Nutrient Cycling in Land Plants

OCN 401 - Biogeochemical Systems

Reading: Schlesinger, Chapter 6

Outline

1. Nutrient requirements and sources
   • Nutrient uptake by plants
   • Nutrient balance

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

- **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)
- Animals and plants **protein** contains ~ 16% N (by weight)
- C:N ≈ 50 in leaf tissue. Thus, global NPP of 60 x 10¹⁵ g C/yr implies requirement of 1.2 x 10¹⁵ 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

<table>
<thead>
<tr>
<th>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*</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Process</strong></td>
</tr>
<tr>
<td>Growth requirement (Kg ha⁻¹ yr⁻¹)</td>
</tr>
<tr>
<td>Percentage of the requirement that could be supplied by:</td>
</tr>
<tr>
<td>Inter-system inputs</td>
</tr>
<tr>
<td>Atmospheric</td>
</tr>
<tr>
<td>Rock weathering</td>
</tr>
<tr>
<td>Intra-system transfers</td>
</tr>
<tr>
<td>Reabsorptions</td>
</tr>
<tr>
<td>Detritus turnover (includes return in throughfall and stemflow)</td>
</tr>
</tbody>
</table>

* 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).

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

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

- Ion exchange and solubility control initial availability of nutrients
- However, plants can increase uptake rates:
  - **Passive uptake**: plant uptake alters equilibrium distribution -- thus, more dissolution from host rock
    - Plants use passive uptake (in water) of some ions when concentrations are adequate.
  - **Deliberate uptake**: release of enzymes to promote solubility
    - 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 lower P levels in cold soils (due to slower 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 rapid -- keeps levels low, causes diffusion limitation
• High concentration ions can be actively excluded at the root zone -- e.g., Ca excluded as CaCO$_3$ in desert regions with calcareous soils

• Root growth rate correlates with N assimilation (i.e., N is “controlling”):

![Graph showing the relationship between root growth rate and N assimilation.](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)
Nutrient Balance

- Plants need all nutrients simultaneously — imbalance leads to slow growth, but deficiency symptoms only appear when a nutrient abundance is very low

- 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$^*$ |
|-----------------------------|---------|---------|---------|---------|---------|---------|---------|---------|
|                           | 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 %              |        | −37.2   |         |         | +143.1  |         |         |         |

| Imbalance in mEq %        | Depends on chem species | Anions | Cations |
| (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 $\text{NH}_4^+$ and $\text{NO}_3^−$ uptake.

Or…..

N uptake as $\text{NH}_4^+$ leads to more acidification around roots

N uptake as $\text{NO}_3^−$ leads to release of $\text{HCO}_3^−$ 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>

## Nitrogen Biogeochemical Cycle

- **Nitrogen fixation**: N$_2$ → (NH$_3$)
- **Nitrification**: NH$_4^+$ → NO$_3^-$
- **Nitrate reduction and assimilation**: (NO$_2^-$) → (NH$_3$)
- **Decomposition / mineralization**: Organic matter → NH$_4^+$
- **Nitrogen fixation**: N$_2$
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 $\text{O}_2$ levels)
  - Deserts and forests -- mainly $\text{NO}_3^-$ (higher $\text{O}_2$ levels)

- Many species show preference for $\text{NO}_3^-$, except where nitrification is inhibited ($\text{Nitrification} = \text{NH}_4^+ + \text{O}_2 \rightarrow \text{NO}_3^-$)

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

- 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.
Nitrogen Fixation

- Some bacteria and blue-green algae 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\textsuperscript{-1} yr\textsuperscript{-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\textsuperscript{-1} yr\textsuperscript{-1}. On new lava: up to 18 kg N ha\textsuperscript{-1} yr\textsuperscript{-1}.

- Global N fixation ≈ 0.1 x 10\textsuperscript{15} g N yr\textsuperscript{-1}, ~ 10% of annual total N used in NPP.

- Acetylene (HC=CH) reduction to ethylene (H\textsubscript{2}C=CH\textsubscript{2}) is performed by nitrogenase and can be used to measure nitrogenase activity.
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:

\[ \delta^{15}N \propto \frac{^{15}N}{^{14}N} \]

Atmospheric N\(_2\): 99.63% \(^{14}N\), 0.37% \(^{15}N\)

\[ \delta^{15}N_{\text{atmospheric N}_2} = 0 \]

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

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

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

*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:

Figure 6.5  Relationship between infection of the roots of lebiody pine by ectomycorrhizal fungi and the sucrose concentration in the root. From Marx et al. (1977).