Reports

Phosphorus Cycling in a Northern Hardwood Forest: Biological and Chemical Control

Abstract. *Phosphorus is tightly conserved within the northern hardwood forest ecosystems at Hubbard Brook, New Hampshire. Detailed analyses of the soil system indicate that biological and geochemical processes, stratified within the profile, regulate phosphorus retention.*

Of the six major plant nutrients, phosphorus is typically one of the most tightly conserved within forested ecosystems. Hydrologic exports of dissolved inorganic phosphorus (DIP) with stream water and deep seepage rarely exceed 0.05 kg ha^{-1} $year^{-1}$, whereas losses of dissolved calcium, magnesium, potassium, nitrogen, and sulfur generally fall in the range of 2 to 20 kg ha^{-1} $year^{-1}$ (*1*). Forest plants, their mycorrhizal associates, and other microorganisms can contribute to phosphorus retention through close coupling of decomposition and uptake processes. Such coupling has been reported for moist tropical forests where dense surficial root mats absorb large portions of the nutrients released from decomposing litter (*2*). Phosphorus can also be retained in forest soils through geochemical fixation on calcium, iron, and aluminum minerals (*3*). Thus, a thorough understanding of phosphorus cycling and retention in forest ecosystems requires detailed study of the actions and interactions of biological and geochemical control mechanisms.

For the past 15 years, scientists at the Hubbard Brook Experimental Forest in central New Hampshire have been conducting intensive long-term studies of forest biogeochemistry, using the small watershed approach (*1*). The results of their work indicate that the phosphorus cycle within this 55- to 65-year-old northern hardwood forest ecosystem is both dynamic and exceedingly tight. Plants take up an estimated 12.5 kg of phosphorus per hectare per year from the soil. About 1.5 kg ha^{-1} $year^{-1}$ are stored in accumulating biomass, and 11.0 kg ha^{-1} $year^{-1}$ are returned to the soil with aboveground and belowground litter, throughfall, and root exudates. More than 10.0 kg ha^{-1} $year^{-1}$ of organic phosphorus are mineralized through decomposition processes in the soil. Weathering of primary soil minerals releases an additional 1.5 to 1.8 kg of phosphorus per hectare to soil solutions each year (*4*).

Despite these large intrasystem fluxes, only 0.007 kg ha^{-1} $year^{-1}$ of DIP are lost from these forests in stream water (*5*). Concentrations of DIP in Hubbard Brook streams remain at ≤ 1 μg $liter^{-1}$ throughout the year. These exports and concentrations are among the lowest reported in the literature, and, in the absence of other significant vectors of output, they indicate the strong degree to which phosphorus is conserved within this forest ecosystem. Questions remained, however, concerning the degree to which biological versus geochemical processes contribute to phosphorus retention, and in 1977 we initiated studies to address this problem. Some results are reported here.

Hubbard Brook soils are generally acid, well-drained spodosols (haplorthods) of sandy loam texture. Mature profiles, undisturbed by windthrow, are typically characterized by five distinct horizons [AO or forest floor, A2, B2lh, B2ir, and Cx (*6*)], which differ markedly in their chemical and physical characteristics (Table 1). In this study, the A and B horizons were extensively sampled to determine the abundances and distributions of biological agents (nonwoody roots, bacteria, and fungi) and geochemical agents (iron and aluminum sesquioxides) that typically govern phosphorus movements and solubilities in acid soils (*7*). The Cx horizon, a discontinuous fragipan, is impermeable to deep seepage and root growth, and, as such, does not directly influence phosphorus biogeochemistry.

Table 1. Select characteristics of Hubbard Brook soils. Values are the means from ten profiles.

Soil horizon	Depth (cm)	Loss on ignition (%)	*p*H (water)
AO	0 to 9	54.1	3.42
A2	9 to 15	2.5	3.88
B2lh	15 to 18	12.6	3.82
B2ir	18 to 80	7.1	4.63
Cx	> 80	0.9	5.16

We surveyed the populations of roots, bacteria, and fungi during the 1977 growing season by first extracting intact soil cores from specified depths within the profile. Fine (≤ 0.6 mm in diameter) nonwoody roots were carefully removed from cores, and their lengths, diameters, numbers of intact root tips, and oven dry weights were measured (*7*). Bacteria and fungi were inventoried by direct microscopic counts of soil homogenates (*7, 8*).

Peak concentrations of fine roots occurred in the surface 2 cm of the forest floor. Abundances declined with depth in a near exponential fashion with a slight discontinuity in the A2 and B2lh horizons (Fig. 1). We calculate that there are, during the growing season, a total of 24.7 ± 3.2 km, 24.6 ± 3.2 m^2, and 707 ± 103 g of fine root length, surface area, and biomass, respectively, beneath each square meter of soil surface. Root tips total $(3.8 \pm 0.6) \times 10^6$ per square meter. Forty to 50 percent of these totals occur in the top 10 cm of the profile.

Soil microbes were similarly distributed with peak concentrations of $(10.4 \pm 2.2) \times 10^9$ bacteria per cubic centimeter of soil and 402 ± 299 m of fungal hyphae per cubic centimeter occurring in the AO horizon. Bacterial abundance declined to $(1.1 \pm 0.4) \times 10^9$ per cubic centimeter in the A2, rose to $(3.0 \pm 1.0) \times 10^9$ in the B2lh, and then fell with depth through the B2ir where densities averaged $(0.8 \pm 0.3) \times 10^9$. Fungal hyphae followed a similar decline with depth: 32 ± 19 m cm^{-3} in the A2, 100 ± 31 in the B2lh, and 40 ± 26 in the B2ir. Approximately 60 percent of the soil bacteria and fungi occurred in the upper 10 cm of the profile.

Many factors, including moisture and oxygen availability, may shape distributions of roots and microbes, but peaks in the AO and B2lh suggest the importance of annual litterfall and soil organic matter as sources of carbon and nutrients for growth (Table 1). Codistributions of roots, microbes, and organic matter, in turn, suggest localized transfers of nutrients between living and dead biomass, a

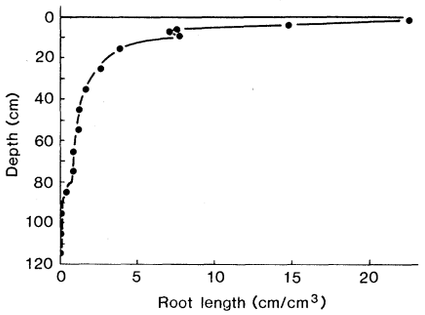

Fig. 1. The distributions of fine roots (≤ 0.6 mm in diameter) in Hubbard Brook soils. Mean root densities are expressed as root length (in centimeters) per cubic centimeter of soil. Profiles for fine root surface area, biomass, and root tip density were similar.

key process for biological regulation of phosphorus cycling and retention.

We examined chemical regulation of phosphorus retention through a series of equilibrium experiments designed to measure (i) the capacities of soils taken from designated horizons to sorb and release dissolved inorganic phosphorus when shaken for 24 hours with KH_2PO_4 solutions ranging in concentration from 0 to 2 m*M* (*7, 9*) and (ii) the equilibrium phosphorus concentrations maintained when sorption and release processes came into balance (*10*). These analyses showed that AO and A2 horizon soils were relatively inert with respect to phosphorus geochemistry. Composed primarily of organic matter and siliceous residues of heavily weathered minerals, these surface soils chemically removed only small amounts of phosphorus from solution. Their sorption capacities averaged less than 0.05 mg of phosphorus per gram of soil. AO horizon soils released significant amounts of phosphorus to distilled water, and they tended to weakly buffer solution phosphorus concentrations at 2000 to 7000 μg of DIP per liter. A2 horizon soils tended to release little phosphorus to solution and weakly maintained equilibrium phosphorus concentrations at 109 ± 42 μg of DIP per liter.

In contrast, soil from B2lh and B2ir horizons chemically fixed large amounts of dissolved phosphorus (their sorption capacities for phosphorus exceeded 1.5 mg g^{-1}) and released only trace amounts of phosphorus when equilibrated with distilled water. As such, they strictly buffered equilibrium phosphorus concentrations at 6 ± 2 and 1 ± 0 μg of DIP per liter, respectively. The latter result is important. B2ir horizon soils regulate solution phosphorus concentrations at levels also found in first-order streams draining the forest ecosystem.

In acid soils, iron and aluminum sesquioxides typically dominate phosphorus fixation through replacement of hydroxyl groups by phosphate (*3*). This mechanism appears active in Hubbard Brook spodosols. Phosphorus sorption capacities of ten soil samples from each of the five horizons were highly correlated ($r^2 = 0.95$; $P \leq 0.001$) with concentrations of free, surface-reactive iron and aluminum measured by HCl extraction (*7, 11*). Correlations with concentrations of extractable calcium, magnesium, and manganese, other metals that can chemically fix phosphate, were insignificant.

Three representative profiles showed low concentrations of free iron and aluminum in the AO and A2 horizons (Fig. 2). Concentrations of free iron peaked in the B2lh and then diminished through the remainder of the profile. Free aluminum was more deeply distributed, with concentrations peaking in the upper B2ir.

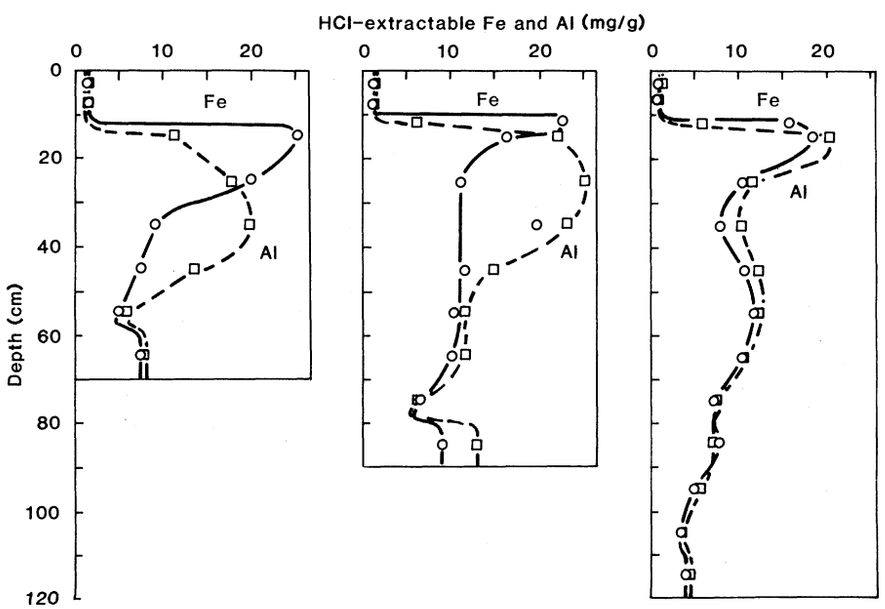

Fig. 2. Distributions of HCl-extractable iron and aluminum in three soil profiles at Hubbard Brook.

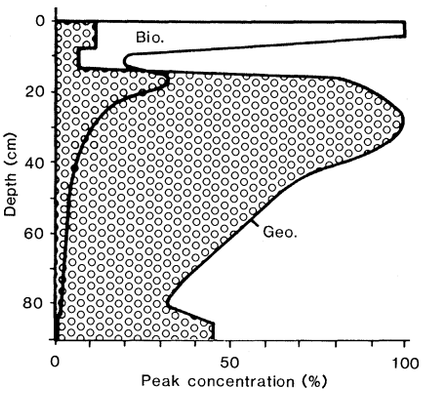

Fig. 3. Comparison of the relative distributions of biological agents (fine roots, bacteria, and fungi) versus geochemical agents (surface-reactive iron and aluminum sesquioxides) that contribute to phosphorus retention in Hubbard Brook soils.

Soils in the B horizons can also sorb large amounts of organic phosphorus through coprecipitation of dissolved organic matter with iron (*12*). Equilibration experiments showed B2ir soils to be capable of sorbing more than 0.3 mg of dissolved organic carbon (DOC) per gram of soil and of maintaining equilibrium DOC concentrations at 2.0 to 3.0 mg $liter^{-1}$ (*13*). Phosphorus associated with this organic carbon is, of course, fixed in tandem.

The above surveys indicate that Hubbard Brook soils are highly stratified with respect to phosphorus biogeochemistry (Fig. 3). The forest floor, rich in roots, bacteria, and fungi but poor in free iron and aluminum, is a zone of potentially high biological control but minimal geochemical control over phosphorus movements. Underlying B horizons, with high concentrations of free metals and relatively low densities of roots and microorganisms, are just the opposite.

We used this stratification to distinguish the relative roles of biological and chemical processes in shaping phosphorus movements within and through the soil system. Soil solutions were collected during two growing seasons from 12 lysimeters placed in the lower A2 horizon and from six lysimeters placed in the middle of the B2ir. Solutions were analyzed for their phosphorus contents, and results were used to examine phosphorus flux through the soil profile. Solutions collected from the lower A2 horizon contained only 24 ± 18 μg of total phosphorus per liter and 1 ± 1 μg of DIP per liter. These concentrations were far

below those chemically maintained by A horizon soils in laboratory equilibrations, an indication of regulation through biological uptake. Using computer-based estimates of hydrologic flow across the A horizon–B horizon interface (*7, 14*) and assuming that the phosphorus contents of these solutions did not vary seasonally, we calculated that 0.23 kg per hectare of total phosphorus leach from the A horizons to the B horizons annually. This amount is only 3 percent of the 8.35 kg ha^{-1} $year^{-1}$ estimated to be released within the A horizons (*15*), and it indicates strict biological retention of phosphorus within surface soils. Solutions collected from lysimeters placed in the middle of the B2ir invariably contained ≤ 1 μg of total phosphorus per liter, substantiating the hypothesis of geochemical control of dissolved inorganic and organic phosphorus in subsoils and eventually stream waters.

Our results indicate dual and stratified regulation of phosphorus cycling and retention at Hubbard Brook. Phosphorus is biologically conserved within this forest community by close coupling of biological decomposition and uptake processes in the surface soils. Underlying iron- and aluminum-rich B horizons, in turn, function as massive geochemical buffers that regulate the constant and low-level losses of dissolved phosphorus with stream water.

These findings are significant in explaining changes in phosphorus biogeochemistry after forest disturbance. Experiments at Hubbard Brook have demonstrated massive increases in stream water exports of calcium, potassium, and nitrate-nitrogen after clear-cutting. Losses were attributed to disruption of biological retention mechanisms as well as to acidification of cation-exchange sites in the profile (*6, 16*). Stream water losses of dissolved inorganic phosphorus did not increase after clear-cutting (*17*), presumably because chemical processes in the B horizons continued to function. With disruption of biological controls in surface horizons, however, it is likely that large amounts of phosphorus migrated from the forest floor to sinks in the B horizons. Recovery of phosphorus stored in those subsoils may represent an important aspect of forest regrowth after disturbance.

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References and Notes

1. G. E. Likens *et al.*, *Biogeochemistry of a Forested Ecosystem* (Springer-Verlag, New York, 1977).
2. N. Stark and C. F. Jordan, *Ecology* **59**, 434 (1978).
3. R. L. Parfitt and R. J. Atkinson, *Nature (London)* **264**, 740 (1976); L. J. Evans and G. W. Smillie, *Ir. J. Agric. Res.* **15**, 65 (1976).
4. Values for the phosphorus fluxes are as published (*1*), with modifications based on revised estimates of root turnover and of the amounts of organic and inorganic phosphorus in Hubbard Brook soils (*7*).
5. J. L. Meyer and G. E. Likens, *Ecology* **60**, 1255 (1979).
6. Soil Survey Staff, *Soil Taxonomy* (Agriculture Handbook No. 436, Government Printing Office, Washington, D.C., 1975).
7. T. E. Wood, thesis, Yale University (1980).
8. J. E. Hobbie, R. J. Daley, S. Jasper, *Appl. Environ. Microbiol.* **33**, 1225 (1977); E. A. Paul and R. L. Johnson, *ibid.* **34**, 263 (1977).
9. S. R. Olsen and F. S. Watanabe, *Soil Sci. Soc. Am. Proc.* **21**, 144 (1957).
10. A. W. Taylor and H. M. Kunishi, *J. Agric. Food Chem.* **19**, 824 (1971).
11. Soils were extracted for 1 hour with 12*N* HCl. We analyzed extracts for iron and aluminum, using methods in M. L. Jackson, [*Soil Chemical Analyses* (Prentice-Hall, Englewood Cliffs, N.J., 1958)] and in W. K. Dougan and A. L. Wilson [*Analyst* **99**, 413 (1974)].
12. M. Schnitzer, *Soil Sci. Soc. Am. Proc.* **33**, 75 (1969).
13. W. H. McDowell and T. E. Wood, *Soil Sci.*, in press.
14. C. A. Federer and D. Lash, *Research Report 19* (Water Resources Research Center, Durham, N.H., 1978).
15. The estimate of annual phosphorus release within the AO plus A2 horizons (8.35 kg ha^{-1} $year^{-1}$) was calculated as the sum of phosphorus inputs to these strata with precipitation (0.04), throughfall and stemflow (0.56), aboveground and belowground litter (7.02), root exudates (0.10), and mineral weathering (0.90), minus the net annual accretion of phosphorus in the A horizons with accumulating organic matter (0.27). Complete documentation is given by Wood (*7*).
16. G. E. Likens, F. H. Bormann, N. M. Johnson, D. W. Fisher, R. S. Pierce, *Ecol. Monogr.* **40**, 23 (1970).
17. J. E. Hobbie and G. E. Likens, *Limnol. Oceanog.* **13**, 734 (1973).

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Microwave Measurements of Carbon Monoxide on Titan

Abstract. *The ratio of the flux density of Titan was measured in two 200-megahertz bands, one centered on the (1–0) rotation line of carbon monoxide at 115.3 gigahertz and the other 2600 megahertz lower. The measurements were made with a complex-correlation technique on the new millimeter-wavelength interferometer at the Owens Valley Radio Observatory, Big Pine, California. The excess flux in the carbon monoxide band is interpreted as a strong detection of carbon monoxide and a mixing ratio, assumed constant, of* 6×10^{-5}. *The brightness temperature of Titan at 112.6 gigahertz is 69 ± 10 kelvins, consistent with atmospheric emission from just below the tropopause.*

Until recently, the known constituents of the Titan atmosphere were CH_4, C_2H_6, C_2H_2, and CH_3D. Experiments on Voyager during its flyby of Titan established that N_2 was the primary constituent, with no more than 3 percent CH_4 (*1*). Numerous other species were detected, all of which could be products of the parent compounds N_2 and CH_4. We began a series of measurements in early 1982 to detect the first rotational transition of CO at 115.271 GHz, since that line is very strong in the terrestrial planets and the detection of an oxygen compound in Titan would be extremely important (*2*). Concurrently, Samuelson *et al.* (*3*) interpreted an emission feature in the Infrared Interferometer Spectrometer (IRIS) spectrum at 667 cm^{-1} as CO_2, and recently prepared a paper in which they predicted a constant CO mixing ratio of 1.1×10^{-4} based on their photochemical model and a CO_2 mixing ratio of 1.5×10^{-9}. In their model the CO/CO_2 ratio is very large because of the low abundance of H_2O, which is an important source of OH, a critical molecule in the conversion of CO into CO_2. Lutz *et al.* (*2*) detected CO in Titan with Earth-based measurements in the (3–0) rotational-vibration bands near 6350 cm^{-1} and interpreted their measurement with a constant mixing ratio of 6×10^{-5} with an uncertainty of a factor of 3. This uncertainty arises from a multitude of causes, including the possible presence of aerosol, cloud, and haze layers in Titan's atmosphere, which would seriously influence their interpretations. The microwave lines offer a more direct means of measuring the abundance, since the emission is only affected by gaseous absorption and confusion from other chemical species is very unlikely. Any liquid droplets in clouds would probably be nonpolar and, consequently, would not be significant absorbers. The primary problem is one of signal-to-noise ratio.

Titan was observed on 7 and 8 May 1983 by use of the millimeter-wavelength, two-element interferometer at the Owens Valley Radio Observatory, Big Pine, California. The interferometer consisted of two 10.4-m telescopes (*4*) positioned to give a baseline of 50 m east-west. At a nominal wavelength of 2.6 mm the fringe spacings on the sky in the direction toward the Saturn system ranged from about 10.6 to 21.4 arc seconds. The interferometer fringes were continuously positioned on Titan with computer-controlled phase tracking, using a precise Titan ephemeris (*5*). During