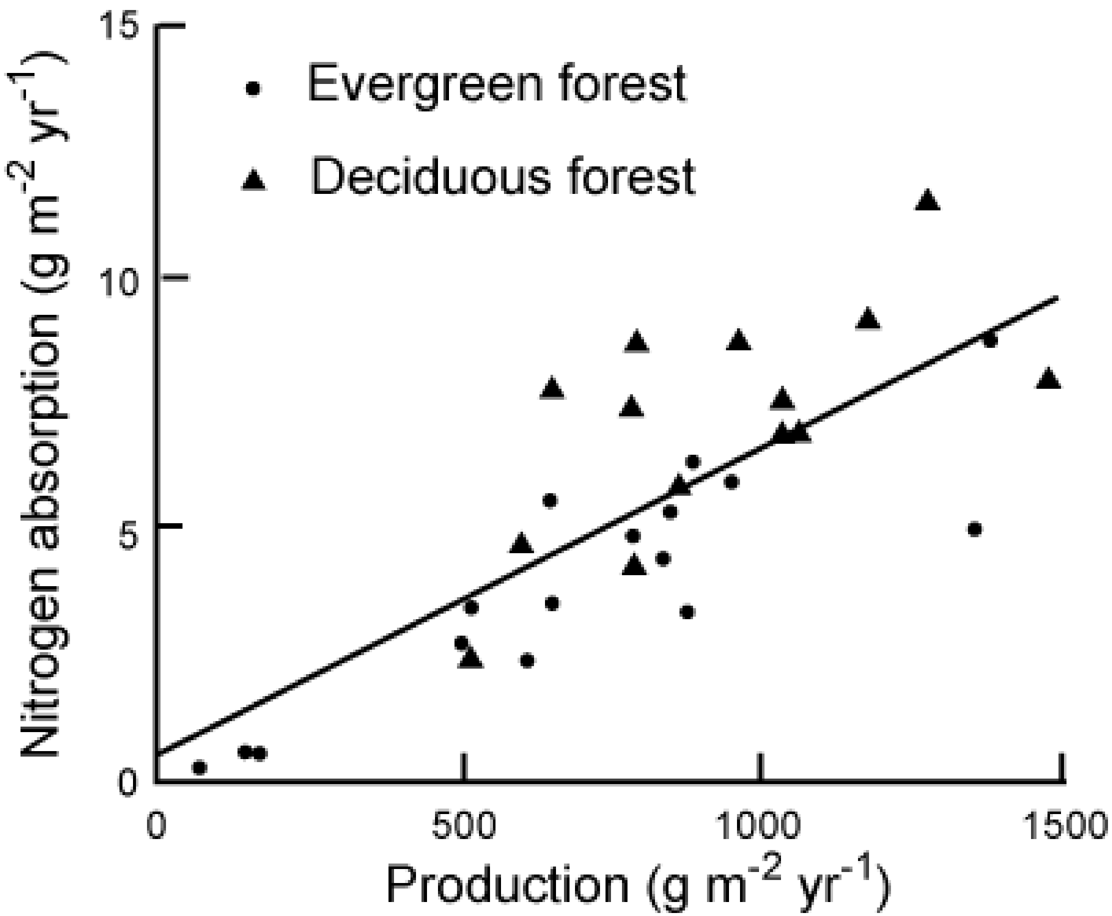
Stress	Ion absorbed	Absorption rate by stressed plant (% of control)
Nitrogen	Ammonium	209
	Nitrate	206
	Phosphate	56
	Sulfate	56
Phosphorus	Phosphate	400
	Nitrate	35
	Sulfate	70
Sulfur	Sulfate	895
	Nitrate	69
	Phosphate	32
Water	Phosphate	32
Light	Nitrate	73

Data are from Lee (1982), Lee and Rudge (1987), and Chapin (1991b)

Plant Nutrient Uptake & Use

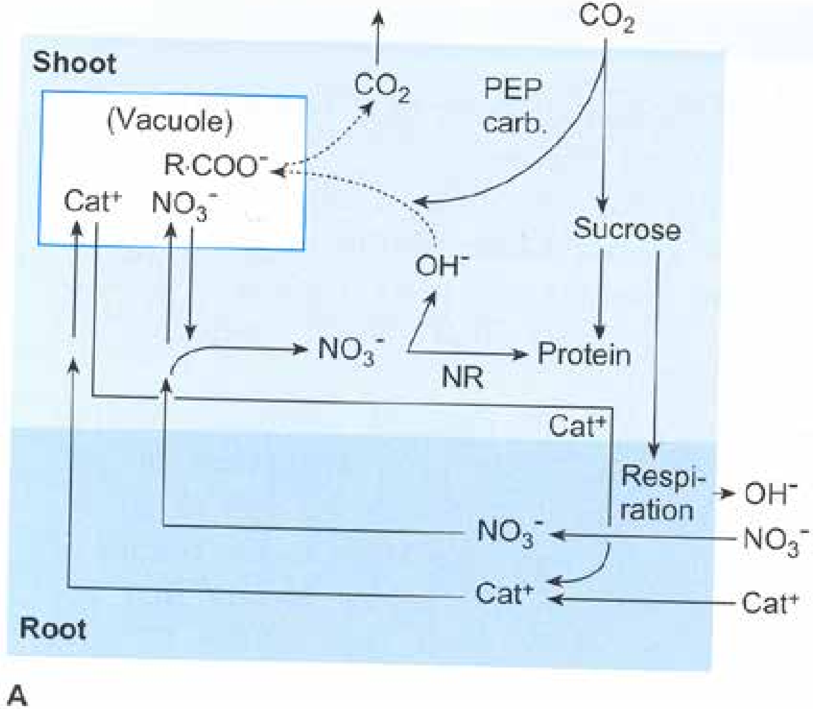
- Strong correlation between nutrient uptake & NPP

- Chicken vs. egg?
  - Does ↑ supply lead to ↑ uptake, and ↑ NPP?
  or
  - Does ↑ NPP lead to ↑ supply & ↑ uptake?



Plant Nutrient Uptake & Use

- Nutrient uptake influences rhizosphere
  - Reduces rhizosphere nutrient concentrations
    - Increases diffusion gradient (diffusion shell)
  - Exudation can enhance decomposition
    - ‘Priming’ of microbial community
  - Changes pH
    - H^+ is secreted when cations are absorbed
      - Lowers pH (more acidic)
    - OH^- secreted when anions are absorbed
      - Raises pH (more basic)



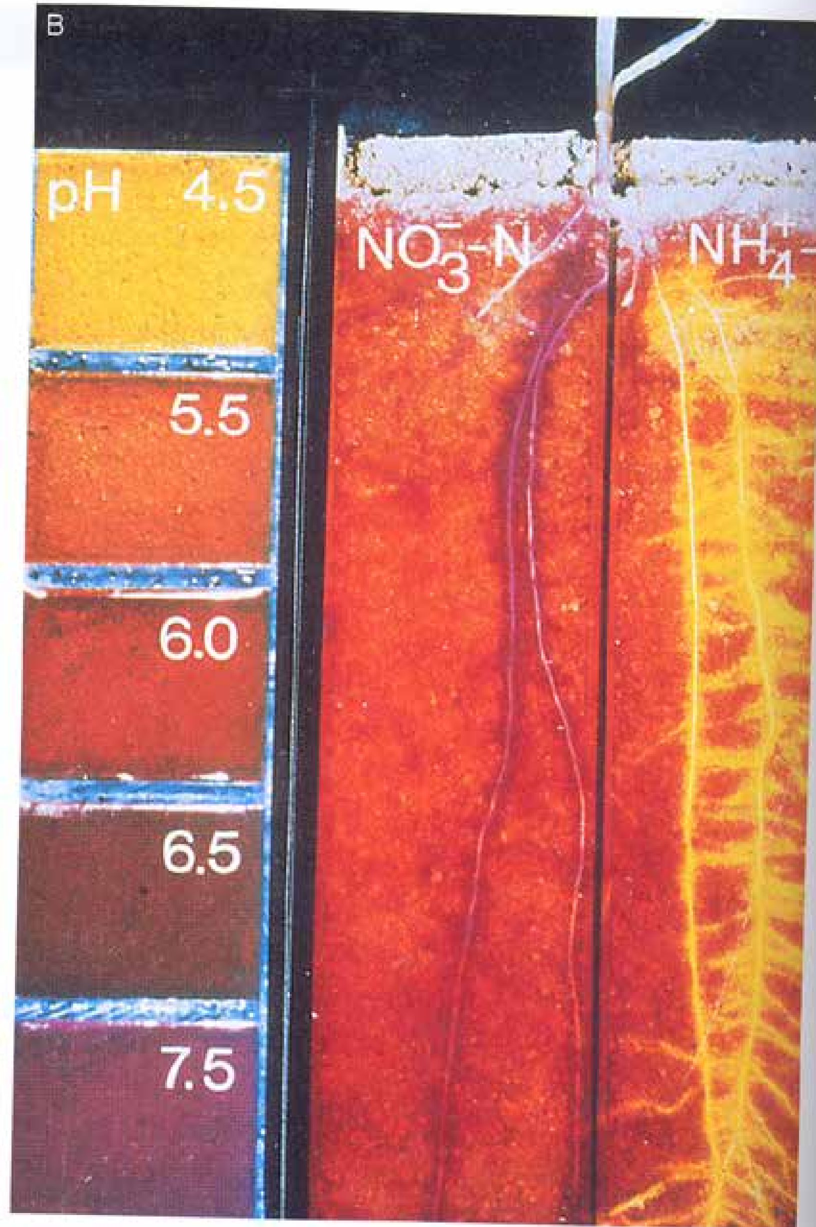


Fig. 2.3.9. A Exchange and transport processes involved in the uptake of nitrate. To balance the charges, OH^- ions are released into the soil, i.e. the soil pH rises. Nitrate can be stored in the vacuole until reduction (Marschner 1995). B Changes in soil pH after nitrate or ammonium uptake. Roots of plants were divided between two compartments: in one the N source was nitrate and in the other ammonium. The *yellow colouration* shows the fall in pH in the proximity of the root during ammonium uptake. The *red colour* shows nitrate uptake and the corresponding pH rise. (Photo E. George)

Plant Nutrient Uptake & Use

- In addition to limitation (i.e., need), nutrient cycling is also controlled by plant stoichiometry (ratios of nutrients in biomass)
  - Relatively constant proportions of nutrients (C:N:P)
    - 1212:28:1 for foliage in forest ecosystems globally (McGroddy et al. 2004)
      - Varies by biome (nutrient availability)
      - Varies within a biome by species (storage in stems & vacuoles)
      - Higher for litter than live tissues (= resorption globally important mechanism)
  - *The most strongly limiting element controls the cycling of all elements*
    - ↑ the supply of nutrients ↑ growth much more than % conc.

Plant Nutrient Uptake & Use

- Summary of plant nutrient uptake
  - Nutrient supply constrains uptake
    - Diffusion is main mechanism of supply
  - Plants adjust uptake rate to meet demands
    - Root : shoot ratio
    - Root growth into “hotspots”
    - Mycorrhizae
    - Uptake capacity (ion transporters)

Plant Nutrient Uptake & Use

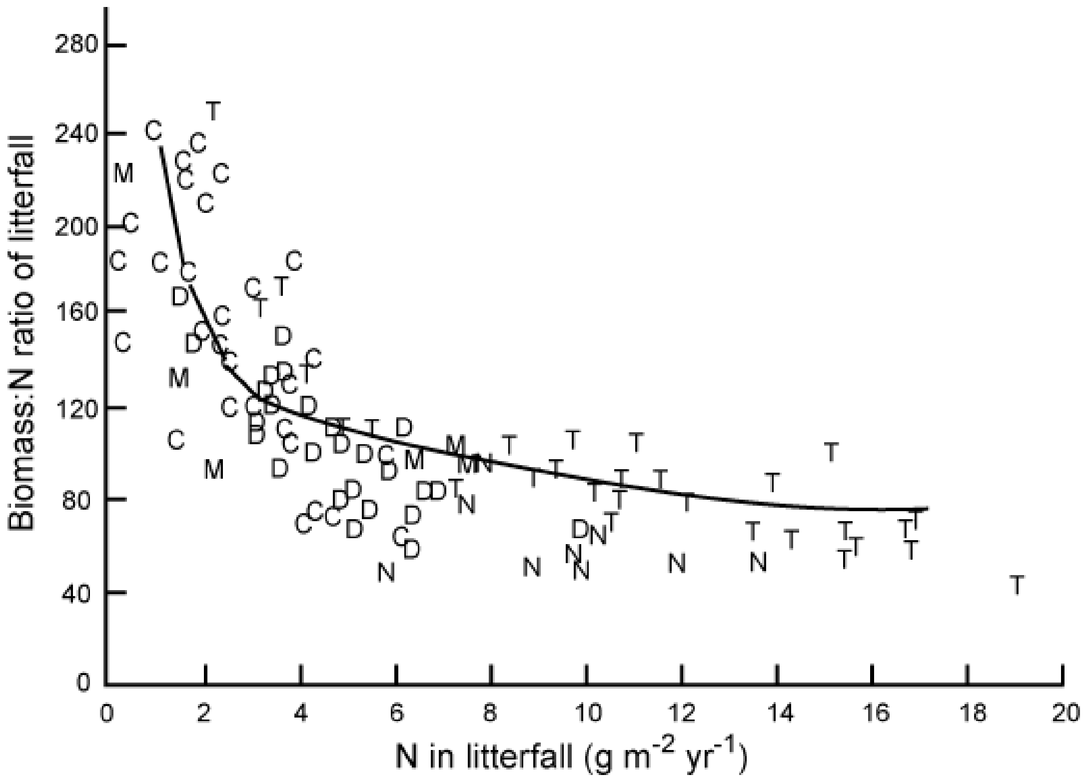
- Nutrient Use
  - Nutrients are used for new growth
    - Leaves and metabolic tissues have high nutrient concentrations of N, P, and K
    - Woody, structural tissues have low concentrations N, P, and K, but high Ca conc.
  - Sometimes there are enough nutrients left over for storage
    - Leads to some variability in nutrient ratios (i.e., stoichiometry) in biomass

Plant Nutrient Uptake & Use

- Nutrient use efficiency (NUE)
  - NUE = Production per unit of plant nutrient
    - Can also incorporate tissue longevity
  - Physiological approach (leaf or plant level)
    - NUE = a*t
      - a = nutrient productivity (photosynthesis / g N / yr)
      - t = residence time of nutrient in plant (yr)
        - » Main way plants ↑ NUE in nutrient limited sties
  - Ecosystem approach (stand-level)
    - NUE = g nutrient / g biomass in litter
    - or NUE = NPP / g nutrient in biomass produced
      - Nutrient productivity
      - Inverse of concentration

Plant Nutrient Uptake & Use

- NUE is highest when production is nutrient limited
- Unproductive sites tend to have slow-growing plants with low nutrient content and long-lived tissues



- Conifers occur in unproductive sites
- Tropical systems have low NUE
    - Often not N limited

Plant Nutrient Uptake & Use

- NUE can be increased by 1 of 2 mechanisms:
  - NUE = a*t
  - Increase nutrient productivity (a)
  - Increase tissue residence time (t)

Table 8.6 Nitrogen use efficiency and its physiological components in a heathland evergreen shrub and a grass

Process	Evergreen shrub[a]	Grass[a]
Nitrogen productivity (g biomass $(gN)^{-1}$ yr^{-1})	77	110
Mean residence time (yr)	1.2	0.8
Nitrogen use efficiency (g biomass $(gN)^{-1}$)	90	89

[a]Species are a low-nutrient-adapted evergreen shrub (*Erica tetralix*) and a co-occurring deciduous grass (*Molinia caerulea*) that is adapted to higher soil fertility.

Plant Nutrient Uptake & Use

- Nutrient loss from plants
  - 1. Tissue senescence / death
    - Major avenue of nutrient loss from plants
    - Reduced by increasing longevity of biomass and/or resorption
  - 2. Leaching of dissolved nutrients (~15% of N & P)
  - 3. Root exudation (including diffusion out of roots)
  - 4. Consumption by herbivores (& loss to parasites)
  - 5. Disturbances
    - 1-3 transfer nutrients to soils, so no loss from the ecosystem
    - 4-5 can lead to large losses of nutrients from ecosystem (esp. #5)

Plant Nutrient Uptake & Use

- Plants reabsorb ~50% of N, P, & K before senescence

Table 8.7 Nitrogen and phosphorus resorption efficiency of different growth forms

Growth form	Resorption efficiency (% of maximum pool)[a] Nitrogen	Phosphorus
All data	50.3 ± 1.0 (287)	52.2 ± 1.5 (226)
Evergreen trees and shrubs	46.7 ± 1.6 (108)[b]	51.4 ± 2.3 (88)[b]
Deciduous trees and shrubs	54.0 ± 1.5 (115)[c]	50.4 ± 2.0 (98)[b]
Forbs	41.4 ± 3.7 (33)[b]	42.4 ± 7.1 (18)[b]
Graminoids	58.5 ± 2.6 (31)[c]	71.5 ± 3.4 (22)[c]

[a]Data are averages ± SE, with number of species in parenthesis. Different letters within a column (b or c) indicate statistical difference between growth forms ($P < 0.05$)
Data from Aerts (1995)

- Species are similar in the proportion of nutrients leached by throughfall

Table 8.8 Nutrients leached from the canopy (throughfall) as a percentage of the total aboveground nutrient return from plants to the soil

Nutrient	Throughfall (% of annual return)[a] Evergreen forests	Deciduous forests
Nitrogen	14 ± 3	15 ± 3
Phosphorus	15 ± 3	15 ± 3
Potassium	59 ± 6	48 ± 4
Calcium	27 ± 6	24 ± 5
Magnesium	33 ± 6	38 ± 5

[a]Data are averages ± SE, for 12 deciduous and 12 evergreen forests
Data from Chapin (1991b)

Plant Nutrient Uptake & Use

- Herbivory can be a major avenue of nutrient loss in some systems
  - Herbivores consume only ~1-10% of NPP in most systems, but prefer nutrient-rich tissue
  - Grassland consumption may be 10-60% of NPP
  - Chemical and morphological defenses are most common in long-lived tissues
    - Reduces nutrient concentration
  - Belowground herbivory is often ignored
    - Nematodes can consume as much belowground biomass as is consumed aboveground

Plant Nutrient Uptake & Use

- Summary
  - Belowground resource availability is the major constraint on ecosystem processes (e.g., NPP)
  - Nutrient supply constrains uptake
    - Diffusion is main mechanism of supply from bulk soil to root surface
    - Augmented by mass flow & root elongation
    - The most limiting elements limits uptake of other elements
  - Plants adjust uptake rates to meet demands
    - Root growth (partitioning of C belowground)
    - Root growth concentrated in “hotspots” of nutrients
    - Mycorrhizae increase nutrient uptake (esp. P)
    - NUE tradeoffs (productivity vs. residence time)