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Phosphorus budget of a 70-year-old northern hardwood forest

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Abstract. Recent measurements have made it possible to revise and improve the phosphorus budget of the Hubbard Brook Experimental Forest, including partitioning P uptake by vegetation from the forest floor and mineral soil and estimating net P mineralization in the forest floor. Both living biomass and forest floor are accumlating P (at rates of 1.3 and 0.16 kg P ha^{-1} yr^{-1} respectively) in this 70-yr old northern hardwood forest. About 61% of the P taken up by the vegetation each year comes from the forest floor (5.9 kg P ha^{-1} yr^{-1} of a total 9.6 kg P ha^{-1} yr^{-1}), even though the P content of this pool is just 5% of that in mineral soil. The turnover rate of P in the forest floor is 7% yr^{-1}, while that of the mineral soil is 0.3% yr^{-1}. Recycling of P in the forest floor is very efficient; of the 5.6 kg P ha^{-1} yr^{-1} net mineralization in the forest floor, only 0.3 kg P ha^{-1} leaches into the mineral soil; the rest is taken up by plants. This tight recycling of P is important because P is less readily available in the mineral soil than in the forest floor.

Introduction

Recent studies at the Hubbard Brook Experimental Forest (HBEF) make it possible to construct a phosphorus budget for the 70-year-old northern hardwood forest that is more detailed and more accurate than earlier budgets reported by Likens et al. (1977), Ryan (1979), and Wood (1980). This paper describes the amounts of P held in different parts of the ecosystem and the movements of P among those parts. Net P mineralization in the forest floor, a process difficult to measure directly, is calculated by a new method. Measurement of P transfer out of the forest floor in soil solution (Yanai 1991) makes it possible to calculate P uptake from the forest floor as well as total P uptake by vegetation. Although the forest floor is known to be the site of active mineralization and uptake, the amount of P uptake from the forest floor by trees has rarely been quantified.

Methods

Site description

The Hubbard Brook Experimental Forest (HBEF), located in the White Mountains of north central New Hampshire, was established after logging between 1910 and 1917 (Bormann et al. 1970). The resulting uneven-aged forest had 230 t ha^{-1} aboveground biomass in 1985. Dominant species include beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh), and yellow birch (*Betula allegheniensis* Britt.). Red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.), and white birch (*Betula papyrifera* Marsh) dominate at higher elevations (Bormann et al. 1970). Slopes average 12—13° with a SE aspect (Bormann et al. 1970); elevation ranges from 510 m to 750 m. The climate is humid continental with mean temperatures of −9 °C in January and 19 °C in July; annual precipitation is 130 cm, with 39 cm falling as snow (Likens et al. 1977).

Soils of the HBEF have developed in granitic glacial till overlying granitic gneiss. Most of the soils are Typic to Lithic Haplorthods of the Tunbridge, Lyman, and Berkshire series (Hungtington et al. 1988). The forest floor (O_i, O_e, and O_a horizons) of Watershed 5 has a mean thickness of 7 cm; the mineral soil averages 54 cm deep (Hungtington et al. 1988).

Structure of the P budget

Phosphorus occurs in a variety of forms in forest ecosystems. The pools I define are forest floor, mineral soil, aboveground biomass, roots in the forest floor, and roots in the mineral soil. Phosphorus is transferred among the pools in throughfall and stemflow, litterfall, root death, root exudation, and leaching from the forest floor to the mineral soil. Because P pool sizes change as the forest develops, the rates of change of P pools, or P accumulation rates, are also calculated.

The time scale of the budget is that of an average annual cycle; seasonal variation is not described here. The spatial scale is that of the stand or small watershed ecosystem.

Selection and compatibility of measurements

One purpose of constructing this budget was to provide a baseline description of the undisturbed HBEF prior to the whole-tree harvest conducted on Watershed 5 (W-5) in 1983—1984 (Yanai 1990). The age

of the forest at that time was between 67 and 74 years; I have chosen to call it a 70-yr old forest.

The timing of the observations used to construct this budget was less consistent than their locations (Table 1). Biomass and soils were inventoried on W-5 in 1982 and 1983, respectively. Litterfall and root exudates were measured between 1968 and 1971; P concentrations and allometric relations for aboveground biomass date from 1966. I have assumed that P cycling remained constant enough during the last 15 years that an informative picture could be constructed by combining these data.

Soil and forest floor

The most reliable data on the amount of forest floor and mineral soil at the Hubbard Brook forest were obtained from 60 0.5-m^2 pits excavated in 1983 in W-5 (Huntington et al. 1988). The forest floor was measured in two parts. The combined O_i and O_e horizons had a dry mass of 22 ± 2 t ha^{-1}; the O_a horizon had a mass of 65 ± 7 t ha^{-1}. The mineral soil, defined as the fine earth (< 2 mm) fraction, had a mass of 3200 ± 210 t ha^{-1}. Mineral soil was excavated to the depth of the fragipan or of unaltered glacial till (54 cm on average).

Total P concentrations in forest floor samples were measured by Johnson (1989) using an HCl-HF digestion (Friedland & Johnson 1985). He calculated mean forest floor P content to be 85 kg P ha^{-1}, using forest floor mass of Huntington et al. (1988). Total P was not determined for mineral soil strata in the 60-pit study; I applied the total P concentration of the B_s horizon (0.50 mg P g^{-1} soil, determined by HF-$HClO_4$ digestion; Wood 1980) to the whole mineral soil mass. The B_s horizon accounts for 75%, on average, of mineral soil thickness (Johnson et al. 1991).

To calculate the amounts of available, organic, and primary and secondary mineral P in both forest floor and mineral soil, I apportioned total P using the fractionation reported by Wood (1980; see Yanai 1990). Dilute acid-extractable P represented available P; primary mineral P was calculated as the difference between total P and organic P (extractable with HCl after ignition) plus secondary mineral P (extractable by citrate-dithionite).

To estimate the rate of P accumulation in the forest floor, I fit a function relating forest floor organic matter content to stand age based on data from 27 northern hardwood stands collected by Covington (1981) and Federer (1984). The amount of forest floor organic matter (t ha^{-1}) is

$$-15.03\ \text{t ha}^{-1} * t^{0.3757} * e^{-0.0004622\ \text{yr}^{-1} * t^{2.135}} + 82.3\ \text{t ha}^{-1}$$

Table 1. Sources of values used in constructing the P budget of the 70-yr old forest.

Measurement	Area sampled	Time	Primary references
Soil mass	W-5; 60 pits at random	1983	Huntington et al. (1988)
Forest floor total P	W-5; 60 pits at random	1983	Johnson (1989)
Soil P concentrations	2 profiles near W2 and 8 profiles adjacent to W6 selected for drainage and presence of an E horizon	1977—78	Wood (1980)
Tree diameter and species	W-6, complete survey	1982	T. G. Siccama (pers. comm.)
Biomass P concentrations	in and near W-6	1966	Likens and Bormann (1970)
Allometric relations	in and near W-6 tree heights	1966 1982	Whittaker et al. (1974) T. G. Siccama (pers. comm.)
Lateral roots	W-5; 60 pits at random	1983	Fahey et al. (1988)
Fine roots	near W-5; 29 soil cores	1987	Fahey et al. (1988)
Aboveground biomass accumulation	W-6, complete survey	1965—82	T. G. Siccama (pers. comm.)
Forest floor accumulation	chronosequence of stands White Mountains, NH		Covington (1976) and Federer (1984)

Table 1. (Continued)

Measurement	Area sampled	Time	Primary references
Precipitation volume	HBFF	1963—80	Likens (1985)
Precipitation P concentration	W-6; one collector	1972—80	Likens (1985)
Streamwater volume	4 watersheds, HBEF	1963—80	Likens (1985)
Dissolved P concentration	W-6	1972—80	Likens (1985)
Particulate matter mass	W-6	1968—69	Likens et al. (1977) Bormann et al. (1974)
Litterfall	W-6	1968—69	Gosz et al. (1972)
Canopy leaching	W-6	1978—79	Wood (1980)
Root turnover rate	Harvard Forest, MA	1978—79	Aber et al. (1985)
Root exudation	below W-4 in the Integrated Plot Study	1968—71	Smith (1976)
Leaching from forest floor to mineral soil	adjacent to W-6; 8 sites	1984—85	Yanai (1990)

where t is the time since clearcutting (yr). The form of this equation follows Covington (1981) but it is an improvement on Covington's original equation because it includes Federer's 13 stands.

I applied the predicted accumulation rate of forest floor organic matter at age 70 to the measured P content of the forest floor to calculate the accumulation rate of P in the forest floor. The concentration of P in the forest floor was assumed to be constant through time, because seven northern hardwood stands of varying age showed no evident pattern of P concentration with forest floor mass or age (Table 2).

Table 2. Phosphorus and organic matter in forest floors of northern hardwood stands of varying ages. Forest floors were sampled by Federer (1984) and analyzed for P by Yanai (1990).

Age	P/OM (mg/g)	Total OM (Mg/ha)	Total P (kg/ha)
1	1.1 ± 0.1	65 ± 12	68 ± 9
4	2.3 ± 0.2	52 ± 5	115 ± 5
10	2.4 ± 0.2	41 ± 7	97 ± 18
24	1.6 ± 0.1	49 ± 2	80 ± 3
31	2.1 ± 0.2	72 ± 5	149 ± 14
34	3.0 ± 0.3	47 ± 3	141 ± 19
70	1.3 ± 0.0	84 ± 9	109 ± 14

Mean ± standard error; $n = 5$.

Aboveground biomass

The amount of P in aboveground living biomass in Watershed 6 (W-6) was calculated by T. G. Siccama (pers. comm.) based on tree inventories, allometric equations relating tree diameter to biomass, and concentration data relating biomass to P content. Diameters of all stems >2 cm diameter at breast height in W-6 were measured in 1982. The allometric equations of Whittaker et al. (1974), which predict the biomass of tree parts (twigs and leaves, branches, bark, stemwood and heartwood) from diameter and species, were modified to correct various errors in the published equations (T. G. Siccama, pers. comm.). Phosphorus concentration data for the same species and tree parts (Likens & Bormann 1970) were derived from samples collected in 1965 in conjunction with the study by Whittaker et al. (1974). This calculation assumes that P concentrations of tissues have not changed since 1965.

The accumulation rate of P in aboveground biomass was calculated from changes in the estimated P content of aboveground biomass in W-6 between 1965 (35.3 kg ha^{-1}; Whittaker et al. 1979) and 1982.

Litterfall and woody litterfall

I used data from Gosz et al. (1972), who reported deposition rates in W-6 from October 1968 to October 1969 of 1.9 kg P ha^{-1} in leaves, 0.8 kg P ha^{-1} in other deciduous tissues (bud scales, flowers, fruit and frass), 0.9 kg P ha^{-1} in branches, stems, and bark, and 0.4 kg P ha^{-1} from the shrub and herb strata.

Roots

Phosphorus content of lateral roots (>0.6 mm diameter) in the forest floor and the mineral soil was calculated based on measured biomass and concentrations in the 60 soil pits described above (Fahey et al. 1988). Phosphorus in fine roots (<0.6 mm diameter) was measured in 29 randomly distributed soil cores taken to a depth of 30 cm or the depth of obstruction (Fahey et al. 1988). Of these fine roots, 46% were found in the forest floor (T. J. Fahey, pers. comm.). Phosphorus in root crowns was calculated from allometric equations for biomass (Fahey et al. 1988) and measured P concentrations of large lateral roots; 75% of root crown P was assumed to be in the forest floor.

I assumed that P accumulated in roots at the same proportional rate as in aboveground living biomass (annual P accumulation was 1.9% of P content). I apportioned P accumulation in roots between the forest floor and mineral soil based on the calculation that 58% of P in large roots (>5 mm dia) and root crowns was in the forest floor (Yanai 1990). Roots smaller than 5 mm diameter were ignored because they were assumed to be near steady state for biomass and P in the 70-yr old forest (Vitousek et al. 1988).

I estimated rates of P return to the soil via root death by different methods for large and fine roots. In the absence of data on large root death, I assumed that woody roots and root crowns turn over at 1.7% per year, the same proportion as aboveground woody litterfall (Gosz et al. 1972) as a fraction of aboveground woody biomass (Whittaker et al. 1974), and that 58% of these roots are in the forest floor.

Fine root turnover was assumed to be 66% per yr, the rate reported for another northern hardwood forest on similar soils (Aber et al. 1985). This turnover is consistent with observations made at HBEF of fine roots growing through screens placed in the soil (T. J. Fahey, pers. comm.), but

it should be noted that the year-to-year variation in root longevity was very high. Resorption of P by senescing roots was assumed to be negligible (Nambiar 1987). I further assumed that fine root turnover is distributed in proportion to fine root biomass, 46% of which is in the forest floor (T. J. Fahey, pers. comm.).

Smith (1976) measured root exudation of phosphate from new woody root tips of the three codominant hardwood species at the HBEF during 1968—1971. He calculated a P exudation rate based on surveys of the number of new woody root tips per unit ground area. I assumed that his value applied to the 70-yr old forest, and that the amount exuded in the forest floor or mineral soil was proportional to the mass of fine roots. The rate of exudation of organic P by roots is unknown.

Precipitation

The P content of bulk precipitation at the HBEF was calculated as the product of volume-weighted annual mean P concentrations measured from 1972 to 1980 and average annual precipitation measured from 1963 to 1980 (Likens 1985).

Throughfall and stemflow

Wood (1980) measured average total P concentration in throughfall in 1978 and 1979; he multiplied this concentration by a calculated throughfall and stemflow water flux. Since the biomass and species composition of foliage changed little from the 55 to the 70-yr old forest, I made no correction for stand age.

Leaching from the forest floor

Phosphorus transfer from the forest floor to the mineral soil was calculated by combining monthly mean total P concentrations of O_a horizon soil solution (collected by lysimeters) and estimated water flux from this horizon to the mineral soil (based on a simulation model) (Yanai, 1991).

Streamwater export

Streamwater has been sampled at weekly intervals for analysis of dissolved constituents (Bormann et al. 1969) and streamflow is monitored continuously at gaging stations using flumes and weirs. Dissolved P concentrations were weighted by weekly streamflow from 1972 to 1980, and annual

average P flux was based on streamflow measured from 1963 to 1980 (Likens 1985).

Particulate matter exported from the ecosystem was collected in stilling basins behind the weirs. Suspended particulate matter was collected by sieving the escaping water through a 1-mm mesh net and the netted water through a 0.5-μm Millipore filter (Bormann et al. 1974). Annual P loss in particulate matter was estimated based on the mass of exported inorganic and organic material in 1968—69 and the assumption that P concentration in these materials was the same as other forms of organic debris and geologic material at the HBEF (Likens et al. 1977; Bormann et al. 1974).

Calculation of non-measured P transfers

Transfers of P that were not measured were calculated from mass-balance constraints on forest floor and vegetation P pools (denoted by asterisks in Table 3 and Fig. 1). The calculations can be reproduced as follows, with all the terms in units of kg P ha^{-1} yr^{-1}.

(1) Transfer from roots to aboveground biomass = litterfall + throughfall (excluding the atmospheric contribution) + aboveground biomass accumulation.

(2) Uptake from the forest floor = litterfall + throughfall (including precipitation) + forest floor root turnover and exudation − leaching − forest floor accumulation.

(3) Transfer from roots in the forest floor to aboveground biomass = uptake from the forest floor − root litter and exudates − root accumulation in the forest floor.

(4) Transfer from roots in the mineral soil to aboveground biomass = transfer from roots to aboveground biomass − transfer from roots in the forest floor to aboveground biomass.

(5) Uptake from mineral soil = transfer from roots in the mineral soil to aboveground biomass + mineral soil root turnover and exudation + root accumulation in the mineral soil.

Finally, net P mineralization from organic materials in the forest floor can be calculated using a budgetary approach. Instead of estimating the P mineralization rate of organic materials in the forest floor, I calculated the amount of mineralized P leaving the forest floor (corrected for the amount of phosphate entering the forest floor). Thus,

(6) Net P mineralization in the forest floor = P uptake from the forest floor (assumed to be all phosphate) + phosphate leaching from forest floor into mineral soil (assumed to be half of the total dissolved P, based on my measurements) − phosphate added in throughfall and stemflow (measured at about half the total P by Wood (1980)) − root exudation of

Table 3. Phosphorus budget for the 70-yr old northern hardwood forest: P pool sizes, P accumulation rates and P transfer rates. Insignificant digits for many values are shown to facilitate reproduction of the calculations.

Phosphorus pool sizes (kg P ha^{-1})	
Living biomass	
Aboveground biomass	51.6
Roots in the forest floor	9.6
Roots in the mineral soil	9.7
Total	70.9
Forest floor	
Available	0.68
Organic matter	61
Primary mineral	20
Secondary mineral	4
Total	85
Mineral soil	
Available	0.13
Organic matter	540
Primary mineral	670
Secondary mineral	390
Total	1600
Ecosystem total	1756
Phosphorus accumulation rates (kg P ha^{-1} yr^{-1})	
in Aboveground biomass	0.96
in Roots in the forest floor	0.21
in Roots in the mineral soil	0.16
in Forest floor	0.16
Total	1.49
Phosphorus transfer rates (kg P ha^{-1} yr^{-1})	
Precipitation	0.04
Streamwater export	0.02
Litterfall	4.0
Throughfall and stemflow	0.57
Root death (forest floor)	1.66
Root death (mineral soil)	1.88
Root exudation (forest floor)	0.10
Root exudation (mineral soil)	0.12
Leaching from forest floor	0.30

Table 3. (Continued)

Uptake by vegetation*	9.62
Uptake from the forest floor*	5.87
Uptake from the mineral soil*	3.75
Net P mineralization in the forest floor*	5.63

* Asterisks denote fluxes calculated by mass balance from those calculated independently.

phosphate in the forest floor (based on measured phosphate). The amount of mineralized P stored on soil surfaces was assumed to be constant at the time scale of interest.

Turnover rates of P in soil

The rate of turnover of P in the forest floor can be calculated by assuming that the forest floor is in steady state for P storage. The annual additions to the forest floor are litterfall, throughfall, root death, and root exudation. The input rate is divided by the pool size to give a turnover rate.

The release of P from primary minerals (weathering) must be subtracted from the rate of P uptake from mineral soil before calculating the turnover of P in the mineral soil. I calculated the rate of P release from primary mineral P by assuming that precipitation P inputs have balanced erosional P losses and that primary P transformation has been constant over the course of soil development (10,000 years). The average rate of P release from primary minerals required to accumulate 1066 kg P ha^{-1} (the sum of living biomass, soil organic matter, and secondary mineral P) in this time period is 0.11 kg P ha^{-1} yr^{-1}.

The rate of P cycling through organic and secondary mineral P in the mineral soil can be calculated from their pool sizes and the rate of P uptake from these forms (P uptake from the mineral soil minus the rate of P supply from primary minerals).

Results

Phosphorus pools

Most of the P in the northern hardwood ecosystem resides in the mineral

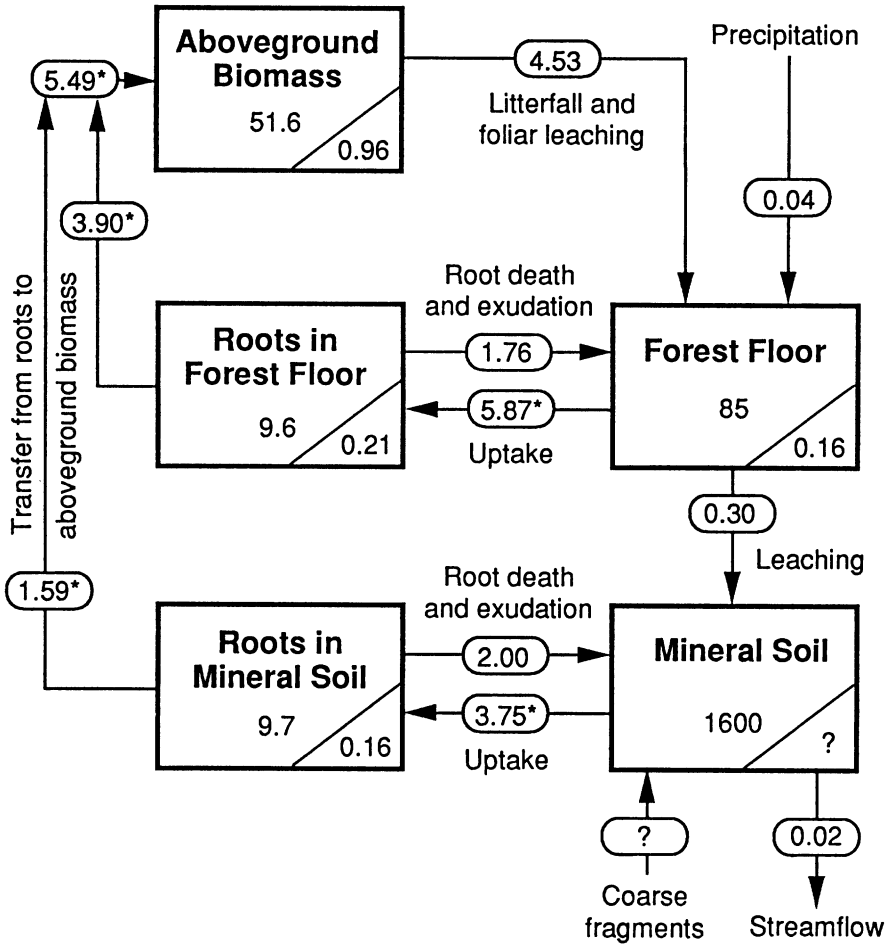


Fig. 1. Phosphorus budget for the 70-yr old northern hardwood forest. Values in rectangles are P stores (kg P ha^{-1}); values in triangles are annual accumulation rates (kg P ha^{-1} yr^{-1}). Arrows represent fluxes (kg P ha^{-1} yr^{-1}). Asterisks denote fluxes calculated by mass balance from those calculated independently. Insignificant digits for many values are shown to facilitate reproduction of the calculations.

soil, which contains 1600 kg P ha^{-1} (Table 3). Little of the P in the mineral soil is readily available; the greatest fraction is in primary mineral form. One third of mineral soil P is in organic form (540 kg P ha^{-1}); this soil organic P far outweighs the P in aboveground biomass (52 kg P ha^{-1}) and the forest floor (85 kg P ha^{-1}, 74% of which is organic). Dilute acid extractable P, chosen to represent P readily available to the biota, is only 0.13 kg P ha^{-1} in the mineral soil and 0.68 kg P ha^{-1} in the forest floor.

Phosphorus accumulation

Above- and belowground living biomass is accumulating P at about 1.3 kg P ha^{-1} yr^{-1} in the 70-yr old northern hardwood forest, or about 2% per year (Table 3). According to the equation describing the dynamics of the forest floor, organic matter accumulates in the forest floor at the rate of only 0.2% per year in the 70-yr old forest. The forest floor is close to steady state, accumulating P at only 0.16 kg P ha^{-1} yr^{-1}.

The rate of P accretion in the mineral soil by weathering of rock fragments and parent material or by addition of organic and mineralized P from the biologic cycle is unknown. Since soil is defined as the <2 mm fraction of material in the zone of biological activity and weathering, it is possible that living biomass, organic matter, and soil, so defined, could all be accumulating P, at the expense of the underlying parent material or the >2 mm rock fragments in the soil.

Phosphorus transfers

Annual P uptake by vegetation, the transfer of P from soil to living biomass, is 9.6 kg P ha^{-1} (Table 3; Fig. 1). Most of this P, 5.9 kg ha^{-1} yr^{-1}, is taken up from the forest floor, although the forest floor contains only 5% of soil P stores. Based on this calculation, roots in the forest floor take up twice as much P per unit root mass as do roots in the mineral soil, assuming P uptake occurs only through fine roots, 46% of which are found in the forest floor.

Annual P uptake is only slightly greater than the return of P from living biomass to soil: litterfall, throughfall and stemflow, and root exudation and root death contribute 8.3 kg P ha^{-1} yr^{-1} to the combined forest floor and mineral soil pools. Most of the P return to soil is received by the forest floor (6.3 kg P ha^{-1} yr^{-1}). Of P return to the forest floor, 70% (4.5 kg P ha^{-1} yr^{-1}) occurs aboveground, in litterfall, throughfall and stemflow. The return of P belowground, via root exudation and root death, is somewhat greater in the mineral soil (2.9 kg P ha^{-1} yr^{-1}) than in the forest floor (1.8 kg P ha^{-1} yr^{-1}). The net transfer of P from mineral soil to accumulation in living biomass and the forest floor is 1.4 kg P ha^{-1} yr^{-1}.

The calculated transfers between soil, roots, and aboveground vegetation are independent of any assumptions about the amount of absorbing root surface, the availability of soil P, or the mechanism of P uptake. Because they are calculated by mass balance, their accuracy depends only on the measured transfer and accumulation rates. They are not dependent on estimates of pool sizes.

Turnover rates of P in soil

The difference in P cycling activity between the forest floor and the mineral soil can be quantified by calculating average P turnover rates. About 7% of forest floor P turns over each year; the mean residence time of P in the forest floor is 14 years (from a pool of 85 kg P ha^{-1}, 6.33 kg P ha^{-1} yr^{-1} is removed by uptake or leaching).

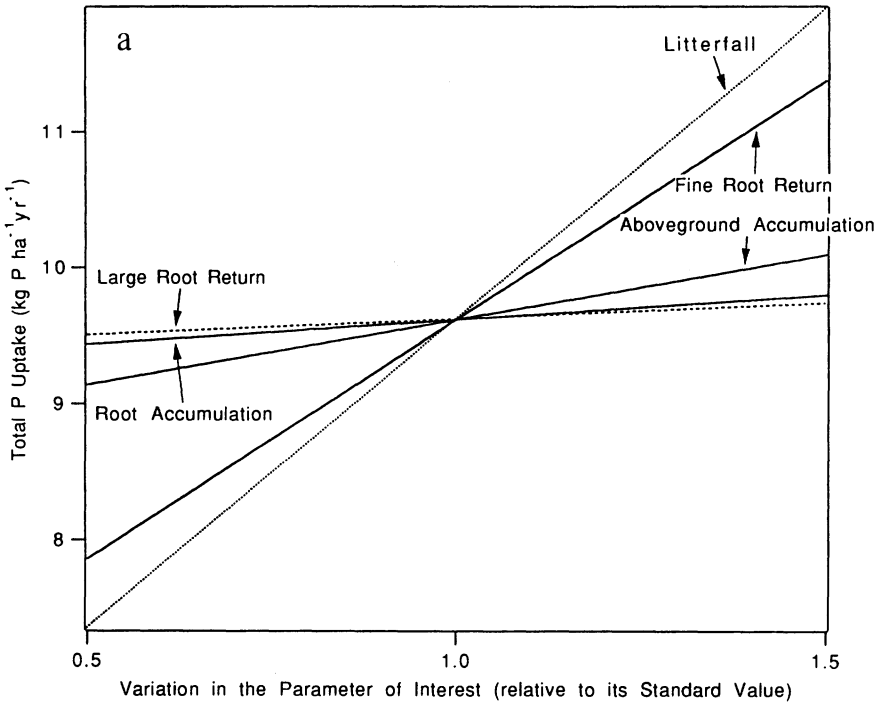
Secondary mineral P and organic P in the mineral soil are recycled, much as P in the forest floor. They are converted to soluble forms and taken up by plants via soil processes such as dissolution, desorption and mineralization. The turnover rates of all forms of organic and secondary mineral P in the mineral soil are combined in the calculated turnover rate of mineral soil P. Only 0.3% of the 1066 kg P ha^{-1} in these pools turns over each year; the mean residence time is 290 years. Primary mineral P in the mineral soil is converted at the rate of 0.02% yr^{-1}.

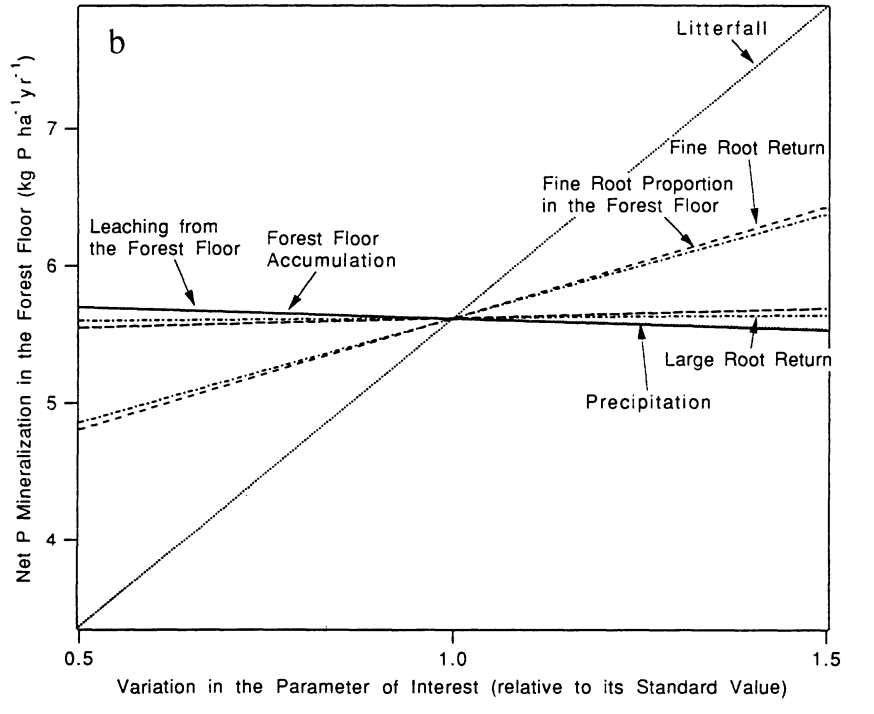
Sensitivity analysis

To provide an indication of the reliability of this budget, the sensitivity of calculated values in the P budget to changes in the measured variables can be graphically displayed. The calculated values of most interest are total P uptake, net P mineralization in the forest floor, and the proportion of P uptake obtained from the forest floor (Fig. 2). Each of the measured variables was varied from 0.5 to 1.5 times the value used in constructing the budget; the effect on the calculated value was graphed as a function of the 0.5 to 1.5 multiplier. In many cases the sensitivity of output to a given measured variable depends on the value of other parameters. Such interactions are not illustrated here; each measured value was varied independently.

Calculated total P uptake was most sensitive to variation in aboveground litterfall and fine root litter (including P exudation). An error of 50% in estimating litterfall P would result in a 2 kg P ha^{-1} yr^{-1} difference in P uptake (Fig. 2a). Uncertainty in living biomass and forest floor accumulations of P were less important because they contributed only a small fraction of the calculated result. Leaching of P in soil solution and the distribution of roots did not enter into the calculation of P uptake rate.

Net P mineralization in the forest floor, like total P uptake, was very sensitive to the estimate of litterfall. This calculation also depended on the estimate of the rate of return of root P to soil, but only on that portion occurring in the forest floor. In consequence, the effect of uncertainty in root P return on P mineralization was less than on P uptake, but the distribution of root return between forest floor and mineral soil was





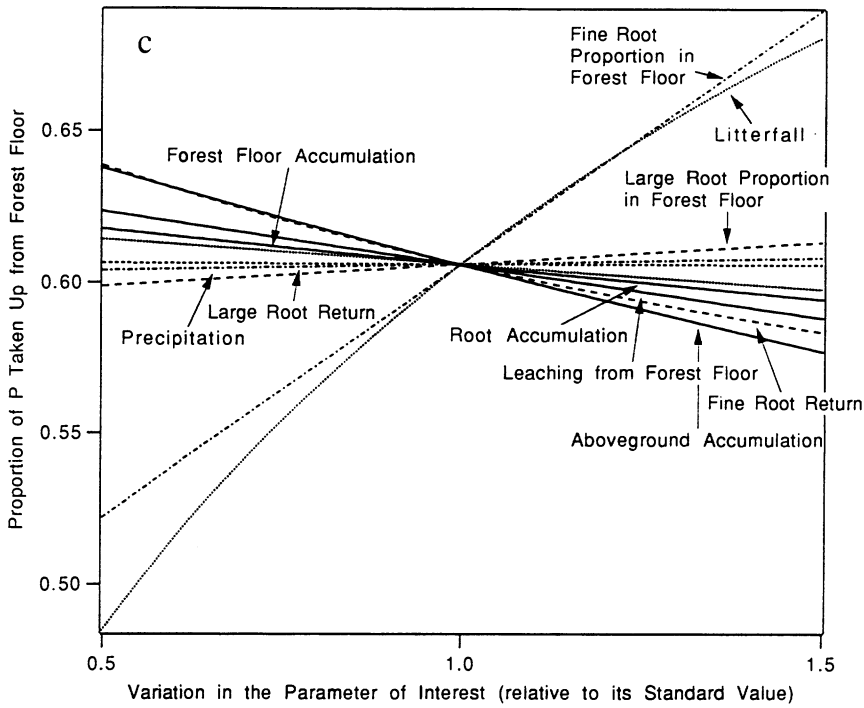


Fig. 2. Sensitivity of (a) total P uptake, (b) net P mineralization in the forest floor, and (c) the proportion of total P uptake obtained from the forest floor to changes in the values of the measured variables from which they were calculated. Each of the measured variables was varied from 0.5 to 1.5 the standard value used in constructing the budget; the 0.5 to 1.5 multiplier serves as the x-axis.

important (Fig. 2b). If estimated root return were higher, the importance of the root distribution estimate would increase accordingly. The distribution of fine roots was more important to the result than was the distribution of large roots because estimates of P return via fine roots were larger.

The proportion of P uptake from the forest floor was sensitive to the estimate of fine root distribution, because only root turnover and exudation in the forest floor contributed to the calculation. Increases in estimates of root return and biomass and forest floor accumulation rates would lead to decreases in the calculated proportion of P obtained from the forest floor (Fig. 2c). Nonetheless, this proportion would remain above 50% unless litterfall were underestimated by more than 45% or the fraction of fine roots in the forest floor (currently estimated at 46%) were less than 17%.

Discussion

Sources of error

The purpose of constructing a nutrient budget is that processes difficult or impossible to measure, such as plant P uptake and net P mineralization, can be estimated on the basis of better-known quantities (Schlesinger 1991). It is difficult to assess the accuracy of these calculated results; in this study the components of the budget were measured at such a range of spatial scales and locations that the budget cannot be replicated. Sensitivity analysis provides an approach to assessing the reliability of calculated values in the budget without making assumptions about the accuracy or validity of measurement methods.

The largest potential source of error in the P budget is in litterfall. Wood litterfall has high year-to-year variation, because tree death is a rare but important contributor to total litterfall and because branch death is strongly influenced by extreme weather conditions. Sollins (1982) suggests that average woody litterfall rates based on less than 10 years observation are potentially misleading.

The mass of leaf litterfall has been consistently measured at 2.8 to 3.0 t ha^{-1} yr^{-1} in northern hardwood forests (Gosz et al. 1972; Covington & Aber 1980; J. Hughes, pers. comm.) but P content varies considerably (1.0 to 1.9 kg P ha^{-1}; J. Hughes, pers. comm.; Gosz et al. 1972). The factors controlling annual variations in P concentration of falling leaves have not been determined.

Previous estimates of P in root turnover at the HBEF ranged from 0.9 kg P ha^{-1} yr^{-1} (Whittaker et al. 1974) to 6.2 kg P ha^{-1} yr^{-1} (Wood 1980) in part because root biomass was poorly known. Although root biomass and its P content have been more systematically measured (Fahey et al. 1988), the rate of root turnover assumed in this budget contributes an important source of uncertainty to the calculations.

The current estimate of root exudation of P omits exudation of organic P and depends on measurements made on roots grown in glass tubes in solution culture (Smith 1976). The calculation assumes that unsuberized tips of new woody roots are the major source of root exudate, that exudation of organic P is unimportant, and that P exudation is unaffected by microbial activity or by soil conditions. According to the current estimates, however, root exudation is a much less important source of P return to soil than is root turnover.

Rates of P accumulation in biomass and forest floor were found to be relatively unimportant in the budget calculations due to their small magnitudes. That the forest floor is near steady state at present is corroborated

by T. G. Siccama (Yale University, unpublished data), who found no significant change in HBEF forest floor biomass from 1976 to 1987 over seven repeated samplings. (Grand mean was 65 ± 1 t ha^{-1}.) Whittaker et al. (1979) reported low biomass P accumulation rates from 1961 to 1965 (0.7 kg P ha^{-1} yr^{-1}). Meyer (1978) and Eaton et al. (1973), like Wood (1980), found small throughfall fluxes of P in the HBEF.

An additional possible source of error in defining pools and flux rates is the absence of data on the fallen dead wood pool. Dead wood dynamics are difficult to quantify and are often omitted from forest ecosystem budgets. In this budget, standing dead wood was included with the inventory of aboveground biomass. Dead roots were included in the inventory of large roots but not of fine roots. Fallen dead wood that was not yet part of the forest floor (i.e., it would not pass a 2 mm screen) was assumed to be in steady state — litterfall losses from aboveground biomass, including dead wood, were equated with litterfall input to the forest floor, including fragmentation and leaching of dead wood. The omission of the fallen dead wood pool does not affect any other calculations in the budget.

The assumption that P flux from the forest floor, excluding plant uptake, is adequately described using tension-free lysimeters is another potential souce of error in the P budget. First, the concentration of P in soil water sampled with lysimeters may differ from that of the average leaching water. Second, the rate of solution flux cannot be measured directly and must be estimated. Finally, the role of soil disturbance, for example by treefall, in moving P among soil horizons is ignored. If lysimeter losses underestimate P loss from the forest floor, then actual P uptake from the forest floor is less and P uptake from the mineral soil more than calculated here.

Net P mineralization in the forest floor

The mineralization of P from organic matter by decomposers is difficult to measure directly under field conditions (Pastor et al. 1984; Walbridge & Vitousek 1987; Adams et al. 1989), but the net amount of organic P mineralized to phosphate in the forest floor can be calculated using a budgetary approach. Net P mineralization in the forest floor can be conceptualized as the amount of phosphate exported from the forest floor (by plant uptake and leaching) minus that delivered to the forest floor (in throughfall and stemflow and root exudates). Net P mineralization, by definition, excludes the retention and release of mineralized P in microbial biomass. Gross P mineralization, the total amount of P converted from organic form to phosphate, was not estimated because changes in P storage in and rates of P cycling though microbes were unknown.

An important assumption of this method of estimating annual net P mineralization is that the amount of mineralized P stored on soil surfaces is the same at the beginning and end of a year. Since Wood (1980) found no P adsorption by the forest floor at ambient soil solution P concentrations and the forest floor mass is near steady state, this assumption is probably valid. The high P adsorption capacity of the mineral soil prohibits the use of this method in estimating P mineralization in the B horizons.

Phosphorus uptake from forest floor and mineral soil

In the forest floor, large inputs of decomposable organic matter combine with low P adsorption capacity to promote rapid P mineralization and P uptake. In the mineral soil, in addition to organic matter mineralization, P is supplied by abiotic sources. Weathering of primary minerals in the mineral soil is important as the ultimate source of new P for biological cycling. The formation and release of P from secondary mineral sources is also more important in the mineral soil than in the forest floor. Because precipitation provides little P (0.004 kg P ha^{-1} yr^{-1}), the mineral soil is necessarily the primary source of the 1.4 kg P ha^{-1} yr^{-1} accumulating in above- and belowground living biomass and the forest floor.

The Hubbard Brook forest, like other ecosystems (Cole et al. 1977; Chapin et al. 1978; Sollins et al. 1980), obtains the majority of its annual P requirements from biological recycling rather than from geochemical sources. Resorption of P from senescing leaves provides about 40% as much P to the Hubbard Brook forest as does uptake of P from soil (Ryan & Bormann 1982). In the soil, decomposer organisms, bacteria and fungi, and absorbing roots are concentrated in the forest floor (Wood et al. 1984), where the bulk of biologically cycling P (from above- and belowground detritus, leaf leachate, and root exudate) enters the soil system. Thus P mineralized from litter by decomposers can pass directly to plant roots without reaching mineral soil. An extreme case of such "direct cycling" of P was observed in a Venezuelan moist tropical forest in which less than 1% of ^{32}P applied to litter leached into the mineral soil (Stark & Jordan 1978); electron micrographs showed funal hyphae connecting living roots and decomposing leaves (Herrera et al. 1978).

Net P mineralization and P uptake in the forest floor of the undisturbed northern hardwood forest appear to be efficiently coupled. Most of the 5.6 kg P mineralized in the forest floor in excess of microbial immobilization each year is uesd by the vegetation; a relatively small amount (0.3 kg P ha^{-1} yr^{-1}) leaches into the mineral soil. The tight cycling of P in the forest floor may be important to P supply, because P in the mineral soil is

less available to plants than is P in the forest floor (Hoyle & Bjorkbom 1969; Wood 1980).

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