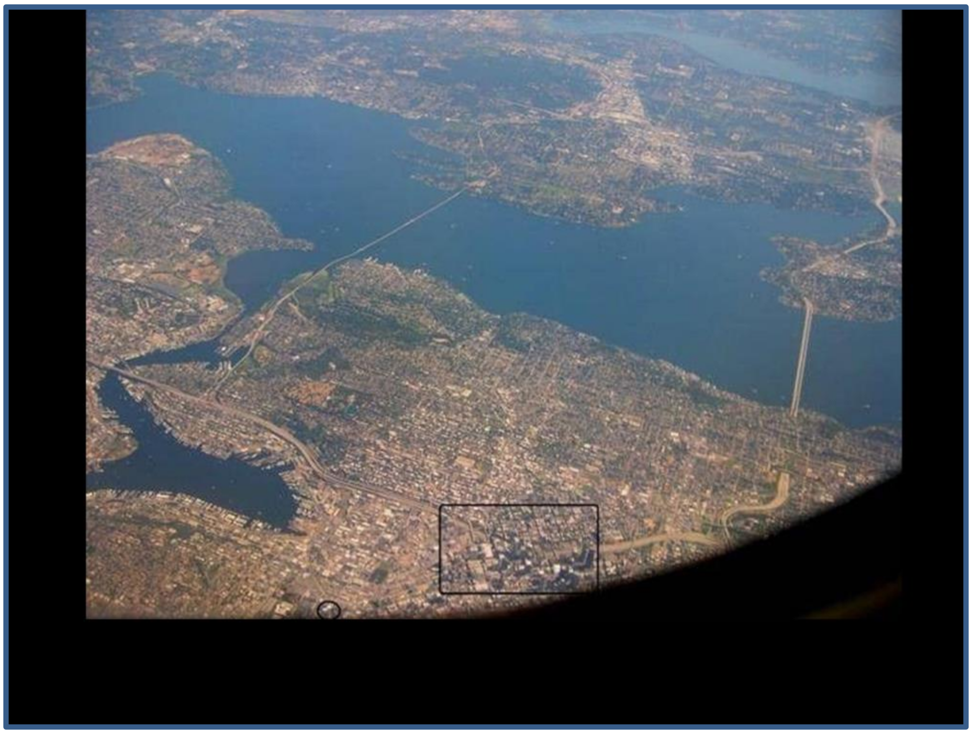
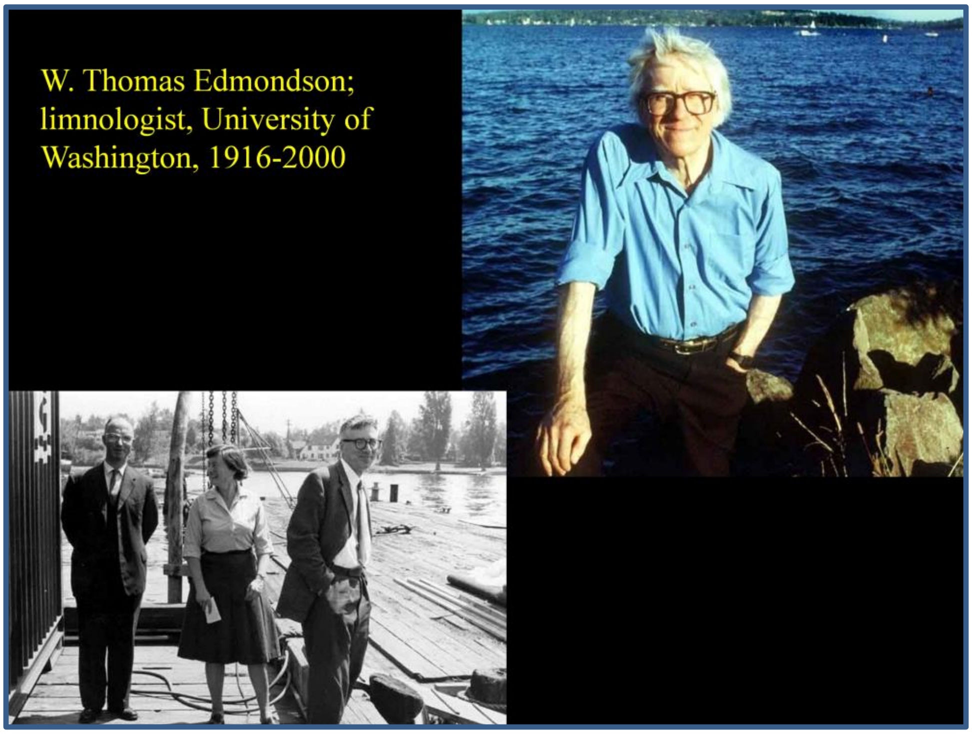
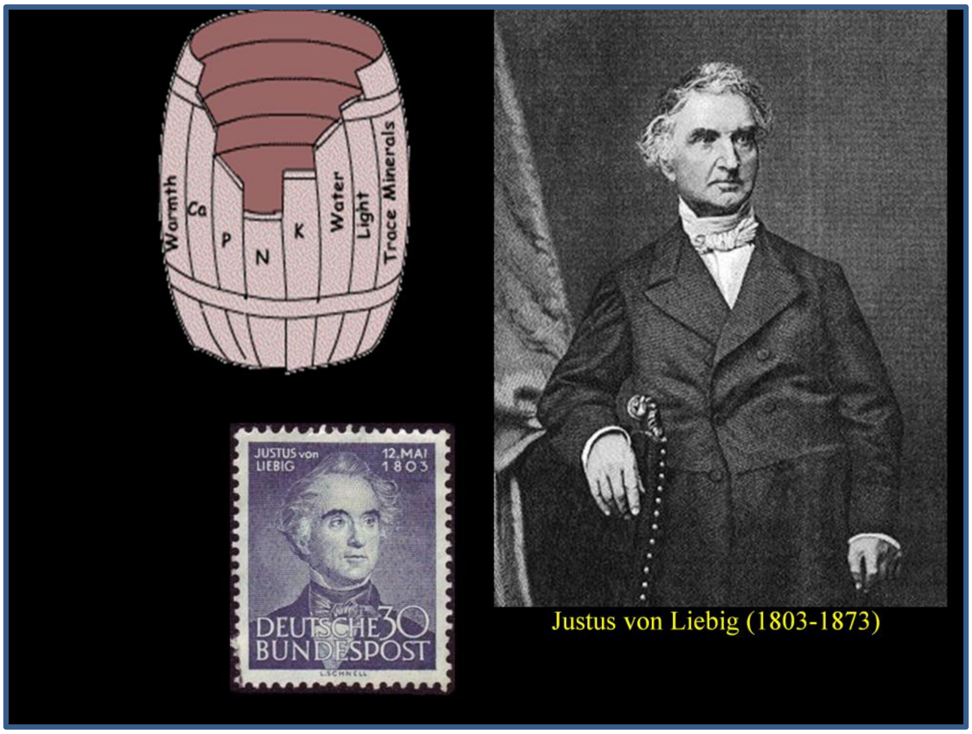


Lake Washington in Seattle: when Seattle exploded in population during and after WWII, sewage input to Lake Washington increased proportionally.  10 sewage plants were added to the lakes watershed from 1941-1953, and they applied only minimal treatment.  The lake changed from a clear-water lake to an algae-clogged and putrid state.  Fish died in large numbers and mats of algae washed ashore along with the fish carcasses and the whole mess rotted; Lake Washington became known as 'Lake Stinko'.  In the 1950s, the Mayor of Seattle appointed a commission to solve the problem.  In consultation with  limnologist Tommy Edmondson the commission determined the cause of the phenomenon and designed a solution – one of the first times a governmental agency explicitly brought understandings from ecological science to bear in application. Edmondson pointed out that fresh-water systems like Lake Seattle are generally *phosphorus-limited* – meaning that, of all the resources required for growth by the organisms at the base of the food chain – the photosynthetic *'primary producers'* (here, planktonic algae) – phosphorus is in *shortest supply relative to proportional need by the algae.*  Marine systems are typically nitrogen-limited.  Terrestrial systems are often water-limited, but sometimes nitrogen-limited.  There are many other nutrients that CAN be limiting in particular circumstances.

Edmondson explained that sewage is relatively rich in phosphorus, so adding phosphorus meant INCREASED ALGAL GROWTH.  As algae increased in abundance, they blocked more light.  Eventually, as phosphorus became more abundant, it ceased being limiting and nitrogen became the limiting resource.  (Algae require carbon, nitrogen, and phosphorus roughly in the ratio  C:N:P=106:16:1 – this is called the 'Redfield ratio'; thus if phosphorus is much more than 1/16 as abundant as nitrogen, nitrogen may be more limiting).



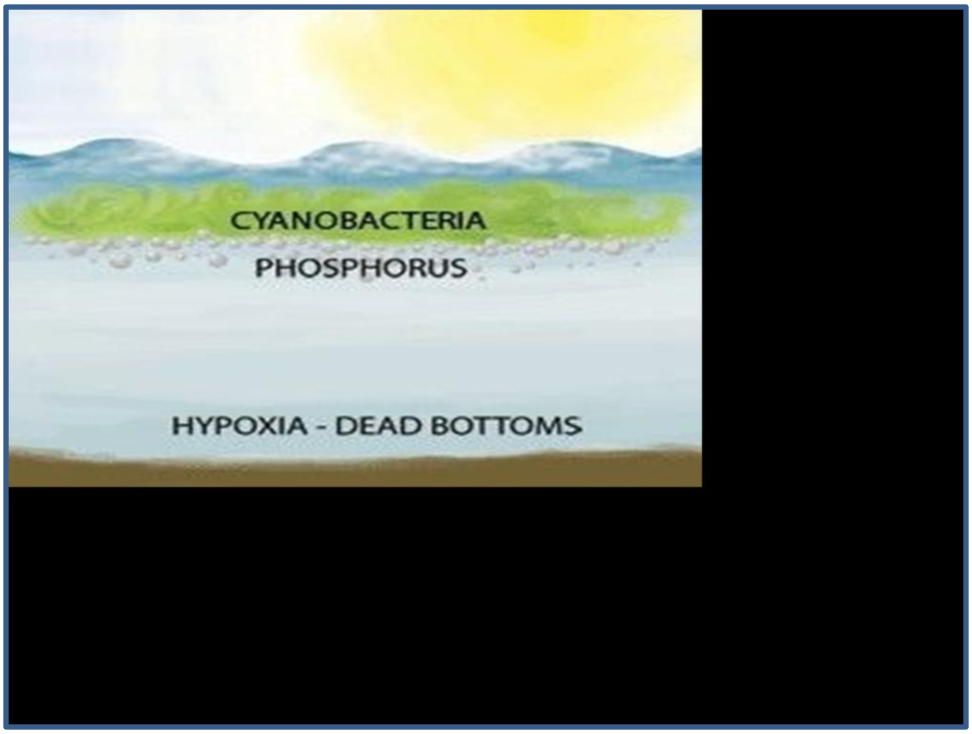

Tommy Edmondson in the 1990s (right) and in the 1960s (left), with his wife, Yvette Edmondson. Yvette Edmondson was also an important limnologist who worked closely with one of the most important ecologists of the 20th century (G. Evelyn Hutchinson at Yale Univ.); she was a member of the second graduating class of Bennington College.



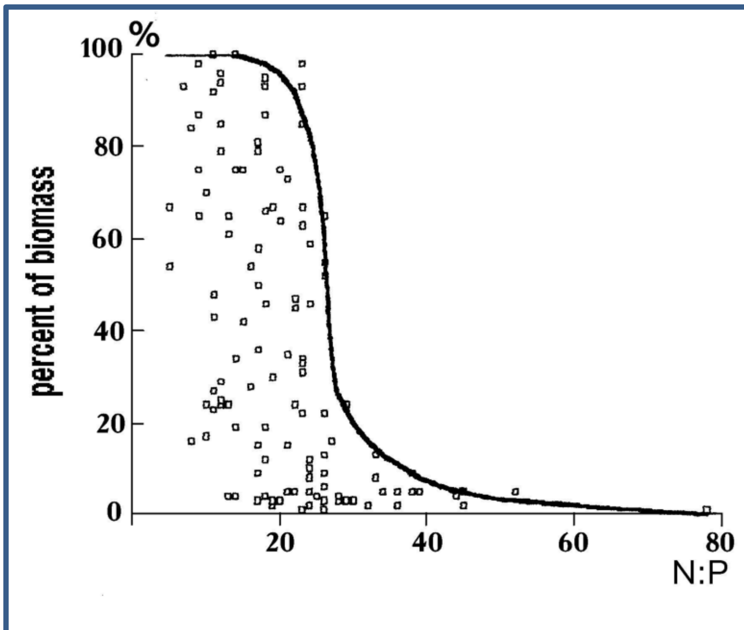

The notion of the limiting resources is rooted in the thinking of 19th-century German chemist, Justus von Liebig, and is sometimes referred to as 'Liebig's Law of the Minimum'. Von Liebig used the metaphor of a rotting barrel; the amount of water the barrel can hold is limited by the height of the shortest stave; it doesn't matter how much water or phosphorus is available (in the case represented above); you can't increase the amount of water the barrel can hold unless you make the nitrogen stave taller (make nitrogen more available). If you do that, however, eventually some other resource will become limiting. NOTE that this isn't really about the ABSOLUTE abundance of these things, but their abundance relative to each other and to the organism's needs. Water is always much commoner than phosphorus – but organisms need lots more water than phosphorus…

In lakes with low phosphorus, *green algae* dominate the plankton community (these are single-cell relatives of true plants). However, when *nitrogen* becomes limiting – potentially due to addition of phosphorus – green algae are out-competed by *blue-green algae* or, more accurately, *cyanobacteria* (look up bacteria for the difference!). Cyanobacteria are photosynthetic 'prokaryotes' (look it up), capable of using gaseous nitrogen from the atmosphere for their necessary N intake (ONLY some bacteria, among all organisms can do this). This is called 'fixation' of N. Thus, while green algae are now N-limited, cyanobacteria are unlikely to ever by so limited since nitrogen is extremely abundant in the atmosphere. (N-fixation is energy-expensive, but if all possible competitors are nitrogen-limited the energy cost is compensated for.) This is a cyanobacterial 'bloom' in a nutrient-enriched lake in South America. Such nutrient enrichment of a system is called *eutrophication;* it can happen naturally or, as in this case, be a consequence of human culture.

Cyanobacteria are not eaten by much (fish or anything else) because they are distasteful to toxic. Thus, with increased growth due to fertilization, and with little consumption, cyanobacteria form massive mats on the water surface.




As the cyanobacterial mats block their own sunlight, the shaded, deeper cells die and sink into the deeper waters, where they are subject to decay by bacteria. Decomposers consume oxygen in the processing of their food (just as you do), but many bacterial decomposers CAN live without oxygen (they can function *anaerobically*). Thus, the lake waters become depleted in oxygen, even to the point of complete absence (especially in the summer – figure out the reason for the seasonality). No multi-cellular organism (fish, worms, whatever) can survive complete hypoxia for long, so they die, and wash up on shore and stink. This was essentially Edmondson's hypothesis for what was going on.




Nitrogen to phosphorus ratio vs. abundance of cyanobacteria in lakes (Smith, 1983).

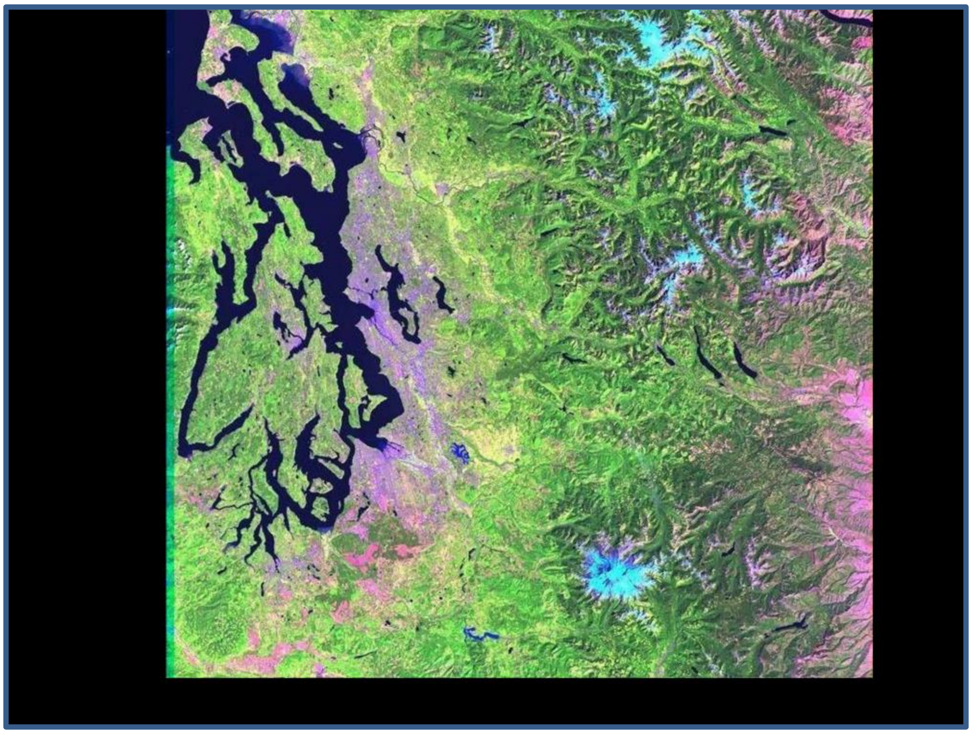
Later research compiled information on algal communities and nutrient rations for many lakes. It turns out that, when the N:P ratio drops is about 30, cyanobacteria OFTEN (but not always) are domimant; they're never domimant when nitrogen is relatively abundant. Note TWO THINGS ABOUT THIS PATTERN:

First, it's not about the ABSOLUTE AMOUNTS of N or P – only their PROPORTIONAL abundance.

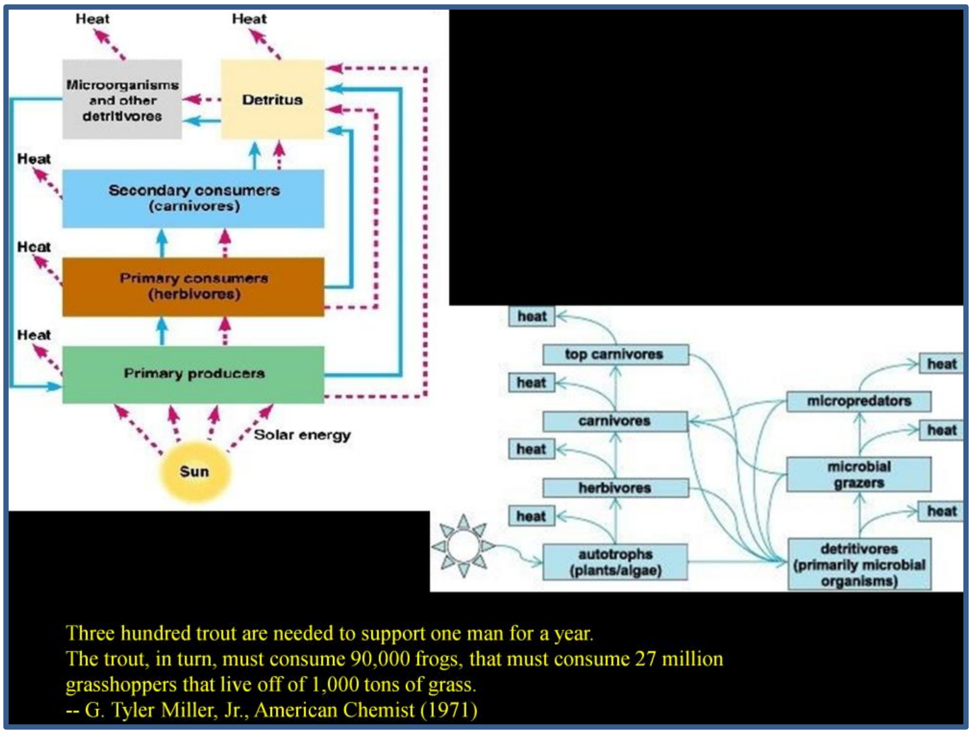
Second, this pattern – the correlation between algal community composition and N:P ratio is not strong evidence that one thing causes the other. We do not know if there is some other correlated phenomenon that causes both, or if chnages in N:P within a single lake would lead to changes in algal community; *correlative/descriptive evidence* can show patterns that suggest causal relationships, but they're not powerful tests of a hypothesis of causality.

David Schindler, a Canadian limnologist, subsequently (in the 1970s) did extensive experiments involving small, similar lakes in Ontario. Some were fertilized with N, some with P (among many other experiments. In the lower photo, the bottom lake was P-fertilized, and has become cyanobacteria dominated; the upper lake was N-fertilized and showed very little change, suggesting that N was NOT limiting.

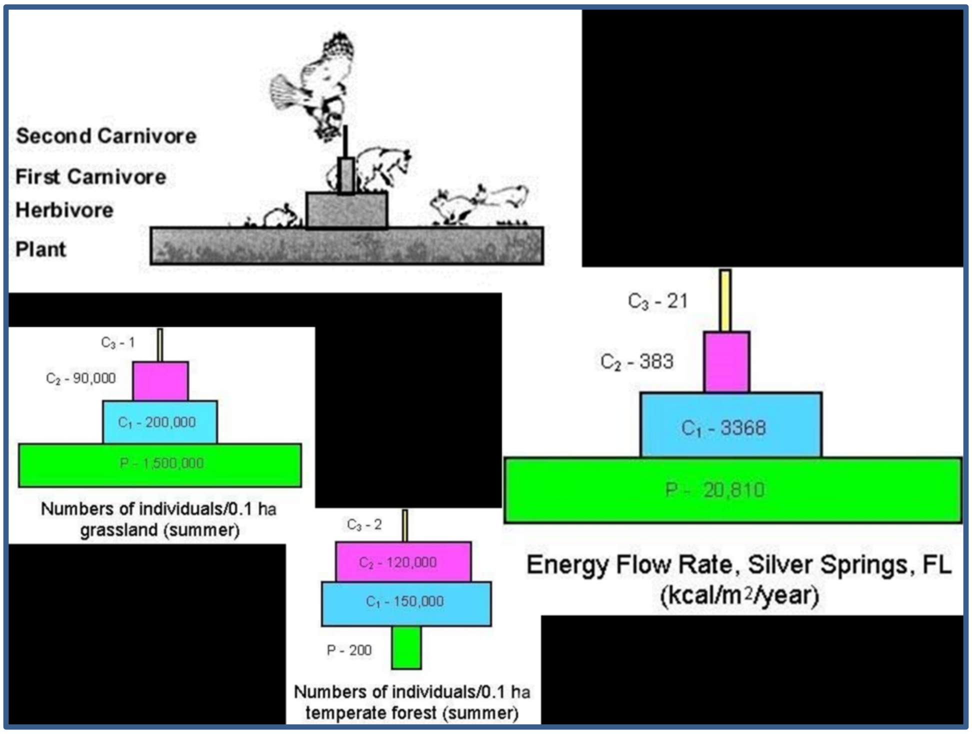
A similar experiment in a single lake basin, with a curtain separating the lake into two basins; the greenish-blue side was P-fertilized.



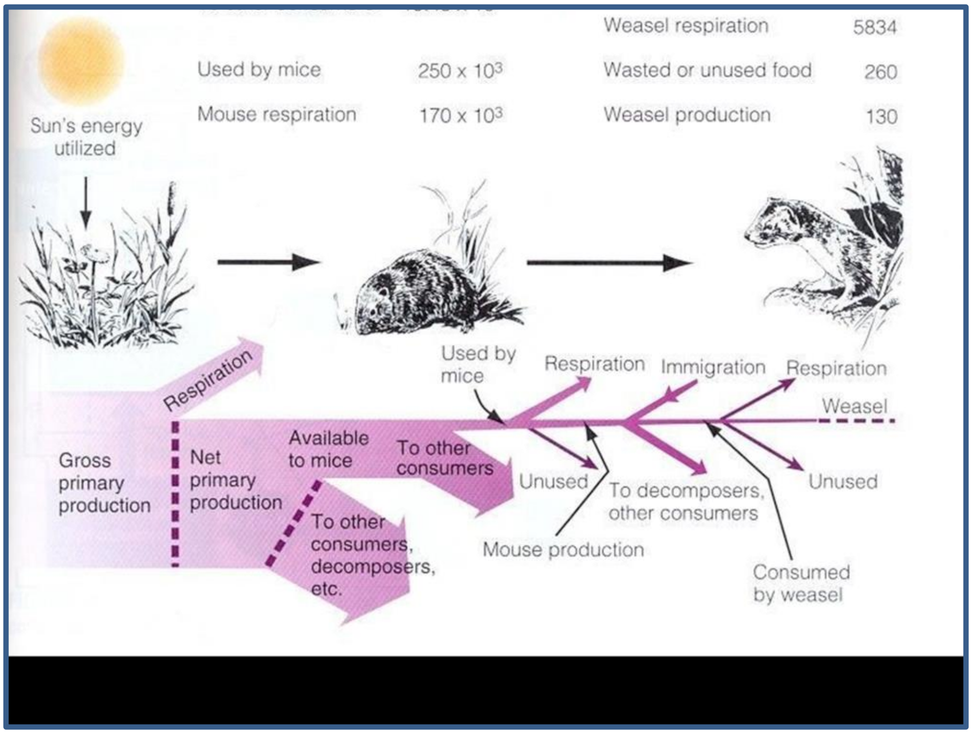
Edmondson's ultimate recommendations included more intensive treatment of sewage before putting it in the lake – but removal of P is very difficult. He also recommended diverting most of it directly to Puget Sound, which sounds irresponsible at first. BUT, remember that a) the volume of water is thousands of times greater (so inputs much more diluted) AND it's flushed by tides directly into the Pacific, and b) *marine systems are not generally phosphorus limited*, so adding a P-rich input would have comparatively modest effects. So that's what they did, and it worked pretty well. A very short version – but one of the first explicit applications of ecological principles in a public policy arena, and a good introduction to ECOSYSTEM-LEVEL THINKING.



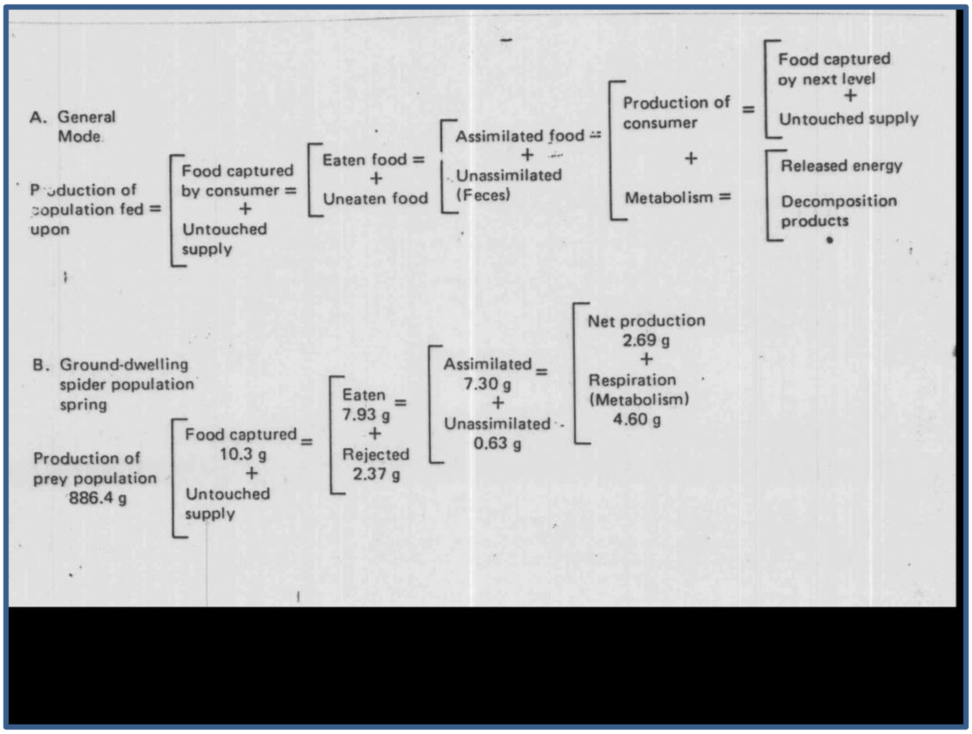

Now, look at ecosystem ecology more closely…. Ecosystem ecologists tend to focus on the way *energy* and *materials* move through ecosystems, treating the systems in quite generalized terms. We'll look first at the way energy behaves in ecosystems. The boxes and arrows here represent 'reservoirs' or places where energy resides (the boxes) and 'fluxes' or flows (the arrows). These graphics both make the point that a) all energy flowing through the system originates as sunlight (captured by photosynthetic *autotrophs* and converted to *chemical bond energy* in organic molecules like sugar). Energy then flows from box to box as organisms consume each other and convert energy from one form to another (from energy tied up in food molecules, to energy used for the consumer's metabolic needs). *But, at each transfer, some of that energy is 'lost' as heat*. It's not truly lost; the first law of thermodynamics says that 'energy is neither created nor destroyed' in such conversions – but diffuse heat is not *useful* energy; it can't be used to 'do work'. The *Second Law of Thermodynamics* states that, no energy conversion can be 100% efficient; some energy will be converted to diffused heat and become 'unuseful'. In other terms; 'organization' of the energy always *decreases* or *ENTROPY*always increases. THUS, energy is continually lost from the ecosystem, and must continually be replaced by newly captured energy if the system is not to run down and die. LIFE IS AN INTERMEDIATE SYSTEM; it can only exist if there's energy input from a concentrated (organized) energy source (here, the sun) because dispersed energy is always, necessarily, being lost.



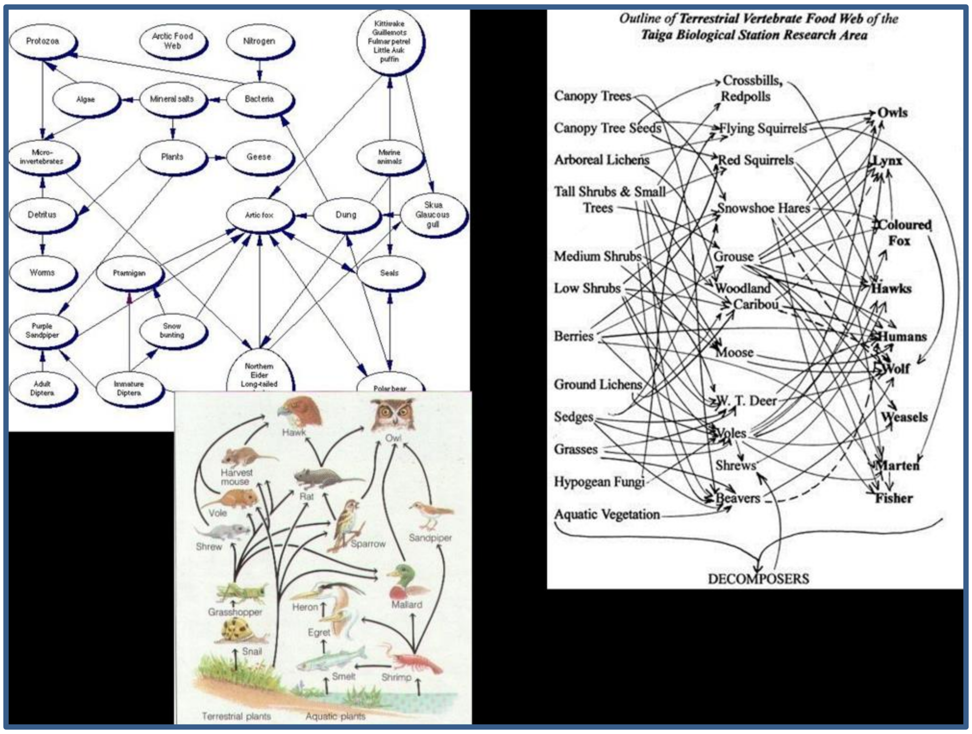

This, then, limits the number of *trophic levels* that can be supported; after three to five levels, usually, so little of the originally captured energy (primary production) remains that a viable population of higher-level consumers simply can't persist. Trophic pyramids are always very broad-based and rapidly tapering… (note that ENERGY pyramids, however, aren't the same as numbers pyramids, or even biomass pyramids)



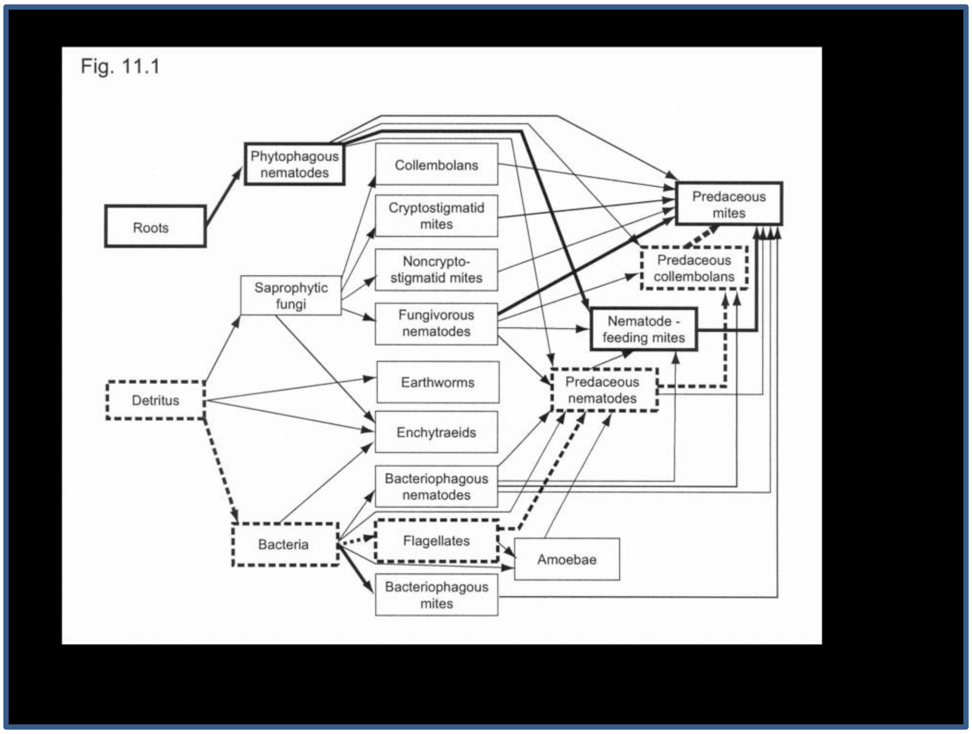

Thus, one view of ecosystems – the energetic view – sees a strictly directional flow; from sun, to photosynthetic organisms (*primary producers*), to consumers of plants (herbivores), to consumers of consumers, to decay organisms, and so on. BUT, AT EACH TRANSFER, some of the available energy is lost as respiratory heat and through inefficiencies of energy transfer. You've heard this structure referred to as a 'food chain', or perhaps a food pyramid; it's more strictly referred to as the *trophic (energetic) structure* of the ecosystem.



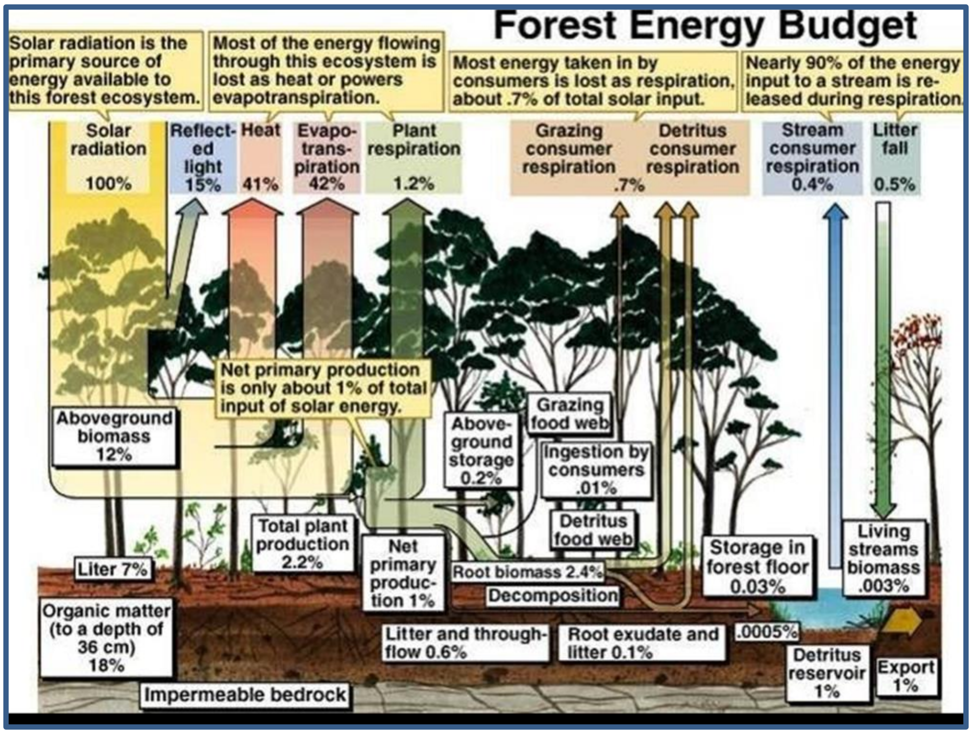

The transfer of energy from one trophic level to the next involves multiple steps. None CAN be 100% efficient. The proportion of energy available at one trophic level that's actually usefully captured by the next level is the *product* of all these efficiencies. Multiplying fractions by fractions makes smaller fractions, so the final *trophic efficiency* – the percentage of energy actually usefully transferred from one trophic level to the next is typically *very low*; often on the order of 1-5% and almost never more than 10%.. In other words, the amount of energy incorporated into biomass of a higher trophic level (say carnivores), is typically 1-10% of the amount of energy available in the biomass of the next-lower trophic level that they consume (e.g., herbivores or primary consumers).



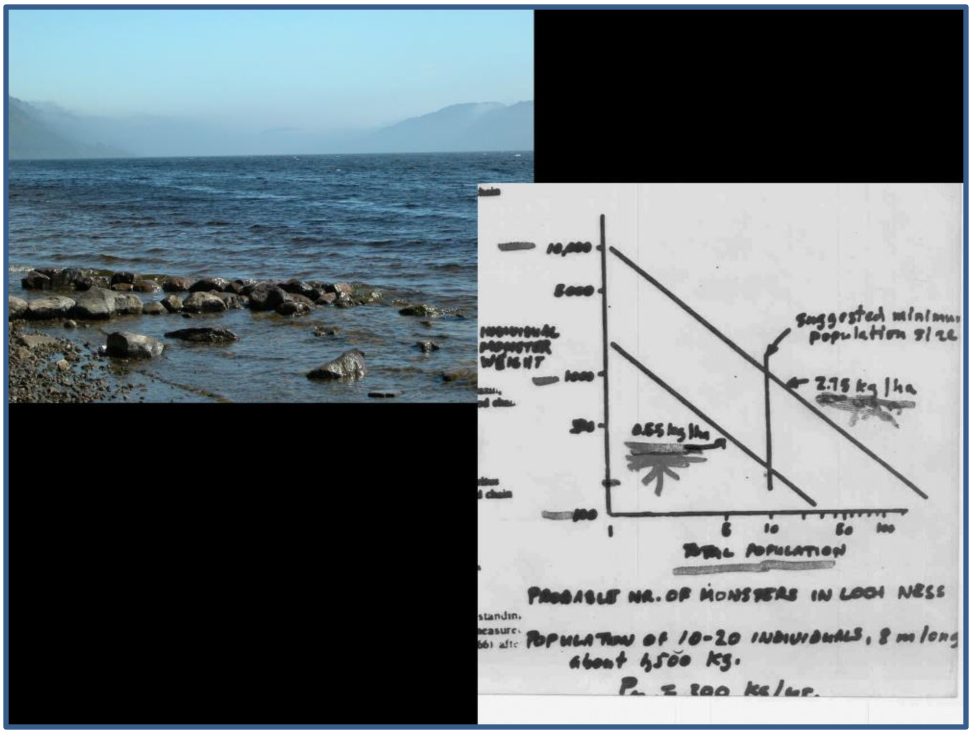
Or, when mapped in more detail, as a ‘food-web’ (a much better metaphor than a chain). It’s still a trophic structure. But such detailed mapping is extremely difficult and rare; usually we look at ecosystems more in terms of the generalized ‘boxes’ we call ‘trophic levels’ – primary producers, consumers, predators, top predators, decomposers…



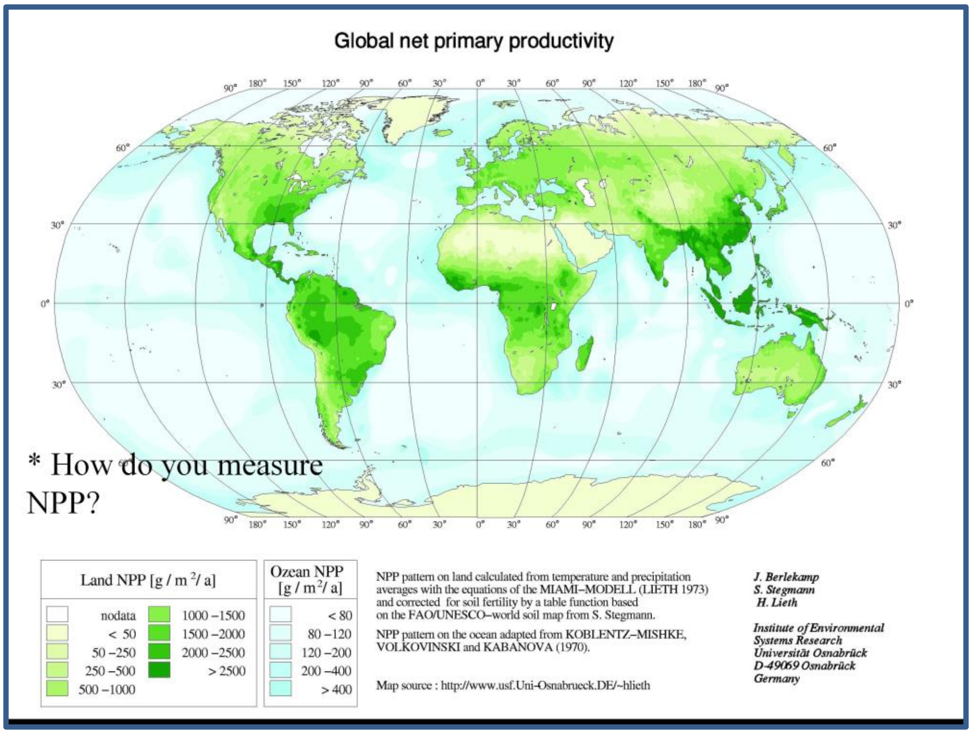

A more conceptual diagram of a food-web or trophic structure; it does not show the loss of diffuse heat energy at each step, but it's there.




Trophic/energy budgets can be developed at higher resolutions; the ‘big box’ of the ecosystem can be broken down into smaller boxes (trophic levels) with exchanges between them, and even smaller boxes as here. It’s a lot of work, but reveals very important aspects of ecosystem function.




Aquatic systems often have more trophic levels than terrestrial ones, suggesting that trophic efficiencies might be higher in aquatic systems. Why might that be. Even so, it appears that the Loch Ness monster is, at best, only marginally plausible from an energetics viewpoint; the trophic structure of the lake is such that a viable number of monsters could be supported only if they were pretty small monsters…




The most important part of all of this is *NET PRIMARY PRODUCTION (or NPP)*; the rate (*production* is, remember, a *rate* – an amount of biomass produced or energy captured *per unit time*) at which solar energy is converted into new biomass of primary producer (plants, algae). *Gross primary production* is the total amount of photosynthesis that happens – the total amount of light energy 'captured' -- but plants use some of this captured energy to run their own metabolism, or for *respiration*. Thus, NPP = GPP – R. (This is quite closely parallel to economic models: net income, or profit, is equal to gross income minus expenditures). NPP may be allocated to growth OR reproduction – new biomass of any type. Note that, even though NPP is really a measure of energy flow, it is given here as mass per area per year. Since biologically useful energy is in the bonds between carbon atoms in organic molecules (like glucose), and most organic matter is built around a carbon-chain skeleton, it's reasonable to measure *energetics* in terms of the amount of biomass built or consumed. So NPP is typically given in biomass accumulated per area per year (it's a RATE), or sometimes simply in units of carbon ( C) per area per time. If NPP is greater than the rate of herbivore consumption (or other processes destroying plant biomass), then biomass accumulates; think of biomass as an energy reserve in this context. HOW IS NPP MEASURED?

You could simply monitor, over the long-term, how the amount of biomass present changes, but this doesn't get at the underlying processes. As with any chemical (or other) reaction, you can measure *rates* if you can measure *changes in amounts* of the reactants or the products. Thus the NET rate of photosynthetic creation of biomass (NPP) is generally measured by measuring the change in carbon dioxide concentration in the air in the presence of a photosynthesizing surface (leaf, whole plant…)

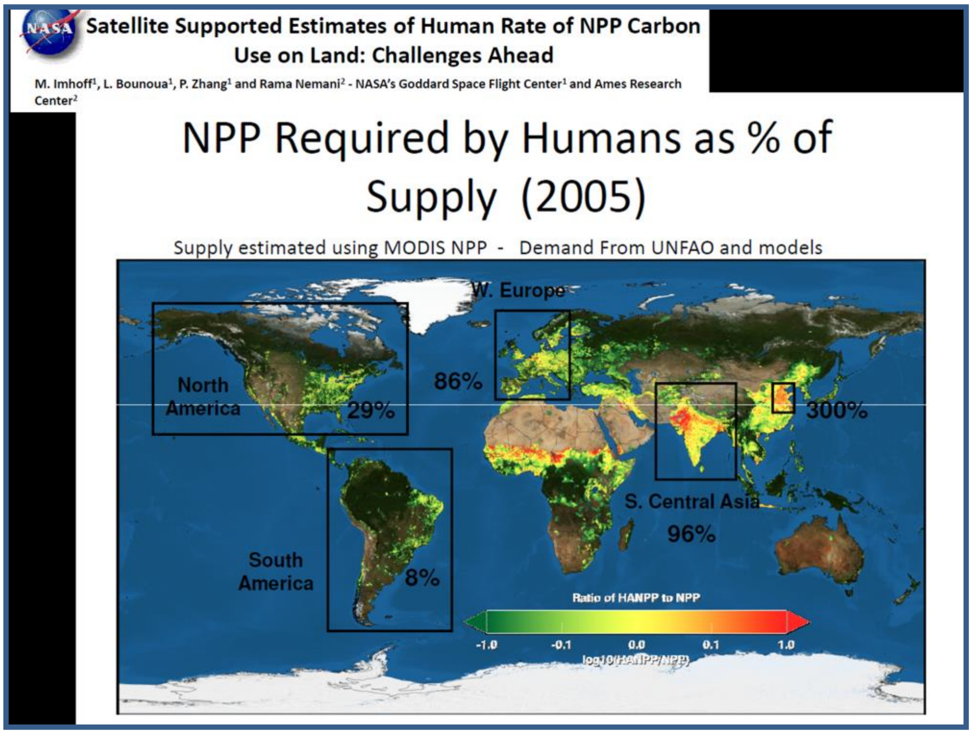
This can also be done at whole-ecosystem scales; how does carbon dioxide concentration change as air passes over and through a forest?

Lots of instruments measuring gases and other things in a vertical transect through a forest canopy.

Pipes and wires lead from the instruments on the tower

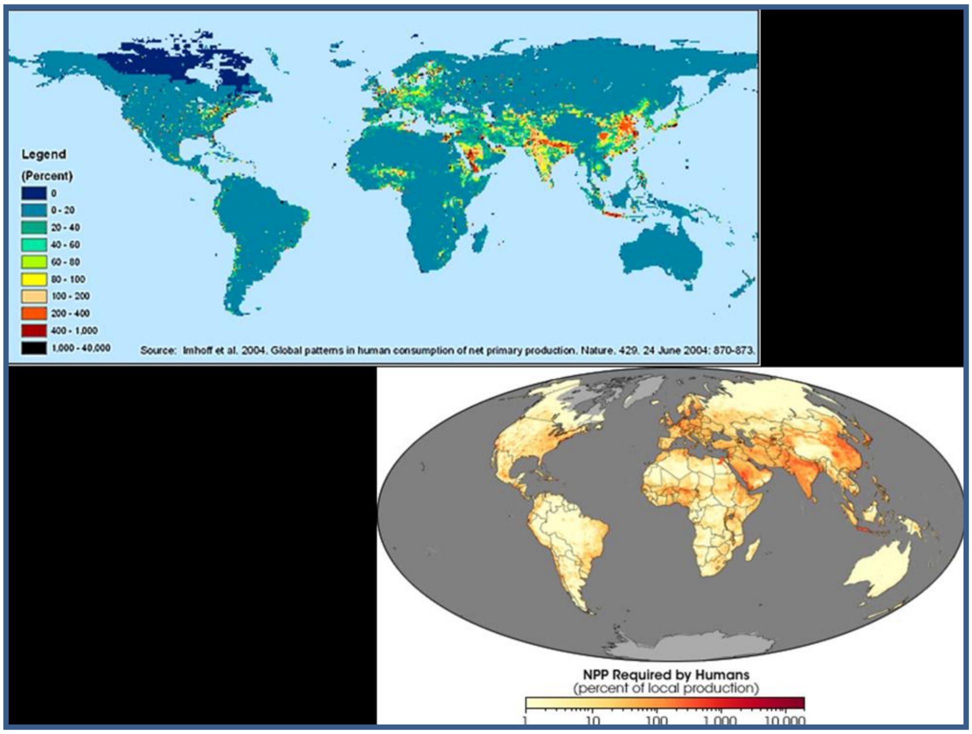
Into the lab at its base

Measurements of biomass lost (in the form of ‘litter’ – fallen leaves, twigs, buds, etc.) are important in understanding the flows of energy/biomass… This is a ‘litter trap’.




Ecosystem net primary productivity is, ultimately, the basis for all life on the planet, including humans. All human food is derived from current NPP, directly or indirectly (through animal products); we also depend on ecosystem production for building materials (wood, bamboo), many of our fabrics (cotton, linen, etc.), fuel (wood, manure) and a variety of other things. (‘Fossil fuels’ supplement current ecosystem production in providing fuels, fertilizers, etc. – but these may be regarded as stored NPP from the geological past).

Over the last 10-15 years, several efforts have been made to estimate how much of TOTAL, global NPP is claimed by all of these human uses; this is sometimes referred to as Human Appropriation of Net Primary Production, or HANPP. While estimates vary quite a bit depending on assumptions and approaches, it appears that HANPP is somewhere in the ballpark of 30% of *all terrestrial NPP*. Think about what this means for human carrying capacity (with human population still growing from current 7 billion to around 10 billion); of course ALL OTHER organisms on the planet must make do with what’s left over after human appropriation. ALSO consider what would be required without fossil fuel subsidies; it has been estimated that replacing all fossil fuel uses with current NPP (e.g., for fuel, fertilizer, etc.) would push HANPP well over the 100% mark.



Legend
(Percent)
0
0 - 20
20 - 40
40 - 60
60 - 80
80 - 100
100 - 200
200 - 400
400 - 1,000
1,000 - 40,000
Source: Imhoff et al. 2004. Global patterns in human consumption of net primary production. Nature. 429. 24 June 2004: 870-873.
NPP Required by Humans
(percent of local production)
1
10
100
1,000
10,000

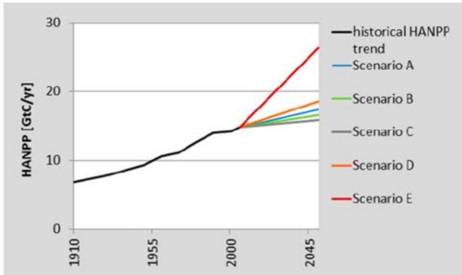



**Fig. 4.** Scenarios for the development on HANPP until 2050. Whereas scenarios A–C assume a continuation of past trends, scenarios D and E add additional primary biomass harvest to scenario B (see text and *SI Appendix* for details). Based on upper and lower boundary values for deployment levels of biomass for energy, we assumed an additional harvest for energy production of 50 EJ/y (scenario D) and 250 EJ/y (scenario E) over the present value. Continuation of past trends would result in moderate growth of HANPP until 2050. Increasing the production of bioenergy, however, could dramatically increase global HANPP (scenario E).

[redacted]

[redacted]

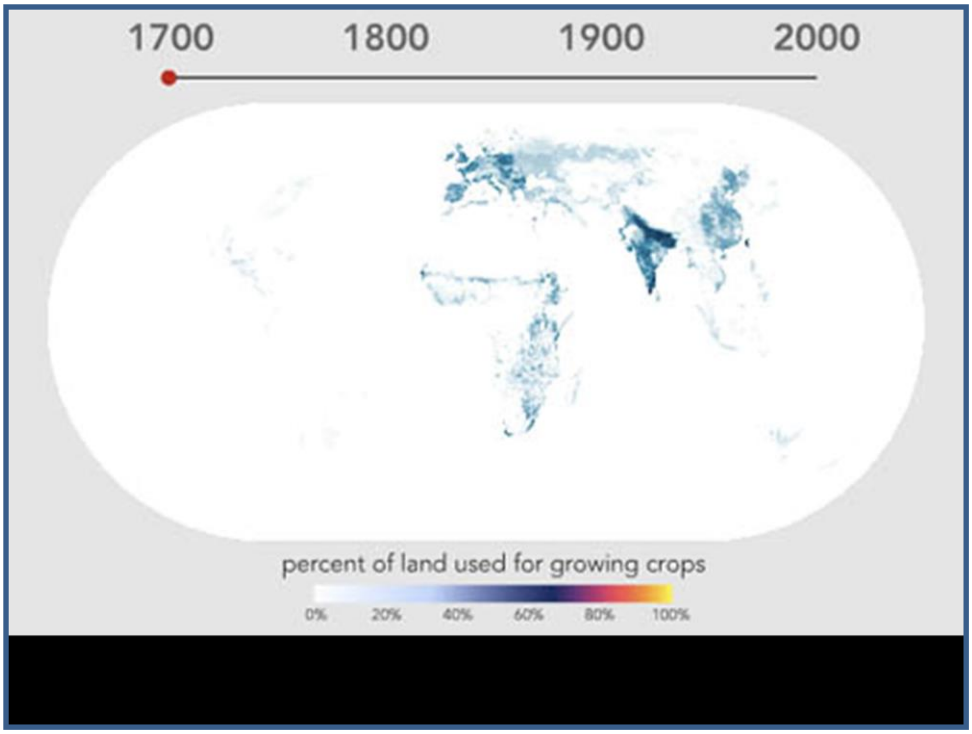
Table 1. Overview of estimates of global HANPP given by different authors.

| Study | Reference time | HANPP absolute* [Pg C/yr] | HANPP relative* [%]** |
|---|---|---|---|
| Whittaker and Lieth (1973) | 1950s | 1.6 | 3% |
| Vitousek et al. (1986) low | 1970s | 2.6 | 3% |
| Vitousek et al. (1986) intermediate | 1970s | 20.3 | 27% |
| Vitousek et al. (1986) high | 1970s | 29.5 | 39% |
| Wright (1990) | 1970s-1980s | 17.7 | 24% |
| Rojstaczer et al. (2001) | 1980s-1990s | 19.5±14 | 32% (10-55%) |
| Imhoff et al. (2004) | 1995 | 11.5 (8.0-14.8) | 20% (14-26%) |
| Haberl et al. (2007) | 2000 | 15.6 | 24% |

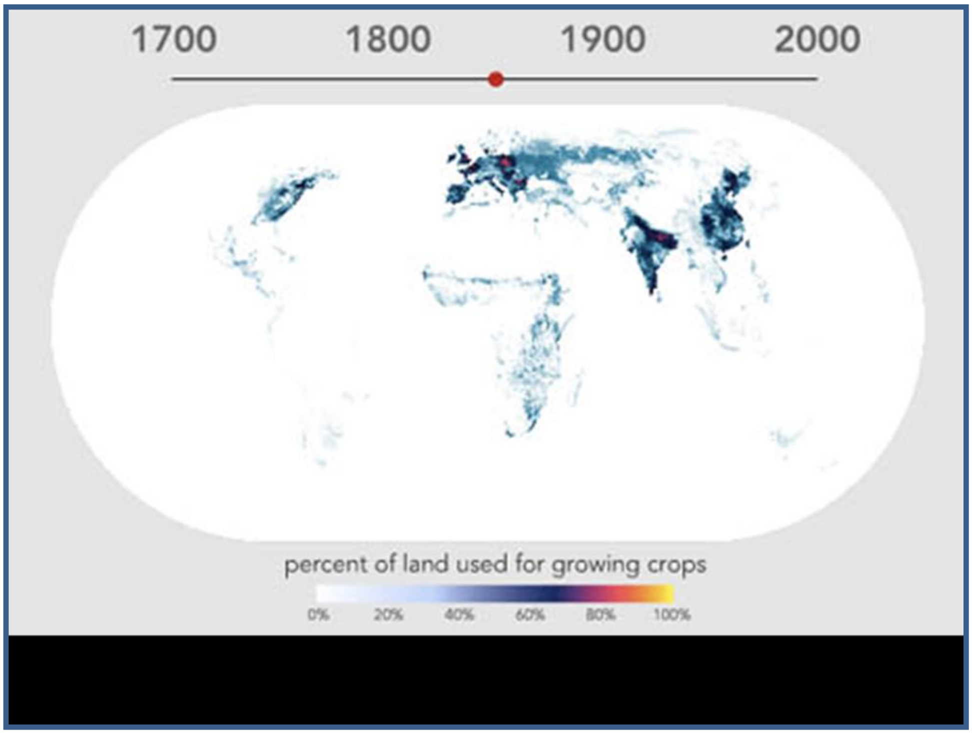
* Note the differences in definitions used in each study discussed in the text.

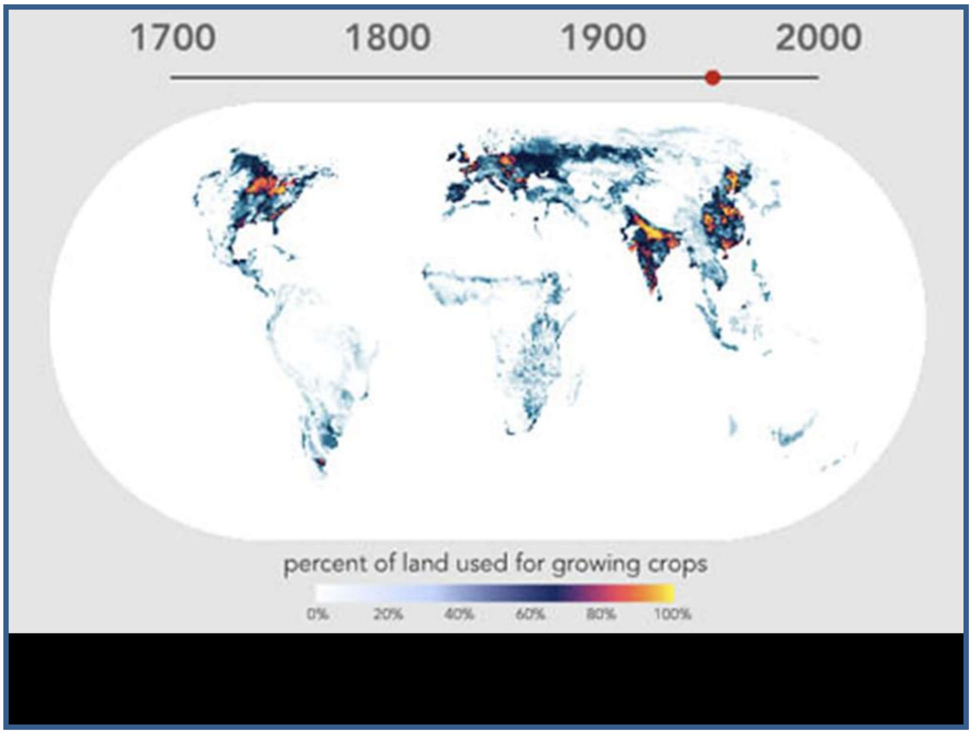
** Per cent of actual or potential NPP. Note that estimates of $NPP_{act}$ and $NPP_0$ also vary considerably; for example Whittaker and Lieth's value of $NPP_{act}$ (54 Pg C/yr) was much lower than Vitousek et al's estimate (75 Pg C/yr). The current "best guess" of $NPP_0$ is 66 Pg C/yr and that of $NPP_{act}$ 59 Pg C/yr (Haberl et al. 2007).

The right-hand table gives several estimates of HANPP, both in absolute amounts (a Pg is a quadrillion grams – about a billion tons) and proportion of total NPP.  The range of estimates is large, but most relatively recent ones put the total in the range of ¼ to 1/3 of global totals.  The graph shows projected increases in HANPP under vbarious scenarios.




This series of figures shows increase in agricultural ‘intensity’ – the proportion of land, by region, used for crops. The situation in 1700 certainly reflects a large *decrease* in the Americas because of massive mortality (perhaps > 90%) of American Indian populations due to disease introduced from Eurasia and Africa. Most of those populations were agricultural.


1700
1800
1900
2000
percent of land used for growing crops
0%
20%
40%
60%
80%
100%


1700
1800
1900
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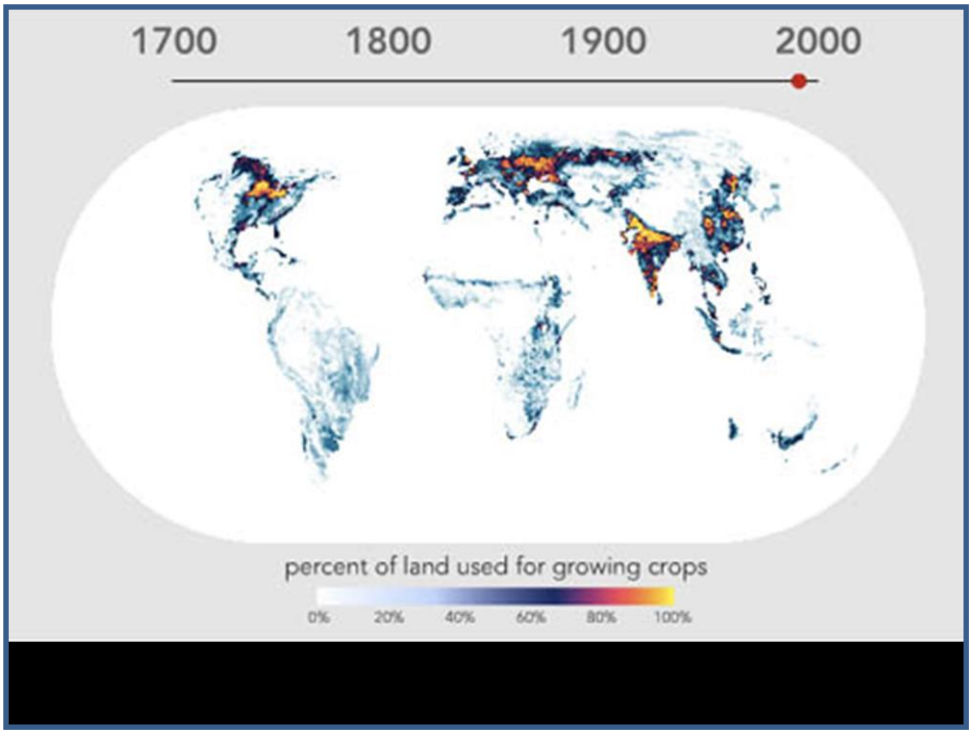
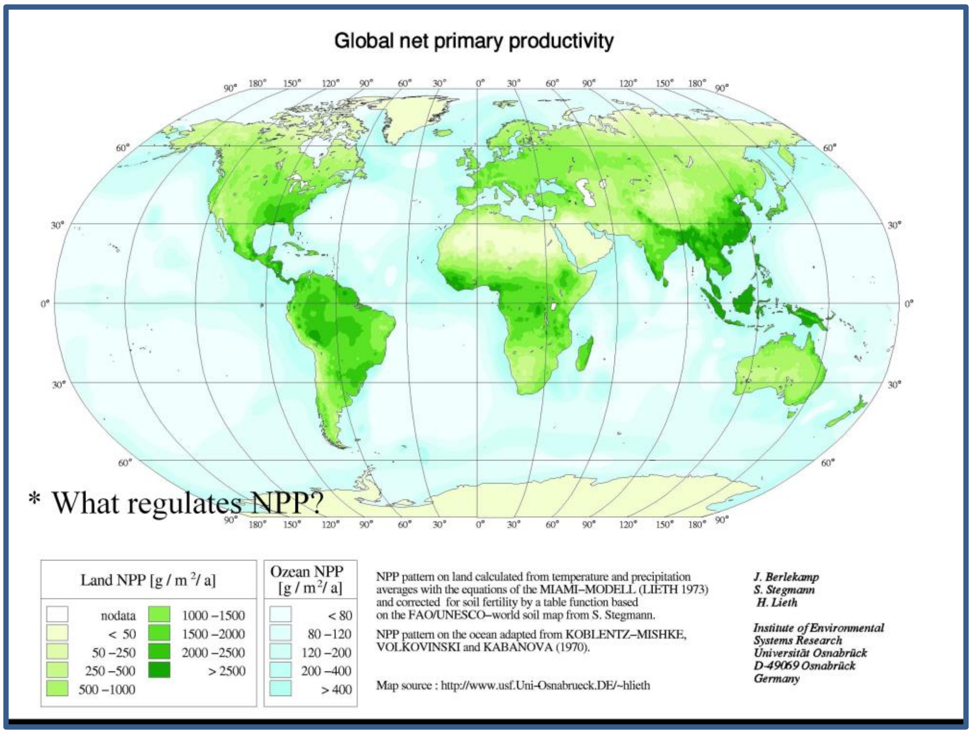
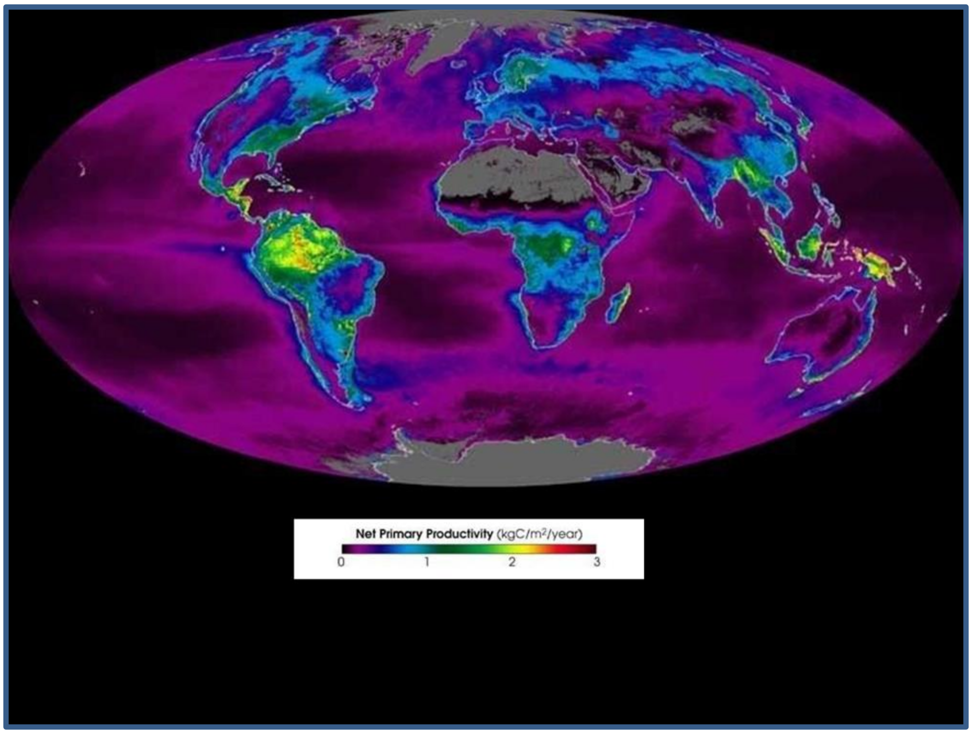
percent of land used for growing crops
0%
20%
40%
60%
80%
100%



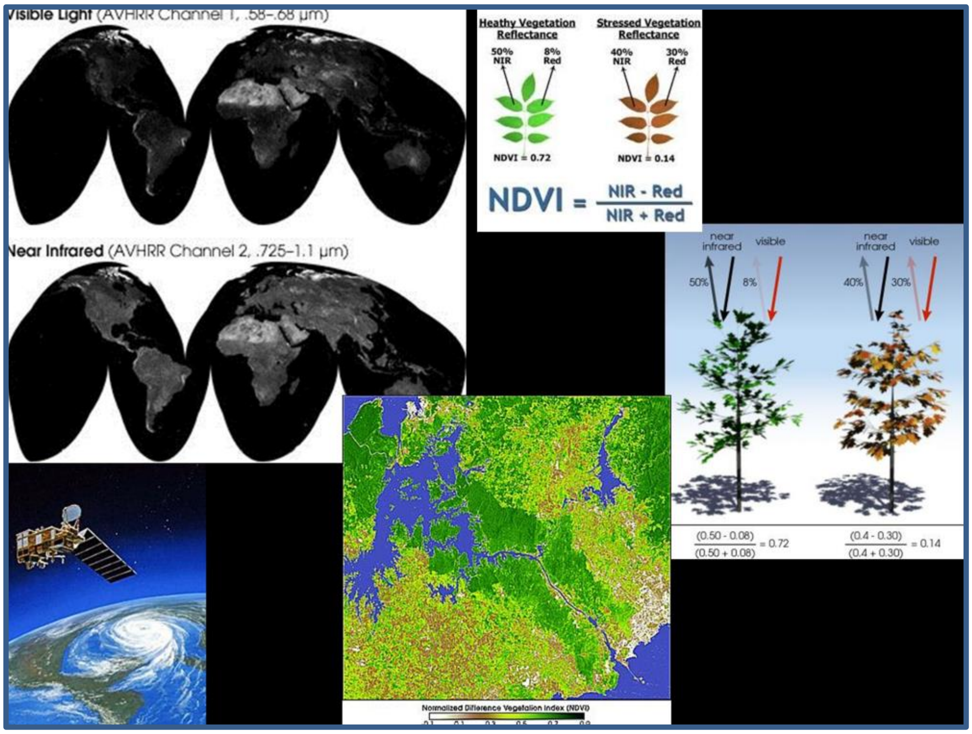

By 2000, large portions of the most fertile areas of the world and of the most densely populated areas have approached 100% conversion to agriculture – for those regions, HANPP also approaches 100%



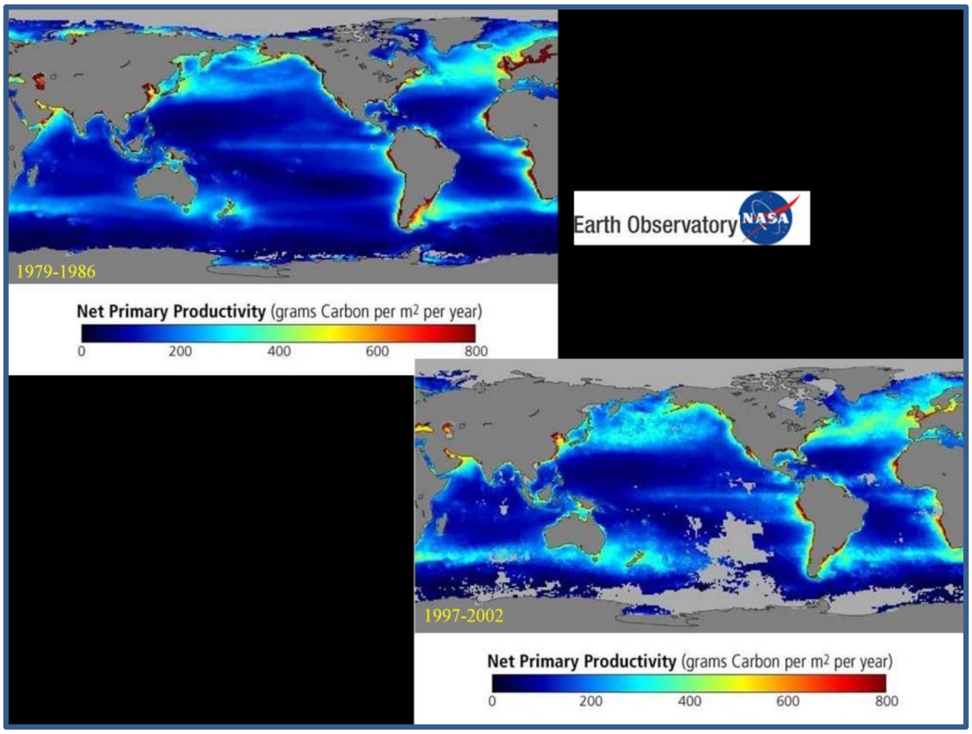

So, what ultimately REGULATES the amount of NPP? It varies hugely over the planet's surface (the estimates shown here are actually quite crude, but they're about the best we have; we don't really have a very precise understanding of amounts of NPP or biomass globally). Clearly, regulation of of NPP is not just about the availability of light energy for photosynthesis; light energy input per square m declines gradually as you move away from the equator, but not so much as to cause the declines in NPP shown here – and all the other variations must be driven by something else. But NPP requires an 'infrastructure'; the organism has to maintain a physical machine to process energy. This takes us back to the notion of limiting resources; if NPP is not limited by the availability of light only (if it were, what would the pattern look like here?), it MUST be limited by other resources involved in maintaining that machine – OR by environmental factors that simply make it impossible for primary producers (plants) to function (for example, ice-caps). Patterns here might suggest some hypotheses as to what factors/resources are *limiting* to net primary productivity (sometimes simply referred to as 'ecosystem function'). Note particularly that ocean NPP is typically MUCH lower than terrestrial. Why? Candidates for limiting resources might include water, carbon dioxide (the basic inputs to photosynthesis), but also a long list of chemical nutrients/elements. Start with the 'BIG SIX' elements that ALL organisms require in some amount: C, H, O, N, P, S.



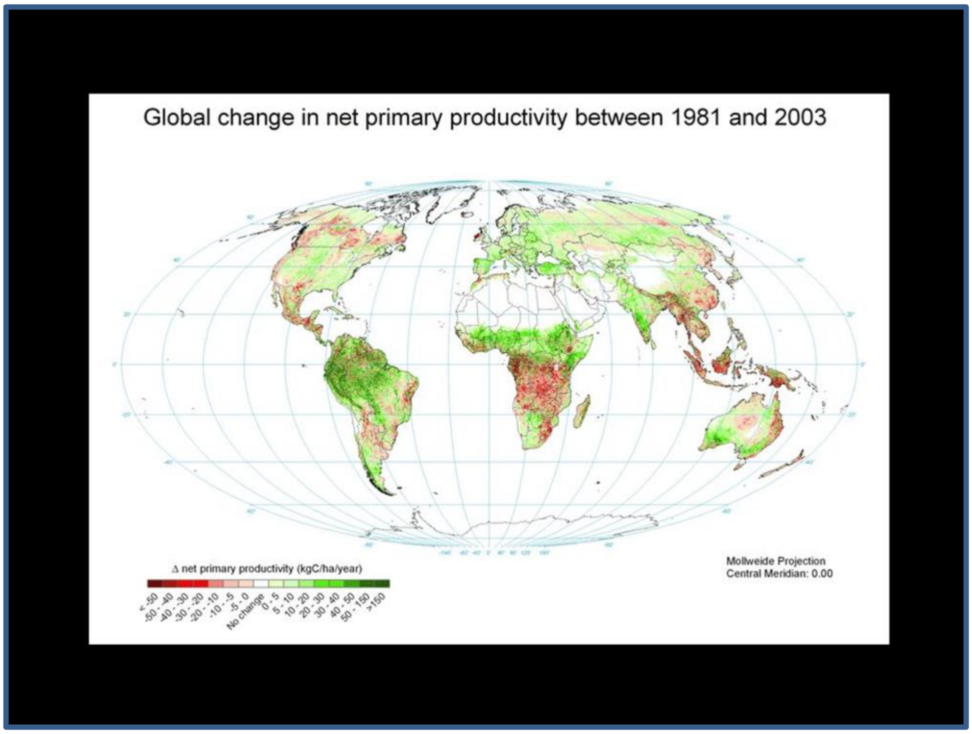

This map more clearly illustrates the extremely low NPP of the oceans compared to most terrestrial systems. This confirms that something besides water and energy can limit productivity, since neither of these should be more limiting in oceans than on land. But how are estimates like this derived?



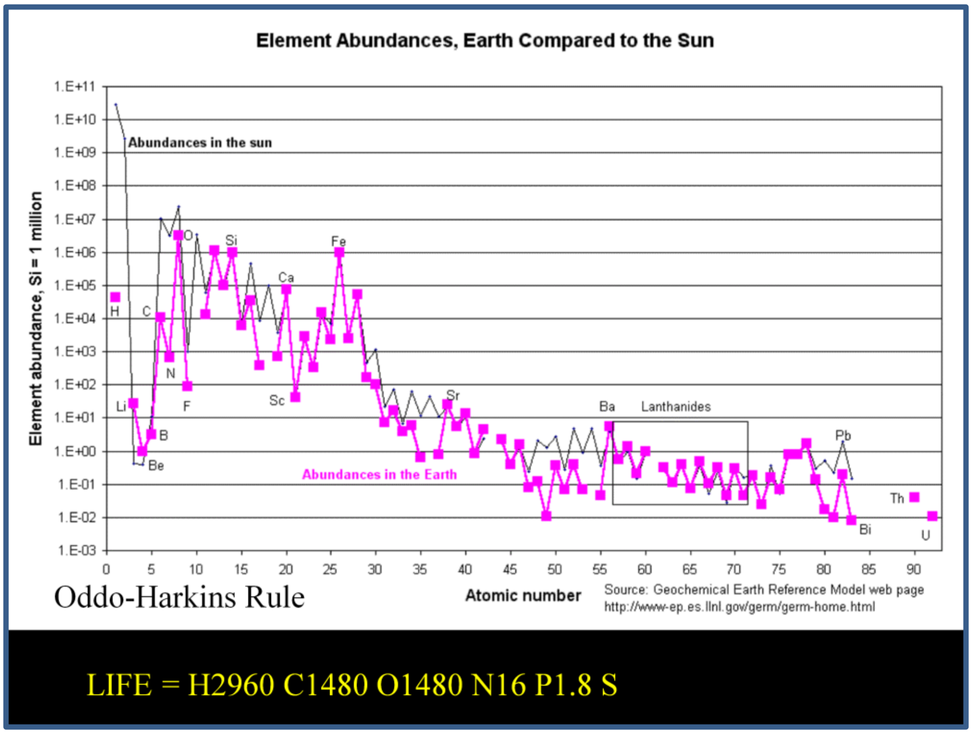

Modern estimates of global NPP (and of geographical patterns of NPP) typically rely heavily on satellite remote sensing. Estimates are based on optical properties of foliage and of chlorophyll. Chlorophyll is strongly absorptive in RED wavelengths (these are the wavelengths that drive photosynthesis), and leaves are strongly reflective in NEAR INFRARED wavelengths (this is partly about reducing heat loads). Thus, ratios involving measurements of reflected light in these wavelengths can tell a lot about the amount of chlorophyll in an area on the ground, and this, in turn, is indicative of photosynthetic rates (which is really more closely related to GPP than NPP…)



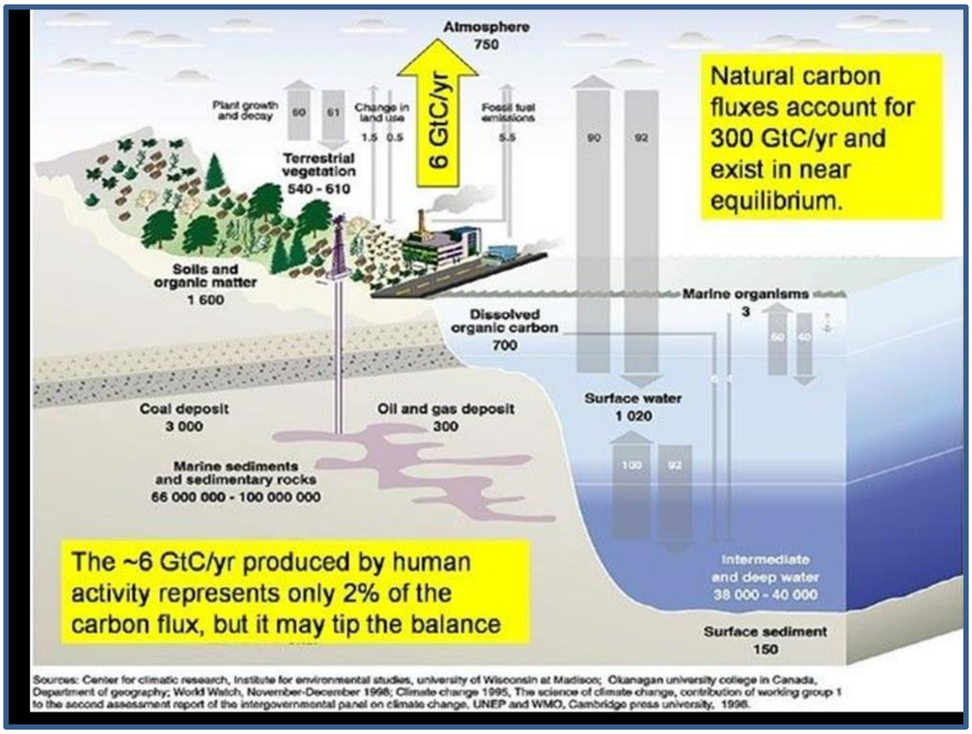

An easier-to-see map of ocean NPP. Aquatic NPP (almost entirely by planktonic algae) can be measured much more accurately than terrestrial using satellite-based sensors…



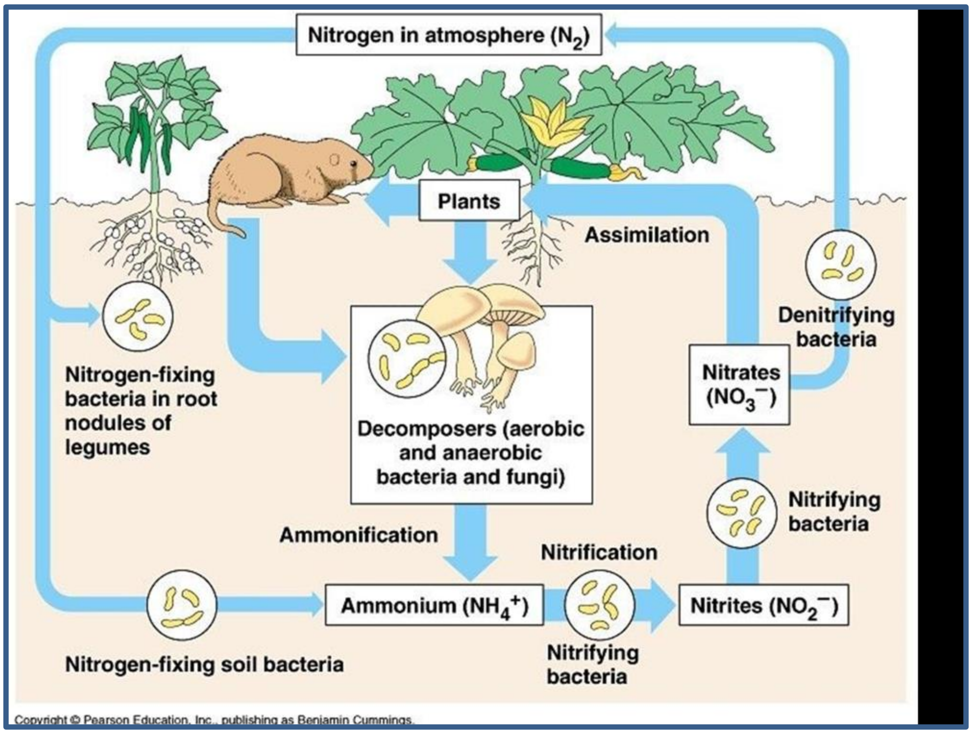

Satellite data suggest that there have been complex changes in NPP across the world. Some of this is related to climate.



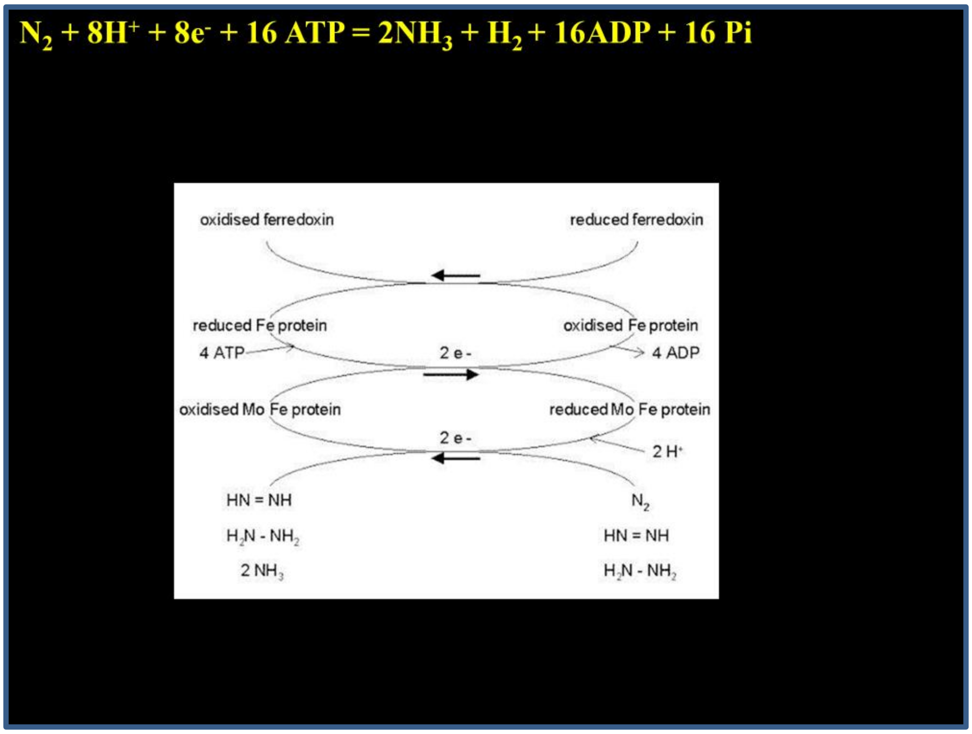

It is in consideration of what resources limit NPP that we find the point of connection between the ‘energetics’ view of ecosystems, and the ‘mineral cycling’ view. Over 20 elements are required by some organisms, but six – the ‘big six’ – are required by ALL organisms, and generally in larger quantities than ‘micronutrients’. These are H, C, O, N, P, and S. Think about why each of these is important… The Oddo-Harkins rule describes the odd fact that odd-numbered elements are much rare than adjacent even-numbered elements. Who knows why – but the consequence is that some elements might be more likely to become limiting than others. N is odd-numbered. (Note that this would appear to argue against thoughtful design of life; a good designer would have build life to use resources proportional to availability?)



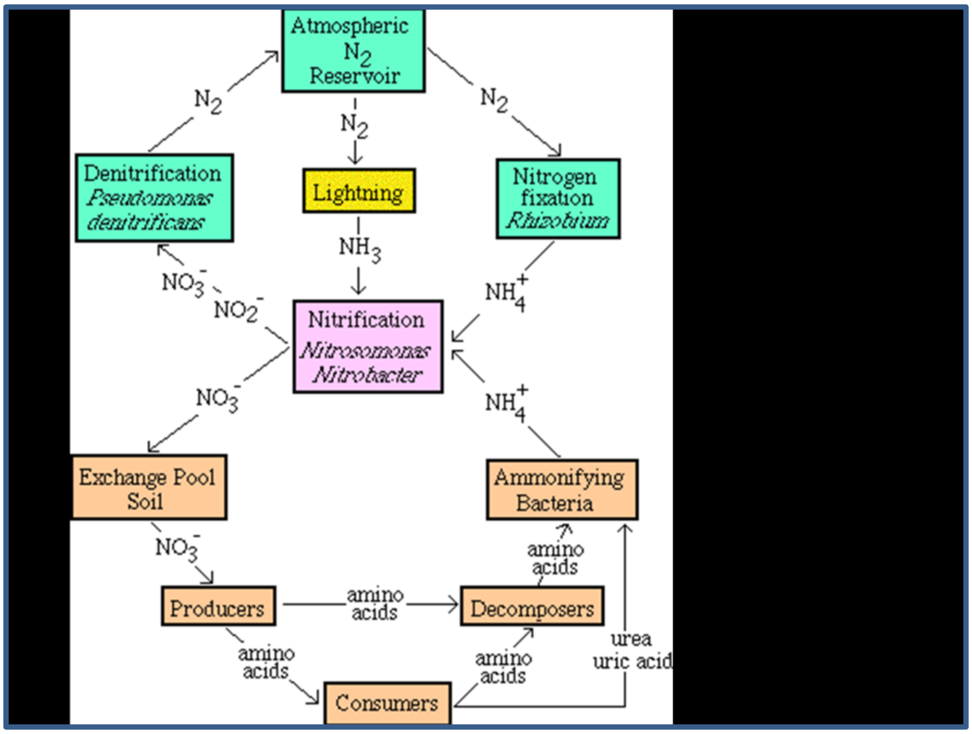

Mineral (or nutrient) movements can be represented in much the same way as energy flow – with arrow (fluxes) and boxes (reservoirs). The BIG difference is that the system is CLOSED materially while it is energetically OPEN. Materials don't leave the planet but travel in closed circuits (even though parts of those circuits may be VERY slow). This is a cartoon-diagram of the CARBON cycle. The arrows leaving the atmosphere are almost entirely through photosynthesis (connecting this material cycle to the energy dynamics of the global ecosystem). Arrows returning to the atmosphere are mostly respiration, but there are some geological ones (including fossil fuel burning). Most of the planet's C is (now) in geological formations, although it was once in the atmosphere. This kind of visualization should suggest that the processes involved in fluxes will shape availability in reservoirs – and, ultimately, what resources are likely to be limiting. Changes in key fluxes, even if they're not that large, can have huge effects as they propagate through the system. *FLUXES are what ultimately shape availability of a nutrient in any particular place.* NOTE THAT CARBON MOVES FREELY THROUGH THE ATMOSPHERE in the form of carbon dioxide, so it does not seem likely that it would generally limit plant net production very often or for long (However, it can be depleted in the short term; a rapidly photosynthesizing cornfield, on a still day, can draw CO2 levels down to the point where photosynthesis stops for a while).



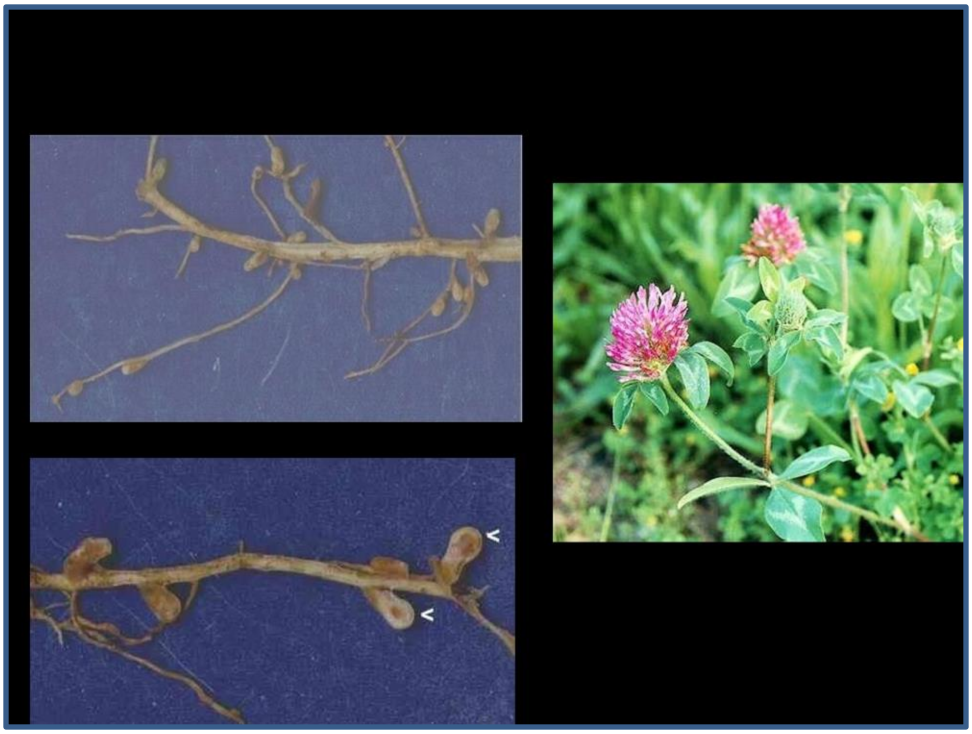

Here's a similar diagram of the NITROGEN (N) cycle. It's much more complicated – but extremely important. MOST of the world's N is in the atmosphere. 'Fixation' – conversion of nitrogen from N2 to other chemical forms – is done almost entirely by bacteria (some high-energy non-biological processes can do it, too). Other bacteria drive conversions among the various chemical forms of N. PLANTS – the dominant primary producers – must acquire N as nitrates (although ammonium is quickly converted to nitrates by bacteria). Thus, even though N travels freely through the atmosphere as gaseous nitrogen, it's availability to plants might be limited by the rate of nitrogen fixation. In fact, it is frequently the resource most immediately limiting NPP. N-fixation is costly in terms of energy. Some plants have symbiotic relationships with N-fixing bacteria; these relationships are costly to the plants, who provide photosynthate (sugar) to the bacteria to power N-fixation; if N were not a limiting resource, this investment by the plant would be quite a disadvantage (the same resources might be used to grow larger and compete more successfully for light).



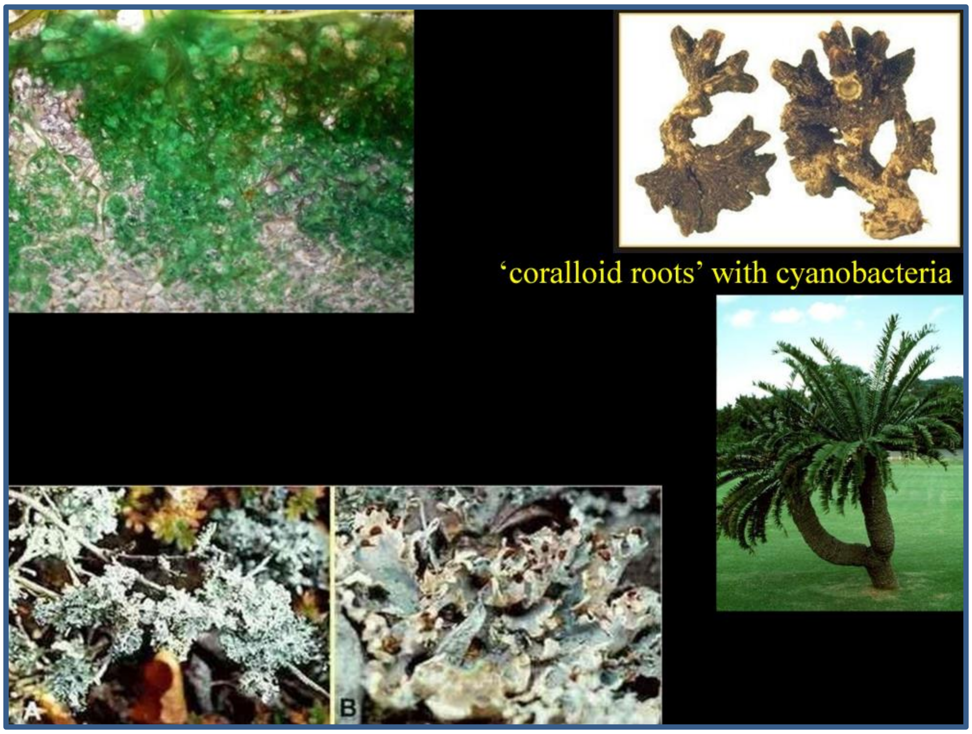

Energy costs of N-fixation – 16 ATP molecules for 2 molecules of ammonia produced.




Lots of bacterial groups regulate critical steps in the N-cycle.



Nodules on the roots of leguminous plants (a family of plants) house one type of N-fixing bacteria; that's why legumes have relatively high protein concentrations compared to other plants (protein has high concentrations of N). But remember that this costs the plants something – so when is it 'worthwhile' to the plant? Under some circumstances, plants appear to 'break' the partnership and reject the bacteria. Why?




Some other N-fixing symbioses – lichens, cycads, etc.

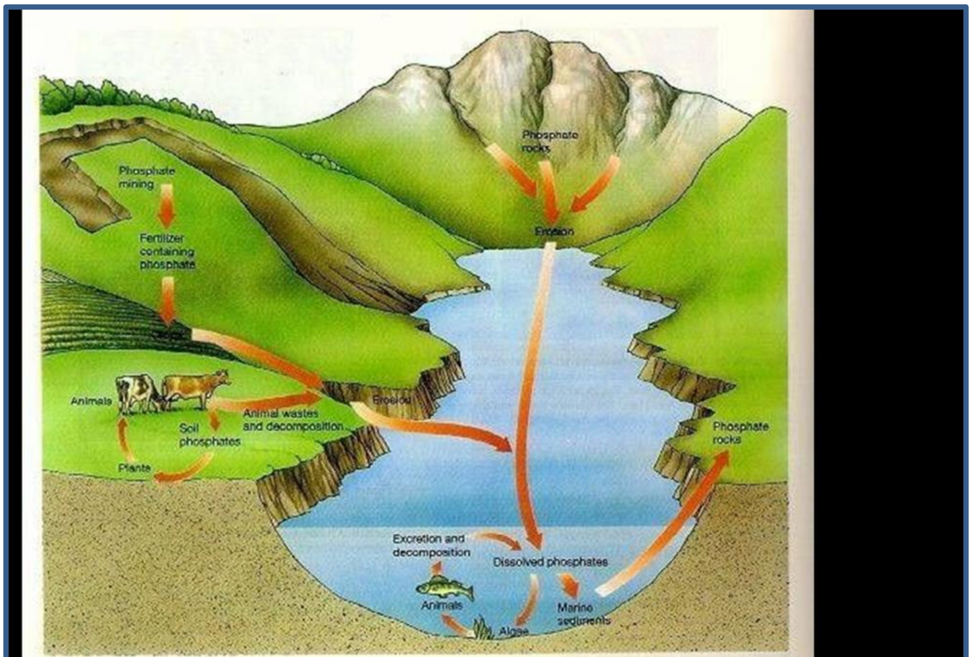
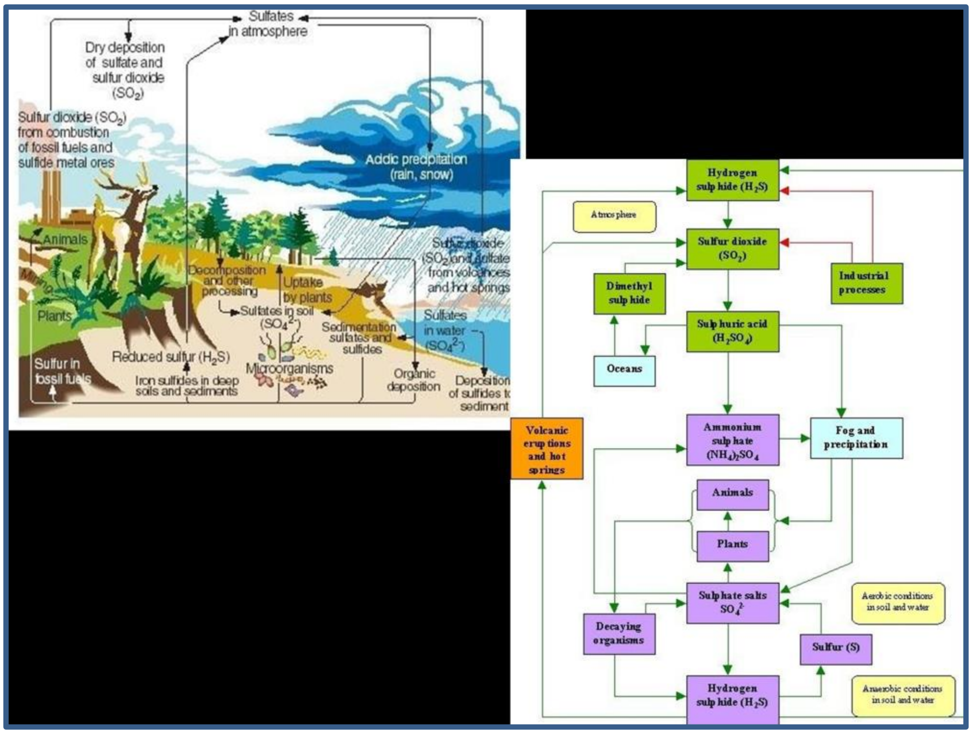
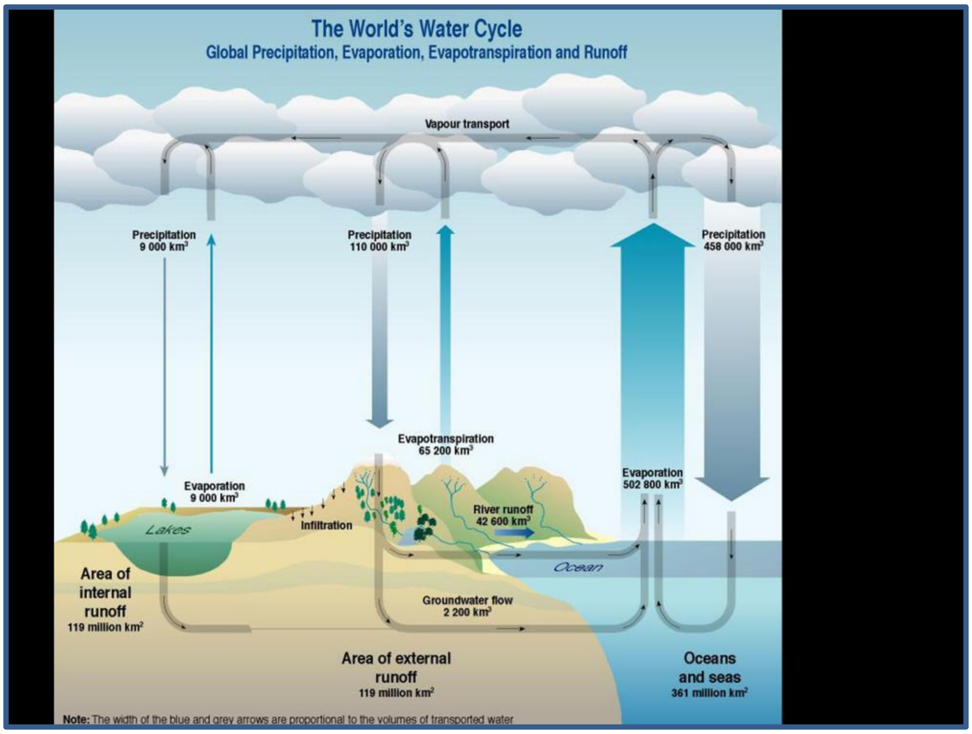



**Figure 54–5** The phosphorus cycle in terrestrial and aquatic environments. Recycling of phosphorus (as phosphate, $PO_4^{3-}$) is slow because no biologically important form of phosphorus is gaseous. Phosphate that becomes part of marine sediments may take millions of years to solidify into rock, uplift as mountains, and erode again to become available to living things.

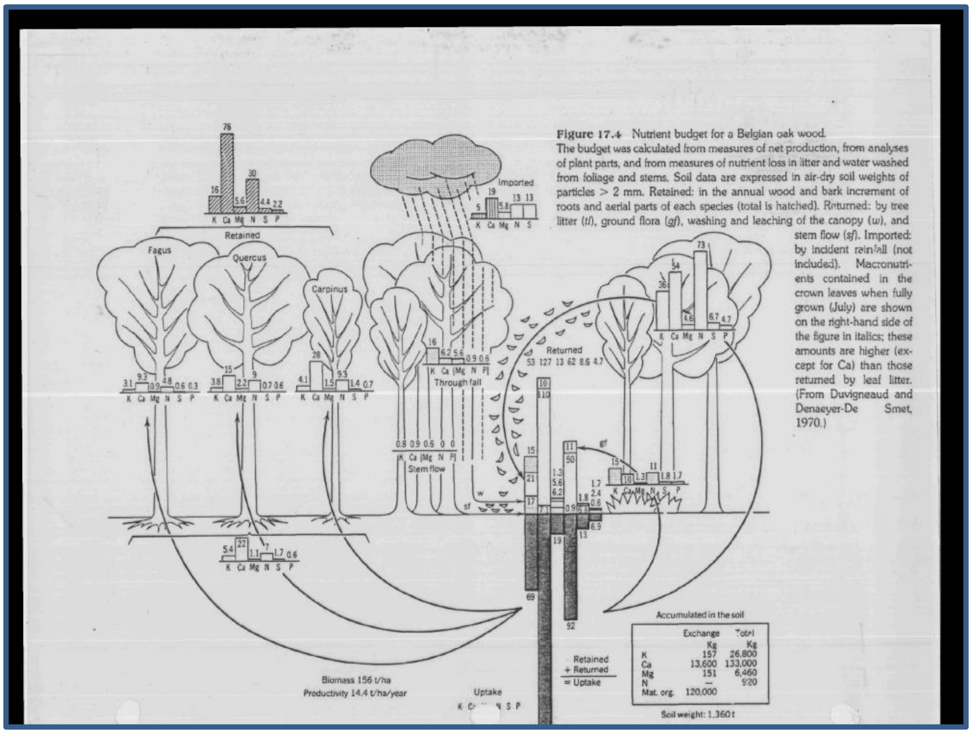
The ‘phosphorus cycle. It is important to note that there is no gaseous form of phosphorus. It moves through the biosphere ONLY in dissolved forms in liquid water; in other words it goes mostly DOWN-HILL (animals can provide an occasional uphill detour). Once it finally reaches the ocean sediments, it can return to the terrestrial biosphere only through geological processes. What are the consequences of this in terms of nutrient cycling dynamics and the likelihood of P becoming limiting? It is not surprising that, after nitrogen, phosphorus fertilizers are what farmers and gardeners most generally add to their soil. Nutrient cycles like those for C, O, N, S that have commonly occurring gaseous forms are referred to as ATMOSPHERIC CYCLES; if there is no gaseous form of an element, it has a SEDIMENTARY CYCLE. Nutrients with sedimentary cycles can be depleted in a particular ecosystem more easily because they're not easily replaced.



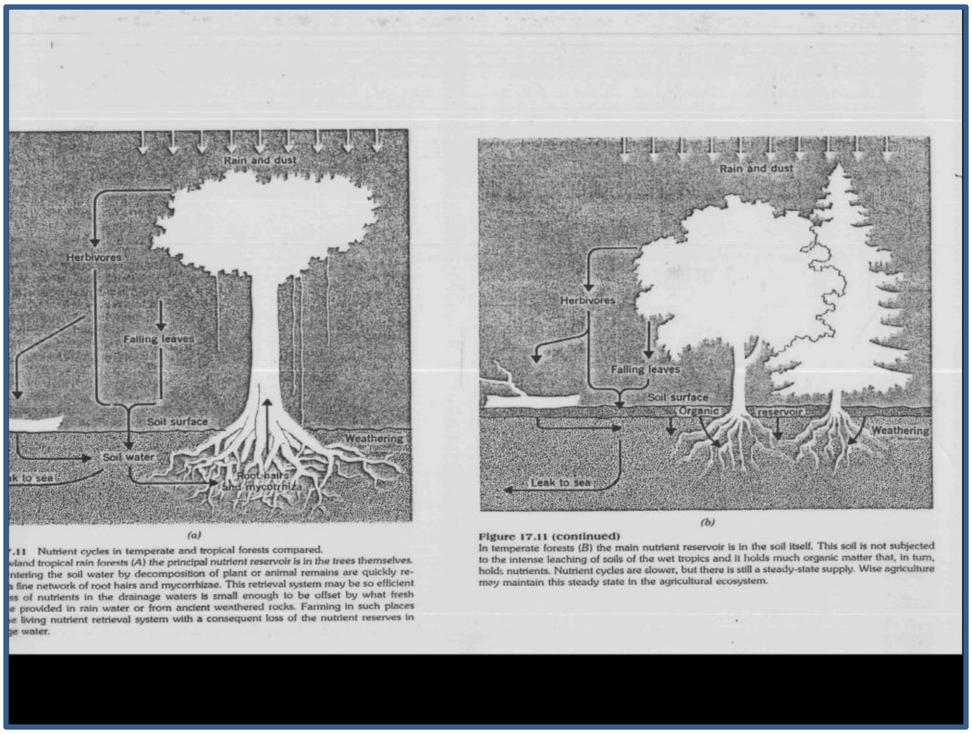

Sulfur cycle; sulfur has gaseous forms that move freely in the atmosphere. It's also fairly common in the waters and rocks of the planet; it's rarely limiting to ecosystem productivity.




Water cycle; even though water is not an element, it's often studied in the same way in terms of ecosystem processes. It is, of course, frequently limiting NPP; consider that deserts, when irrigated, are often highly productive agriculturally.



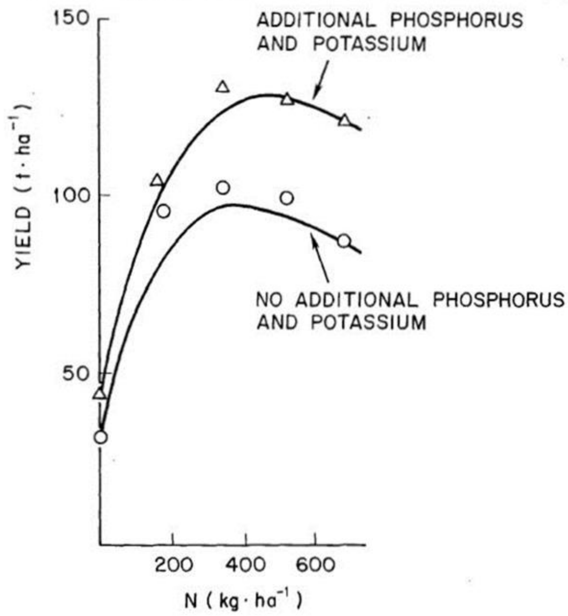

Just as with energy flows, nutrient cycling can be studied at finer scales – and COMPARED among systems. Here is a 'map' of movement of a number of important mineral nutrients among biomass (living and dead) 'compartments' in a temperate European forest. It shows inputs, pools, and fluxes, just like diagrams for larger regions, but here they have more accurate numbers attached to them.



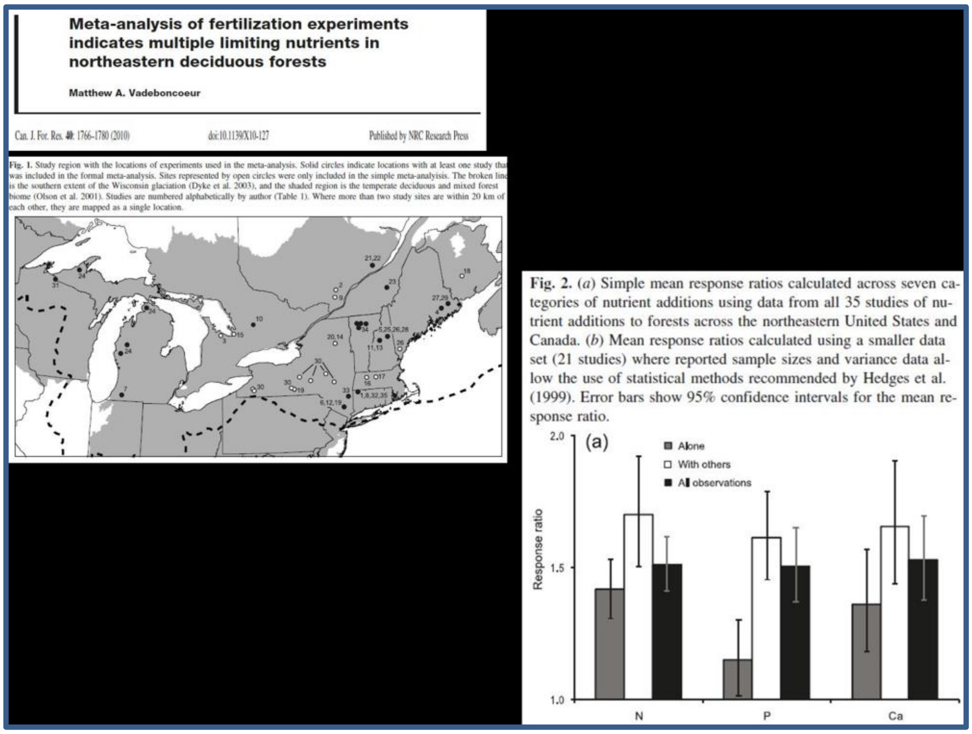

Here are such ‘local nutrient cycles’ portrayed, generically, for a tropical forest and a temperate forests. Look for the salient differences (e.g., the lack of a thick organic layer in tropical forest soils), and consider their consequences. Dead materials decay much more rapidly in the hot, wet tropics. The lack of a large 'reservoir' of dead organic matter – detritus – on and in the soil means that nutrients are quickly liberated and EITHER taken back up quickly by living vegetation OR potentially lost by 'washing out' ('leaching') to rivers and the sea.


This makes the high productivity of some tropical regions, like the Amazon basin, a little mysterious. Recent discoveries suggest that critical sedimentary nutrients are supplied to the Amazon basin by wind-blown dust from Africa!

*Figure 4.* *Yield of cabbage grown in Midlands region of England plotted as a function of N fertilizer applied at two levels of P and K fertilizer application. Modified from Milthorpe and Moorby (1974).*




An example of the effects of adding a limiting resource; adding N increases yield of cabbages quite a lot (at first). Note that N fertilization is even MORE effective if some P and K are added along with it, suggesting that the ‘law of the minimum’ doesn’t apply simply…



**Meta-analysis of fertilization experiments indicates multiple limiting nutrients in northeastern deciduous forests**

Matthew A. Vadeboncoeur

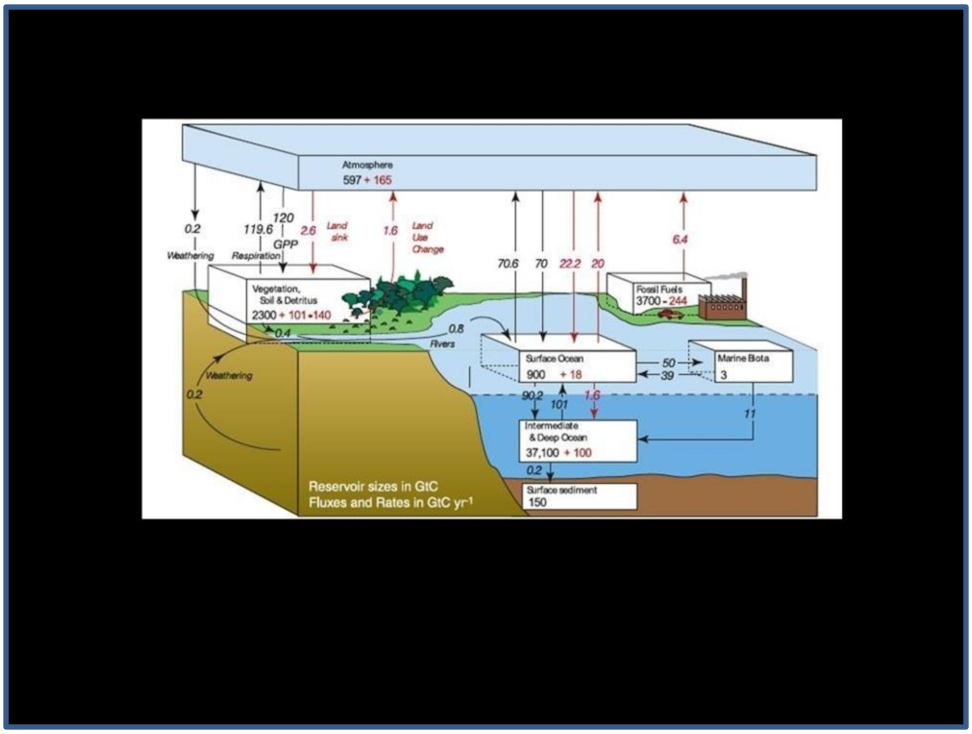
Can. J. For. Res. 40: 1766–1780 (2010) doi:10.1139/X10-127 Published by NRC Research Press

**Fig. 1.** Study region with the locations of experiments used in the meta-analysis. Solid circles indicate locations with at least one study that was included in the formal meta-analysis. Sites represented by open circles were only included in the simple meta-analysis. The broken line is the southern extent of the Wisconsin glaciation (Dyke et al. 2003), and the shaded region is the temperate deciduous and mixed forest biome (Olson et al. 2001). Studies are numbered alphabetically by author (Table 1). Where more than two study sites are within 20 km of each other, they are mapped as a single location.

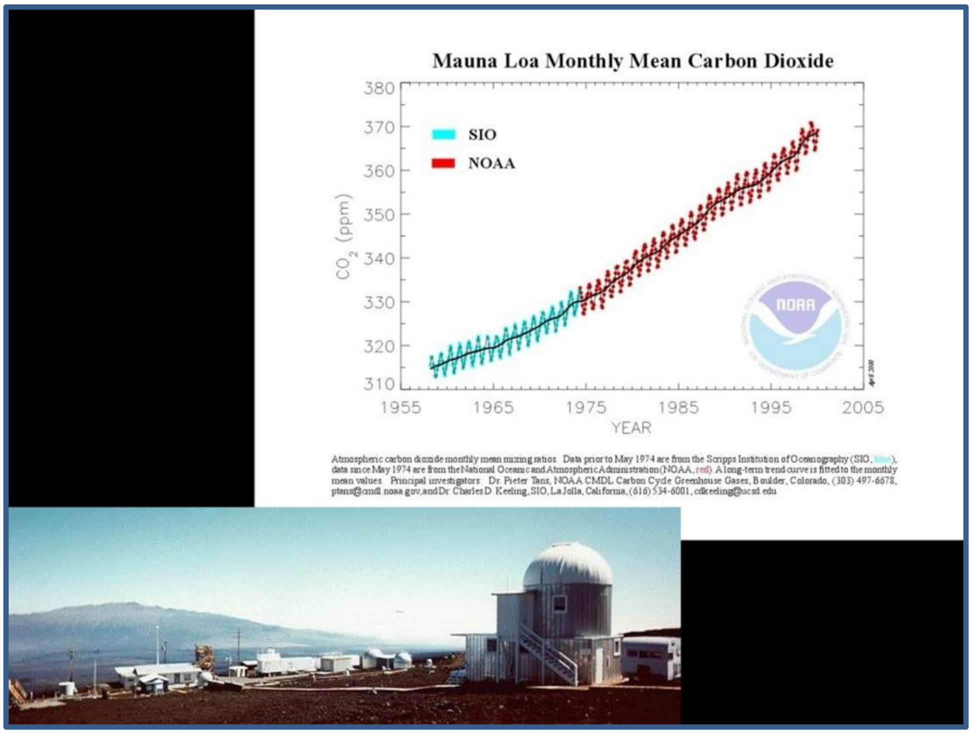
**Fig. 2.** (*a*) Simple mean response ratios calculated across seven categories of nutrient additions using data from all 35 studies of nutrient additions to forests across the northeastern United States and Canada. (*b*) Mean response ratios calculated using a smaller data set (21 studies) where reported sample sizes and variance data allow the use of statistical methods recommended by Hedges et al. (1999). Error bars show 95% confidence intervals for the mean response ratio.



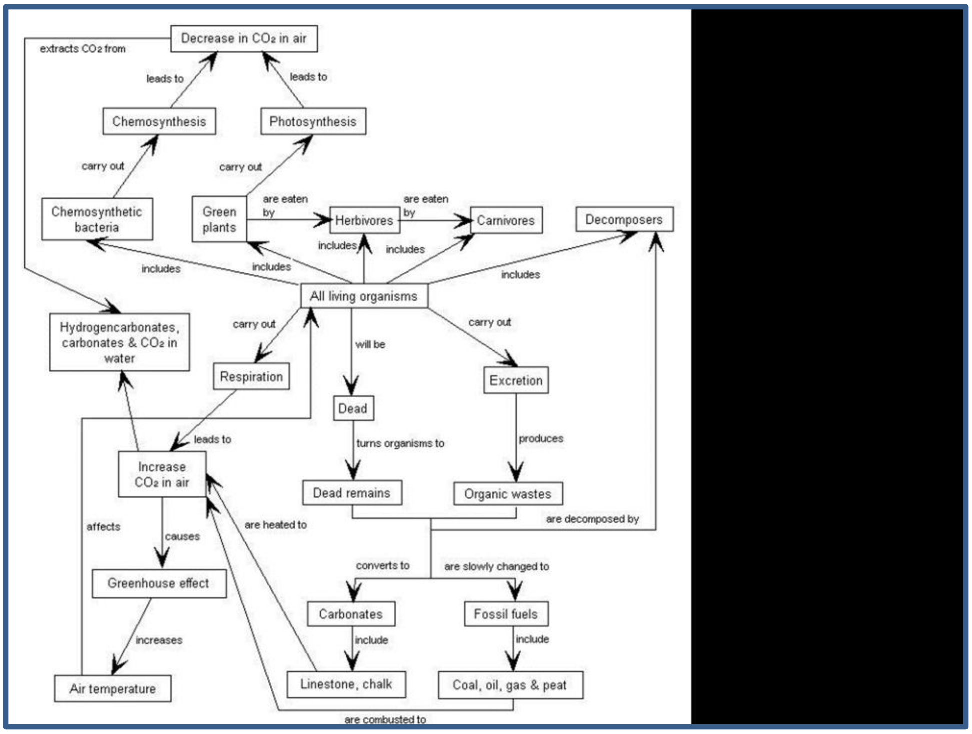
N, P, and Ca additions can increase NPP in natural forests of the northeast



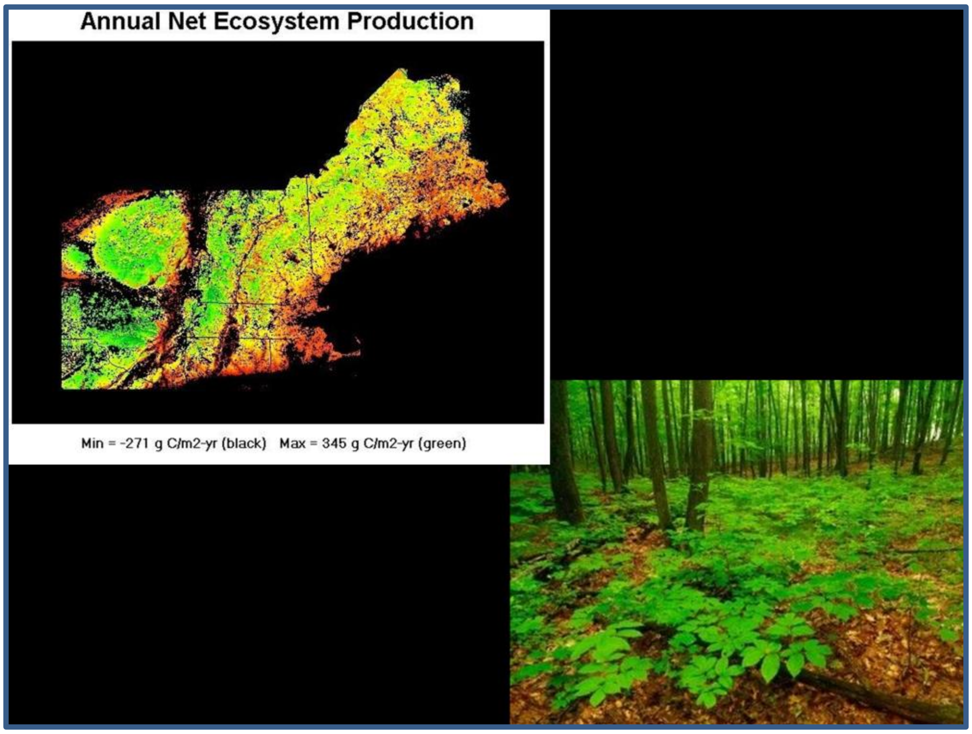

Human activity can have great influence on nutrient cycles and so shift ecosystem function in substantial ways – not just locally as with Lake Washington, but regionally and globally. Almost certainly, the most consequential such influence right now is our alteration of the global carbon cycle through fossil fuel burning, deforestation, reforestation, etc.




The graph shows the concentration of carbon dioxide in the atmosphere at the summit of Mauna Loa in Hawaii (it's often called the 'Keeling Curve' after the scientist who maintained the study over the long term); it has been called the most important data-graphic ever because it is one of the most powerful illustrations of the consequences of human activities for greenhouse-gas concentrations. The gradual rise in carbon dioxide is due, primarily, to fossil-fuel burning; essentially a 'short-circuit' of the carbon cycle, moving carbon rapidly from otherwise very long-term sedimentary reservoirs into the atmosphere. However, current biological processes also affect the curve. Why does it 'wiggle' on an annual cycle? Realize, also, that the if the *total amount of biomass on the planet* changes, that, too will affect atmospheric concentrations of carbon dioxide; biomass is a *carbon reservoir*. Increases in biomass 'sequester' carbon from the atmosphere through photosynthesis. (Note also how this all ties the energy/trophic viewpoint of ecosystems together with the nutrient cycling viewpoint).




This change in the carbon cycle is almost certain to have far-reaching consequences for ecosystem function – but, as with the Lyme disease story, there are MANY FEEDBACKS in the network of cause and effect, so it's VERY difficult to predict exactly what those consequences will be.

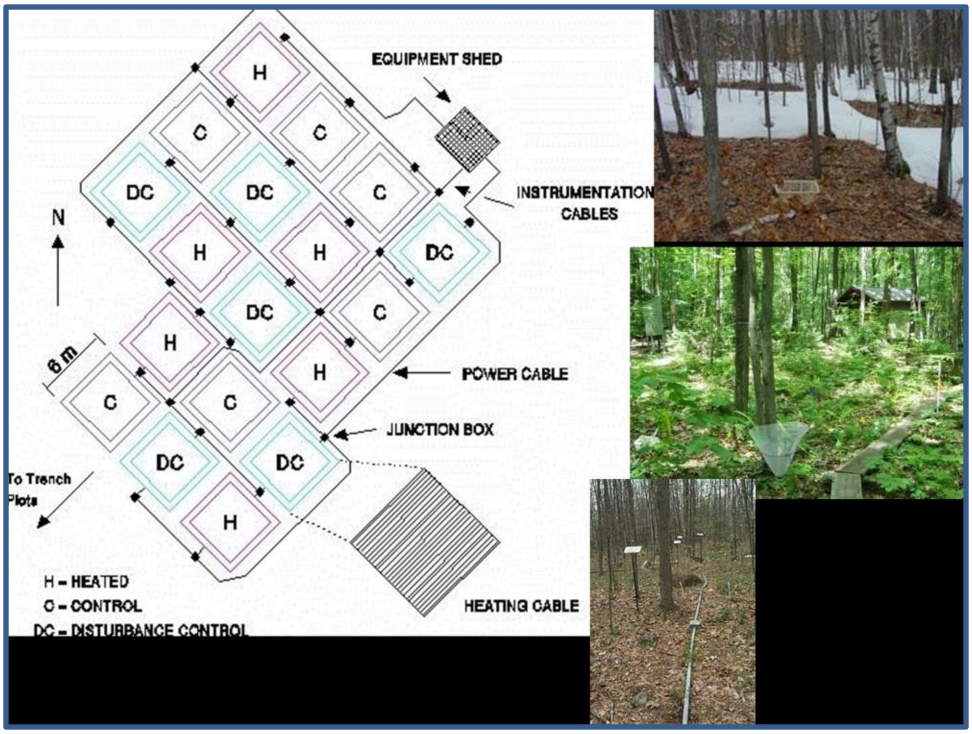



NET ECOSYSTEM PRODUCTION is the difference between total photosynthesis (GPP) and the respiration of ALL organisms in the ecosystem (at all trophic levels). If it’s positive, the total amount of biomass in the system must be increasing – i.e., CARBON IS, on average, FLOWING INTO and ACCUMULATING IN the ecosystem from the atmosphere. In the northeast is, over the majority of the landscape NEP is POSITIVE (the yellow and green colors in the map); biomass is increasing and the northeatern U.S. is a CARBON SINK; the ecosystems of the region are, on net, REMOVING carbon dioxide from the atmosphere (in fact, they’re removing more than people in the same area produce by burning fossil fuels!). How can this happen? Consider the age and nature of most of the forests of the region. Over the long term, can this state of positive NEP production over the large landscape be maintained? We'll explore this kind of question later.

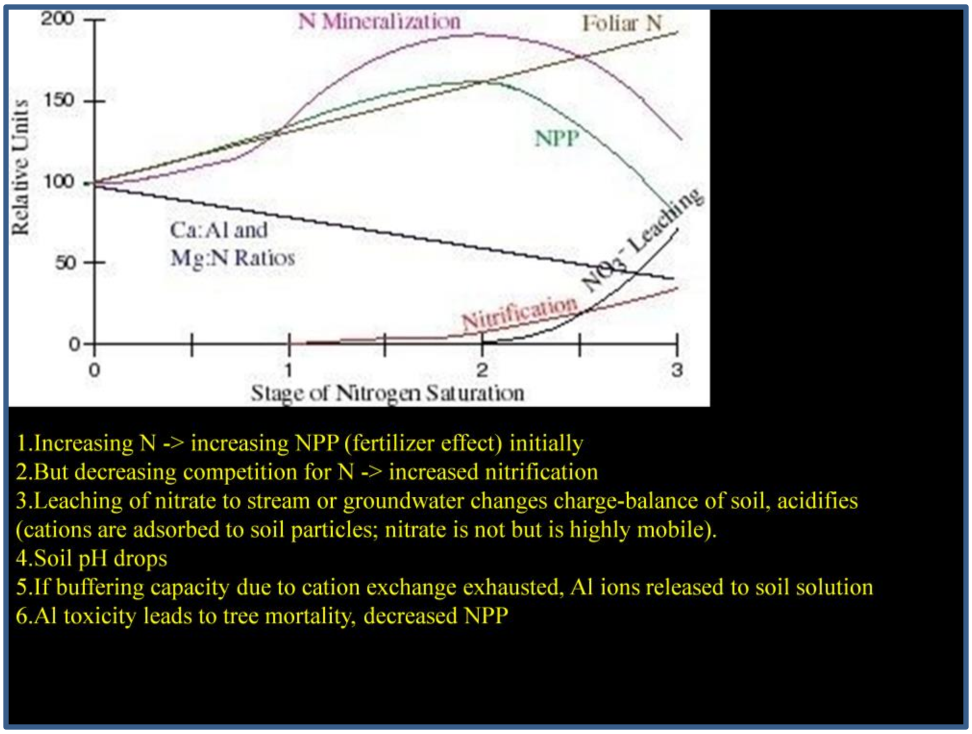

Might increasing carbon dioxide have a fertilizing effect, allowing more rapid plant growth?  If so, increases in NPP might lead to some sequestration of C in increasing biomass pools, therefore providing a negative feedback to greenhouse gas increases. This is one of a number of experiments testing this possibility.  The towers emit carbon dioxide in a rigorously controlled way to increase ambient concentrations in the forest within the rings. Since these forests are otherwise unaltered, these experiments are thought to give more realistic results than experiments done in a lab setting (they're called 'Free-Air Carbon Enrichment' or FACE experiments).  The first and most famous of these experiments was established at the Duke University Experimental Forest.

Similar experiments have now been done at many sites, including other forests, agricultural fields, grasslands,...

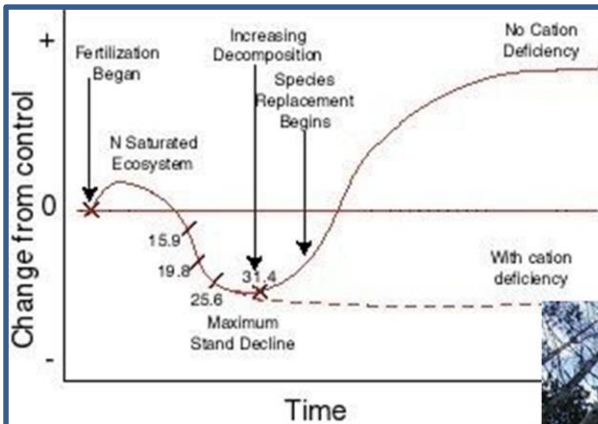
Here's some of the piping involved. The results are interesting, but not easily interpreted or the same across ecosystems. There are often initial increases in total net ecosystem production, but they may not persist over the long term (this may be in part because warming temperatures also increase metabolic rates). But there are also many other effects at 'lower levels'; some species do better at higher carbon dioxide concentrations than others. Poison ivy growth rates increase by 50% or so (and it produces more of the irritant urushiol); ragweed produces more pollen...




Here's another experiment – at Harvard Forest – where heating cables buried in study plots are used to simulate increasing temperature and measure ecosystem effects.




Increasing NITROGEN input in precipitation (due, primarily to changes in atmospheric chemistry resulting from internal combustion engines, but also, in some areas, from N fertilizer used in agriculture) may, in some areas, have effects as great as greenhouse warming.  Note that N in precipication forms nitric acid, contributing to acid rain, but the more significant effect is probably going to be through 'nitrogen saturation' in systems that have usually been N-limited.

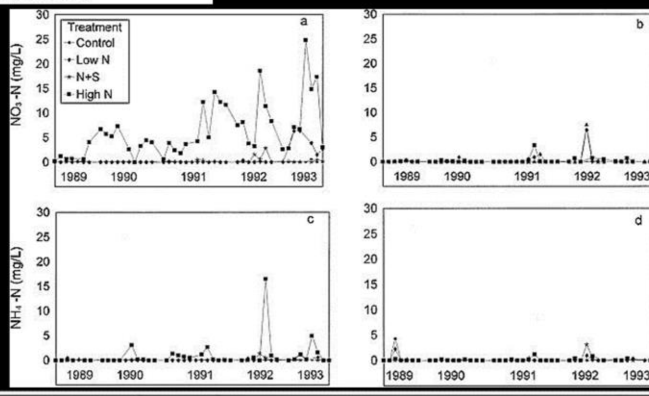



7. BUT, if cations NOT exhausted, shift in species composition (Why?) and potential increases in NPP

*Ecological Applications*, 7(2), 1997, pp. 402–415

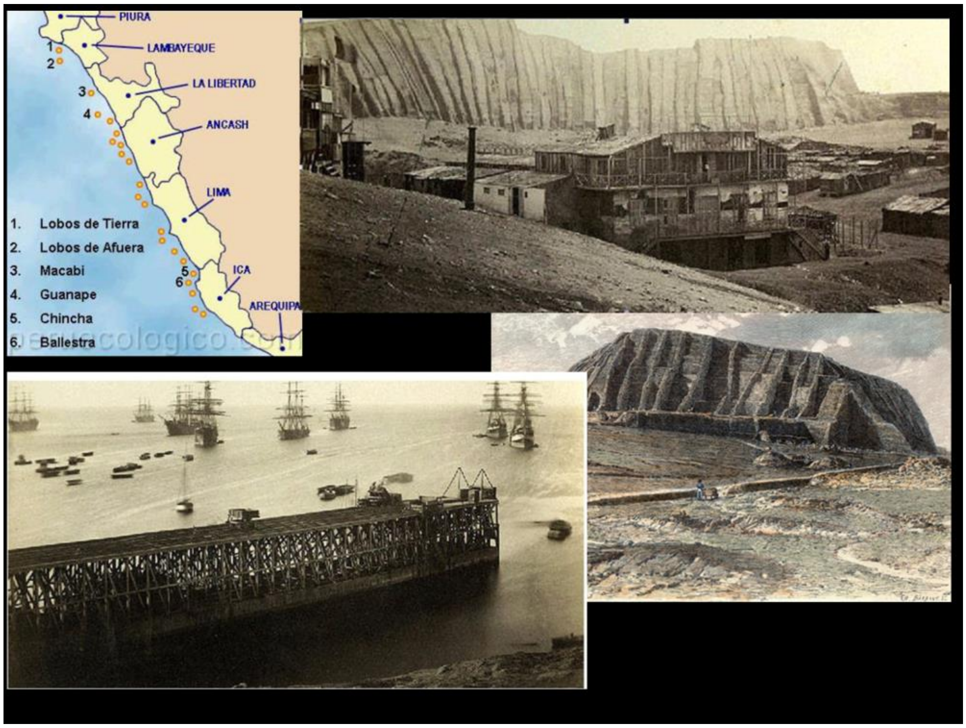

BIOGEOCHEMICAL RESPONSE OF FOREST ECOSYSTEMS TO SIMULATED CHRONIC NITROGEN DEPOSITION

Alison H. Magill,[1] John D. Aber,[1] Joseph J. Hendricks,[1,4] Richard D. Bowden,[2] Jerry M. Melillo,[3] and Paul A. Steudler[3]

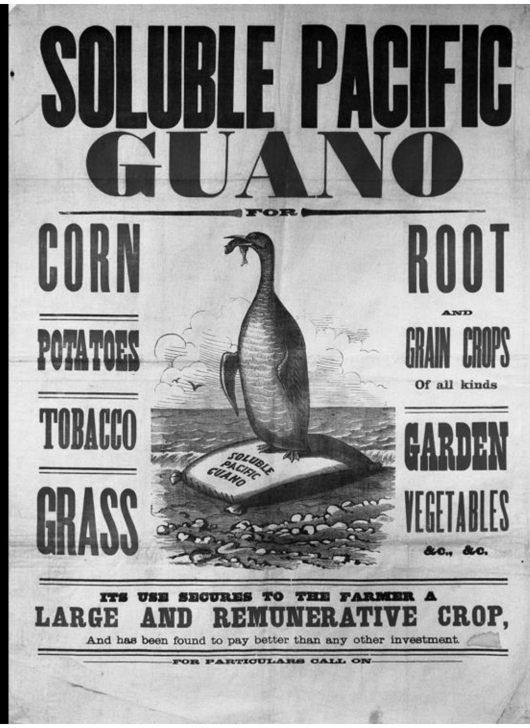



| | Pine stand treatments | | | | Hardwood stand treatments | | | |
|---|---|---|---|---|---|---|---|---|
| | Control | Low N | N+S | High N | Control | Low N | N+S | High N |
| Woody increment | 3.3 | 3.3 | 2.4 | 2.0 | 4.5 | 4.8 | 5.1 | 6.5 |
| Litterfall | 3.2 | 3.7 | 3.8 | 4.1 | 2.9 | 2.9 | 3.0 | 3.3 |
| Total | 6.5 | 7.0 | 6.2 | 6.1 | 7.4 | 7.7 | 8.1 | 9.8 |

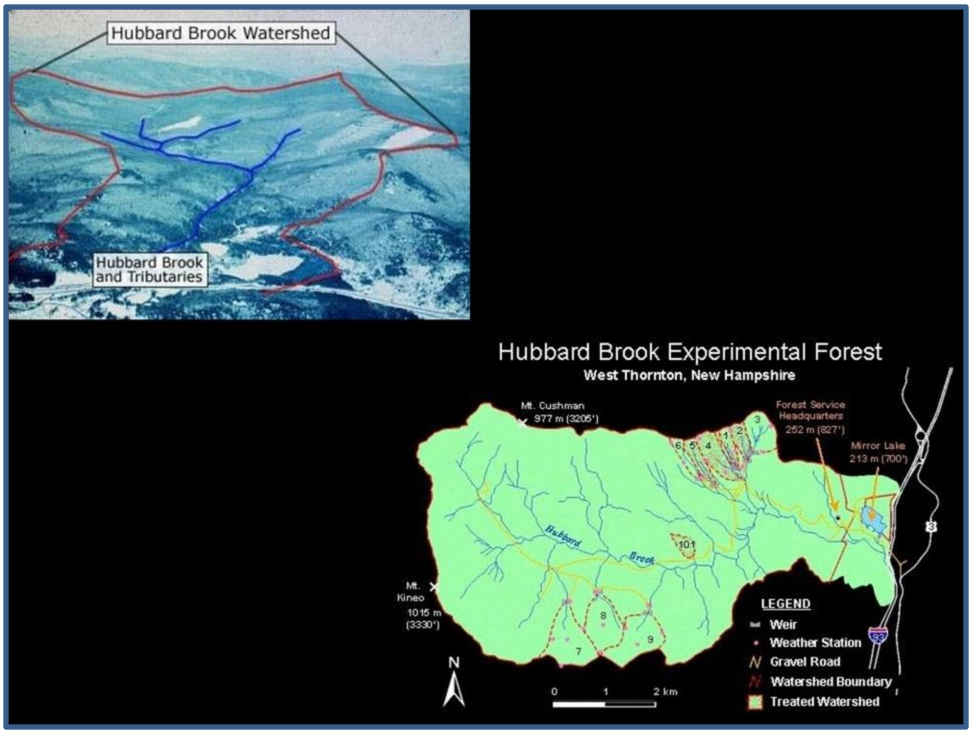
Experiments at Harvard Forest and Hubbard Brook and elsewhere have been exploring the consequences of N saturation. We're still learning...



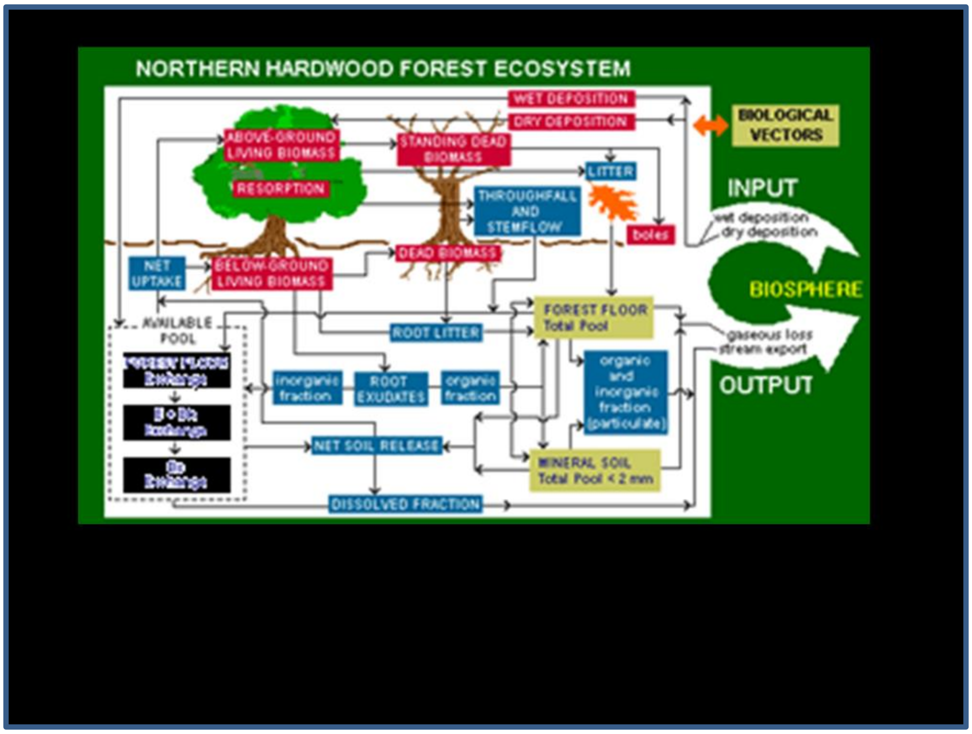

Human manipulation of the PHOSPHORUS CYCLE has been quite extensive; since P can be limiting *and has a sedimentary cycle,* it can be difficult to replace. Phosphorus fertilizers come from various sources, but one of the most important is huge guano deposits on islands off the coast of Peru. These represent a 'short-circuit' of the P cycle. Easterly winds blow surface waters of the Pacific away from the coast; this causes *upwelling* of cold, deep waters that *include high concentrations of P that has 'sunk' below the surface waters and so become unavailable to planktonic algae*; resulting increases in NPP fuel a productive marine foodweb – lots of algae and fish, so ltos of seabirds; birds nest on islands to avoid predation; the very dry climate prevents their guano from washing back into the sea, so it builds up. Some of these islands have (had) deposits hundreds of feet thick. They've been mined for over 200 years and shipped around the world for fertilizer – a very lucrative trade…


SOLUBLE PACIFIC
GUANO
FOR
CORN
POTATOES
TOBACCO
GRASS
ROOT
AND
GRAIN CROPS
Of all kinds
GARDEN
VEGETABLES
&c., &c.
SOLUBLE PACIFIC GUANO
ITS USE SECURES TO THE FARMER A
LARGE AND REMUNERATIVE CROP,
And has been found to pay better than any other investment.
FOR PARTICULARS CALL ON

Walvis Bay platform, Namibia – constructed 1930 as guano-harvesting receptacle:
Made builder millionaire



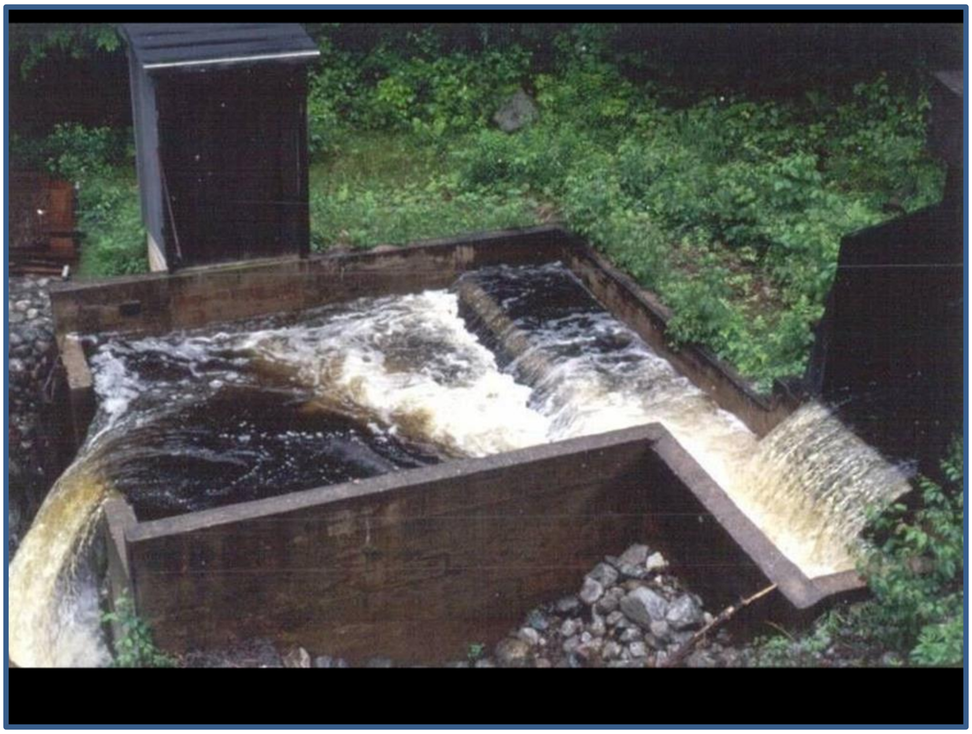

The Hubbard Brook ecosystem study in New Hampshire was the first large-scale *experimental* study of ecosystem processes in an essentially natural landscape. The researchers treated *watersheds* as experimental units and established a number of 'experimental treatments' to see how they effected nutrient cycling. Several of the treatments were designed to understand the effects of forestry management, particularly on the availability of limiting nutrients – and, therefore, ecosystem production/growth. Because these watersheds were very similar, this allows comparisons among treatments and with an unaltered 'control' watershed.




A conceptual diagram of a Hubbard Brook watershed; because the study unit is a watershed, the only meaningful inputs of nutrients were from atmospheric deposition or weathering of rock, while the main outputs were through the streams draining the watersheds (and some gases).

Inputs of nutrients through aerial deposition (in rain water or snow, or in blown dust) were measured by sophisticated weather stations.

Losses of nutrients in stream flow were measured at experimental 'weirs', which allowed monitoring of stream flow rates.  Regular sampling of water and sediments permitted analysis of nutrient composition



Even good plans are sometimes inadequate; this is an extreme storm where the stream overflowed the weir.

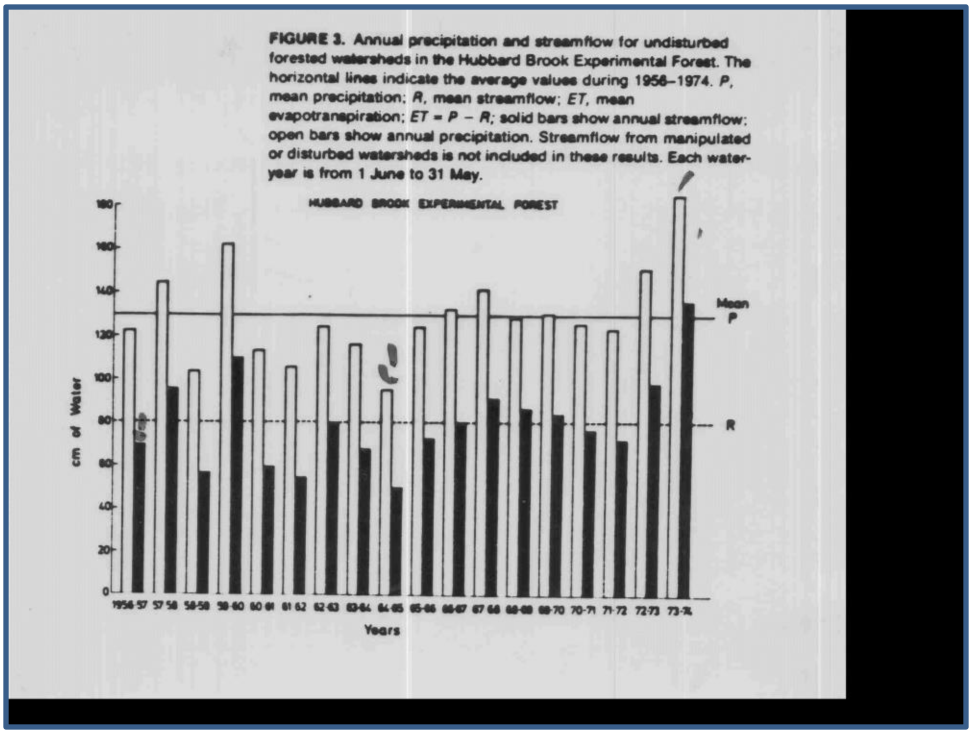
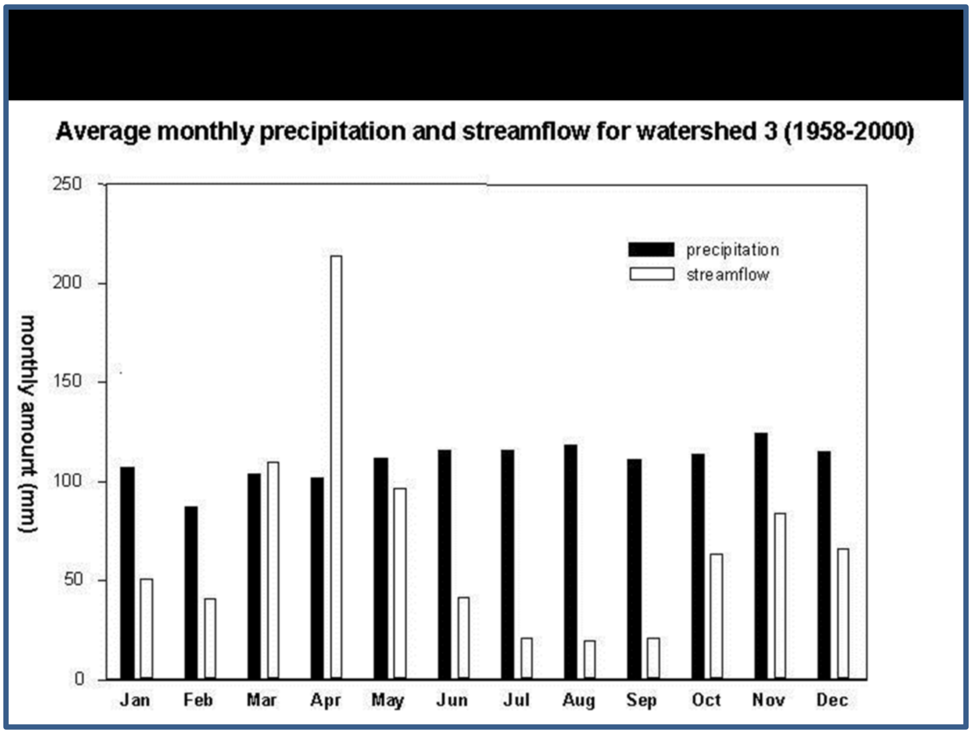


**FIGURE 3.** Annual precipitation and streamflow for undisturbed forested watersheds in the Hubbard Brook Experimental Forest. The horizontal lines indicate the average values during 1956–1974. *P*, mean precipitation; *R*, mean streamflow; *ET*, mean evapotranspiration; $ET = P - R$; solid bars show annual streamflow; open bars show annual precipitation. Streamflow from manipulated or disturbed watersheds is not included in these results. Each water-year is from 1 June to 31 May.

The baseline precipitation record shows a lot of variation from year to year (open bars are rain and snowfall amounts as cm of water). Dark bars are water leaving the watershed in the stream.  Less water leaves through the stream than came in in precipitation. Where did it go?




A similar graph showing average MONTHLY inputs and stream outputs of water. Some striking patterns here. Precipitation is pretty regular across the year, but streamflow is not…

**Table 12.** Summary of Annual Input–Output Budgets for Undisturbed Forested Ecosystems at Hubbard Brook[a]

| Element | Input, kg/ha·yr | Output, kg/ha·yr | Net gain (+) or loss (−), kg/ha·yr |
|---|---|---|---|
| Si | — | 23.8 | −23.8 |
| Ca | 2.2 | 13.9 | −11.7 |
| Na | 1.6 | 7.5 | −5.9 |
| Al | — | 3.4 | −3.4 |
| Mg | 0.6 | 3.3 | −2.7 |
| K | 0.9 | 2.4 | −1.5 |
| Organic C | 1484[b] | 12.3 | +1472 |
| N | 20.7 | 4.0 | +16.7 |
| Cl | 6.2 | 4.6 | +1.6 |
| S | 18.8 | 17.6 | +1.2 |
| H | 0.96[c] | 0.10[c] | +0.56 |
| P | 0.036 | 0.019 | +0.017 |

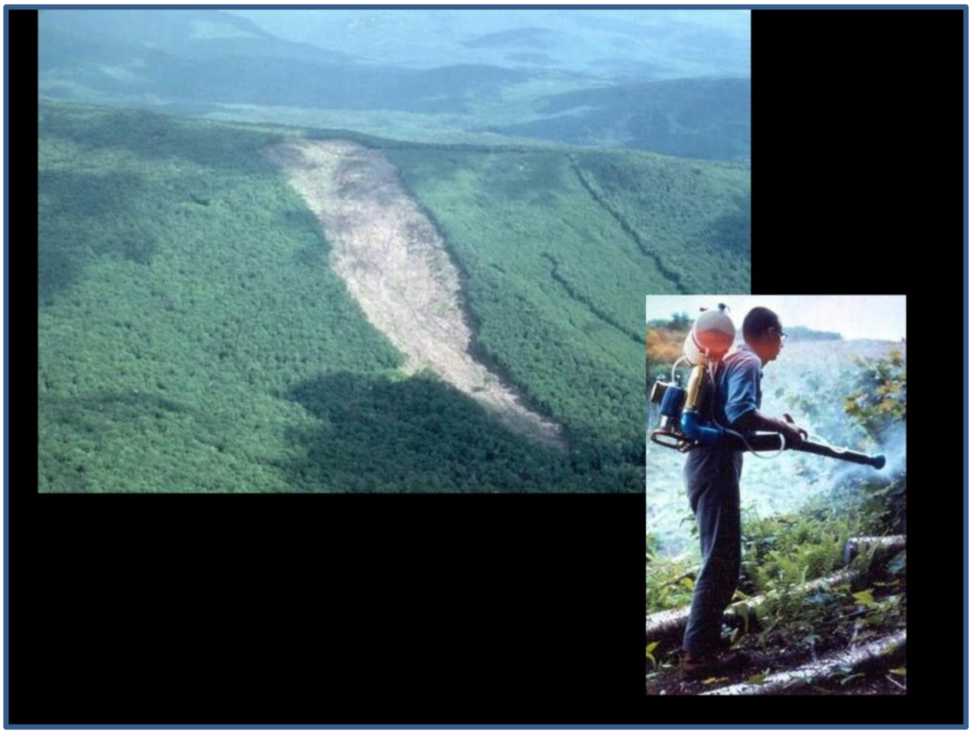
[a]Input values for organic C, N, and S include bulk precipitation, estimates of aerosol impaction, and net gaseous uptake; all others are based on bulk precipitation only. Output values include both dissolved substances (Table 10) and particulate matter (Table 9) in stream water.

[b]Includes ecosystem biomass accretion (*net* ecosystem gaseous uptake of $CO_2$) based on the period 1961–1965 (Whittaker, et al., 1974); therefore output does not include respiration losses of $CO_2$.

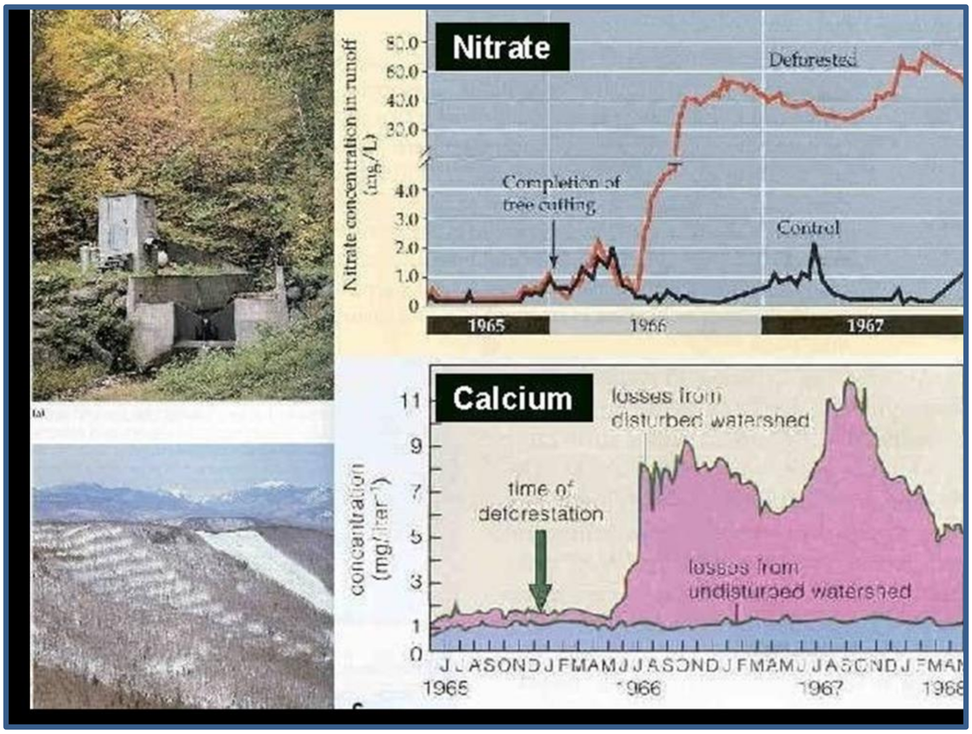
[c]Dissolved form only.

Here are the nutrient ‘budgets’ for the control watershed at Hubbard Brook. Note that the watershed is RETAINING some nutrients – less is leaving the watershed than is falling precipitation – so these nutrients must be accumulating in biomass or soils. Note that these include some important, ofen-limiting elements. Others are leaving the watershed in quantities larger than they were added in precipitation; this must be due to inputs from erosion of bedrock. (There is virtually no N or P in the bedrock at Hubbard Brook; why is that important to know?)

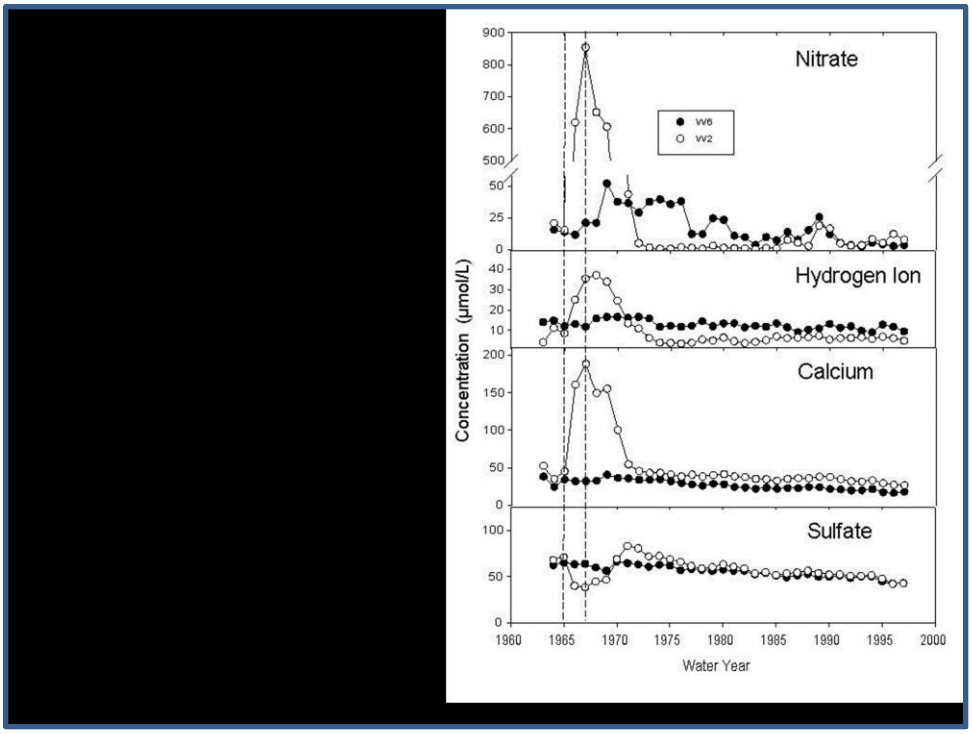
Some of the ‘experimental’ watersheds; these were logged by various standard commercial methods (one was herbicided for two years after cutting as an experiment to see how quickly regrowing vegetation re-established ‘control’ over nutrient losses).



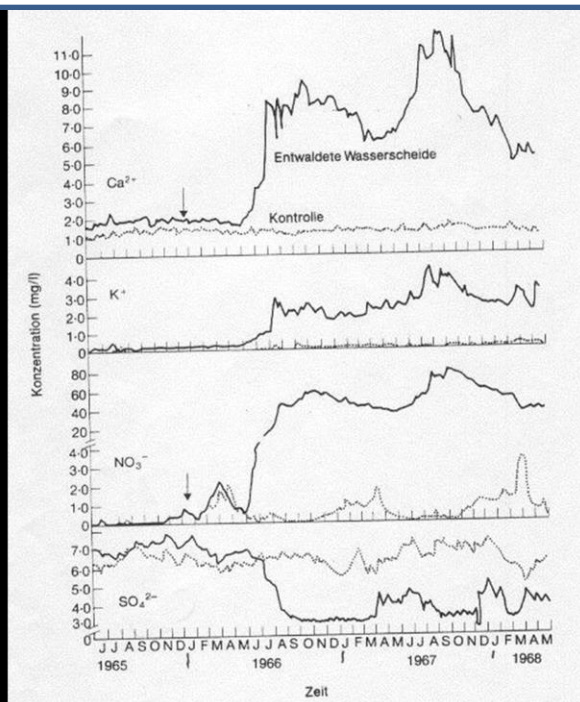
Upper left: the herbicided watershet.  Lower right: regrowth, dominated by pin-cherry very soon thereafter.  Pin-cherry seeds are present in the soil seed bank in vast numbers. Each year for several years after clearing pin cherry seedlings came up at densities of HUNDREDS per square m.



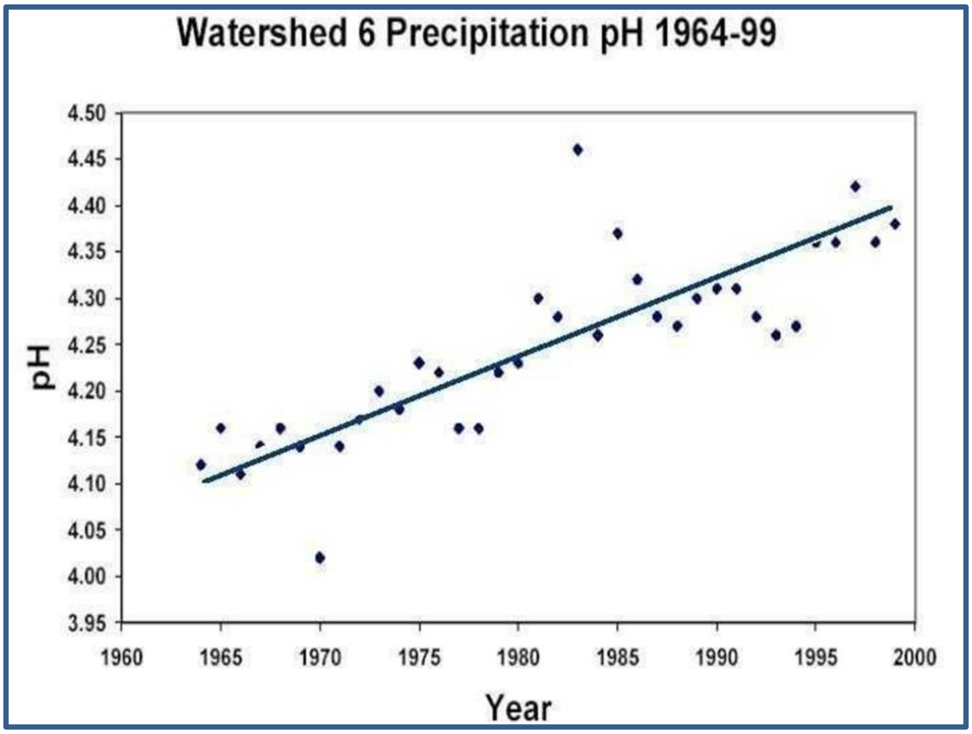

Nutrient concentrations in runoff increased dramatically after logging, but losses began to decline within two years of cutting, and returned to levels similar to the control after several years. Even with the rapid reassertion of nutrient-cycling 'efficiency' with regrowing vegetation, however, large amounts of the probable limiting resource (nitrogen) were lost; this must affect the time it takes for the forest to 'recover'. An experimental cutting method (lower left), where the watershed was cut in contoured 'strips' over several years had virtually no elevation of nitrate in stream water.



Nitrate
W6
W2
Hydrogen Ion
Calcium
Sulfate
Concentration (µmol/L)
Water Year
900
800
700
600
500
50
25
0
40
30
20
10
200
150
100
50
0
100
50
0
1960
1965
1970
1975
1980
1985
1990
1995
2000



Entwaldete Wasserscheide
Kontrolle
$Ca^{2+}$
$K^+$
$NO_3^-$
$SO_4^{2-}$
Konzentration (mg/l)
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
1965
1966
1967
1968
Zeit



Watershed 6 Precipitation pH 1964-99
4.50
4.45
4.40
4.35
4.30
4.25
4.20
4.15
4.10
4.05
4.00
3.95
pH
1960
1965
1970
1975
1980
1985
1990
1995
2000
Year

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ECOSYSTEMS


# The Effects of Land-use History on Soil Properties and Nutrient Dynamics in Northern Hardwood Forests of the Adirondack Mountains

Erika F. Latty,[1,2*] Charles D. Canham,[2] and Peter L. Marks[1]

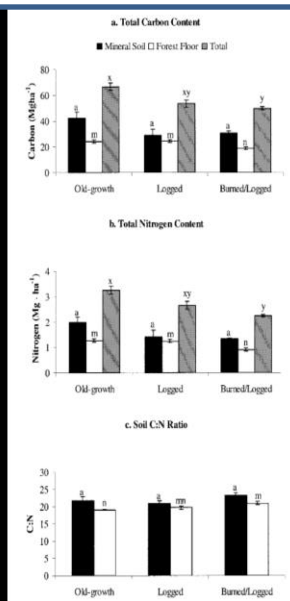



**Figure 2.** Average midsummer **(a)** total carbon (C) content ($g{\cdot}m^{-2}$), **(b)** total nitrogen (N) content ($g{\cdot}m^{-2}$), and **(c)** C–N ratio in the forest floor and upper 0–15 cm of the mineral fraction in old-growth, logged, and logged/burned soils. *Bars* are mean values (± 1 SE) of four stands per forest-history class. *Lowercase letters* indicate Tukey's honestly significantly different (HSD) test at $P < 0.05$

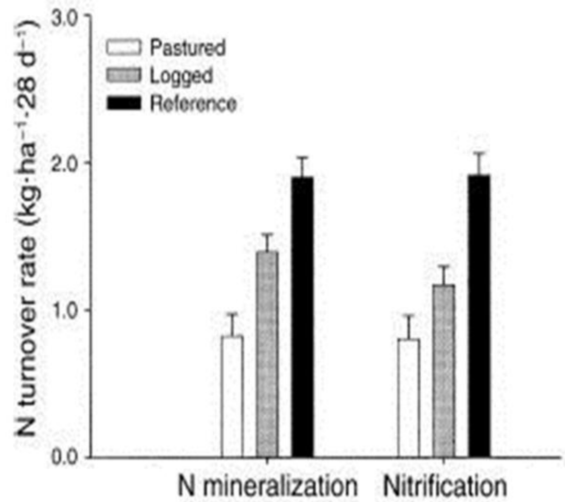



FIG. 4. Mean potential net N mineralization and nitrification per hectare in 0–15 cm mineral soil collected during June 2002. Error bars indicate +1 SE. Samples were converted using corrected bulk density (without the coarse fraction).

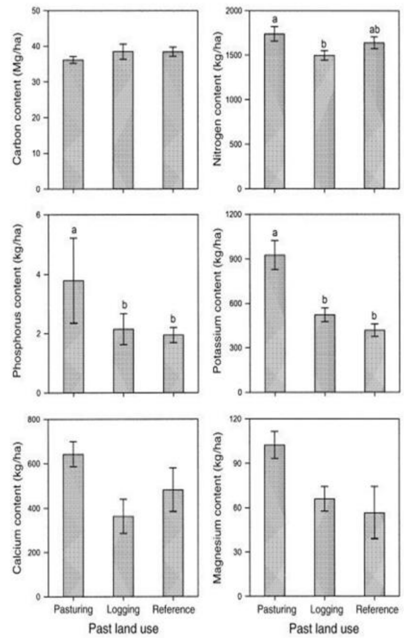
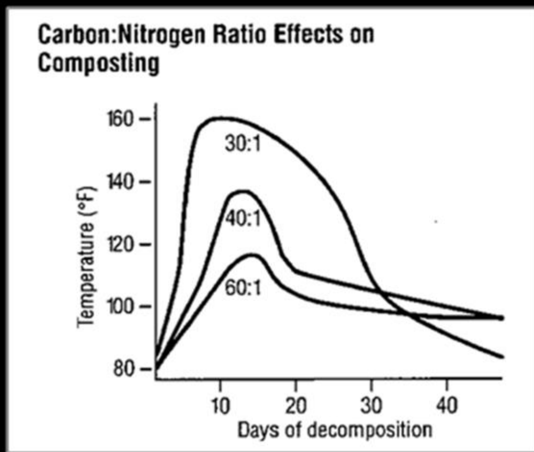



FIG. 3. Nutrient stocks (mean ± 1 SE) in the 0–15 cm mineral soil by land-use history. Samples were converted using corrected bulk density (without the coarse fraction). Bars with different letters are significantly different ($P < 0.05$).




| C/N FOR COMPOST PILE MATERIALS | |
|---|---|
| **Material** | **C/N** |
| autumn leaves | 40-80:1 |
| grass clippings | 20-25:1 |
| manure | 14:1 |
| paper | 170:1 |
| pine needles | 60-110:1 |
| sawdust | 400-500:1 |
| straw | 50-100:1 |
| vegetable scraps | 25:1 |