Nutrient Cycling in Land Plants

OCN 401 - Biogeochemical Systems
12 September 2013

Reading: 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 = 20 - 50 in leaf tissue. Thus, global NPP of 60 x 10¹⁵ g C/yr implies a global N 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

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**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 *

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Ca</th>
<th>Mg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth requirement (Kg ha⁻¹ yr⁻¹)</td>
<td>115.4</td>
<td>12.3</td>
<td>66.9</td>
<td>62.2</td>
<td>9.5</td>
</tr>
<tr>
<td>Percentage of the requirement that could be supplied by:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Intersystem inputs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Atmospheric</td>
<td>18</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>Rock weathering</td>
<td>0</td>
<td>13</td>
<td>11</td>
<td>34</td>
<td>37</td>
</tr>
<tr>
<td><strong>Intrasystem transfers</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reabsorptions</td>
<td>31</td>
<td>28</td>
<td>4</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Detritus turnover (includes return in throughfall and stemflow)</td>
<td>69</td>
<td>67</td>
<td>87</td>
<td>85</td>
<td>87</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” (“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:

Carex = grassy sedge

- 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”):

![Graph showing the relationship between root N assimilation and root growth rate.](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
  (shoot = plant material above soil line)

• 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 CaCO₃ 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 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 | Depends on chem species | Anions | Cations |
| Imbalance in mEq | $+37.2$ | $+143.1$ |

*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>NO₃⁻</td>
<td>N (+5)</td>
</tr>
<tr>
<td>Nitrite</td>
<td>NO₂⁻</td>
<td>N (+3)</td>
</tr>
<tr>
<td>Dinitrogen</td>
<td>N₂</td>
<td>N (0)</td>
</tr>
<tr>
<td>Ammonium</td>
<td>NH₄⁺</td>
<td>N (-3)</td>
</tr>
<tr>
<td>Organic N</td>
<td>R-NH₂</td>
<td>N (-3)</td>
</tr>
</tbody>
</table>

Note: NH₃ is ammonia (non-ionic, volatile)

Nitrogen Biogeochemical Cycle

- **Nitrogen fixation**
- **Nitrate reduction and assimilation**
- **Decomposition / mineralization**
- **Ammonium assimilation**
- **Nitrification**

\[
\begin{align*}
\text{N}_2 & \quad \text{Nitrogen fixation} \\
(\text{NH}_3) & \quad \text{Nitrogen fixation} \\
\text{Organic matter} & \quad \text{Nitrate reduction and assimilation} \\
\text{R-NH}_2 & \quad \text{Ammonium assimilation} \\
\text{NH}_4^+ & \quad \text{Nitrification} \\
\text{O}_2 & \quad \text{NH}_4^+ \\
\text{NO}_3^- & \quad \text{N}_2
\end{align*}
\]
Nitrogen Assimilation

• Availability as NO$_3^-$ or NH$_4^+$ depends 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 (Nitrification $\equiv$ NH$_4^+$ + O$_2$ $\rightarrow$ NO$_3^-$)

• Assimilated NO$_3^-$ is chemically reduced to form -NH$_2$ groups attached to organic compounds -- uses the enzyme “nitrate reductase”, which consumes energy

• A puzzle: Why do some plants prefer NO$_3^-$ over NH$_4^+$ despite extra energy needed for reduction of NO$_3^-$? Possible reasons:
  • NH$_4^+$ adsorbed onto soil cation-exchange sites -- whereas NO$_3^-$ is more soluble, so less root growth needed
  • NH$_4^+$ uptake may involve competition with uptake of other cations (e.g., K$^+$)
    • Potential toxicity of relatively low levels of 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 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\(_2\) 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

• 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* \(O_2\) *levels*

• N fixation may be as energy efficient as NO\(_3^-\) 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\(^{-1}\), \(\approx 10\%\) of annual total N used in terrestrial NPP

• Nitrogen fixation rates are commonly estimated by measuring acetylene (HC≡CH) reduction to ethylene (H\(_2\)C=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 Fe and P. (Low availability of Mo in NW U.S. soils may limit N fixation.)

N isotope can be used to understand N dynamics:

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

\[
\delta^{15}N = \frac{[^{15}N]}{[^{14}N]} \times 1000
\]

- $\delta^{15}N_{\text{atmospheric N}_2} = 0$

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

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 (mg/nodule/hr)</td>
<td>0</td>
<td>0</td>
<td>27.85</td>
<td>40.46</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></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>0.32</td>
<td>0.30</td>
<td>1.24</td>
<td>1.31</td>
</tr>
<tr>
<td>P</td>
<td>0.08</td>
<td>0.07</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td>Ca</td>
<td></td>
<td></td>
<td>1.07</td>
<td>1.15</td>
</tr>
</tbody>
</table>

*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

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

![Diagram showing relationship between percentage of mycorrhizae and sucrose concentration.](image)

\[ r^2 = 0.85 \]

**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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**The next lectures:**

Discussion of Peer Reviewed Mini-essays
Assign Extended Essay Topics
Review of Rubrics
Library Research Methods

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**Nutrient Cycling in Land Vegetation and Soils**

We will extend the topics covered today to an examination of nutrient cycling in terrestrial ecosystems.