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Vitousek P M & Reiners W A. Ecosystem succession and nutrient retention: a hypothesis. *Bioscience* 25:376-81, 1975.
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Theoretical considerations suggest that the storage of essential plant nutrients in biomass (living and dead) is an important cause of variation in watershed-level nutrient losses. We demonstrate that New Hampshire watersheds supporting forests that have never been harvested (and therefore are not accumulating biomass rapidly) lose larger quantities of nutrients than those supporting young forests in which biomass is accumulating. [The *SCI*® indicates that this paper has been cited in more than 130 publications.]

Ecological Succession and Nutrient Budgets

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We did not start a study to examine succession and nutrient cycling. Rather, we thought we were taking preliminary steps in a study evaluating the effects of nitric versus sulfuric acid rain on alpine tundra when we collected and analyzed water samples from a subalpine stream that might have been used as a source of irrigation water. However, that possible Dartmouth PhD thesis was dropped when we found relatively high concentrations of nitrate in the stream.

At that time (1972), the conventional wisdom held that mature vegetation was conservative of nutrients, while disturbance (such as forest cutting) caused elevated losses from watersheds. The mechanisms causing that pattern weren't all clear, and indeed the terminology itself was a bit fuzzy (what does "mature" mean when applied to an ecosystem?). But, the overall difference was (and is) clear. The observation of reasonably high nitrate concentrations in a stream draining a seemingly undisturbed forest was therefore puzzling.

We placed the results from that stream in context by sampling and analyzing many other streams in the area and got the still more puzzling result that where forests had been harvested more than 30 years previously, nitrate concentrations in streamwater were low during the growing season; where they had never been cut, nitrate concentrations were moderately high—though never as high as those in recent (three year old) clearcuts.

We decided that the overall pattern could be explained by a single mechanism if nitrogen losses were controlled by net nitrogen storage in biomass (living or dead), which itself could be controlled by net ecosystem productivity (NEP—the net change in living plus dead biomass, which can be positive or negative). NEP is negative immediately after disturbance, as decomposition exceeds plant production; it is positive in developing systems and can average zero if a steady-state biomass is reached late in succession.

Calculations based on the literature showed that the magnitude of macronutrient storage was sufficient to affect nutrient losses from whole ecosystems (as E. Gorham[1] had demonstrated earlier), and measurements over an annual cycle showed that the reduction in losses of particular nutrients from older harvested areas compared to uncut areas was dependent on forest demand for that particular nutrient. We suggested, therefore, that biomass dynamics in succession could be a general mechanism controlling nutrient losses from terrestrial watersheds; we also speculated on the forest dynamics that could lead to a steady-state biomass.[2]

All of this seems obvious in retrospect, as indeed it is obvious that other general mechanisms interact with or offset this one in controlling overall nutrient budgets.[3] However, the paper provoked discussion at the time. Reactions ranged from immediate incorporation as a null hypothesis and rapid appearance in the abstracts of publications to rather strong rejections on the grounds that it was simplistic (which is true, by itself) or that it was a tautology (which it is not). Looking back, we can only conclude that the field was then hungry for testable generalizations about mechanisms controlling nutrient cycling.

The overall conclusion that biomass dynamics after disturbance and during succession of terrestrial ecosystems, especially forests, represent one of the major controls over nutrient losses is widely accepted; it is used in models and studies of regional trace gas fluxes[4] and in aquatic systems[5] as well as in studies of nutrient budgets of particular terrestrial ecosystems.[6]

1. **Gorham E.** Factors influencing supply of major ions to inland waters, with special reference to the atmosphere. *Geol. Soc. Amer. Bull.* 72:795-840, 1961. (Cited 125 times.)
2. **Reiners W A & Lang G E.** Vegetational patterns and processes in the balsam fir zone, White Mountains, New Hampshire. *Ecology* 60:403-17, 1979.
3. **Gorham E, Vitousek P M & Reiners W A.** The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annu. Rev. Ecol. Syst.* 10:53-84, 1979.
4. **Robertson G P & Rosswall T H.** Nitrogen in West Africa: the regional cycle. *Ecol. Monogr.* 56:43-72, 1986.
5. **Grimm N B.** Nitrogen dynamics during succession in a desert stream. *Ecology* 68:1157-70, 1987.
6. **Vitousek P M, Fahey T, Johnson D W & Swift M J.** Element interactions in forest ecosystems: succession, allometry, and input-output budgets. *Biogeochemistry* 5:7-34, 1988.

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