The Carbon Cycle 3

I. Introduction: Changes to Global C Cycle (Ch. 15)
II. C-cycle overview: pools & fluxes (Ch. 6)
III. Controls on GPP (Ch. 5)
IV. Controls on NPP (Ch. 6)
V. Controls on NEP (Ch. 6)

IV. Controls on NPP
A. Components of NPP
B. Physiological Controls on NPP
   1. Plant Respiration
   2. Allocation
C. State Factor and Interactive Controls on NPP
   1. Climate
   2. Parent material/nutrient availability
   3. Organisms
   4. Time
V. Controls on NEP
A. Measuring NEP
B. Controls on NEP
   1. Uptake/release imbalance
   2. Disturbance

NPP = GPP - R_{plant}
NPP = \Delta \text{Plant}/\Delta t + C_{lost}
C_{lost}: exudates, volatilization, herbivory, tissue turnover (litterfall), disturbance (fire, harvest)

• NPP is total energy available to rest of ecosystem

Table 6.2 Components of NPP

<table>
<thead>
<tr>
<th>Components of NPP</th>
<th>% of NPP</th>
</tr>
</thead>
<tbody>
<tr>
<td>New plant biomass</td>
<td>40-70</td>
</tr>
<tr>
<td>Leaves and reproductive parts (fine litterfall)</td>
<td>10-30</td>
</tr>
<tr>
<td>Apical stem growth</td>
<td>0-10</td>
</tr>
<tr>
<td>Secondary stem growth</td>
<td>0-30</td>
</tr>
<tr>
<td>New roots</td>
<td>30-40</td>
</tr>
<tr>
<td>Root secretions</td>
<td>20-40</td>
</tr>
<tr>
<td>Root exudates</td>
<td>10-30</td>
</tr>
<tr>
<td>Root transfers to mycorrhizae</td>
<td>10-30</td>
</tr>
<tr>
<td>Losses to herbivores, mortality, and fire</td>
<td>1-40</td>
</tr>
<tr>
<td>Volatile emissions</td>
<td>0-5</td>
</tr>
</tbody>
</table>

What do we usually measure??
Litterfall
Stem growth
Sometimes roots
That leaves ~30% or more unaccounted for

What do we really care about?
• Biomass increment and carbon storage
• Energy available to other trophic levels
• Energy transfer to mycorrhizae (maybe)
• Root exudates (maybe)
• Volatile emissions (maybe; important for atmos chem but less so for C accounting).
B. Physiological controls on NPP

1. Respiration
   - NPP = GPP - Respiration

   Respiration provides energy for essential plant processes
   \[ R_{\text{plant}} = R_{\text{growth}} + R_{\text{maint}} + R_{\text{ion}} \]

   - Repair of Proteins
   - Repair of Membranes
   - Repair of Other stuff

   Probably correlates with GPP

   Respiration cost of growth is similar among species and plant parts

2. Allocation (pp. 132-135)
   Plants allocate most growth to tissues that maximize capture of limiting resources
   - Allocate to roots when dry or nutrient poor
   - Allocate to stems, leaves when light is limiting
   - Constantly adjust allocation
     - Prevents overwhelming limitation by any one resource
     - Tends to make plants limited by multiple resources

NPP is about half of GPP when looking across biomes
Table 6.3. Net Primary Productivity of the Major Biome Types Based on Biomass Harvests.

<table>
<thead>
<tr>
<th>Biome</th>
<th>Aboveground NPP (g m⁻² yr⁻¹)</th>
<th>Belowground NPP (g m⁻² yr⁻¹) (% of total)</th>
<th>Total NPP (g m⁻² yr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical forests</td>
<td>1,400</td>
<td>1,100</td>
<td>2,500</td>
</tr>
<tr>
<td>Temperate forests</td>
<td>950</td>
<td>600</td>
<td>1,550</td>
</tr>
<tr>
<td>Boreal forests</td>
<td>230</td>
<td>150</td>
<td>380</td>
</tr>
<tr>
<td>Mediterranean shrublands</td>
<td>500</td>
<td>500</td>
<td>1,000</td>
</tr>
<tr>
<td>Tropical savannas and grasslands</td>
<td>540</td>
<td>540</td>
<td>1,080</td>
</tr>
<tr>
<td>Temperate grasslands</td>
<td>250</td>
<td>500</td>
<td>750</td>
</tr>
<tr>
<td>Deserts</td>
<td>150</td>
<td>100</td>
<td>250</td>
</tr>
<tr>
<td>Arctic tundra</td>
<td>80</td>
<td>100</td>
<td>180</td>
</tr>
<tr>
<td>Crops</td>
<td>530</td>
<td>80</td>
<td>610</td>
</tr>
</tbody>
</table>

NPP varies 14-fold among biomes.

Half of global biomass and a third of global NPP is in tropical forests (total area x production/area).

Table 6.4. Biomass distribution of the major terrestrial biomes.

<table>
<thead>
<tr>
<th>Biome</th>
<th>Shoot Root (g m⁻²)</th>
<th>Root Total (%) of total (g m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical forests</td>
<td>30,400</td>
<td>8,400</td>
</tr>
<tr>
<td>Temperate forests</td>
<td>21,000</td>
<td>5,700</td>
</tr>
<tr>
<td>Boreal forests</td>
<td>6,100</td>
<td>2,200</td>
</tr>
<tr>
<td>Mediterranean shrublands</td>
<td>6,000</td>
<td>6,000</td>
</tr>
<tr>
<td>Tropical savannas and grasslands</td>
<td>4,000</td>
<td>1,700</td>
</tr>
<tr>
<td>Temperate grasslands</td>
<td>250</td>
<td>500</td>
</tr>
<tr>
<td>Deserts</td>
<td>350</td>
<td>350</td>
</tr>
<tr>
<td>Arctic tundra</td>
<td>250</td>
<td>400</td>
</tr>
<tr>
<td>Crops</td>
<td>530</td>
<td>80</td>
</tr>
</tbody>
</table>

Data from [Roy, 2001 #3858]. Biomass is expressed in units of dry mass.

Table 6.5. Global distribution of terrestrial biomes and their total carbon in plan biomass.

<table>
<thead>
<tr>
<th>Biome</th>
<th>Area (10⁶ km²)</th>
<th>Total C pool (Pg C)</th>
<th>Total NPP (Pg C yr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical forests</td>
<td>17.5</td>
<td>340</td>
<td>21.9</td>
</tr>
<tr>
<td>Temperate forests</td>
<td>10.4</td>
<td>139</td>
<td>8.1</td>
</tr>
<tr>
<td>Boreal forests</td>
<td>13.7</td>
<td>57</td>
<td>2.6</td>
</tr>
<tr>
<td>Mediterranean shrublands</td>
<td>2.8</td>
<td>17</td>
<td>1.4</td>
</tr>
<tr>
<td>Tropical savannas and grasslands</td>
<td>27.6</td>
<td>79</td>
<td>14.9</td>
</tr>
<tr>
<td>Temperate grasslands</td>
<td>15.9</td>
<td>6</td>
<td>5.6</td>
</tr>
<tr>
<td>Deserts</td>
<td>27.7</td>
<td>10</td>
<td>3.5</td>
</tr>
<tr>
<td>Arctic tundra</td>
<td>5.6</td>
<td>2</td>
<td>0.5</td>
</tr>
<tr>
<td>Crops</td>
<td>13.5</td>
<td>4</td>
<td>4.1</td>
</tr>
<tr>
<td>Ice</td>
<td>15.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>149.3</td>
<td>652</td>
<td>62.6</td>
</tr>
</tbody>
</table>

Data from [Roy, 2001 #3858]. Biomass is expressed in units of carbon, assuming that plant biomass is 50% carbon.

C.1. Climate

Global patterns of NPP vary with climate:
- Increases with ppt (up to max at ~2-3 m/yr)
- Increases exponentially with temperature
- High variance due to variation in other state factors

AET does better than temp or ppt alone.

What the heck is AET?

Molles 2004
PET responds mostly to changing temp (and wind)
AET is PET as constrained by available precip.

PET decreases
AET decreases

PET same
AET decreases

PET responds mostly to changing temp (and wind)
AET is PET as constrained by available precip.

AET does better than temp or ppt alone.

Molles 2004

NPP per unit leaf area and time is fairly similar across biomes

Table 6.6. Productivity per day and per unit leaf area.

<table>
<thead>
<tr>
<th>Biome</th>
<th>Season length (days)</th>
<th>Daily NPP per ground area (g m⁻² d⁻¹)</th>
<th>Total LAI (m² m⁻²)</th>
<th>Daily NPP per leaf area (g m⁻² d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical forests</td>
<td>365</td>
<td>6.8</td>
<td>6.0</td>
<td>1.14</td>
</tr>
<tr>
<td>Temperate forests</td>
<td>250</td>
<td>6.2</td>
<td>6.0</td>
<td>1.03</td>
</tr>
<tr>
<td>Boreal forests</td>
<td>200</td>
<td>2.5</td>
<td>3.5</td>
<td>0.72</td>
</tr>
<tr>
<td>Mediterranean shrublands</td>
<td>200</td>
<td>2.5</td>
<td>3.5</td>
<td>0.72</td>
</tr>
<tr>
<td>Tropical savannas and grasslands</td>
<td>200</td>
<td>5.0</td>
<td>2.0</td>
<td>2.50</td>
</tr>
<tr>
<td>Temperate grasslands</td>
<td>150</td>
<td>5.4</td>
<td>5.0</td>
<td>1.08</td>
</tr>
<tr>
<td>Deserts</td>
<td>150</td>
<td>5.0</td>
<td>5.0</td>
<td>1.43</td>
</tr>
<tr>
<td>Arctic tundra</td>
<td>100</td>
<td>2.5</td>
<td>1.0</td>
<td>2.50</td>
</tr>
<tr>
<td>Crops</td>
<td>200</td>
<td>3.1</td>
<td>4.0</td>
<td>0.76</td>
</tr>
</tbody>
</table>

Leaf Area Index Correlates with NPP

Length of the Growing Season Correlates with NPP
This suggests that LAI and season length are strong controllers of NPP as well as GPP.

2. Parent material/soil resources

a. Nutrient limitation of NPP
   - Soil fertility gradients
   - Fertilization

   Which nutrients limit production?
   What do we mean by “limitation”?

   Simplistic view: Liebig’s law of the minimum – only one resource is limiting, that in most limited supply

   But, multiple resource limitation of NPP is frequently observed...

   Why is NPP often limited by multiple resources?

   • Adjustment of allocation to prevent overwhelming limitation by one resource
   • Environment changes seasonally and from year to year
   • Different resources limit different species
b. Climate effects are in part mediated by belowground resources.

In ecosystems where correlations suggest a strong climatic limitation of NPP...

...experiments and observations indicate that this is mediated primarily by climatic effects on belowground resources.

c. Interactive effects of nutrients & vegetation: Soil/vegetation feedback

Low nutrient environment → Low RGR, high C:N, low biomass turnover → Slow decomposition → Low productivity → Slow mineralization

Chapin 1980

3. Organisms

a. Vegetation composition determines growth potential – both across and within biomes

Potential Vegetation

Atlas of the Biosphere

b. Organisms x Climate interactions:

Direct effects of climate on growth: short-term temporal variation

Effects on species composition: spatial variation (which determines growth potential) (takes time to adjust to climate)

4. Time: Disturbance and succession are major causes of variation in NPP within a biome

NPP (kg m⁻²)

Stand age (yr)
V. Net ecosystem production (NEP)

\[ \text{NEP} = \text{GPP} - \text{Recosyst} \]

\[ \text{Recosyst} = \text{R}_{\text{plant}} + \text{R}_{\text{het}} \]

\[ \text{NEP} = \text{NPP} - \text{R}_{\text{het}} \]

\[ \text{NECB} = \text{GPP} - \text{R}_{\text{E}} +/\text{F}_{\text{lat}} \]

\[ \text{NECB} = \frac{dC}{dt} \quad \text{(Chapin et al. 2006)} \]

\[ = (\Delta \text{Plant} + \Delta \text{Het} + \Delta \text{SOM})/\Delta t +/\text{F}_{\text{lat}} \]

See Box 6.1

NEP and NECB (NBP at large scales) is most relevant to long-term sequestration of CO₂ from atmosphere

The problem of definition vs. measurement

A. Measuring NEP

NEP is the balance between two large fluxes: GPP and ecosystem respiration

![Graph showing carbon exchange](image)

A. Measuring NEP

![Diagram of net ecosystem exchange](image)

- NEE = net atmospheric CO₂ flux

Measuring NEE - chambers
Measuring NEE - Eddy covariance towers (eddy flux)

Comparison of Tundra and Spruce energy

B. Controls on NEP, NEE, NECB
1. Represents net carbon storage in ecosystem (imbalance between C uptake and C loss)
2. Strong dependence on disturbance
   - Negative when disturbance frequent (fire, tillage)
   - Positive during recovery from disturbance (succession)

Schlesinger 2001

Why is NEP positive (NEE negative) in most ecosystems?

- Maybe all ecosystems accumulate C between disturbances
- Maybe bias in site selection
  - Researchers prefer productive sites?
- Maybe carbon loss by leaching is significant
- Maybe terrestrial biosphere is gaining carbon
  - due to elevated CO2 and N deposition

Summary
1. Controls on NPP are similar to those on GPP.
2. $R_{\text{plant}}$ consists of respiration for growth, maintenance, and ion uptake.
3. While variable temporally within ecosystems, across ecosystems NPP is ~50% of GPP.
4. NEP, NECB reflect net storage of C within an ecosystem.
5. Disturbance regime is the main controller of difference between NEP and NECB in natural systems.
6. Humans are influencing many factors (temp, nutrient avail, disturbance regimes) that could alter the balance of GPP and $R_{\text{ecosyst}}$ and thereby alter NEP and NECB.