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Forests weather soil cations and lose them to streams

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Models of forest ecosystem dynamics (1, 2) and their response to human impacts have time scales of decades, yet data supporting these models are almost never as long. To solve this problem, ecologists have used paleoecological approaches (3) or space for time substitution (4, 5). Such chronosequence approaches are powerful, but nonetheless have limitations (6). Best would be a time series from a single location. Hubbard Brook Experimental Forest (Hubbard Brook), has such a record with weekly measures of precipitation inputs and stream water exports of elements for >60 y. Such a time series record can show biogeochemical change over forest development via direct observation combined with whole watershed experiments. Canonical studies from Hubbard Brook have shown the long-term effects of acid rain (7) and response to forest disturbance (8). This ever-extending time series allows new understanding of forest biogeochemical dynamics, clearly shown in ref. 9. This paper examines the biogeochemical basis of forest recovery following harvest across a backdrop of acid precipitation to show how plant-driven mineral weathering can drive long term change in watershed cation export (9).

Biogeochemical trajectories at Hubbard Brook are a function of long term impacts, and now recovery, from acid deposition superimposed on recovery from initial forest harvest >100 y ago (7). More recent deforestation experiments have shown additional strong biotic control

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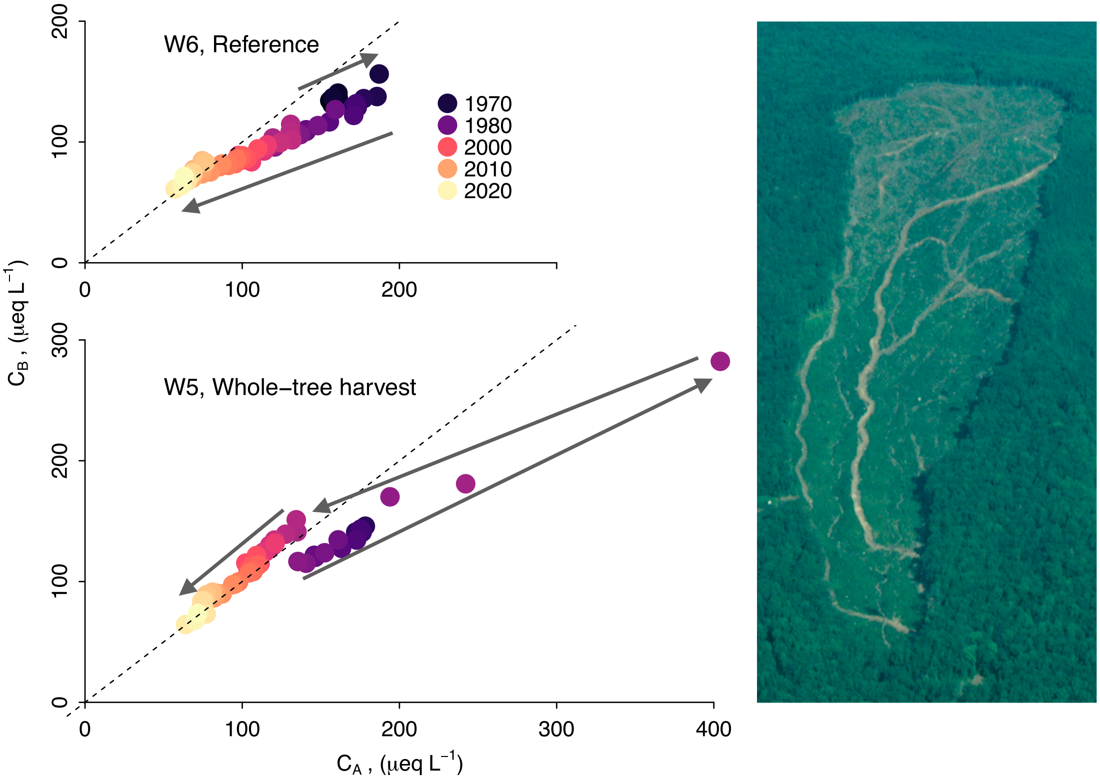

Fig. 1. Forest harvest of Watershed 5 at Hubbard Brook altered the time trajectory of stream export of base cations and acid anions relative to the biogeochemical reference, Watershed 6. Base cations (C_B) are the sum of charges of Na^+, K^+, Ca^{2+}, Mg^{2+}. Acid anions (C_A) are the sum charges of NO_3^-, SO_4^{2-}, and Cl^-. Points are connected by time flowing from dark to light on the color scale. Gray arrows show the time trajectory. Note that following an initial flush of anions and cations following harvest of W5, cation export (mostly Ca^{2+}) increased relative to anions due to increasing weathering of Ca^{2+}. The dotted line is 1:1. Photo is post-harvest Watershed 5. Photo courtesy of the US Forest Service, Northern Research Station. Data derive from ref. 11. Image credit: US Forest Service, Northern Research Station, licensed under CC BY-SA 4.0.

over element export via huge losses of NO_3^- and cations following harvest and rapid recovery upon plant regrowth (8, 10). But long-term data show that these experimentally cut watersheds do not fully recover to the reference condition; instead they continue to lose Ca^{2+}. For example, Hubbard Brook researchers clear cut Watershed 5 (W5) in 1983–1984 and removed all aboveground tree biomass from the watershed. Following harvest, base cation export increased immediately, a response that mirrored previous experiments (10). Bernhardt et al. show that following this initial flush of ions, Ca^{2+} export remained increased for the past 40 y relative to that from the biogeochemical reference, Watershed 6 (W6) (Fig. 1) (9). Varying hypotheses suggested mechanisms, from calcium oxalate in soils to weathering of apatite (12). Bernhardt et al. expand on these ideas and suggest that plant driven weathering of subsurface soils is increasing Ca^{2+} export by streams.

> **This paper examines the biogeochemical basis of forest recovery following harvest across a backdrop of acid precipitation to show how plant-driven mineral weathering can drive long term change in watershed cation export (9).**

The key clue in ref. 9 was linking SiO_2 exports with Ca^{2+}. High SiO_2 exports had been noted before and ascribed to a large pool of amorphous silica. But the ratio of Ca^{2+} to SiO_2 exports provided evidence that increased mineral weathering of silicate-armored apatite provides the source of both Ca^{2+} and SiO_2. This Ca^{2+}:SiO_2 ratio is remarkably similar in both W5 and the reference W6. The ratio is much higher in W1, the watershed with experimentally added, and highly weatherable, $CaSiO_3$. The mechanism of this increased weathering was organic acids produced by photosynthesis and exuded via roots. Evidence for this mechanism lies in a third element of interest: increased dissolved inorganic carbon (DIC) in stream water because of both increased root respiration and respiration of these organic acid exudates. This DIC enters streams in baseflow and is much higher in W5 during summer than in the reference watershed, W6. Further evidence supporting the mechanism of plant-driven weathering is that American beech (*Fagus grandifolia*) is the dominant tree on W5 versus sugar maple (*Acer saccharum*), a tree with declining dominance throughout Hubbard Brook. Beech has ectomycorrhizal fungi that can produce organic acids promoting weathering of apatite (12), and it has lower nutrient requirements than sugar maple.

Why have trees increased mineral weathering? Bernhardt et al. suggest severe nutrient limitation, in particular phosphorus (P), following harvest drives this response (9). Phosphorus is locked up in apatite and weathering releases it, albeit slowly. This response take decades and has not yet met the demand of the recovering plant production. A simple mass balance provided evidence. Whole tree harvest of W5 in 1983–1984 removed an estimated 90 kg P ha^{-1} from the watershed as plant matter. This amount represents a large fraction of the biologically cycling P. (13). Given stoichiometry of Ca^{2+} to P in apatite it is possible to estimate the P released from this plant-enhanced weathering: ~70 kg P ha^{-1}, which is in the range of what was lost from the watershed as harvest. A simpler way to address this hypothesis would be to examine fluvial outputs of phosphorus, but P is cycled so tightly, no matter the watershed fertility status, that only a vanishingly small amount exits via the stream. Thus there is no way to use stream P export as a measure of the degree to which P might be limiting productivity in a watershed. Stream fluxes are about 0.04 kg P ha^{-1} y^{-1} and are mostly due to transported leaf litter (14), which is not under any sort of biological control. Internal cycling and stocks within the watershed are much higher; vegetation uptake flux is 10 kg P ha^{-1} y^{-1} and standing stock in the vegetation and forest floor is 150 kg P ha^{-1} (13). Thus the weathering inputs, 2 kg P ha^{-1} y^{-1} greatly exceed fluvial export, yet are only 20% of annual P uptake by vegetation in a mature forest (13).

Implications of this increased weathering of Ca^{2+} may extend to downstream ecosystems. Increased Ca^{2+} in stream water will increase alkalinity and pH, thus giving the impression that streams are recovering from acidification while the forest continues to lose base cations. Watershed 1 (W1) received a $CaSiO_3$ treatment (1,200 kg Ca^{2+} ha^{-1}) in 1999 that essentially doubled the stock of exchangeable Ca^{2+}. This Ca^{2+} increased stream water export in W1 relative to the reference watershed by 200 kg Ca ha^{-1}. Watershed 5 had a different response, export of Ca^{2+} derives from weathering mineral soil and the watershed is losing Ca^{2+} as it recovers from harvest. In addition to increased Ca^{2+} export, higher DIC in stream water from root and soil respiration increases both CO_2 emissions from streams and alkalinity export to downstream ecosystems. Streams are large sources of CO_2 to the atmosphere, and much of this CO_2 derives from groundwater transporting terrestrially derived CO_2 to streams (15). Thus it is possible that the root derived CO_2 will emit to the atmosphere, but not through the soil, but rather via the stream at a location further down the river network.

Three lessons emerge from this research. 1) Whole watershed experiments are necessary to allow testing of biogeochemical mechanisms. Disturbing biogeochemical cycling allows understanding controls upon these cycles. This point was clear in 1970 (10), and Bernhardt et al. show how we can still learn from these experiments, even four decades after the manipulation. Future large scale experiments will continue to provide these insights. 2) Watershed-scale studies need to address multiple elements, because often the behavior of one element can be only understood by that of another (16). The stoichiometric match of Ca^{2+} export to SiO_2 provides strong evidence of weathering liberating the crucial element, P, for plant nutrition. Increased DIC export suggested plant exudates as the cause. Studying any one element in isolation would have provided insufficient means to identify the plant-enhanced weathering mechanism (9). 3) The third lesson is easy to state, but harder to execute: Maintaining long term biogeochemical records, such as those at Hubbard Brook, is essential to understand how ecosystems will respond to long term environmental change. The biogeochemical record at Hubbard Brook (and anywhere else) becomes more valuable as it lengthens. Decadal- and soon century-level changes are simply not predictable or even visible with shorter time series. Even without invoking secular changes to biogeochemical cycling, solute exports from watershed vary over no characteristic time scale (17). Bernhardt et al. (9) provide yet more evidence how assessing a forest response to disturbance requires decades to assess. Climate change is another forcing variable for watershed ecosystem function (18), and it may be another 5 to 100 y to evaluate these responses. The invaluable (and easily accessible) biogeochemical time series record from Hubbard Brook (19) is ones of the best possible tools that ecologists can use to understand how climate change, pollution, and land management will alter ecosystems in unforeseen ways.

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