Nutrient Cycling in Land Plants

OCN 401 - Biogeochemical Systems

7 September 2017

Reading: Chapter 6

Outline

1. Plant nutrient requirements and sources
2. Nutrient uptake by plants
    - Nutrient balances
3. Biogeochemical nitrogen cycle
    - Nitrogen speciation
    - Nitrogen biogeochemical cycle
    - Nitrogen assimilation
    - Nitrogen fixation
    - Mycorrhizal fungi

Nutrient Requirements & Sources – The Big Picture

- Plant organic matter is mainly C,H, and O (*i.e.*, CH_2O), with traces of 20 other elements needed for growth (*e.g.*, N, P, Ca, Mo, S, Fe, Mg)
- C:N = 20 - 50 in leaf tissue   N:P = 10 – 20 in vegetation
- Availability of N or P may control rate of NPP (since other elements are rarely limiting): P is a major limiting nutrient in older tropical soils, N is the major limiting nutrient in younger temperate and high-latitude soils
- Biological processes affect geochemical cycling of biologically important elements -- less effect on elements with small biological role in global cycles (*e.g.*, Na, Cl)
- Atmosphere is dominant source of C, N and S to terrestrial systems; rock weathering is dominant source for Mg, Ca, K, Fe, P →

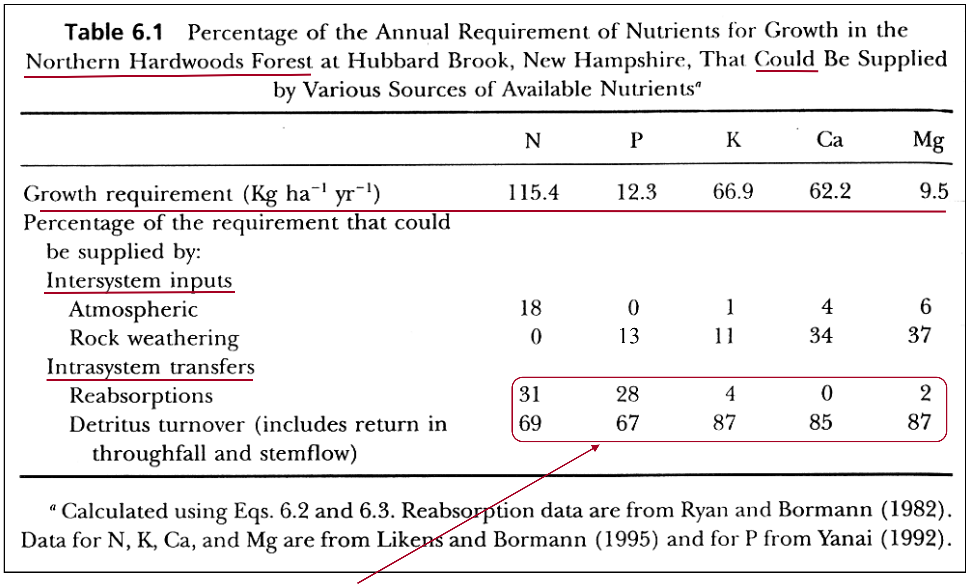

Table 6.1 Percentage of the Annual Requirement of Nutrients for Growth in the Northern Hardwoods Forest at Hubbard Brook, New Hampshire, That Could Be Supplied by Various Sources of Available Nutrients[a]

	N	P	K	Ca	Mg
Growth requirement (Kg ha^{-1} yr^{-1})	115.4	12.3	66.9	62.2	9.5
Percentage of the requirement that could be supplied by:					
Intersystem inputs					
Atmospheric	18	0	1	4	6
Rock weathering	0	13	11	34	37
Intrasystem transfers					
Reabsorptions	31	28	4	0	2
Detritus turnover (includes return in throughfall and stemflow)	69	67	87	85	87

[a] Calculated using Eqs. 6.2 and 6.3. Reabsorption data are from Ryan and Bormann (1982). Data for N, K, Ca, and Mg are from Likens and Bormann (1995) and for P from Yanai (1992).

1 hectare (ha) = 2.5 acres

Retention and internal recycling of essential nutrients is largest source of chemicals supporting growth

Inputs from external sources support "new growth" ("new production" in the ocean)

Nutrient Uptake – A Wide Range of Strategies!

- Ion exchange and solubility in soil control basic availability of nutrients

- However, plants can increase uptake rates by:
  - Passive uptake: plant uptake alters soil:root equilibrium -- thus, more dissolution from host rock

    Used when concentrations are relatively high

  - Deliberate uptake: release of enzymes to promote solubility or transport

    E.g., low-concentration, biogeochemically important ions (*e.g.*, N, P, K) are actively transported by enzymes in root membranes

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Enzyme systems can adapt to availability of elements

E.g., there are low P levels in cold soils (due to slow weathering rates), so arctic plants have fast uptake at low temperatures:

Carex = grassy sedge

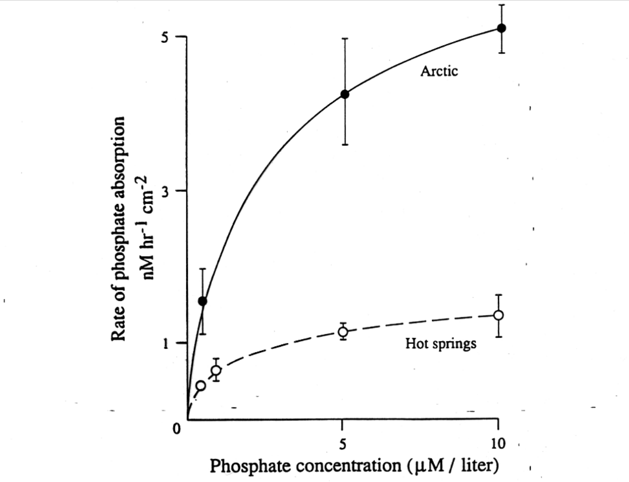


Figure 6.1 Rate of phosphate absorption per unit of root surface area in populations of *Carex aquatilis* from cold (Arctic) and warm (Hot Springs) habitats measured at 5°C. From Chapin (1974).

- Presumably due to lower temperature optima for arctic plant enzymes
- In both populations, enzymes allow rapid uptake at low concentrations

- Uptake of P and N is typically rapid, and soil concs are low – so diffusion within the adjacent soil is commonly the limiting factor
- Moreover, root growth rate correlates with N assimilation rate (*i.e.*, N is “controlling”):

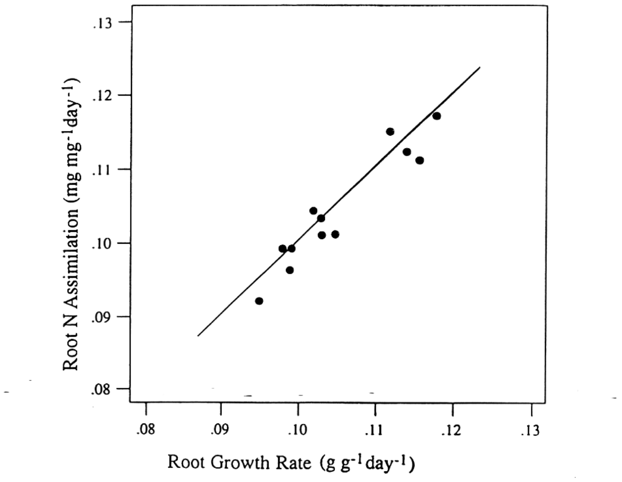
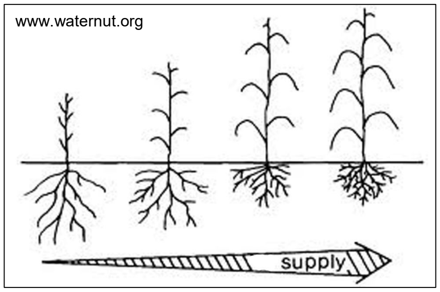


Figure 6.2 The rate of N uptake in tobacco as a function of the relative growth rate of roots. From Raper et al. (1978).

- P is commonly immobilized in soils, but plants can increase “root/shoot ratio” to get more P if needed

(shoot = plant material above soil line)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- Phosphatases released by higher plants and microbes remove P from organic matter -- enzyme activity varies inversely with P availability

In low-P environments, phosphatase activity can provide majority of P (*e.g.*, up to 69% in tundra)

In contrast to low-conc ions….

- High concentration ions may be actively excluded at the root zone -- *e.g.*, Ca excluded as $CaCO_3$ in desert regions with calcareous soils

Nutrient Balances

- Element Balance: Plants need all nutrients simultaneously -- imbalance leads to slow growth (but deficiency symptoms only appear when a nutrient abundance is very low)
- Charge Balance: Most nutrients are positively charged ions *(cations)*, but charge balance must be maintained across the cell membrane
  - Excess cation uptake is balanced by release of H^+ from roots -- leading to acidification of soil around root regions, which releases other cations (*e.g.*, K^+) (see Fig. 6.3 in text)
  - Excess anion uptake is balanced by release of HCO_3^- and organic anions to balance charge

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Large amount of N in plants causes the form of plant N uptake to dominate soil charge balance (note sums in table):

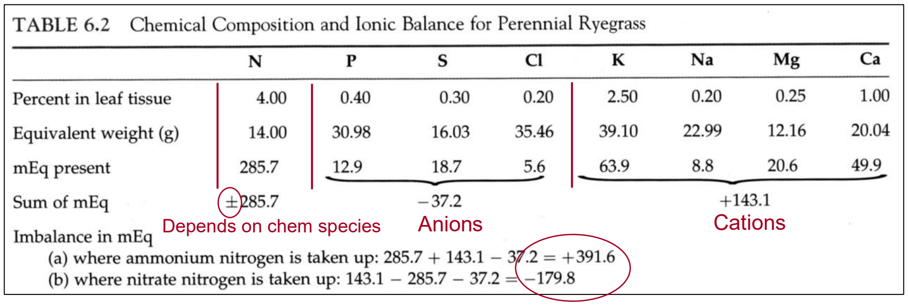


TABLE 6.2 Chemical Composition and Ionic Balance for Perennial Ryegrass

	N	P	S	Cl	K	Na	Mg	Ca
Percent in leaf tissue	4.00	0.40	0.30	0.20	2.50	0.20	0.25	1.00
Equivalent weight (g)	14.00	30.98	16.03	35.46	39.10	22.99	12.16	20.04
mEq present	285.7	12.9	18.7	5.6	63.9	8.8	20.6	49.9
Sum of mEq	±285.7		−37.2			+143.1		

Depends on chem species

Anions

Cations

Imbalance in mEq

(a) where ammonium nitrogen is taken up: 285.7 + 143.1 − 37.2 = +391.6

(b) where nitrate nitrogen is taken up: 143.1 − 285.7 − 37.2 = −179.8

Equivalents = moles x charge

Implies a combination of NH_4^+ and NO_3^- uptake.

Or…..

N uptake as NH_4^+ leads to more acidification around roots

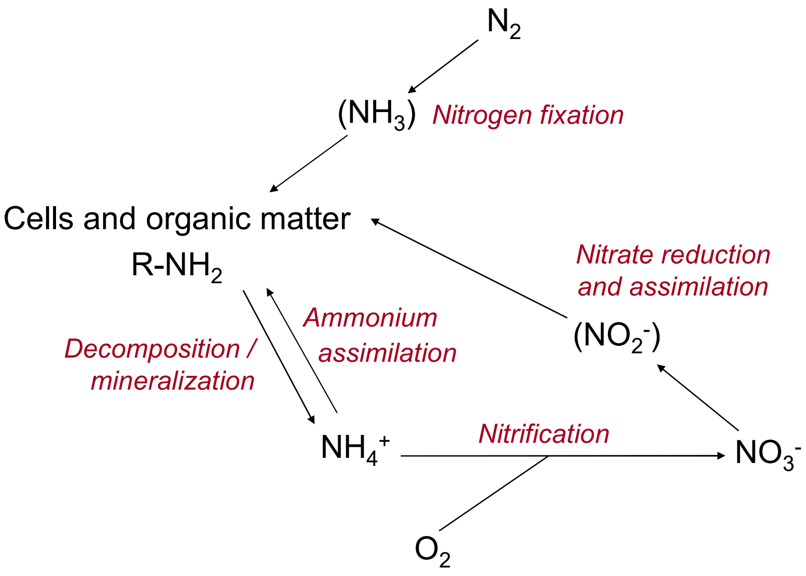
N uptake as NO_3^- leads to release of HCO_3^- and/or organic anions to balance charge

Nitrogen Speciation

Name	*Chemical formula*	*Oxidation state of N*
Nitrate	NO_3^-	+5
Nitrite	NO_2^-	+3
Dinitrogen	N_2	0
Ammonium	NH_4^+	-3
Organic N	$R\text{-}NH_2$	-3

Note: NH_3 is *ammonia* (non-ionic, volatile compound)

Nitrogen Biogeochemical Cycle



Nitrogen Assimilation

- Soil N is available as NO_3^- or NH_4^+ depending on soil conditions and bacterial action during regeneration
- Two extremes:
  - Waterlogged tundra -- NH_4^+ (low O_2 levels)
  - Deserts and forests -- mainly NO_3^- (higher O_2 levels)
- Many species show preference for NO_3^-, except where nitrification is inhibited because of low O_2 levels (Nitrification: $NH_4^+ + O_2 \rightarrow NO_3^-$)
- Assimilated NO_3^- is chemically reduced to form $-NH_2$ groups attached to organic compounds – this uses the enzyme "nitrate reductase", which consumes energy
- A few plants get N from an organic source -- *e.g.*, insect digestion

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Nitrogen Fixation

- Some bacteria and cyanobacteria possess the enzyme *nitrogenase*, which reduces atmospheric N_2 to NH_3 -- some are free-living, others are *symbionts* with plants

- N fixation needs a large amount of energy -- symbionts get carbohydrates from the host's root system

- N fixation rates can be similar to rates of wet and dry deposition from atmosphere, but importance of N fixation depends on conditions

- Free-living N fixation is favored in soils with large amounts of organic C (*e.g.*, rotting logs) which is a C source for the microbes -- *these environments also usually have low O_2 levels*

- N fixation may be as energy efficient as NO_3^- uptake + reduction in root systems

- Nitrogen fixation rates are commonly estimated by measuring acetylene *(HC≡CH)* reduction to ethylene *($H_2C{=}CH_2$)*, which is also performed by nitrogenase

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N fixation inhibited at high levels of available N:

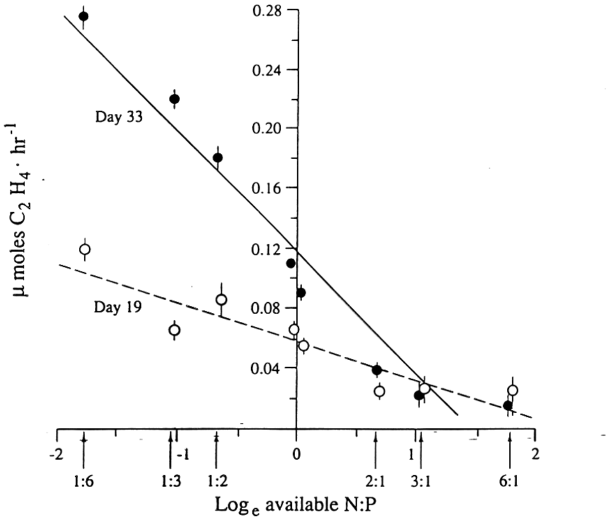


Figure 6.4 Acetylene reduction, an index of nitrogen fixation by asymbiotic N-fixing bacteria, as a function of the N:P ratio in soil. From Eisele et al. (1989).

N fixation can be stimulated by addition of P in low-N environments

Nitrogenase also needs Mo and Fe. Plants with symbiotic N-fixers may acidify root zone to release Fe and P.

N isotopes can be used to understand N dynamics

Atmospheric N_2: 99.63% ^{14}N, 0.37% ^{15}N

$\delta^{15}N \propto [^{15}N] / [^{14}N]$

$\delta^{15}N_{\text{atmospheric N2}} \equiv 0$

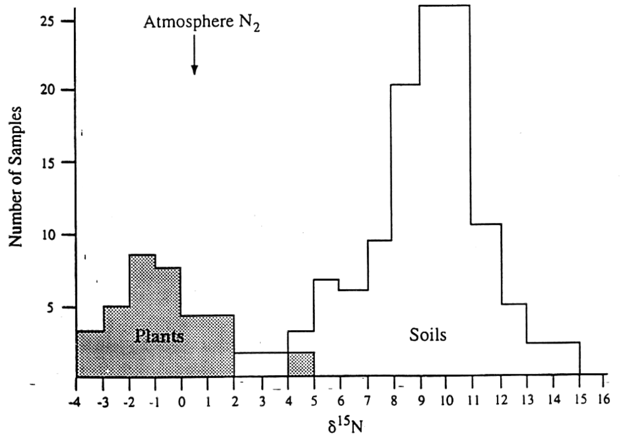


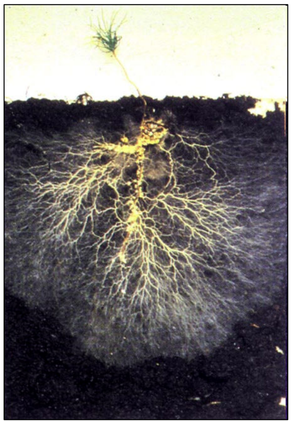
Figure 6.5 Frequency distribution of $\delta^{15}N$ in the tissues of 34 nitrogen-fixing plants and in the organic matter of 124 soils from throughout the United States. Plotted using data from Shearer and Kohl (1988, 1989).

N-fixers have $\delta^{15}N \approx 0$ (little "discrimination") -- N in soil organic matter has higher $\delta^{15}N$ values

Can use $\delta^{15}N$ to estimate fraction of N from fixation (40-60 % of uptake in some plants)

Mycorrhizal Fungi

- Symbiotic relationship with plants -- form sheath around fine roots and extend hyphae into soil and sometimes into root cells
- Mycorrhizae transfer nutrients to roots (important in infertile soils) and can stimulate N-fixation
- May release cellulases and phosphatases, enzymes that help break down organic matter, releasing C and P
- May release acids that help to weather rock
- But….N from fertilizers and atmospheric NO_x is beginning to decrease the effectiveness of N-fixing mycorrhizal fungi!



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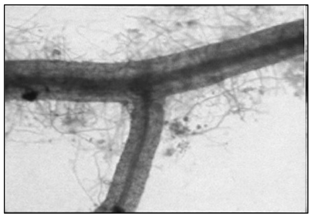

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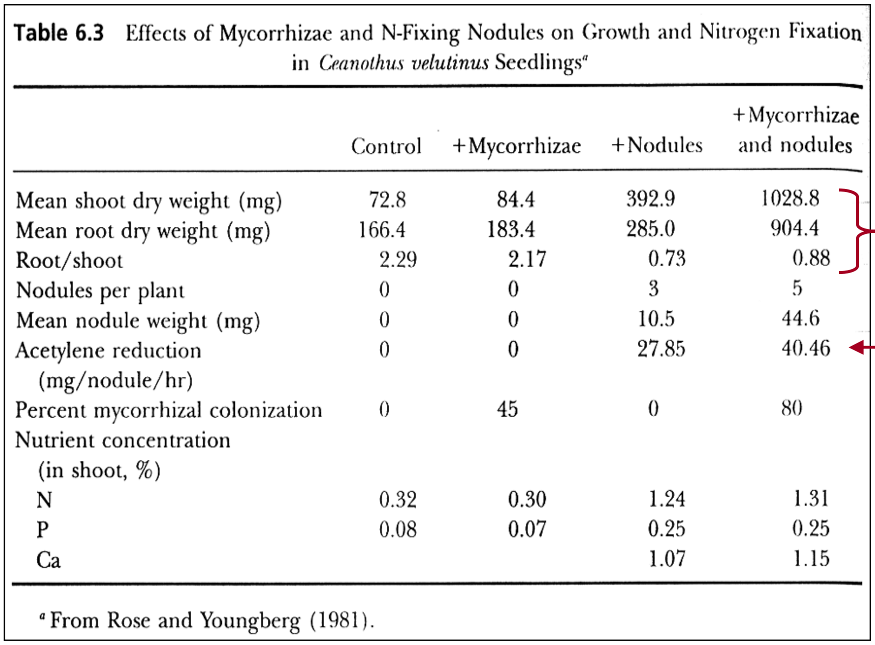

Table 6.3 Effects of Mycorrhizae and N-Fixing Nodules on Growth and Nitrogen Fixation in *Ceanothus velutinus* Seedlings[a]

	Control	+Mycorrhizae	+Nodules	+Mycorrhizae and nodules
Mean shoot dry weight (mg)	72.8	84.4	392.9	1028.8
Mean root dry weight (mg)	166.4	183.4	285.0	904.4
Root/shoot	2.29	2.17	0.73	0.88
Nodules per plant	0	0	3	5
Mean nodule weight (mg)	0	0	10.5	44.6
Acetylene reduction (mg/nodule/hr)	0	0	27.85	40.46
Percent mycorrhizal colonization	0	45	0	80
Nutrient concentration (in shoot, %)				
N	0.32	0.30	1.24	1.31
P	0.08	0.07	0.25	0.25
Ca			1.07	1.15

[a] From Rose and Youngberg (1981).

Ceanothus = hedgerow shrub

- Mycorrhizal fungi can be as much as 70% of stored carbon in boreal forests!
  (Clemmensen *et al.* 2013 *Science*)
- During nutrient deficiency: plant growth slows, photosynthesis remains high

Possible reason: Extra carbohydrate passed to roots, which encourages mycorrhizal infections and increased nutrient uptake:

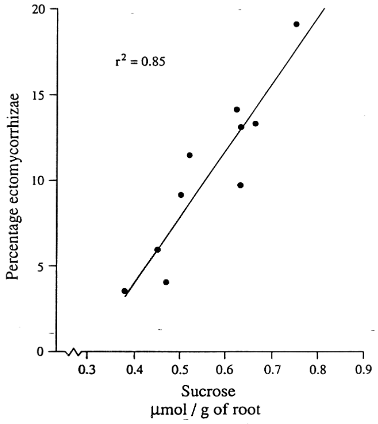

Figure 6.6 Relationship between infection of the roots of loblolly pine by ectomycorrhizal fungi and the sucrose concentration in the root. From Marx et al. (1977).