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Tree Harvest in an Experimental Sand Ecosystem: Plant Effects on Nutrient Dynamics and Solute Generation

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Abstract

The hydrochemical signatures of forested ecosystems are known to be determined by a time-variant combination of physical-hydrologic, geochemical, and biologic processes. We studied subsurface potassium (K), calcium (Ca), and nitrate (NO_3) in an experimental red -pine mesocosm to determine how trees affect the behavior of these nutrients in soil water, both during growth and after a harvest disturbance. Solution chemistry was monitored for 2 years at the end of a 15-year period of tree growth, and then for 3 more years after harvest and removal of aboveground biomass. Concentrations were characterized by three distinct temporal patterns that we ascribe to changes in solute generation mechanisms. Prior to harvest, K soil-water concentrations were relatively uniform with depth, whereas Ca soil-water concentrations doubled with depth. Nitrate concentrations were below detection in soil water and discharge (drainage) water. Plant uptake and water/nutrient cycling exerted strong control during this interval. During the 1st year after harvest, K concentrations tripled in shallow soil water, relative to preharvest levels, and showed a strong seasonal peak in discharge that mimicked soil temperature. Summer soil temperatures and annual water flux also increased. Decomposition of labile litter, with complete nitrogen (N) immobilization, characterized this interval. In the third interval (years 2 and 3 after harvest), decomposition shifted from N to carbon (C) limitation, and Ca and NO_3 concentrations in discharge spiked to nearly 200 and 400 μM, respectively. Relatively stable ionic strength and carbonate chemistry in discharge, throughout the study period, indicate that carbonic-acid weathering was sustained by belowground decomposition long after the harvest. This stable chemical weathering regime, along with the persistence of N limitation for a long period after disturbance, may be characteristic of early-phase primary-successional systems.

Key words: biocycling; nutrient cycling; ecosystem disturbance; ecosystem regulation; mesocosm; calcium; potassium.

Introduction

Bormann and Likens (1967) described the use of small monitored watersheds to study nutrient cycling of intact and experimentally manipulated

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forested ecosystems through time. They proposed a nutrient flux and cycling model focused on biologic, geologic, and meterologic processes, both internal and external to the system, that govern ecosystem nutrient status as it responds to development or to disturbance (Likens and Bormann 1995; Bormann and Likens 1979). Application of the nutrient flux and cycling model to studies of ecosystem disturbance has borne fruit at the Hubbard Brook Experimental Forest (HBEF) (Bormann and others 1974; Hornbeck and others 1986) and elsewhere (for example, Jewett and others 1995). There is now broad recognition that nutrient losses associated with disturbance are due to combinations of changes in water and nutrient uptake, chemical weathering, and decomposition processes that together constitute transient loss of ecosystem control over internal nutrient pools (for example, Likens and others 1970; Dahlgren and Driscoll 1994; Schlesinger 1997). However, watershed-scale mass balance models are limited in their ability to test ideas about how specific sources and/or processes contribute to the nutrient losses, and how these contributions vary with stage of ecosystem development (for example, Vitousek and Reiners 1975; Gorham and others 1979).

The Hubbard Brook sandbox experiment was established in 1982 to reapply the small-watershed technique to outdoor mesocosms characterized by carefully documented construction and uniform initial conditions in the subsurface (Bormann and others 1987). Three sandboxes have water samplers along soil-water flowpaths and are plumbed to measure water drainage from the system. With this experimental control, researchers have isolated and examined processes obscured by complexity and heterogeneity in larger natural systems such as sources of nitrogen (N) to plants (Bormann and others 1993, 2002), chemical weathering and cation exchange (Berner and Rao 1997; Berner and others 1998), hydrology (O'Brien and others 2004), and weathering rates and consequences for nutrient availability (Bormann and others 1998; Kauffman and others 2003).

More recently, we conducted a tree harvest experiment in one of the sandboxes. Our goal was to further elucidate the mechanisms of ecosystem control that result from the interaction of biota and their resources (energy, nutrients, water, space). In this work, we observe how vascular plants affect potassium (K), calcium (Ca), and nitrate (NO_3) in soil water, both during growth and after a harvest, and we identify the processes generating these solutes. By harvesting only the aboveground biomass and minimizing physical disturbance to the soil, we examined compensatory ecosystem processes when root uptake and photosynthesis are abruptly terminated. We also compared growth and harvest effects to baseline changes in an adjacent undisturbed, nonvascular sandbox.

Our objective was to address the following research questions: (a) How do the distributions and dynamics of K, Ca, and NO_3 change in response to aboveground biomass removal and what causes these changes? (b) How does the degree of soil development influence the response to such a disturbance? We hypothesized that immediate increases in soil temperature, soil moisture, decomposition rates, and water discharge would cause large and immediate increases in all nutrient concentrations and fluxes (for example, Bormann and Likens 1979). However, due to small amounts of organic matter and weak soil development in the sandbox, we also hypothesized that our observed concentration changes would be smaller, and of shorter duration, than changes reported from an analogous harvest of a forested watershed with a well-developed soil.

Background and Methods

Study Location

The HBEF is located in the White Mountains of north-central New Hampshire, USA, and encompasses an area of 3,160 ha. In 1982, 18 sandboxes were constructed and planted with various tree species to study N cycling (Bormann and others 1987). The sandboxes are located approximately 200 m east of HBEF weather station 22, where daily temperature, precipitation amount, and wet/dry deposition data are collected. Mean daily air temperatures at HBEF range from 19°C in July to −9°C in January (Federer 1973). Precipitation averages nearly 130 cm/y for the Hubbard Brook area, averaging 70% as rain and 30% as snow (Bormann and Likens 1979).

Forest floor soil was removed to facilitate the mechanical excavation of square holes for the sandboxes in the underlying well-drained glacial deposits (Bormann and others 1993; details in Ingersoll and others 1987). Three of the larger sandboxes, measuring 7.5 × 7.5 × 1.5 m, were fully lined with impermeable Hypalon geomembrane. Slotted polyvinylchloride (PVC) pipe was placed in a 15-cm layer of 1.9–3.8 cm–diameter gravel in the bottom of these boxes to collect drainage water. The pipes drain into tipping buckets to enable volumetric discharge measurements. The boxes were filled to

ground level with 1.3 m of granitic glaciofluvial sand (no more than 0.95 cm). Then 5 cm of native topsoil was rototilled into the top 20 cm of the sand. Beneath this depth, the average grain-size distribution of the sandboxes was 94% sand, 4.5% silt, and 1.5 % clay particles (O'Brien and others 2004).

Two of these sandboxes were studied for this work. One sandbox, referred to as the ''nonvascular'' box, was actively weeded of vascular plants until it was eventually colonized by a lichen (*Cladonia cristatella* Tuck.) and moss (*Polytricum* spp.). Another sandbox, called the ''red pine'' box, was planted with 196 red pine (*Pinus resinosa* Ait.) seedlings in a 0.5-m nodal grid, providing each tree with 0.25 m^2 of growing space. The sandboxes have been as undisturbed as possible, with minimal intrusions including occasional weeding, soil sampling, installation of sampling equipment, and one-time replanting of failed red pine seedlings (Ingersoll, and others 1987). Statistical inference is limited to changes through time in the red pine and nonvascular sandboxes. Standard deviations are provided to describe sample variation within the boxes.

On 1 May 1998, the trees in the red pine box were carefully harvested by hand and all aboveground biomass was removed from the box, leaving only the stumps, roots, and a 5–8 cm-thick layer of twigs, branches, and needles (referred to hereafter as the ''litter layer'') in place. Physical disturbance of the box during the harvest was minimized by the use of wood planks placed upon the stumps to stand and walk on.

Data Collection

Precipitation amounts and samples for chemical analysis were collected from US Department of Agriculture Forest Service weather station 22. Bulk precipitation samples were analyzed at the Institute of Ecosystem Studies, Millbrook, NY for major cations and anions (Na^+, K^+, Ca^{2+}, Mg^{2+}, NH_4^+, NO_3^-, Cl^-, and SO_4^{2-}) (O'Brien 2000). In 1995, soil-water samplers consisting of a fritted glass plate on a cylindrical collection chamber (approximately 50 cm^3), connected to a vacuum pump maintaining a negative pressure equivalent to 255 cm H_2O, were installed laterally in both boxes at depths of 15, 35, and 95 cm below ground surface, with three replicate samplers at each depth (O'Brien 2000; O'Brien and others 2004). Samplers were flushed of any resident liquid prior to each 24-h sampling period.

Soil-water samples were filtered through a 0.2-μm nylon filter in the field, with one aliquot frozen for anion analysis and a second aliquot acidified to below pH 2.0 with HCl for cation analysis. Anions were quantitatively determined by ion chromatography (IC), and cations by either IC (1996–1997) (O'Brien 2000) or inductively coupled plasma spectroscopy (ICP) (1998–2000) (Havig 2002). Discharge-water samples were collected from both sandboxes, volume-weighted, and analyzed at Yale University for major cations using ICP and anions using IC. All ICP and IC analyses had a standard deviation of <5% (Berner and others 1998). Dissolved organic carbon (DOC) and total dissolved N (TDN) were measured by high-temperature catalytic oxidation; dissolved organic N (DON) was determined by the difference between TDN and dissolved inorganic N.

When the trees were removed, aboveground living biomass was separated into foliage, stem, and branches for analysis of biomass weight and nutrient content. Soil cores were collected in each sandbox at multiple locations and at three different times for cation extraction using a conventional ammonium-acetate procedure (Havig 2002). Extractable concentrations reported here correspond to ''exchangeable'' pools in much of the literature (for example, Jobbagy and Jackson 2001).

Results

Data are presented in the context of the three distinct periods that emerged: preharvest, 1 year after harvest, and 2–3 years after harvest.

Preharvest Period

For the 2 years prior to harvest, there were large differences in sandbox discharge and soil temperature between the red pine and nonvascular sandboxes. Water discharge from the red pine sandbox was less than one-half of the discharge from the nonvascular box in water year 1996 and one-fourth of the nonvascular discharge in water year 1997 (Figure 1). The difference in maximum summer soil temperature in the upper 35 cm between the sandboxes was approximately 10°C, with the red pine sandbox having a lower temperature.

Clear patterns in red pine subsurface concentrations of K (Figure 2a) were difficult to discern prior to harvest; red pine ranges were similar to those observed in the nonvascular sandbox (Figure 2d). At some times, the K concentration was greater in shallow red pine soil water than in discharge. However, Ca concentration during the same time period was distinctly different between the boxes.

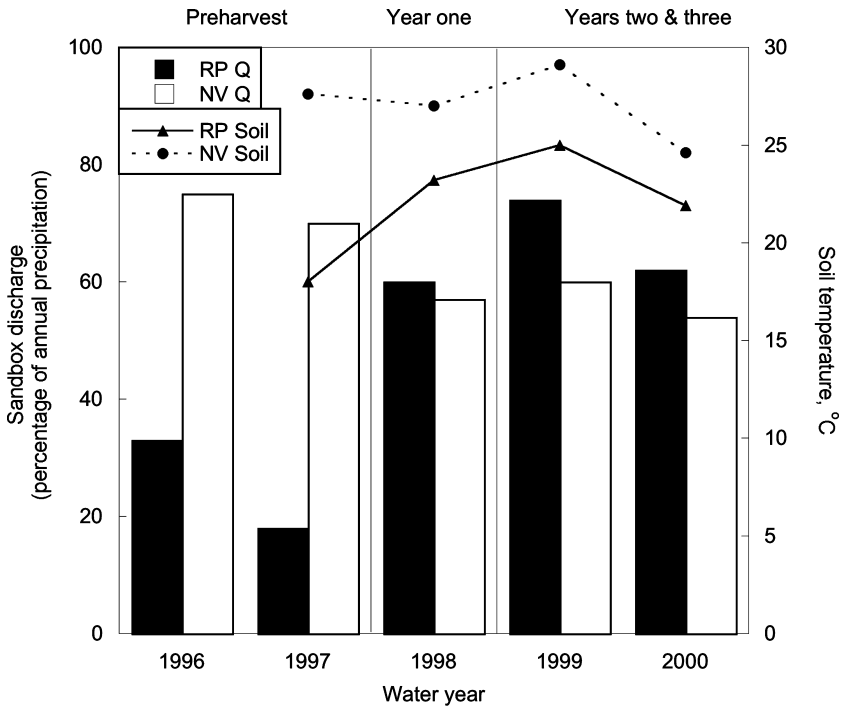

Figure 1. Discharge and soil temperature patterns over time for the red pine (RP) and nonvascular (NV) sandbox ecosystems. Discharge is reported as the percentage of total precipitation for each water year. Soil temperature is mean maximum for the upper 35 cm in each sandbox.

Soil-water concentrations in the red pine sandbox increased with depth, with mean concentrations at 95 cm more than twice as large as concentrations at 15 cm (Figure 2b). In the nonvascular sandbox, no such increase was evident (Figure 2e). While trees were growing, there was also a difference between the two sandboxes in NO_3 patterns. Preharvest NO_3 concentrations in the red pine sandbox (both soil water and discharge) were almost always below the detection level of 2 μM (Figure 2c). Shallow NO_3 concentrations in the nonvascular sandbox (15-cm depth) were as large as 50–100 μM, but concentrations in deeper soil-water and discharge never exceeded 40 μM (Figure 2f).

Soil-extractable cation concentration profiles (Figure 3) reflect 1998 conditions immediately before red pine harvest. At many depths, the differences between the sandboxes were not statistically significant, but the consistencies of the differences over substantial depth intervals are important. The red pine extractable-K profile showed enrichment relative to the nonvascular profile, particularly in the upper 15 cm. The Ca profile, by contrast, showed general depletion in the upper part of the sandbox relative to the nonvascular profile, with slight enrichment in the top 15 cm. The red pine patterns are similar to the patterns shown by the depth profiles of red pine soil-water concentrations described above: little change in K with depth below 15 cm and large increases in Ca with depth below 15 cm.

Year 1 after Harvest

After removal of the trees, water discharge from the red pine box increased significantly during the first year and was equivalent to nonvascular discharge (Figure 1). Loss of tree canopy increased the maximum summer red pine soil temperature by approximately 5°C in the upper 35 cm of the sandbox (Figure 1).

In shallow red pine soil water (15-cm depth), K concentrations more than doubled during the first growing season after harvest (Figure 2a). Concentrations of K in red pine discharge began to show a clear seasonal pattern with a strong correlation to soil temperature; red pine discharge concentrations were two to three times larger than those from the nonvascular sandbox (compare Figures 2a, d). In contrast, the range of subsurface Ca concentrations in the red pine sandbox did not deviate from the preharvest period (Figure 2b). Nitrate concentrations in the red pine sandbox also remained unchanged through out the first growing season, but they increased slightly during the first winter (Figure 2c). The observed stability of Ca and NO_3 is contrary to our hypothesis of rapid increases in all nutrient concentrations after harvest.

Years 2 and 3 after Harvest

Water discharge from the red pine sandbox exceeded discharge from the nonvascular sandbox by

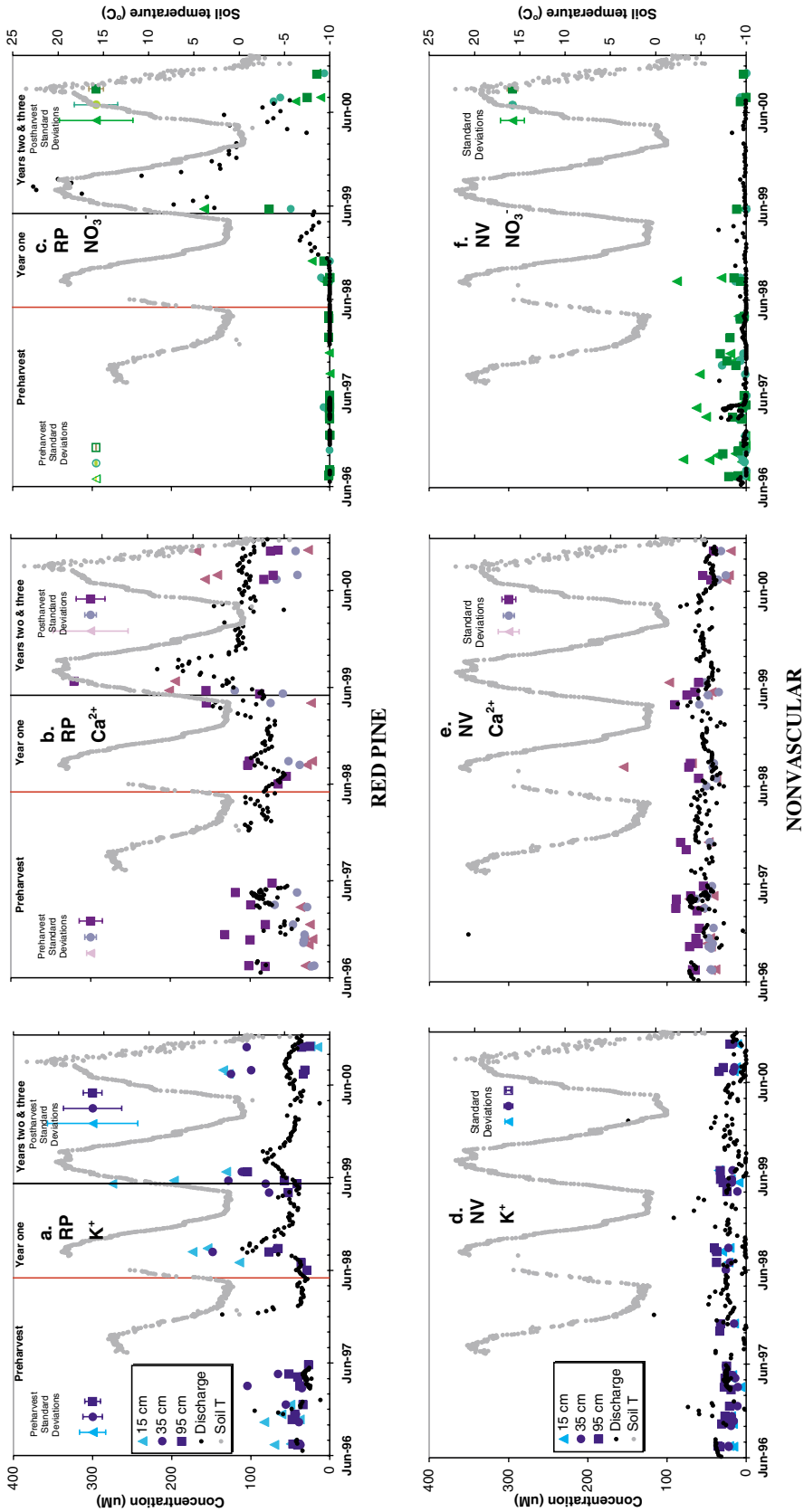

Figure 2. Nutrient concentrations over 5 years in *RP* and *NV* sandbox ecosystems. Red vertical line indicates harvest. *Black dots* represent sandbox discharge samples; *color symbols* represent soil-water samples at various depths (*triangles*: 15 cm; *circles*: 35 cm; *squares*: 95 cm). Standard deviations are reported among replicates. Soil temperature (*grayscale*) is at 95-cm depth. *K*, potassium, *Ca*, calcium, NO_3 nitrate.

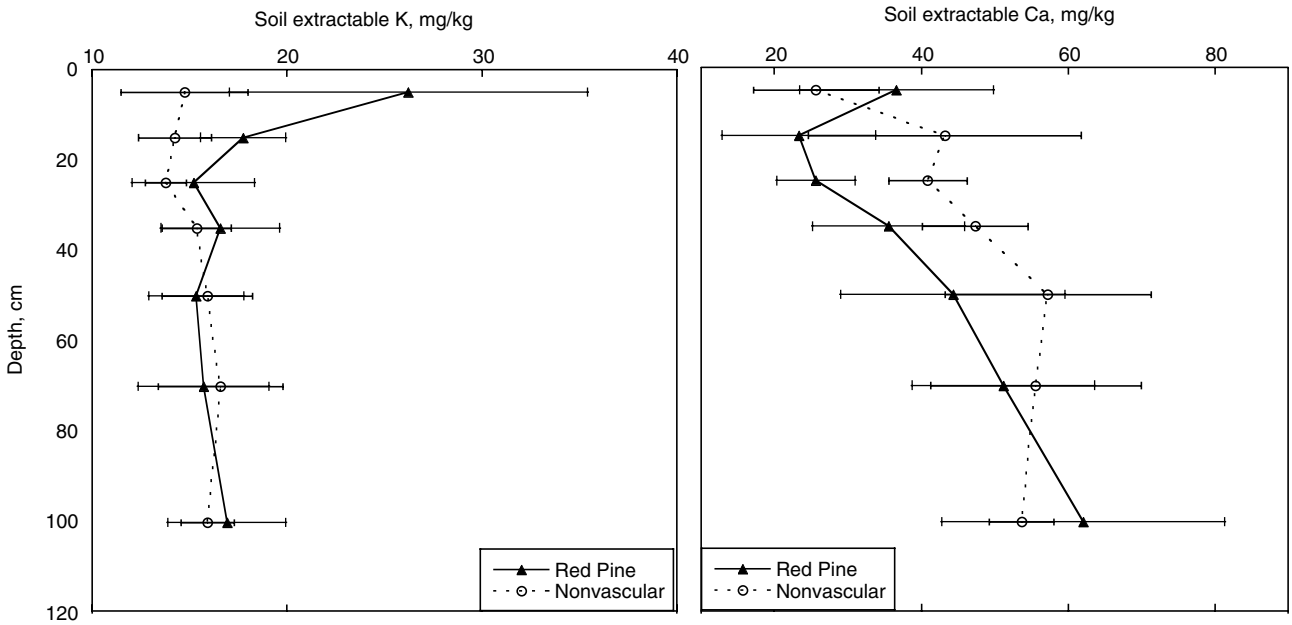

Figure 3. Depth profiles of soil-extractable potassium (K) and calcium (Ca) concentrations for the RP and NV sandboxes. Soils were sampled in 1998 immediately prior to RP harvest. Each point represents the mean of eight replicate cores centered at the plotted depth.

14 and 8% during years 2 and 3, respectively. Maximum soil temperature in the red pine sandbox continued to increase; by year 3 after harvest, there was less than a 3°C temperature difference between the sandboxes (Figure 1).

Potassium concentration patterns in the red pine sandbox continued from year 1 into years 2 and 3. Elevated concentrations occurred in shallow soil water, and the seasonal variation in discharge continued (although the magnitude of variation decreased each year). Dramatic changes to both Ca and NO_3 concentrations occurred during year 2 after harvest, when concentrations more than doubled and discharge began to clearly show seasonal fluctuations that mimicked soil temperature. The magnitude of the concentration fluctuation for NO_3 during year 2 was almost double that for Ca (Figure 2b,c).

By year 3, observed increases for all measured solutes (K, Ca, NO_3) had decreased to levels only slightly elevated relative to preharvest conditions (Figure 2a–c). In watershed 2 (W2) of the HBEF, concentrations of these nutrients in streamwater remained strongly elevated for at least 5 years after harvest, that is, through 3 years of regrowth suppression and a substantial period afterward (Bormann and Likens 1979). Thus, our hypothesis of a shorter-duration response to harvest appears to be supported.

Discussion

The observed time sequence of hydrochemical patterns results from abrupt cessation of plant uptake and cycling of water and nutrients, and accompanying changes in decomposition regimes. These events are superposed upon ongoing carbonic-acid weathering. Our understanding of the progression of these processes is illustrated in Figure 4.

Plant Cycling of Nutrients and Water (top row, Figure 4)

Potassium and Ca play different roles in plant growth and metabolism, so their preharvest distributions, and responses to disturbance, may be expected to differ. Potassium is actively redistributed by biochemical cycling within plants (for example, Perry 1994) and subject to relatively large rates of leaching from the labile components of tree canopy and litter tissues (Chapin 1980). We attribute the occasional preharvest elevation of shallow soil-water K relative to discharge (Figure 2a), and the accompanying increase in extractable K for shallow soil (Figure 3), to the presence of dissolved K in shallow soil water generated by leaching of canopy and litter tissue and by plant-driven weathering in the rhizosphere (April and Keller 1990). Rapid uptake from soil water by the roots of the growing trees is likely in the surface soil, because this is

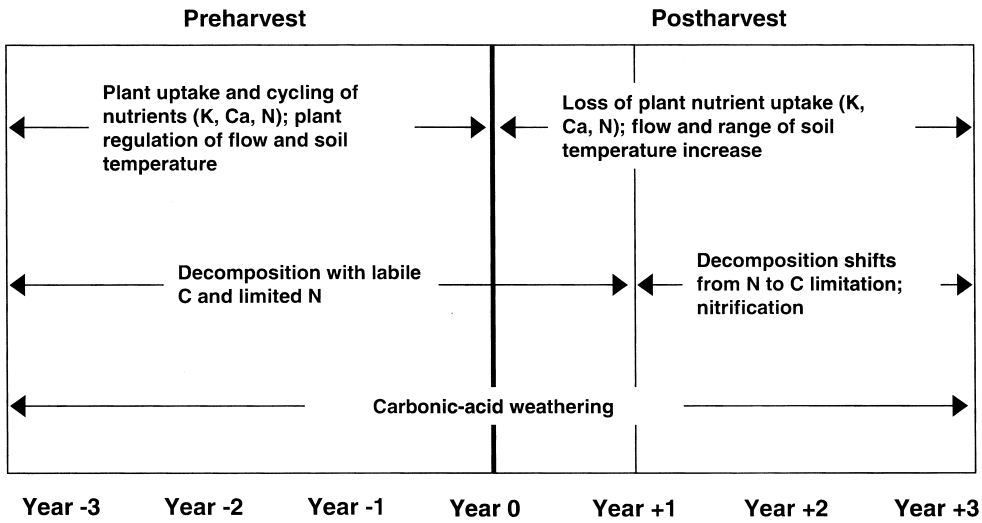

Figure 4. Conceptual model for progression of subsurface processes in response to aboveground biomass removal, based on results of the sandbox harvest experiment. *K*, potassium, *Ca* calcium, *N* nitrogen, *C* carbon.

where availability is the highest. The shallow accumulation of soil K is typical of global soil exchangeable-K patterns (Jobbagy and Jackson 2001), where such a pattern is characteristic of a nutrient for which plant demand is large relative to soil supply. The relatively small K concentrations typical of deep soil water and discharge during the preharvest interval (Figure 2a) may thus be understood as the consequence of strong biocycling of a limiting nutrient. The chemical signal observed in the discharge water is generated by the processes taking place in the active shallow layer. When plant uptake stopped at harvest, K concentrations in soil water and discharge increased rapidly.

Calcium, by contrast, is concentrated in structural components of plant tissue and is much less subject than K to internal redistribution and release during tree growth (Chapin 1980). However, decomposition of leaf tissue and fine roots still creates a recycled flux of soluble Ca as evidenced by the slight reversal in the depth profile of extractable Ca in the topmost layer of soil (Figure 3). This profile, coupled with the observation of lower bulk water concentrations of Ca in shallow samples in the pre-harvest condition (Figure 2b), suggests that in contrast to K, preharvest discharge-water chemistry is dominated by solute-generation processes in the lower part of the soil profile.

Because there was approximately as much Ca as K in red pine biomass when the trees were cut (T. Coe, personal communication), and given the negligible inputs of both elements to the sandbox in precipitation (Havig 2002; O'Brien 2000), cumulative tree Ca uptake from shallow sandbox soil over the 15 years prior to harvest must have been similar in magnitude to cumulative tree K uptake. Given this, our preharvest observation of small soil-water Ca concentrations in the shallow subsurface (Figure 2b) is noteworthy and implies that growing tree roots and their fungal associates take up Ca directly from mineral and/or exchanger surfaces, rather than from solution in bulk soil water. Variants of this idea have been proposed in the context of Ca-budget and microscopic weathering studies by, for example, Blum and others (2002), Wallander (2000), and Balogh and others (2004). The lack of rapid increases in shallow, soil-water Ca- concentration after harvest (Figure 2b)—unlike those seen with K—is consistent with the sequestration of Ca in relatively recalcitrant plant tissue. The shallow depletion of Ca in preharvest shallow red- pine sandbox soil (Figure 3) is typical of the global pattern of exchangeable Ca (Jobbagy and Jackson 2001), where increases with depth are characteristic of a nutrient for which soil supplies are large relative to plant demand.

The increase of red pine water-discharge after harvest (Figure 1) shows how the growing trees exerted control of subsurface water fluxes by water uptake and transpiration during the preharvest interval. Increased postharvest water fluxes caused increased rates of nutrient loss.

Decomposition and Nitrification (middle row, Figure 4)

Tree harvest terminated subsurface photosynthate supplies and root respiration, making decomposition the dominant postharvest biologic process generating solutes. During the year-1 growing season, an unprecedented 5-month pulse of K was observed in discharge (Figure 2a), with K concentrations exceeding Ca concentrations for 6 weeks in August and September (Figure 5). The hydro-

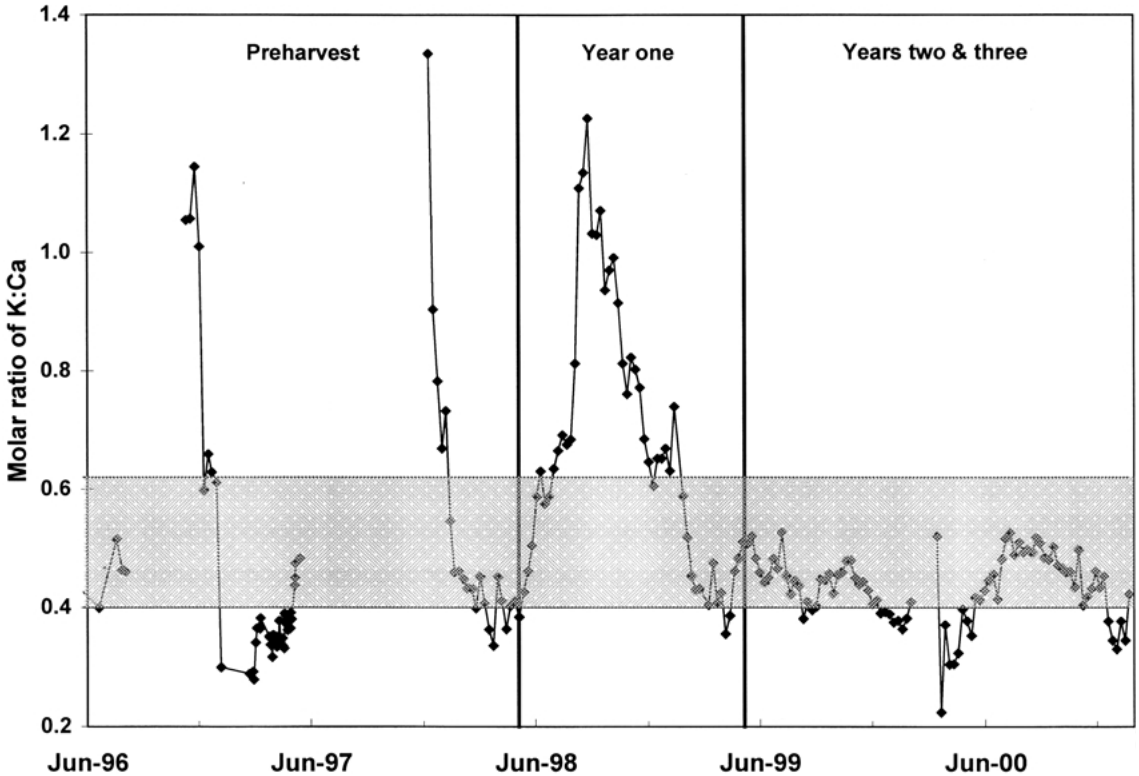

Figure 5. Ratio of potassium–calcium (K:Ca) concentrations in RP sandbox discharge. Gaps in the data sequence prior to harvest are due to elimination of discharge by evapotranspiration. *Shaded area* represents the range of K:Ca ratio for litter, roots, and collars.

chemical signature of this period is this sustained elevation of the K:Ca concentration ratio in discharge, whereas NO_3 concentrations remained below detection (Figure 2c). [Large preharvest K concentration and K:Ca ratio ''spikes'' of K in the first fall flush of discharge water, evident in Figure 5, are explained by evapotranspirative concentration during each preceding growing season; Kauffman and others (2003) noted flushing of Cl, which they attributed to this process, at the same time each year.] Hydrologically, the removal of aboveground biomass eliminated both transpiration and leaching of K from the canopy during this period, and plant-driven weathering would have declined with a decrease in root activity. However, increases in soil temperature (Figure 1) accelerated the release of K from the decomposition of labile components of litter and fine roots. In the absence of plant uptake, this K quickly built up in soil-water; cessation of water uptake also enabled the diffusion of K from roots and mycorrhizae. The large K concentration pulse appeared in discharge (Figure 5) approximately 1 month after the first detection of elevated K in shallow soil water (Figure 2a), which is consistent with typical rates of soil water flow through the sandbox (O'Brien and others 2004).

The appearance of NO_3 in red pine discharge (November 1998) signaled a major shift in the decomposition regime of the red pine sandbox (middle row, Figure 4) and was followed by a large Ca and NO_3 discharge pulse during year 2 after harvest. During year 1, discharge concentrations of DOC and its ratio to DON declined steadily (Figure 6). The DOC and DON represent biologically labile energy and N sources for heterotrophic decomposers. Large DOC:DON ratios indicate N-limited decomposition of labile substrate; this is consistent with immobilization of N within a growing microbial community and the virtual absence of NO_3 and ammonium (NH_4^+) in red pine discharge. When the DOC:DON ratio was depleted below a critical ratio (traditionally assumed to be about 25:1 for tree litter) (Chapin and others 2002), microbial growth and respiration became carbon-limited. At that point, nitrification became an important pathway for the decomposition of increasingly recalcitrant, Ca-rich tissue components, and NO_3 began to appear in discharge water (Figure 6). Nitrification generates NO_3^- and H^+ in a

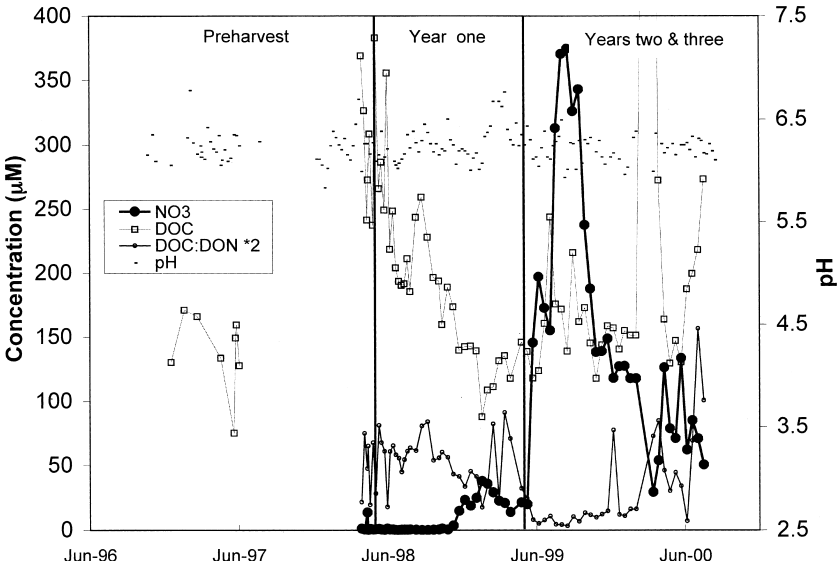

Figure 6. Dissolved nitrate (NO_3) (*dark circles*) and dissolved organic carbon (DOC) (*open squares*) concentrations and molar DOC to dissolved organic nitrogen (DON) ratio (*open circles*) in RP sandbox discharge water. DOC:DON was greater than 25 before NO_3 rose above detection. Discharge pH showed no trend after tree harvest and was consistently 1.5–2 units greater than runoff in nearby Hubbard Brook Experimental Forest (HBEF) streams and more than 2 units above precipitation pH. The DOC spike in March 2000, during snowmelt, peaks at 1,107 μmol.

1:2 molar ratio (for example, Bormann and Likens 1979); the absence of pH change over the entire postharvest period (Figure 6) indicates neutralization of this acid pulse by the soil, whereas mineralized Ca, K, and NO_3 were transported out of the sandbox in discharge water (Figure 2). Thus, decomposition of recalcitrant tissue and associated nitrification were major nutrient sources during years 2 and 3 after harvest.

The discharge-water K:Ca molar-ratio range of 0.3–0.5, which was constant through years 2 and 3, was similar to the average K:Ca molar ratios of litter and roots (Figure 5). This overall agreement is consistent with a decomposition source for both cations. This scenario would suggest that substrate and decomposer K:Ca ratios were stable throughout this period. Root and litter pools in the red pine sandbox at harvest provided sufficient supplies, containing approximately three times the Ca and K lost in drainage water through 2000 (Havig 2002). Furthermore, postharvest soil-water profiles certainly suggest a shallow-depth source.

However, the preharvest K:Ca molar ratio in red pine discharge (Figure 5), as well as discharge from the nonvascular sandbox between 1996 and 2000, showed a similar range. The consistent range of ratio seems independent of plant- activity and suggests a carbon dioxide (CO_2) weathering source for both cations in both sandboxes. It seems likely that in the red pine box both plant-decomposition and CO_2-weathering sources contributed during the nitrification period; as biologic sources of cations were depleted over time, we would expect the carbonic-acid weathering to predominate. Ongoing work is directed at quantifying the contributions from these two sources using cation isotope ratios as tracers.

Carbonic-Acid Weathering (bottom row, Figure 4)

Carbonic-acid weathering occurs when soil CO_2 dissolves into water to form carbonic acid, which attacks mineral structures, yielding base cations to solution and buffering pH. In subsurface settings dominated by silicate minerals, such as the sandboxes, progressive carbonic-acid weathering is conventionally invoked to explain increases in major solute concentrations along groundwater flowpaths (for example, Drever 1997).

Several lines of evidence suggest that carbonic-acid weathering is an important process in the red pine sandbox. Soil-water concentrations of Ca increase progressively with depth except during the growing season of year 2 (Figure 2b), and these patterns are mimicked by soil-water concentration depth profiles for silica and bicarbonate (O'Brien and others 2004; O'Brien 2000). Concentrations of Ca in discharge remain in the 50–100 μM range except for the year-2 growing season (Figure 2b). Because sodium (Na) is relatively unaffected by biological processes, it should therefore be a good tracer of cation release by weathering (for example, Bailey and others 2004); its concentration distributions with depth and over time are like those of Ca, except that its concentration range in discharge is 25–75 μM and the disturbance effect in year 2 is much more subtle than that of Ca (Havig 2002). Discharge pH is approximately 2 units greater than that of precipitation and remains stable from preharvest through years 2 and 3 (Figure 6). Subsurface CO_2 levels, the driving force, show patterns that remain stable with depth and over time: growing-season peak soil concentrations and sea-

sonal cumulative respiration fluxes vary by less than 50% among the preharvest and postharvest intervals (Keller and others in press). Carbonic-acid weathering is a temporally persistent solute generation mechanism in the red pine sandbox (Figure 4).

Selker and others (1999) suggested that the transition from shallow plant-driven weathering control to deeper CO_2-weathering control is a general feature of vadose hydrochemical systems. In the red pine sandbox, carbonic-acid weathering apparently becomes increasingly important the further soil water moves below the zone of greatest rhizospheric activity. The stability of the carbonic-acid weathering regime throughout the study period—evidenced most clearly by pH stability (Figure 6)—is striking. We assume that the sustained driving force,—that is soil CO_2 levels,—is maintained by an increase in microbial respiration that compensates for rapidly dwindling root respiration after harvest.

The Sandbox Harvest Experiment in Context of Classic Watershed Studies

The red pine sandbox harvest was similar by design in several respects to the well-known experimental clear-cut harvest imposed in 1967 on W2 of the HBEF (Likens and others 1970; Bormann and Likens 1979). In both cases, all trees were cut and regrowth was suppressed for approximately 3 years; water-discharge (stream discharge for W2) and concentration data were collected before and after harvest. Because W2 is only 2 km from the sandboxes, the climate was similar. Geologic material in the sandboxes also came from a local bedrock-derived source. There were gross similarities in the responses of the two systems to their respective disturbances: large, immediate increases in water discharge occurred, and similar base cation losses occurred in the 3 years after after disturbance (Table 1). The parallels between the sandbox and W2 outcomes are striking and attest to the essential nature of ecosystem developments of inorganic exchange and water retention capacity, biotic pools of nutrients, and microbial, fungal, and plant biodiversity.

A major hydrochemical difference in the responses occurred with N, both in the amount and timing of N loss after harvest. The increase in the NO_3 flux from the RP sandbox after harvest was only one-third of the increase from w2 following clearcutting (Table 1). We explain this contrast by the extreme N limitation within the sandbox, which persisted through the first season of decomposition after harvest (Figure 6). Intense competition for ammonium is expected under such conditions, and ammonium concentrations in red pine sandbox discharge waters were less than 0.3 μM for most of this time (Havig 2002), compared to approximately 2 μM typical of aggrading HBEF watersheds during 1963–1974 (Bormann and Likens 1979). Previous workers have argued that it takes time under such conditions for nitrifiers to become established after a disturbance (for example, Vitousek and others 1982). Removal of aboveground biomass during the red pine harvest may also account for some reduction of N efflux from the sandbox.

Table 1. Comparison of Increases in Postharvest Solute Fluxes from Hubbard Brook Experimental Forest (HBEF) Watershed 2 (W2) and Red Pine Sandbox

Nutrient	HBEF (W2) (mol/ha/y)	Red pine sandbox (mol/ha/y)
Ca	571	608
K	245	319
NO_3	2,775	897

Ca calcium, K potassium, NO_3 nitrate.
Watershed 2 results are averaged over 36 months of stream discharge data after tree harvest (Bormann and Likens 1979); red pine results are averaged over 32 months of sandbox discharge data after tree harvest.

A second major hydrochemical difference between the systems is evident in how cation chemistry (K, Ca, hydrogen [H]) in discharge changed after harvest. Mean concentration changes in W2 were large (Figure 7), and pH declined by half a unit (Bormann and Likens 1979). In contrast, concentration changes in red pine discharge were small (Figure 7), and pH remained unchanged even through the most intense period of nitrification (Figure 6). The stability of discharge chemistry in the red pine sandbox is due to the relative importance of carbonic-acid weathering in controlling sandbox discharge chemistry, both before and after the harvest.

Relative to typical New England hardwood forest watersheds, the soils in the sandboxes at time of red pine harvest were poorly developed. They had large ratios of primary to secondary minerals (Bormann and others 1998), little horizonation and organic matter, and minimal water-retention capacity coupled with a large vertical hydraulic conductivity (O'Brien and others 2004). Such soil characteristics are associated with early stages of primary-successional ecosystems, where pedogenesis proceeds on recently disturbed, freshly exposed

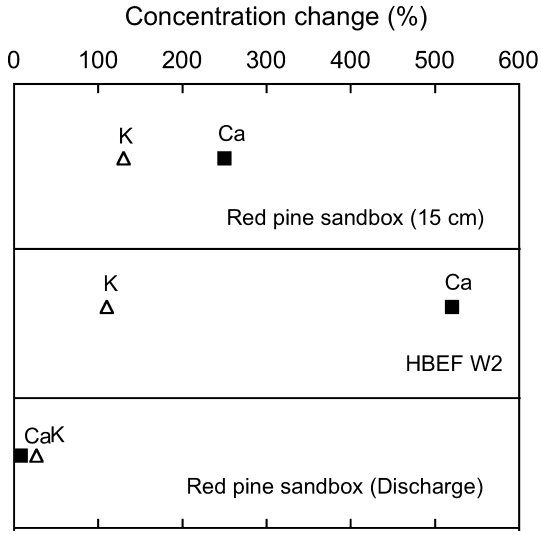

Figure 7. Comparison of change in nutrient concentrations after harvest experiments in Hubbard Brook Experimental Forest (HBEF) watershed 2 (W 2) and the RP sandbox. Change is defined as the difference between mean concentration values before and 32–36 months after harvest, divided by mean values before. *K*, potassium; *Ca* calcium.

substrates (for example, Jenny 1980). In the classic primary-successional chronosequence at Glacier Bay, Alaska, Engstrom and others (2000) observed chronosequences of lake chemistry from high-alkalinity, high-pH conditions (landscapes less than 100 years old) to low-alkalinity, low-pH, and high-DOC conditions (500–10,000-year-old landscapes). They associated the early-phase conditions with lake-water supply by groundwater inflow and later conditions with increasing dominance of lake supply by overland flows across and through shallow soils depleted of minerals that weather rapidly. Sandbox conditions are roughly analogous to the early-phase landscapes at Glacier Bay—that is, they are characterized by deep hydrologic flowpaths where water in contact with fresh mineral surfaces attains well-buffered, high ionic-strength hydrochemistry. Our results imply that disturbance to early-phase primary-successional ecosystems may cause less overall change to the hydrochemistry of terrestrial and aquatic environments than disturbance to later-phase systems.

Summary and Conclusions

We studied the hydrology and solute chemistry of experimental sandbox ecosystems in spatial and temporal detail for 5 years, before and after tree harvest from one of the boxes. In contrast to the findings of previous watershed studies and contrary to our expectations, we observed a distinct sequence of nutrient concentration changes that not only distinguished preharvest conditions from the first year after harvest, but also showed distinct nutrient patterns during years 2 and 3 after harvest. We developed a conceptual model of the progression of subsurface processes we think are causing this sequence. Potassium concentrations and losses responded immediately to harvest-induced elimination of plant uptake and acceleration of decomposition, but Ca and NO_3 concentrations did not increase dramatically until the second growing season after harvest. We attribute this, in part, to differing modes of base-cation uptake, sequestration, and cycling by plants.

A second key factor, underlying the unexpectedly marked delay of NO_3 and Ca concentration and loss pulses, was the strongly N-limited status of the red pine sandbox, which persisted throughout most of year 1 after harvest. In years 2 and 3 after harvest, decomposition substrates and decomposer communities shifted to a carbon-limited, nitrifying regime that mobilized large pulses of NO_3 and Ca from relatively recalcitrant tissue. To the extent that such initial persistence of N-immobilizing conditions occurs in natural systems, it would tend to conserve scant N during reorganization.

Carbonic-acid weathering in the deeper part of the sandbox was also a consistently important solute-generation mechanism conferring notable stability to the bulk hydrochemistry of sandbox water output, such that postharvest cation loss rates showed relatively small increases from preharvest conditions. We hypothesized that the muted nutrient responses to harvest were due to scant accumulation of organic matter, rather than to weathering-regime stability. The chemical stability of the red pine sandbox after disturbance is analogous to early-phase primary-successional systems, which are also characterized by fresh substrates, a paucity of soil organic matter, and deep hydrologic routing.

Our findings underscore the importance of decomposition, as well as plant uptake and cycling of water and nutrients, in controlling nutrient concentrations. Decomposition conserved Ca and and NO_3 for a substantial period after harvest, and it complemented and compensated for root respiration in generating the stable soil-CO_2 driver of carbonic-acid weathering throughout the study period. This suggests that decomposition processes can play a variety of important roles in ecosystem regulation.

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