Nutrient Cycling in Land Plants

OCN 401 - Biogeochemical Systems
11 September 2012

Reading: Schlesinger, Chapter 6
Outline

1. Nutrient requirements and sources
   - Nutrient uptake by plants
   - Nutrient balances

2. Biogeochemical nitrogen cycle
   - Nitrogen speciation
   - Nitrogen biogeochemical cycle
   - Nitrogen assimilation
   - Nitrogen fixation
   - Mycorrhizal fungi
Nutrient Requirements and Sources

- Plant organic matter is mainly C,H, and O (i.e., CH₂O), with traces of 20 other elements needed for growth (e.g., N, P, Ca, Mo, S, Fe, Mg).

- C:N \approx 50 \text{ in leaf tissue}. Thus, global NPP of $60 \times 10^{15} \text{ g C/yr}$ implies a global N requirement of $1.2 \times 10^{15} \text{ g N/yr}$.

- Availability of N or P may control rate of NPP -- other elements are rarely limiting.

- 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.
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

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

• However, plants can increase uptake rates:
  • Passive uptake: plant uptake alters equilibrium distribution -- thus, more dissolution from host rock
    Used when concentrations are adequate
  • 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
Enzyme systems can adapt to availability of element

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

- Presumably due to lower temperature optima for arctic plant enzymes
- In both cases, enzymes allow rapid uptake at low concentrations
• Uptake of P and N is typically rapid, and soil concs are low – so diffusion from adjacent soil is commonly the limiting factor.

• Thus, root growth rate correlates with N assimilation rate (i.e., N is "controlling"): 

![Figure 6.2](image) 

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

• **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 $\text{H}^+$ from roots -- leads to acidification of soil around root regions, which releases other cations (*e.g.*, $\text{K}^+$)

  • *Excess anion uptake* is balanced by release of $\text{HCO}_3^-$ and organic anions to balance charge
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 Imbalance for Perennial Ryegrass<sup>a</sup> |
|-----------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|                 | 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|       |       |       |       |       |       |       |

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

*From Middleton and Smith (1979).*

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 organic anions to balance charge
## Nitrogen Speciation

<table>
<thead>
<tr>
<th>Name</th>
<th>Chemical formula</th>
<th>Oxidation state</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrate</td>
<td>NO$_3^-$</td>
<td>N (+5)</td>
</tr>
<tr>
<td>Nitrite</td>
<td>NO$_2^-$</td>
<td>N (+3)</td>
</tr>
<tr>
<td>Dinitrogen</td>
<td>N$_2$</td>
<td>N (0)</td>
</tr>
<tr>
<td>Ammonium</td>
<td>NH$_4^+$</td>
<td>N (-3)</td>
</tr>
<tr>
<td>Organic N</td>
<td>R-NH$_2$</td>
<td>N (-3)</td>
</tr>
</tbody>
</table>

Note: NH$_3$ is *ammonia* (non-ionic, volatile)
Nitrogen Biogeochemical Cycle

Nitrogen fixation

Organic matter

Decomposition / mineralization

Ammonium assimilation

R-NH₂

NH₄⁺

Nitrate reduction and assimilation

(NO₂⁻)

Nitrification

N₂

NO₃⁻
Nitrogen Assimilation

- Availability as $\text{NO}_3^-$ or $\text{NH}_4^+$ depends on soil conditions and bacterial action during regeneration

- Two extremes:
  - Waterlogged tundra -- $\text{NH}_4^+$ (low $O_2$ levels)
  - Deserts and forests -- mainly $\text{NO}_3^-$ (higher $O_2$ levels)

- Many species show preference for $\text{NO}_3^-$, except where nitrification is inhibited ($\text{Nitrification} \equiv \text{NH}_4^+ + O_2 \rightarrow \text{NO}_3^-$)

- Assimilated $\text{NO}_3^-$ is chemically reduced to form -$\text{NH}_2$ groups attached to organic compounds -- uses the enzyme “nitrate reductase”, which consumes energy
• A puzzle: Why do some plants prefer $\text{NO}_3^-$ over $\text{NH}_4^+$ despite extra energy needed for reduction of $\text{NO}_3^-$? Possible reasons:

  • $\text{NH}_4^+$ adsorbed onto soil cation-exchange sites -- whereas $\text{NO}_3^-$ is more soluble, so less root growth needed

  • $\text{NH}_4^+$ uptake may involve competition with uptake of other cations (e.g., $\text{K}^+$)

  • Potential toxicity of relatively low levels of $\text{NH}_4^+$ in plants

• Another puzzle: Nitrate reduction is more efficient when combined with photosynthesis in leaves, but woody plants concentrate nitrate reductase in roots (maybe due to lower $\text{O}_2$ levels?)

• A few plants get N from an organic source -- e.g., insect digestion
Nitrogen Fixation

• Some bacteria and cyanobacteria possess the enzyme *nitrogenase*, which reduces atmospheric N\textsubscript{2} to NH\textsubscript{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.

• Free-living N fixation favored in soils with large amounts of *organic C* to provide carbohydrates (*e.g.*, rotting logs) to the microbes -- *these environments also usually have low O\textsubscript{2} levels*.

• N fixation may be as energy efficient as NO\textsubscript{3}\textsuperscript{-} uptake + reduction in root systems.
• N fixation rates can be similar to rates of wet and dry deposition from atmosphere, but importance of N fixation depends on conditions

• Asymbiotic N fixation is 1-5 kg N ha\(^{-1}\) yr\(^{-1}\) in most systems

• Invading species in regions of high light levels (i.e., high photosynthetic rates) fix N at rates up to 100 kg N ha\(^{-1}\) yr\(^{-1}\). On new lava: up to 18 kg N ha\(^{-1}\) yr\(^{-1}\).

• Global N fixation \(\approx 0.1 \times 10^{15}\) g N yr\(^{-1}\), \(\sim 10\%\) of annual total N used in NPP

• Nitrogen fixation rates are commonly estimated by measuring acetylene (HC≡CH) reduction to ethylene (\(H_2C=CH_2\)), which is also performed by nitrogenase
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 Mo and Fe. (Low availability of Mo in NW U.S. soils may limit N fixation.)
N isotopes can be used to understand N dynamics

Atmospheric N$_2$: 99.63% $^{14}$N, 0.37% $^{15}$N

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 using a protein
- Speed up access to nutrients -- very important in infertile soils
- May also release cellulases and phosphatases, enzymes that help break down organic matter. Also may release acids that help to weather rock
<table>
<thead>
<tr>
<th>Table 6.3  Effects of Mycorrhizae and N-Fixing Nodules on Growth and Nitrogen Fixation in <em>Ceanothus velutinus</em> Seedlings&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control + Mycorrhizae + Nodules + Mycorrhizae and nodules</td>
</tr>
<tr>
<td>Mean shoot dry weight (mg)</td>
</tr>
<tr>
<td>Mean root dry weight (mg)</td>
</tr>
<tr>
<td>Root/shoot</td>
</tr>
<tr>
<td>Nodules per plant</td>
</tr>
<tr>
<td>Mean nodule weight (mg)</td>
</tr>
<tr>
<td>Acetylene reduction (mg/nodule/hr)</td>
</tr>
<tr>
<td>Percent mycorrhizal colonization</td>
</tr>
<tr>
<td>Nutrient concentration (in shoot, %)</td>
</tr>
<tr>
<td>N</td>
</tr>
<tr>
<td>P</td>
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<tr>
<td>Ca</td>
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</tbody>
</table>

<sup>a</sup> From Rose and Youngberg (1981).

*Ceanothus* = hedgerow shrub
• In a forest: mycorrhizal fungi are only 1% of biomass, but use 15% of NPP

• During nutrient deficiency: growth slows, but rates of photosynthesis remain high.

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

\[
\text{Figure 6.5 Relationship between infection of the roots of loblolly pine by ectomycorrhizal fungi and the sucrose concentration in the root. From Marx et al. (1977).}
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