



Nutrient retention and loss during ecosystem succession: revisiting a classic model

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Abstract. In 1975, Vitousek and Reiners proposed a conceptual model relating the net retention of a limiting nutrient to the net biomass accumulation in terrestrial ecosystems, whereby terrestrial systems should be highly conservative of nutrients during ecosystem succession when plants are actively accumulating biomass, but should be relatively leakier in older stands, when net plant biomass accumulation nears zero. The model was based on measurements in the White Mountains of New Hampshire. However, recent data showing that nitrate output in streams is declining across this region even as forests are aging seem to be inconsistent with this theory. Because the more recent data do not match the predictions of the Vitousek and Reiners model, either new hypotheses, or modifications of the original hypothesis, need to be considered. I suggest that the original model can be amended by accounting for increased woody debris; an accumulation of both above and belowground high C:N coarse woody debris from tree mortality in these regenerating forests can lead to high microbial immobilization of N and can explain the recent patterns of declining stream nitrate. Few studies or models have attempted to calculate the impacts of coarse woody debris (CWD) decomposition products to the retention of C and N in forested ecosystems and their receiving streams, but evidence suggests that CWD can significantly affect stream N exports and should be considered in future models of ecosystem biogeochemical cycles.

Key words: biogeochemistry; coarse woody debris; Hubbard Brook; nitrate; streamwater; succession.

In 1975, Vitousek and Reiners proposed what became a classic conceptual model relating the net retention of a limiting nutrient to the net biomass accumulation in terrestrial ecosystems. According to their model, terrestrial systems should be highly conservative of growth-limiting nutrients during ecosystem succession when plants are actively accumulating biomass, but should be relatively leakier in older stands, when net plant biomass accumulation nears zero. The retention of growth-limiting nutrients was defined by losses of nutrients to streamwater as measured at weirs at the base of watershed streams. They tested their model in watersheds across New Hampshire and found that the concentration of nitrate in streams from late-successional spruce-dominated watersheds was significantly greater than nitrate concentrations from watersheds dominated by early successional forest. Their paper has been cited over 1,000 times, forming a paradigm for biogeochemistry that can be found in modern ecology textbooks (e.g., Waring and Schlesinger 1985, Cain et al. 2017) and in ecosystem ecology courses (e.g., Schlesinger and Bernhardt 2013). Goodale et al. (2000) confirmed the general patterns predicted by the model; they noted that across the White Mountains of New

Hampshire mean nitrate export from old-growth watersheds was four times greater than from previously disturbed watersheds, several decades after the original study.

Lovett et al. (2018) report that more recent streamwater data seem to be inconsistent with this theory. They point out that Goodale et al. (2003) resampled some of the original streams sampled by Vitousek and Reiners (1975) and some additional streams to evaluate stream chemistry after continued forest aggradation that is occurring across New England. Although the relative patterns seen in the 1975 paper remained, nitrate and other ions were significantly lower in all streams 23 yr after the initial sampling, which was not predicted by the original hypothesis. During more than 50 yr of measurements at the Hubbard Brook Experimental Forest (HBEF) in New Hampshire, the forest in the reference watershed has aged from a mid-successional forest to a ~100-yr-old mature forest, and the net rate of live biomass accumulation at HBEF has been near or below zero since the early 1980s (Bernal et al. 2012). However, after a peak in the 1970s, nitrate export in streamwater from this watershed has steadily declined (Likens and Buso 2012, Bernal et al. 2012). Although levels of sulfate in precipitation have declined significantly across the region after passage and implementation of the Clean Air Act, levels of nitrate in precipitation did not respond

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as sharply or as quickly, and nitrate inputs via precipitation remain elevated across New England (Goodale et al. 2003, Bernhardt et al. 2005). Bernal et al. (2012) point out that bulk deposition of nitrate is similar now to levels in the early 1980s, but that nitrate export in streams has dropped by about $4 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. More significantly, they point out that during the 1970s the watersheds retained about 30% of external precipitation inputs, but by 2012 the watersheds retained about 90% of inputs. They concluded that changes in nitrate inputs could not account for declining nitrate export in these streams, as have others (Goodale et al. 2003, Bernhardt et al. 2005). I am proposing that this stream nitrate decline, and the greater N retention efficiency of the Hubbard Brook watersheds, is due to new inputs of high C:N woody debris that is causing the immobilization of dissolved N by microbes.

Vitousek and Reiners considered soil organic matter as part of the larger biomass pool that would be depleted as vegetation was harvested and accumulate as vegetation regrew. Lovett et al. (2018) point out that soil organic matter dynamics can be temporally displaced from vegetation dynamics, and argue that in early and midsuccession when biomass is actively increasing, trees “mine” the soil organic nitrogen (N) pool, and when trees no longer serve as a net sink of N the soil organic N pool reaccumulates. A prediction of this revised model is that N outputs from the ecosystem would not equal inputs until soil organic N reaccumulation ceases, which could lag by decades or centuries behind the N accumulation in vegetation.

Accounting for a pool of soil N that can be mined and rebuilt is certainly a valid and critical revision to the hypothesis, but it is unlikely to be the sole factor explaining the recent decline in nitrate in New England streams, and may not even be the most significant one. I argue that the unique harvest history of New England forests has had a significant effect on the recent pattern of nitrate output in streams. The peak of deforestation and agricultural activity across most of New England occurred from 1830 to 1880 (Thompson et al. 2013), and across much of New England, 60–80% of the land was cleared for pasture, tillage, orchards, and buildings (Peart et al. 1992). Much of the Hubbard Brook valley was heavily logged during the first two decades of the 20th century, and the hurricane of 1938 greatly affected older stands as well. I suggest that because logging and clearing occurred extensively and for over a century, coarse woody debris (CWD) that existed in the primeval forest had long since decayed, and woody debris did not accumulate on the forest floor during periods of active forest use. Similarly, with the absence of large trees, large coarse woody roots did not accumulate in the soil. As the eastern forests have regrown and forest cover of New England has expanded, forests have aged to the point in succession where tree mortality is now a meaningful dynamic in these forests. Yellow birch, the most abundant species in the Hubbard Brook valley, has

experienced the greatest mortality, but balsam fir, paper birch, sugar maple, and beech have all experienced increased mortality (Peart et al. 1992). All of this mortality means that there is an increasing supply of wood with a high carbon nitrogen ratio (C:N) that is being added to the forest floor, and an input of dead and now decaying high C:N coarse roots to the soil. Because microbes have a significantly lower C:N (~8) than wood (generally >200), theories of ecological stoichiometry (e.g., Elser et al. 2000) suggest that microbes will be limited by N when high C:N materials are added to the forest floor, and thus will immobilize available N from soil solution. This immobilization of N by the addition of high C:N materials has been widely observed in both field and laboratory settings (Homyak et al. 2008, Kaleem Abbasi et al. 2015). This suggests that high C:N woody materials can serve as a sink for soil N as the decomposer microbial community, primarily fungi, immobilizes N, leading to lowered leaching losses of N to streams and thus declining streamwater N concentrations.

Multiple lines of evidence suggest that woody debris can reduce N availability and N leaching to streams. Logs felled by hurricanes have been shown to reduce N availability in tropical forested ecosystems (Zimmerman et al. 1995), and woody debris added to forested soils have been shown to reduce N leaching and immobilize significant quantities of N by microbial biomass (Lajtha et al. 2005, Homyak et al. 2008). CWD from tree mortality in New England forests would certainly be expected to do the same. In addition, as old, large trees die, the biomass of decaying high C:N coarse roots in soils will increase, also serving as loci of microbial N immobilization. Thus, the recent accumulation of both above- and belowground CWD in New England forests could explain the lower nitrate concentrations in streamwaters draining mature stands. The effect of an input of high C:N material can be observed at any point along succession: the hurricane of 1938, for example, or any other catastrophic disturbance that resulted in extensive tree mortality, likely causes N immobilization and thus lower streamwater N loss.

The impact of forest cutting in the old-growth forests of the Andrews Experimental Forest in Oregon, where N deposition was several-fold lower than at Hubbard Brook and biomass C density is substantially greater, with large stocks of logs on the forest floor (approaching 200 Mg/ha in some watersheds), can help to illustrate the power of a large CWD sink. Nitrate leaching in the watersheds at the Andrews forest is about an order of magnitude lower than at Hubbard Brook, certainly partly caused by the lack of chronically elevated N in deposition. More significantly, forest harvest has little effect on nitrate loss to streams at the Andrews Forest, likely because of high C:N materials that can readily immobilize N released by N mineralization in slash and soil (Vanderbilt et al. 2003).

Results from Fisk et al. (2002) support this new hypothesis and support a profound role for CWD in ecosystem N dynamics. These authors found that detrital biomass, especially larger pools of CWD in maturing stands, resulted in greater microbial immobilization of N and corresponded to greater N retention in old-growth compared to maturing second-growth forests in northern hardwood forests in the western upper peninsula of Michigan. Patterns of nitrate leaching in their stands did not follow trends predicted by Vitousek and Reiners (1975); only increasing microbial immobilization of N by high C:N materials explained their observations.

Evidence suggesting that these forests can continue to accumulate C in soils come from studies of remnant stands of true old-growth in the eastern United States, which occupy about 1% of the current forested area. McGarvey et al. (2015) found that dead wood C density was 1,800% higher in these remnant old-growth forests than in the surrounding younger forests, suggesting that ecosystem C could increase for periods greater than a single century. Similarly, Zhou et al. (2006) provided evidence from forest age sequences that old-growth forest soils can continue to accumulate C even if live biomass is no longer increasing C stores.

If logs and coarse woody roots decomposed completely, they would serve only as temporary sinks for N during immobilization and not as a true longer-term sink of N. However, organic matter added to soils does not disappear completely even if log structure is no longer visible—if all plant inputs decayed completely, soil organic matter would not exist. Rather, there is ample evidence that woody debris contributes to soil organic matter accumulation. The FACE Wood Decomposition Experiment (FWDE) uses the unique $\delta^{13}\text{C}$ signature of wood that originated from two FACE sites to follow the fate of woody detritus in ecosystems by adding these isotopically labeled logs to the forest floor of forest that were not part of FACE experiments. After less than a decade, the isotopic signal of the wood was found not only in the forest floor but also in mineral soil (Trettin et al. 2018). vandenEnden et al. (2018) similarly saw chemical signatures of woody debris in soils after only 10 yr of woody debris additions to a forest in Michigan. Yanai et al. (2003) point out that CWD can be buried and not directly measured as forest floor material and thus escape ecosystem nutrient budgets. Although the contribution of woody debris to long-term pools of C will vary by ecosystem, Manies et al. (2005) estimate that between 10 and 60% of the deep-soil C along an upland chronosequence in boreal Manitoba is derived from wood biomass, suggesting that CWD can be a mechanism behind long-term soil C accumulation even in old-growth forests.

In many whole-watershed ecosystem models, retention or loss of N from the terrestrial watershed is measured by stream N output. However, we now recognize that stream nutrient output is an incomplete estimate of loss from the terrestrial system because of in-stream uptake

and losses (Burns 1998, Sudduth et al. 2013). Bernhardt et al. (2005) noted that at Hubbard Brook, as tree mortality increased with forest aging and as new organic debris dams formed in streams, heterotrophic assimilation of stream N increased. They also noted that the accumulation of these organic-rich sediments could serve as the loci for denitrification. Similarly, an influx of CWD after an ice storm at Hubbard Brook significantly reduced nitrate concentrations in streams (Bernhardt et al. 2003). In addition, old-growth watersheds with high loads of CWD export significantly more dissolved organic carbon (DOC) to streams than do younger forests (Lajtha and Jones 2018), and this additional dissolved C source can fuel denitrification. Stream DOC concentrations increase with forest age at Hubbard Brook (Cawley et al. 2014), and increasing DOC could be another mechanism for declining nitrate loss with increasing time and woody debris inputs to forests and streams.

These woody sinks are unlikely to saturate until the forests are harvested and/or are disturbed again, and the accumulation of these high C:N materials can serve as the mechanism behind the reaccumulation of the soil organic N pool. The revised model of Lovett et al. (2018) suggests that a replenishable soil organic N pool delays nitrate leaching by a few decades, after which inputs will again equal outputs. Adding an increasing stock of CWD with its associated N-rich microbial community to the model suggests that nitrate leaching will remain low until the forests are disturbed, or soil C accumulation ceases. Nitrate leaching should follow a pattern that diverges from the pattern initially predicted by the Vitousek and Reiners model (Fig. 1A, B). First, during forest regrowth after harvest, N leaching should be low as nutrients are sequestered in growing biomass. As forests age and net ecosystem production in vegetation returns to near zero, N output should increase, in line with the Vitousek and Reiners model. However, if tree mortality and inputs of CWD increase after peak net storage in regrowing vegetation, N losses to streams will remain low as long as accumulation of C in soils continues (Fig. 1C, D). Chronosequence studies suggest that soils in recovering forests sequester in the range of 0.2–3.0 kg C·ha⁻¹·yr⁻¹, and globally soils continue to sequester about 0.4 10¹⁵ g C/yr (Schlesinger 1990, Post and Kwon 2000). Assuming an average C:N ratio of 15 for Hubbard Brook soils (Aitkenhead and McDowell 2000), this results in a potential sink of up to 20 kg N·ha⁻¹·yr⁻¹, which is significantly larger than the N loss that needs to be explained (~4 g N·ha⁻¹·yr⁻¹, Bernal et al. 2012).

Further evidence that soil organic matter and litter C pools are dynamic rather than static, and can affect N leaching and retention, comes from a unique whole-watershed calcium addition experiment at Hubbard Brook. Decades of acidic inputs to eastern forests caused profound changes to soil chemistry, including a lowering of soil pH and declines in acid-neutralizing capacity. Calcium in soil and streamwater has been severely

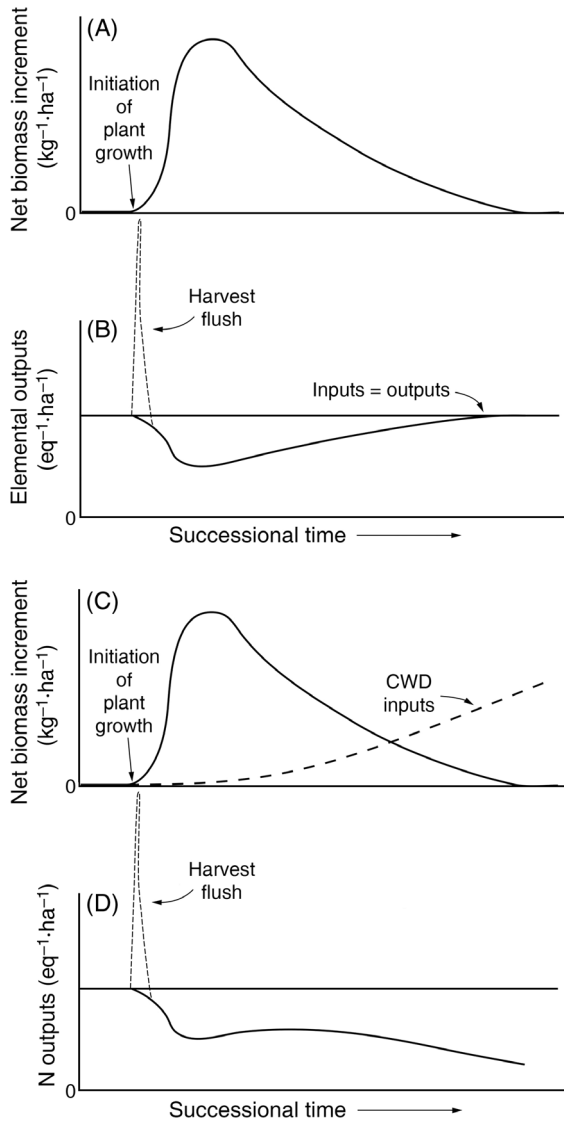


FIG. 1. Upper panels: comparison of the trajectories of (A) net biomass increment and (B) N loss over successional time according to the Vitousek and Reiners (1975) hypothesis. In this model, vegetation biomass increment is the primary control on N loss to streams, and when net biomass increment returns to near zero, N losses equal N inputs in precipitation. Lower panels: the addition of (C) an increasing pool of coarse woody debris causes increased N immobilization by microbes, and thus both vegetation dynamics and the input of high C:N detrital materials control (D) N loss to streams. Because woody debris inputs are greater now in New England forests than during periods of prolonged forest harvest, N loss to streams is declining. A similar critical role of woody debris on stream N dynamics will be observed whenever disturbance causes large inputs of woody debris to the ecosystem.

depleted at Hubbard Brook since the onset of these acidic inputs (Likens et al. 1998), and Goodale et al. (2003) found a 24% reduction in calcium compared to values reported by Vitousek and Reiners in 1975. The calcium addition experiment was initiated in one

watershed at Hubbard Brook in 1999 and had the goal of replacing all the calcium that had been lost historically through the addition of CaSiO_3 , or wollastonite (Cho et al. 2009). This addition increased the pH and acid-neutralizing capacity of soils and streamwater, as expected. Forest growth increased, and researchers expected this additional growth to lead to streamwater reductions in nitrate as N was sequestered in growing biomass. Although initial reports did not find a relationship between calcium status and either nitrification or stream N leaching after wollastonite additions (Groffman et al. 2006), by 2013, 30 times greater dissolved inorganic N was exported from the wollastonite-treated watershed than from reference watersheds (Rosi-Marshall et al. 2016), contrary to trends predicted by the Vitousek and Reiners (1975) hypothesis. However, forest floor and surficial mineral soil C content in the CaSiO_3 -treated watershed declined by 40% over this time period, likely because of enhanced microbial activity (Johnson et al. 2014). Because this loss of soil organic matter was greater than the increase in living biomass, there was a net release of organically bound N from the wollastonite-treated forest. The rise in soil pH may also have increased nitrate production in forest floor soils (Duggin et al. 1991), leading to enhanced nitrate output in streams. These results also suggest that decades of acidic inputs may have enhanced both C and N sequestration in forest floor mass through negative effects on the decomposer microbial community, although this suppression of organic matter decomposition would have to be compared to the depression in forest biomass growth to determine if N sequestration would have been positive or negative.

In summary, the original model developed by Vitousek and Reiners in the 1970s was influenced by the unique history of eastern U.S. forests, including decades of acidic precipitation and elevated N inputs, and historic deforestation and loss of CWD inputs. Adding in a role for the accumulation of high C:N detritus, and documenting the fate of the increased above- and below-ground woody inputs, can only serve to make this model of nutrient response to forest succession more robust and more universal. I am here arguing that the influence of CWD inputs to both soils and streams on N immobilization in both soils and in streams, as well as on denitrification in streams, is a valid hypothesis for consideration to help explain the declining nitrate concentrations observed in Hubbard Brook and the surrounding region. CWD has been shown to be important for ecosystem C budgets (Harmon and Marks 2002, Liu et al. 2006, Manies et al. 2005) as well as for forest ecosystem services and biodiversity. Less well studied are the impacts of inputs of high C:N coarse roots directly to soil (Sollins 1982). Few studies or models have attempted to calculate the impacts of CWD decomposition products to the retention of C and N in forested ecosystems and their receiving streams, but evidence from the literature suggests that CWD can significantly

affect biogeochemical cycles, nutrient retention by terrestrial ecosystems, and stream nutrient exports.

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