Lecture 18. Biogeochemical Cycles

Review:
-recall that the two central processes occurring in ecosystems are:
  - transduction of energy and cycling of materials
-while energy flows through an ecosystem, material recycles around and around and around

Terminology
** cyclic series of transfers of an element from one component to another through an ecosystem is a biogeochemical cycle
-includes transfers to and from rocks and soil over geological time
-relatively rapid transfers among biotic and short-term abiotic components of the ecosystem called element cycles or nutrient cycles
-ecosystem compartments that contain the element are pools,
-connected by fluxes, transfers from one pool to another
-a pool that is a net recipient of an element is a sink;
-if a net efflux, it is a source
-e.g., atmosphere is a source of N to terrestrial ecosystems
-e.g., oceans are sinks for sodium and chloride
-because these elements enter but never leave

/Rant
Na and Cl are said to have “incomplete” cycles because they don’t cycle at all
-this terminology is silly
-this example illustrates ecologists’ fetish for attaching names to things
-even if those names are meaningless and uninformative
“I didn’t flunk out of school, I suffered an incomplete graduation.”
-why don’t we simply say that some elements cycle, some don’t
/end rant
-biogeochemical cycles for all biologically active elements: C, N, P, Fe, Ca, etc.
nitrogen cycle is described in agonizing detail in text, others more briefly
-we will run very quickly through Nitrogen cycle
-you have seen it in Intro Ecology, and will see it again in other courses
-read the text if you want details

Nitrogen Cycle
Figure below shows the essential elements of the nitrogen cycle [also Text Figure 9.6, p. 272]
-Decomp means Decomposition; Immob means Immobilization, the binding of nutrients within tissues of soil micro-organisms, unavailable to plant roots; Min means mineralization, the release of N in inorganic form (ammonia) into the soil when microbial cells die

-as with Carbon, largest N pool is the **atmosphere**
-recall that atmosphere is 78% triple-bonded N₂ (N ≡ N)
-this N is in a stable, inorganic form that most organisms cannot use: **unavailable**
Nitrogen Fixation
-diverse group of soil organisms transform atmospheric N\textsubscript{2} into organic N,
-which they use to make proteins and amino acids
-this is the mechanism of Nitrogen Fixation

-N-fixers are soil bacteria or cyanobacteria (blue-green algae)
-energetically *expensive*: highest rates from autotrophic cyanobacteria or plant root symbioses
-such as on roots of clovers, peas, beans, other legumes

N-fixation nodules on the root of a bean plant.
The nodules contain *Rhizobium* bacteria that fix atmospheric N2. The plant provides energy as sugar from photosynthesis.

N Mineralization
-mineralization refers to transition of organic N into mineral (inorganic) forms, NH\textsubscript{3} and NO\textsubscript{3}
-all fixed N becomes part of living organisms, and eventually, dead organic matter
-may pass through a few consumers along the way,
-but always ends up as detritus

-as organic matter is decomposed, N is released as dissolved organic nitrogen (DON)
-this fraction consists of free amino acids, nucleic acid, other small, N-containing molecules
-plant roots and *mycorrhizal fungi* can take up some DON directly, without mineralization
-unit of N may cycle between organic tissue and DON many times before it is fully mineralized
-the role of DON in N cycling and plant nutrition has only recently been realized

-Amino acids (left) and bases from nucleic acids (right), typical components of DON

-N in DON is eventually fully mineralized to ammonia (NH₃)
(Aside: Ammonia, NH₃, is a base; in water it is mostly found as ammonium, NH₄⁺; the difference is unimportant in the context of N cycling)
-ammonia has two possible fates:
   (1) root or microbial uptake
   ammonia can be taken up by plants from the soil or water
or:   (2) conversion to nitrate (NO₃⁻)

Nitrification
-ammonia not immediately assimilated by plant roots is oxidized to nitrate
-through a two-step process (NH₃ → NO₂ → NO₃)
-involving two specialized genera of bacteria;
-nitrate is also available for uptake by plant roots;
-which sends it cycling through the ecosystem again
** plant roots have three N sources: DON, ammonia, nitrate
-DON and ammonia preferred because nitrate must be reduced to NH₂ for use

Denitrification
-possible for some nitrate to be lost to the atmosphere
-denitrification refers to conversion of nitrate back to atmospheric N₂
-it “completes” the N cycle in the sense that it brings N back to the inert form
-mostly carried out by bacteria growing anaerobically in waterlogged soils
-these organisms use nitrate as a terminal electron acceptor in place of oxygen
**Principles of Element Cycling**

More REVIEW: some general principles of biogeochemical cycles

1. One large abiotic pool holds most of the active supply of the element
   - most C and N are in the atmosphere
   - for almost all other elements (P, Ca, Mg, K) largest pool is in soil and rocks
   - only a small part of total abiotic pool is in flux through the biota at any time

   - therefore, flux of the element from major abiotic pool to biotic pool
     sets upper limit on supply of that element to the ecosystem

e.g., in the N cycle, N-fixation is the critical rate

e.g., in the P cycle, rate of rock weathering is the critical rate

2. Elements change energy state as they are cycled
   - energy flows through the ecosystem;
   - along the way it drives cycling of elements
   - by alternately raising and lowering the energy state
   - abiotic pools contain stable, oxidized forms of the element with a low energy content
   - energy from sunlight is pumped into the elements to transform them into a reduced form
     ** reduced form is more energetically active,
   - therefore more useful as a structural element in tissues
   - ** same general rules apply to all element cycles

3. Decomposition of organic matter renders elements in organic matter available to plant roots
   - decomposition is essential to the functioning of all ecosystems
   - and the cycling of all essential elements
   - plant roots obtain most of their nutrients from decomposition of organic matter
   - weathering and atmospheric inputs replace the small amounts lost through runoff and leaching
4. Micro-organisms are **essential** for all element cycles
-microbes, fungi and bacteria, are responsible for at least one step in cycling of every element
**microbes have a range of metabolic pathways for energy metabolism**
-which are not available to plants and animals
Remember: **micro-organisms run the world**

5. Element cycles are **nested combinations** of many cycles operating at different time scales
-what we call an element cycle is really many cycles, all operating at once

-look at carbon cycle:
some carbon from the atmospheric pool is fixed into organic carbon
-then immediately recycled back to the atmosphere by respiration
-those two fluxes constitute a C cycle

-other carbon becomes litter
-which is returned to the atmosphere when the litter decomposes
-completing a second, longer cycle

-still other C may become stable organic matter in the soil
-or accumulate in a peat bog
-this C cycles over extremely long periods, hundreds or thousands of years

-finally, a small part of the C becomes buried in the earth
-and adds to deposits of coal or oil
-there are thus a whole range of cycles going on, one inside another inside another

-same “nestedness” applies to all element cycles
-we separate longest cycles as **biogeochemical** cycles and the shorter as **nutrient** cycles, but a gradient and all manner of intermediates in between
**shorter cycles are affected more by **biological factors**
-longer cycles are affected more by **geological (abiotic) factors**
  ** hence, shorter the element cycle, the more biologically controlled it is

-more silly terminology:

-closed cycles keep most of a nutrient within soil or biota,
minimizing losses to drainage water or atmosphere
-open cycles have less biological control, more interaction with the large abiotic pools

-whether a cycle appears open or closed depends on the scale of the resolution
-entire nitrogen cycle can occur within a few grams of soil
-imagine a soil particle, surrounded by soil atmosphere
-a free-living *Azotobacter* bacterium can fix nitrogen from the soil air
-then release organic N when the cell dies,
-another bacterium breaks down the DON, releases NH$_3$
-which is oxidized to NO$_3$ by two other species (*Nitrosomonas* and *Nitrobacter*)
-then denitrified back to atmospheric N$_2$ (*Pseudomonas*) when particle becomes water saturated

-at that scale, N cycle is entirely closed; nothing is leaving the ecosystem
-but if we scale up, to the level of a stand of trees, there are fluxes to and from the atmosphere,
-which are considered gains or losses
-also losses of soluble nitrate in **drainage water**
-but nitrate leached out of a forest or field ends up in the nearest stream or lake or wetland,
-so it is an external gain for them

-if we scale up to entire drainage basin, those drainage losses are internal cycling, not losses
-but some N is lost entirely from the drainage basin, to the ocean or the atmosphere
-so at that scale, the cycle is open
-but lost N will still be available for cycling somewhere else

** at level of the entire planet, all biogeochemical cycles are **closed**
[Unless you insist that some elements are lost from the upper atmosphere when molecules become excited to escape velocity by sunlight and are lost to space. The Earth also gains about 40,000 tonnes of mass each year from intercepted space dust, micro-meteorites, and occasional larger particles. So perhaps whole planet has open element cycles. I am not going to go there.]

Kinds of Element Cycles

- return for a moment to first of five principles of element cycling:

1. One large abiotic pool holds most of the active supply of the element

-I posit that we can separate element cycles into three distinct sorts:
   1. Elements with a major abiotic pool in the atmosphere (N and C)
   2. Elements with a major abiotic pool in the lithosphere (most other elements)
   3. Elements with both major pools (chiefly Sulfur)

- look at Text Figure 9.17, p. 292, which diagrams some of the cycles terrestrially
- N and C are withdrawn from the atmosphere biologically
- so biological controls and processes apply
- there is also as flux of these elements back to the atmosphere

- ultimate supply of other elements is controlled by physical processes
  ** so biota cannot control the supply rate, even if an element (P) becomes limiting

- sulphur appears to be a special case
- major reservoir in the soil,
- but atmospheric concentrations may be considerable too
- fittingly, both physical and biological mechanisms important to flux of S to other pools

Carbon is a complicated element
- Carbon has a large lithospheric pool too (coal, gas, oil, C-bearing rocks)
- much of this carbon apparently does not cycle except by human intervention
-some C in minerals, such as CaCO$_3$, may enter the cycle through physical mechanisms (erosion)
-but I don’t think the quantities are significant.

** Carbon also has a very large pool in soil organic matter
** on a global basis, *three times* as much C in soil than in the atmosphere
-this C is dead, but it is organic material (detritus),
-so I think we can count it as part of the biota, not part of the large inorganic pool
-if so, my classification system still works
-but this is just my hypothesis: I could be all wrong.
**Lecture 19: Terrestrial Versus Aquatic Element Cycles**

-can we find predictable differences in element cycles between terrestrial and aquatic ecosystems?

-recall that I defined four kinds of surface ecosystem: terrestrial, freshwater, marine and transitional

**biogeochemical cycles are all fundamentally similar regardless of the kind of ecosystem**

-however, some important differences between aquatic and terrestrial ecosystems

-arising from dominance of aquatic ecosystems by water instead of air

-as summarized below:

1. **Terrestrial subsidies**

-because water flows downhill, aquatic ecosystems receive runoff from terrestrial ecosystems

-therefore, **subsidies** from the surrounding land are an additional influx to aquatic ecosystems

**subsidies accrue to all aquatic ecosystems, from the smallest pond to the largest oceans**

-recall that lakes, rivers receive significant N and P income from surrounding land

-coastal oceans are more productive than offshore because of runoff from continents

-especially near the mouths of great rivers

**these are all subsidies from the land to the water**

**because of the dependence of aquatic ecosystems on subsidies,**

-whatever is recycled effectively (closed cycle) on land is impoverished in water

-recall that binding of P to soil starves freshwater lakes of P

-mature forest ecosystems release very little N, Ca, Mg, etc, in groundwater to streams

-do subsidies ever move the other direction? Only in exceptional cases

-Example: spawning migrations of salmon to west coast streams are a major nutrient transfer from oceans to forest

-Example: sea spray can deposit salts, and perhaps other nutrients, on coastal landscapes

-but by and large, movement of elements is one-way, propelled by gravity

-eventually, everything ends up (or down) in the ocean
2. Separation from the solid phase
-in pelagic environment, biota at surface are permanently or temporarily isolated from sediments
-many nutrient transformations, such as mineralization of N, P, may occur in the sediments
-but these nutrients may not be recycled into the water column until the next overturn
-in the deep ocean, they may not be recycled at all

-therefore, in pelagic ecosystems we find
(A) severe nutrient limitation where land subsidies are small (offshore ocean, Shield lakes)
(B) extremely efficient nutrient recycling within the pelagic zone to offset settling losses

3. Physical mixing controls nutrient recycling
-true for most elements
-especially true for N, P, Fe, which tend to leave the photic zone as solid particles
-then are mineralized in the sediments (or on the way there)
-cannot be re-used by biota until mixing brings them back to the surface, later or never
** aquatic ecosystems have less biological control over all element cycles than on land

4. Water solubility alters flux rates
-large pools of N\textsubscript{2} and CO\textsubscript{2} are in the atmosphere
-for these elements to be fixed by biota, they must first dissolve in water
-both chemicals are very soluble,
-but sometimes atmospheric transfer of CO\textsubscript{2} not fast enough to meet photosynthetic demand
-hence aquatic production can occasionally be limited by CO\textsubscript{2}
-especially since only some CO\textsubscript{2} dissolved in water is available
-rest forms bicarbonate (HCO\textsubscript{3}^-) and carbonate (CO\textsubscript{3}^{2-}) that most plants cannot assimilate

** water solubility of phosphorus a major limitation on recycling of that element
-P is an extremely reactive element
-in oxygenated water, P forms carbonates and oxides with Ca, Fe, Mg and other elements
-these compounds are insoluble, and settle to the sediments
-under anoxic conditions, P may be released in the available, soluble form again
-anoxia is the rule below the surface of the sediments
-but **mixing** is required to bring that P back to the photic zone

** solubility of a second element, oxygen, alters flux rates of P

-on land, P reacts with Ca, Fe, clays and organic matter in soil
-creates occluded P, permanently unavailable
-only a small portion of P in soil is available,
-rest is permanently occluded in soil particles
-which is why so little leaches into runoff or soil water (leading to P limitation of lakes, rivers)

-new available P is produced by weathering of primary minerals, which tend to be P-rich in very long term, P content of the soil may be exhausted,
-leading to permanent P limitation on land
-this has happened in the ancient soils of tropical rainforests,
-which are frequently P limited
-as opposed to N-limited in most terrestrial ecosystems
-relentless leaching by daily heavy rains contributes as well

**5. Spatial variability is much lower in aquatic ecosystems**
-soil processes are famously variable
-entirely different rates of key processes in samples a few metres apart
-because soil is a solid, and doesn’t move around

Example: very different soil chemistry and element cycling beneath an oak tree
-compared with a shallow-rooted spruce tree a few metres away
-because the oak tree draws calcium from deep in the soil
-drops alkaline, Ca-rich leaf litter
-spruce tree drops acid needle litter very poor in Ca
- same variability applies at every spatial scale
- from smallest particles to whole landscape
- need intense and careful sampling to estimate flux rates in soil
- to make matters worse rates of soil processes change after every rain

In contrast:
- aquatic ecosystems are based on water, a fluid
- mixes freely, equalizing concentrations very quickly across all scales
- elements in solution rapidly diffuse throughout the water body, equalizing concentrations
- can estimate concentrations and flux rates in a lake very easily with relatively few samples
- must allow for large-scale, vertical differences (stratification), but not small-scale variability

** maybe sediment-based processes at the bottom of lakes and streams are as variable as on land
- I have never seen data on this

6. Redfield ratios and greater storage in terrestrial ecosystems
- nitrogen and phosphorus occur in strikingly constant proportions (14:1) in all plant tissues
- called Redfield Ratio after the oceanographer who described it in the 1950s

Alfred Clarence Redfield
Always wondered what this fellow looked like
-Redfield observed the fixed ratio in algae,
-but it has since been observed in virtually all plants
-when N:P ratio is greater than 14:1, algae become P limited
-because they are disproportionately lacking in P relative to N
-if P:N ratio is much less than 14:1 then algae are N-limited
-when algae are P-limited, they take up as much P as they can,
** also take up N in a 14:1 proportion to the P absorbed
-same when they are N limited
** consequently, element that is most limiting determines uptake rate for all elements
-this feature of plants is universal enough that it is used to determine fertilizer requirements

-Redfield ratio is complicated by storage of nutrients
-algae absorb non-limiting nutrients in excess of present requirements
-excess nutrient is stored in a vacuole in the cell
-nutrient storage is apparently an adaptation to temporal variability in nutrient availability
-limiting nutrient today may not be limiting tomorrow
-for a small investment in storage, cell can grow and divide under varying circumstances

** storage capacity is much greater on land plants than in phytoplankton
-vascular plants store surplus elements in vacuoles, stems and roots
-again an adaptation to varying nutrient supply
-in perennial plants, an adaptation to predictable seasonal patterns

-in temperate regions, N and P in soil become available in a pulse in the autumn, after leaf fall,
-and again in early spring, when decomposers are more active than plants
-plants absorb these nutrients when they become available, use them to grow later
** nutrient concentrations in vascular plants at any given time may vary from the Redfield Ratio
-in Arctic and alpine regions, growth and decomposition are far out of synchrony
-so much that plants store nutrients to grow the following year
-uptake from roots late in the growing season used primarily to replenish depleted stores
Nutrient Cycling in Wetlands

-let’s briefly consider wetlands, or transitional ecosystems in general
-how are biogeochemical cycles modified in these unique habitats?
-wetlands are characterized by: (1) high and varying water table (2) mostly vascular plants
-they are best characterized as **modified terrestrial habitats** as far as nutrient cycles go

-saturation or inundation complicates the picture

Examples: (1) soils may be seriously leached, reducing nutrient supply

(2) decomposition may be accelerated by moisture, or decelerated by lack of O₂

(3) solution of nutrients in water may complicate availability

(4) may be profound differences in water content through space and time

-nitrogen cycle again provides best examples

-wetland soils tend to be carbon rich, oxygen-poor and rich in nitrate

-these circumstances promote rapid **denitrification** from nitrate to N₂

-by anaerobic bacteria using NO₃ as an electron receptor in the absence of oxygen

-so wetlands tend to be N-poor because of loss of N₂ to the atmosphere

** N-fixing plants have an advantage in wetlands because of high light and water, but low N

-alders, blue-green algae, other N-fixing plants commonly thrive in wetlands

-denitrification requires a supply of nitrate to be reduced to N₂

-if soil is anaerobic, ammonia will not be oxidized to NO₃ (NH₄ → NO₃ requires oxygen)

-this step can limit the amount of denitrification

** nitrate may be supplied by oxidation of ammonia in drier uplands (see Figure next page)

-nitrate then transported to the wetland in surface or groundwater flow

-remember nitrate does not bind strongly to soil (negative charge)

** this mechanism is important in fringing wetlands and floodplains along streams

-especially if upland is farmland given heavy doses of N fertilizer

-denitrification of nitrate from fertilizer may **protect** aquatic ecosystems against excess N
Since we have a little extra space in this discussion of element cycling, can you tell what this is?

**Figure 14.6.** Topographically controlled interactions among ecosystems in a landscape via erosion and solution transfers in subsurface flow or groundwater. Riparian forest trees absorb nutrients primarily from well-aerated soils, whereas denitrification requires anoxic conditions, which generally occur below the water table. Nitrogen uptake and denitrification are the most important mechanisms by which riparian zones filter nitrogen from groundwater between upland ecosystems and streams.

It’s an elephant cycle!