The effect of whole-tree harvest on phosphorus cycling in a northern hardwood forest

Ruth D. Yanai [*]

SUNY, College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA

Abstract

A small watershed ecosystem at the Hubbard Brook Experimental Forest in New Hampshire was whole-tree harvested in the dormant season; all trees greater than 10 cm diameter were removed. This harvest removed 50 kg P/ha, five times more P than the bole-only clearcut of an adjacent watershed. The P content of branches and twigs was nearly twice that of stem wood and bark, which contributed to the intensity of P removal. The amount of P removed in harvest was small compared to total P in the mineral soil (1600 kg/ha) but large compared to the pools of P in the living vegetation (70 kg/ha) and the forest floor (85 kg/ha). Negligible P was lost in streamwater and sediment (0.2 kg P/ha over 3 years), although export of other nutrients increased dramatically. Although leaching of P from the forest floor to the mineral soil in the first 2 years after logging was higher in harvested sites than in undisturbed forest, the increase in P leaching (0.7 kg P/(ha yr)) was much less than the estimated decrease in P uptake from the forest floor (4.8 kg/(ha yr)), suggesting a 70% decline in net P mineralization in the forest floor. Even in areas where P uptake by regrowing vegetation was quite high, calculated net P mineralization was 40% lower in the first 2 years of growth than in the undisturbed forest. Revegetation was rapid: in the first 2 years after logging, P in biomass had accumulated to 3% of the uncut forest; uptake was 12% of that in the uncut forest. Whether intensive biomass removals could induce P deficiency in future rotations is unknown. © 1998 Elsevier Science B.V.

Keywords: Clearcut; Ecosystem disturbance; Nutrient removals; P mineralization; Regeneration

1. Introduction

Clearcutting disrupts nutrient cycling through multiple pathways. Biological regulation is reduced immediately after logging, with consequent increases in water yield and nutrient export (Pierce et al., 1972; Johnson and Swank, 1973; Bormann and Likens, 1979). The amount of nutrients removed in

the harvested biomass is often not large, especially when compared to ecosystem stores. In recent decades, however, increased mechanization and the development of regional and global markets for wood chips have allowed more intensive utilization, such as the harvest of whole trees, with consequent increases in nutrient removals (White, 1974). Whole-tree harvest is a method of clearcutting that removes all aboveground portions of trees above a certain size. The disruption of nutrient cycling and the magnitude of nutrient removal varies depending on the

---

[*] Corresponding author. Tel.: +1-315-470-6955; fax: +1-315-470-6954; e-mail: rdyanai@mailbox.syr.edu.

element and the ecosystem as well as the harvesting method (Federer et al., 1989).

Phosphorus cycling in forested ecosystems can be described in terms of biological and geochemical cycles (Schlesinger, 1991; Walbridge et al., 1991). Biological processes include uptake by plants and microorganisms, production and decomposition of organic residues, and release of mineralized P. Geochemical processes include weathering of primary minerals and the adsorption and desorption of organic and inorganic P by soil surfaces. Most mineral soils can adsorb large amounts of P, which explains the low losses of P in drainage water and the low availability of P in many soils. In such systems, biological cycling of P apart from the mineral soil (through vegetation and the forest floor) helps to maintain P availability (Stark and Jordan, 1978; Wood et al., 1984). Forest disturbance such as clearcutting might be expected to disrupt biological cycling of P, with loss of P to the mineral soil and consequent reduction in P availability. Geochemical adsorption of P might be enhanced, as has been demonstrated for sulfate adsorption (Nodvin et al., 1988), because the increased acidity generated by nitrification increases the positive charge on the adsorbing surfaces.

The whole-tree harvest of a monitored watershed at the Hubbard Brook Experimental Forest (HBEF) in New Hampshire provided an opportunity to study these two aspects of disturbance to ecosystem P cycling. First, I report export of P from the ecosystem, which includes direct removals in harvest and indirect losses in streamwater and sediment. These exports can be compared to that of a bole-only harvest conducted in an adjacent watershed. Second, I describe the P budget of the ecosystem for the first 2 years after the whole-tree harvest disturbance. Processes such as P uptake, leaching, and net P mineralization in the forest floor can be compared to those in an adjacent undisturbed forest (Yanai, 1992).

2. Methods

2.1. Site description

The HBEF is located in the White Mountains of New Hampshire (43°56′N, 71°45′W). The mature forest is dominated by sugar maple (*Acer saccharum* Marsh), yellow birch (*Betula allegheniensis* Britt.), and American beech (*Fagus grandifolia* Ehrh.) at lower elevations and by red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.), and white birch (*Betula papyrifera* Marsh) above about 750 m elevation. The forest was heavily logged early in the century and is largely even-aged. Soils are Typic to Lithic Haplorthods formed in glacial till; the forest floor (O horizon) is well-developed, having an average thickness of 7 cm before the whole-tree harvest (Huntington et al., 1988). The vegetation, soils, climate, hydrology and history of the HBEF are described in detail elsewhere (Bormann et al., 1970; Likens et al., 1977; Bormann and Likens, 1979; Likens, 1985).

2.2. Whole tree harvest treatment

A 22-ha watershed (W-5) at the HBEF was whole-tree harvested in the winter of 1983–1984 by a commercial logger. All trees greater than 10 cm diameter at breast height were cut and removed using feller-bunchers, chain saws, and skidders. Trees at lysimeter sites were removed with care to avoid disturbance to the soil. Elsewhere on the watershed, soil disturbance was quite variable; some 30% of the watershed showed no detectable sign of mechanical disturbance, while 25% retained no visible forest floor (Ryan et al., 1992). This variation in soil disturbance had considerable effect on the growth rate and species composition of regenerating vegetation.

The harvest treatment was temporally as well as spatially non-uniform. Harvesting began in October 1983 and continued until a machine accident in January 1984, at which time the upper third of the watershed remained uncut. The uncut portion was felled in May 1984 and the trees left on the ground. There were therefore no trees standing at the beginning of the growing season to take up water or nutrients. The results of soil water sampling by lysimeters from all sites in the harvested watershed are pooled in constructing the P budget.

After the harvest, vegetation was allowed to reestablish naturally. After 2 years, pin cherry (*Prunus pennsylvanica* L.), red raspberry (*Rubus idaeus* L.), American beech (*Fagus grandifolia*

Ehrh.), and wood fern (*Dryopteris spinulosa* Muell.) dominated living biomass. The growth rate and species composition of the vegetation in the upper third of the watershed were significantly affected by the presence of the felled trees (Hughes, 1987). These trees were finally removed by skidders in May and June, 1985, with renewed disturbance. In July 1985, the time of the vegetation survey, the upper portion of the watershed had considerably less living biomass than the lower section. For this reason, P in vegetation is described for only the lower two-thirds of the watershed. Litterfall measurements were restricted to the same area.

2.3. Harvest removals of P

The amount of biomass and nutrients removed by logging was calculated from a complete survey of tree diameters, regression equations relating tree diameters to the biomass of different tree components by species (Whittaker et al., 1974), and nutrient concentrations of these components (Likens and Bormann, 1970). Corrections to the published regression equations and nutrient concentrations included P concentrations of roots (Siccama et al., 1994).

The biomass and nutrient contents of vegetation calculated by this method were checked against actual removals from three 25 by 25 m plots, in which trees were chipped, weighed, and analyzed for dry weight and nutrient content (Siccama et al., 1994). Measured biomass removals from these plots were within about 10% of aboveground biomass estimated by tree inventory and allometric equations.

2.4. Streamwater and sediment export of P

Streamwater and sediment were monitored at gauging stations at the base of the clearcut (W-5) and reference (W-6) watersheds. Streamwater chemistry was sampled just above these gauging stations (Bormann et al., 1974). Particulate matter was collected in a series of traps and nets below the weirs (Bormann et al., 1969; Martin and Hornbeck, 1994). The pre-treatment similarity of these watersheds is well documented (Likens et al., 1977). I used data for the 3 years from June 1983 to May 1986. At each

collection, organic, mineral, and mixed organic and mineral material was weighed and subsampled for wet to oven-dry weight conversion. These data were provided by R.S. Pierce and C.W. Martin (personal communication).

To convert particulate mass to P content, I applied the P concentration of the parent rock (0.052% P; Johnson et al., 1968) to the mineral fraction and that of the forest floor (0.098% P; C.E. Johnson, personal communication) to the forest floor. For mixed organic and mineral collections, I assumed the mixture had the same proportion (32%) of organic material as the yearly total (Yanai, 1990).

The estimate of nutrient export in particulate matter is biased by missing data, because the collection system failed to capture all particulate matter lost during large storm events. The uncaptured matter might constitute an important fraction of total particulate matter losses (Bormann et al., 1974). Because total particulate matter export from the HBEF is very low, however, the underestimate of P loss by this vector makes little difference to the P output budget.

2.5. Structure of the P budget and sources of data

The compartments and fluxes used in the P budget of the regrowing forest are analogous to those of the undisturbed forest (Yanai, 1992), except that roots were not distributed to specific soil horizons. As a result, P uptake was not divided between the forest floor and the mineral soil. Transfer rates are the average for the first 2 years after harvest; P stores are given for the second growing season. Table 1 gives the timing and location of the measurements used in constructing the budget.

2.6. Above- and belowground biomass

Aboveground biomass was measured in July 1985, the second growing season after whole-tree harvest (Siccama, 1991; Siccama, 1992). Vegetation was clipped in 100 plots each measuring 1 m^2. The plots were placed randomly within three elevational bands. Pin cherry, raspberry, wood fern, and the dominant herb in each plot were collected by species; the remaining biomass was classified as saplings,

Table 1
Sources of values used in constructing the P budget of the recovering forest

Measurement	Area sampled	Time	Source
Aboveground vegetation	Lower two-thirds of W-5 excepting streambed	6/85	Siccama (1991, 1992)
Root-to-shoot ratio	Lower two-thirds of W-5	8/85	Mou (1991)
Precipitation volume	HBEF	1963–1980	Likens (1985)
Precipitation P concentration	W-6; one collector	1972–1980	Likens (1985)
Litterfall mass	Lower two-thirds of W-5	6/84–11/85	Hughes and Fahey (1994)
Litterfall chemistry	Lowest third of W-5	9/86–11/86	J.W. Hughes (pers. comm.)
Leaching from forest floor to mineral soil	W-5, all elevations; sites protected from soil disturbance	1/84–12/85	Yanai (1991)

seedlings, shrubs, and herbs. Leaves were separated from woody material. Each class of material was weighed and subsampled for dry weight and nutrient analysis. Mass and P concentration data were then combined to give P content (Table 2). I used the area-weighted mean of the low- and mid-elevation plots; the high-elevation plots had anomalously low biomass and P content due to the disturbances described above.

The P content of roots was based on the root-to-shoot ratio for P measured as part of another survey of post-harvest vegetation at this site (Mou et al., 1993). The average root-to-shoot ratio for P was 0.19 in the second year (Mou, 1991). This is less than the root-to-shoot ratio for biomass at that time, 0.50

(Mou, 1991), because of the low P concentration of aboveground stems.

The rate of P accumulation in aboveground biomass was calculated as the amount stored in perennial tissues (total P storage minus litterfall and canopy leaching, described below) at the time of the biomass survey in the second growing season, divided by 2 years. The assumption that all this P had accumulated since the whole-tree harvest is valid for seedlings and sprouts, which were not present before the disturbance. However, advance regeneration, which accounted for 8% of stems of the four dominant species at the time of the survey (Hughes, 1987) contained P which accumulated before the disturbance. The undisturbed forest also contained 0.14 kg P/ha in herbs (Whittaker et al., 1979), some of which probably also survived the disturbance. The assumption that P contained in residual vegetation had accumulated since the disturbance would tend to overestimate the P accumulation rate. A second source of error is the omission of P accumulation between July, when aboveground P was measured, and dormancy in autumn. The omission of P uptake after July would tend to underestimate the P accumulation rate.

The rate of P accumulation in belowground biomass was estimated by assuming that all the belowground P accumulated in the first 2 years after harvest. Since the root-to-shoot ratio was measured on seedlings, not stump sprouts (Mou, 1991), its application is probably more accurate for the belowground P accumulation rate than for the belowground P pool. The accumulation rates, not the pool sizes, appear in the calculation of P transfer rates (described below).

Table 2
Aboveground biomass and P content of regrowing vegetation 2 years after whole-tree harvest

	Biomass (kg/ha)			P Content (kg P/ha)		
	Elevation			Elevation		
	Low	Mid	High	Low	Mid	High
Pin cherry leaves	260	50	7	0.44	0.11	0.02
Pin cherry wood	290	50	2	0.17	0.03	0.002
Sapling leaves	230	210	50	0.28	0.26	0.10
Sapling wood	320	480	120	0.15	0.21	0.08
Seedling leaves	110	50	20	0.15	0.07	0.04
Seedling wood	80	50	10	0.06	0.04	0.01
Shrub leaves	150	110	70	0.21	0.23	0.13
Shrub wood	150	40	270	0.11	0.05	0.25
Rubus	320	70	30	0.37	0.09	0.06
Wood fern	50	50	11	0.10	0.11	0.42
Other herbs	150	170	80	0.05	0.07	0.12
Total	2110	1330	770	2.09	1.27	1.23

Seedlings are trees less than 50 cm tall; saplings are taller.

2.7. Precipitation

I used the long-term average P content of bulk precipitation (Likens, 1985) to characterize W-5 during the study period. Although the change in vegetation structure following whole-tree harvest may have affected dry deposition of P, I assume no change in precipitation inputs.

2.8. Litterfall, throughfall and stemflow

Falling litter was collected in W-5 for 3 years beginning in June 1984, the first growing season after whole-tree harvest, by Hughes and Fahey (1994). Thirty-four litter traps (Hughes et al., 1987) were emptied at least three times annually. Litter was separated by species and plant part, oven dried, and weighed. For chemical analysis, additional leaves were collected at two-day intervals during autumn leaf fall in 1986 from 32 sites between 550 and 600 m elevation. Samples were separated by species; those which had been leached by rain after falling were excluded from chemical analysis.

Throughfall and stemflow were not measured in the regrowing forest. In the mature forest at HBEF, 8.8% of foliar P leached into throughfall (calculated

by Yanai, 1990 based on Wood, 1980 and Whittaker et al., 1979). I applied this rate to the foliar P content of the 2-year old vegetation and estimated the foliar P content of the 1-year old vegetation based on the difference in litterfall P between years.

2.9. Root litter and exudates

Root death and root exudation of P were estimated for the regrowing vegetation by assuming they proceed at the same rate, relative to root P, as in the mature forest: 19%/yr (Yanai, 1992, based on Smith, 1976). I further assumed that this rate was attained linearly; i.e., the rate in the first year was half that in the second.

2.10. Leaching from the forest floor

Soil solutions were monitored monthly using tension-free lysimeters for 2 years following harvest (Yanai, 1991). Phosphorus transfer from the forest floor to the mineral soil was calculated as the product of total P concentrations in the Oa horizon and modeled monthly soil water fluxes from this horizon to the mineral soil (Yanai, 1991).
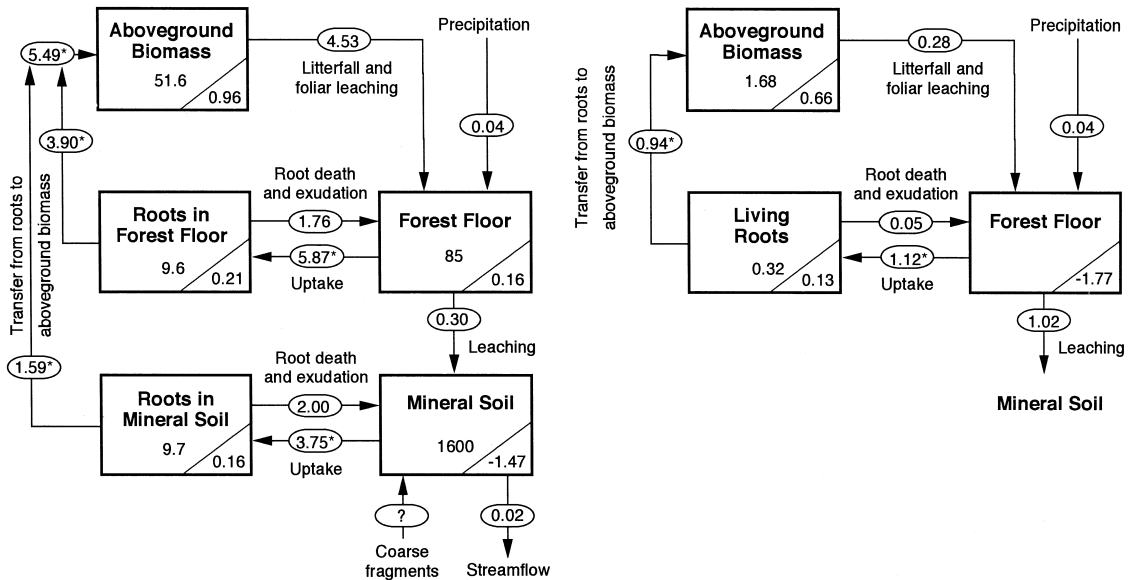

Fig. 1. Phosphorus budgets for the undisturbed forest (from Yanai, 1992) and the recovering forest for the first two years after whole-tree harvest. Values in rectangles are P stores (kg P/ha); values in triangles are annual accumulation rates (kg P/ha yr). Arrows represent fluxes (kg P/ha yr). Asterisks denote fluxes calculated by mass balance from those calculated independently. Insignificant digits for many values are shown to facilitate reproduction of the calculations.

2.11. Calculation of non-measured P transfers

Transfers of P that were not measured were calculated by mass balance on vegetation and forest floor pools (denoted by asterisks in Fig. 1). The calculations can be reproduced as follows (all terms are in units of kg P/ha yr): (1) Transfer from roots to aboveground biomass = litterfall + throughfall (excluding the atmospheric contribution) + aboveground biomass accumulation; (2) Uptake from the forest floor = transfer from roots to aboveground biomass + root accumulation + root turnover and exudation; (3) Change in forest floor = litterfall + throughfall + precipitation + root litter and exudates − uptake from the forest floor − leaching from the forest floor.

In addition to these transfers, which link pools in the budget, net P mineralization in the forest floor can be calculated using a budgetary approach. In the undisturbed forest, net P mineralization in the forest floor was calculated as the excess of phosphate exported from the forest floor over the amount received (Yanai, 1992). Plant uptake from the forest floor cannot be calculated for the recovering forest, because root distribution was not measured; however, an upper limit to net P mineralization in the forest floor can be obtained by assuming that all P is taken up in the forest floor and none from the mineral soil. Therefore, (4) 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 phosphate in the forest floor. Litterfall and root death were assumed to contribute only organic P to the forest floor. The amount of mineralized P stored on soil surfaces was assumed to be constant at the time scale of interest.

3. Results

3.1. The removal of P in biomass by whole-tree harvest

The amount of a nutrient removed during a forest harvest depends not only on the combined biomass of tree parts removed but also on the distribution of the nutrient among the various tree parts. At the HBEF, as elsewhere, concentrations of most nutrient elements are lowest in heartwood and sapwood, intermediate in bark and branches, and highest in leaves and twigs (Likens and Bormann, 1970). Most of the mass of the trees in the 70 yr-old forest was in stemwood; the mass of leaves is relatively small (Table 3). Branches are the greatest reservoir of P in the aboveground biomass of this forest, comprising 56% of the total. Leaves plus twigs, because of their small mass, and stemwood with bark, because of its low P concentration, make up only 13 and 31% of aboveground P, respectively. Other nutrient elements show somewhat different distributions among plant parts: Ca is concentrated in bark, while a greater portion of N and K than of other nutrients occurs in leaves.

Table 3
Mass and nutrient content of aboveground biomass in the 70-yr old northern hardwood forest

Nutrient	Aboveground Total (kg/ha)	Biomass or nutrient content of tree parts as a fraction of aboveground total					Harvest removal ratio
		Stem wood	Stem bark	Branch	Twig	Leaf	
Biomass	199,000	0.63	0.07	0.29	0.006	0.02	1.4
P	52	0.22	0.09	0.56	0.01	0.12	2.8
N	509	0.24	0.16	0.45	0.006	0.15	2.2
K	219	0.34	0.14	0.36	0.005	0.15	1.2
Ca	584	0.17	0.34	0.45	0.003	0.04	1.4
Mg	54	0.42	0.13	0.35	0.004	0.01	1.6
S	59	0.35	0.14	0.36	0.004	0.10	1.8

The Harvest Removal Ratio shows how much more biomass or nutrient is contained in whole-tree harvestable parts (stem wood and bark plus branches and twigs) than in tree parts conventionally harvested (stem wood and bark).

According to these data, if a stem-only clearcut harvest removed all the stemwood and its bark, and if a whole-tree clearcut harvest removed all aboveground biomass except leaves, then the whole-tree harvest would remove 2.8 times as much P as the stem-only harvest. This difference is considerably more than the difference in biomass removal because the P concentration of branches and twigs is greater than that of stems. Of the major nutrient elements, P shows the greatest difference in predicted removals between these two harvest types, because of the proportionately high P content of branches in this data set. The removal of other elements predicted by whole-tree harvest ranges from 1.2 to 2.2 times that of stem-only harvest.

In practice, a stem-only harvest may not remove all stemwood, since not all trees are of usable quality. Steep and inaccessible terrain may further reduce the proportion of stems extracted. The amount of biomass removed in an adjacent stem-only harvest at the HBEF was only 50 Mg/ha (Table 4). The stem-only harvest took place about 10 years earlier than the whole-tree harvest, so part of the difference between the two cases of harvest removal is due to lesser pre-harvest aboveground biomass on the stem-only harvested site (133 Mg/ha, Martin and Hornbeck, 1989), but the fraction removed (0.38) is much less than predicted from Table 3. The removal of aboveground biomass in the whole-tree harvest, in contrast, was nearly complete, with only about 10% (19 ± 2.4 Mg/ha) left as slash (Siccama et al., 1994). Table 4 compares the calculated removals of biomass and nutrients for the whole-tree harvest (these data are corrected for growth following the 1982 diameter survey used to construct Table 3) with the removals from the stem-only harvest. The ratio of removals shows the increase in harvest intensity: three times as much biomass and five times as much P were removed from the whole-tree harvest as from the stem-only harvest, even after correcting for the growth between the two treatments. Other nutrient elements showed three- to four-fold increases in removal.

3.2. Effect of harvest on streamwater export of P

The estimated loss of dissolved P in streamwater from the whole-tree harvested watershed was very small, less than 0.03 kg P/(ha yr) (Table 5). The increase over P loss from the adjacent undisturbed forest was less than 0.01 kg P/(ha yr). Nitrate, Ca, and K, in contrast, were lost at rates 4 to 40 times higher than the loss rates from the undisturbed reference watershed in the second and third years after logging. Increased streamflow from the harvested watershed was responsible for part of the increase in dissolved nutrient export during this period.

Whole-tree harvest increased particulate matter export from an average of 16 kg/(ha yr) to an average of 100 kg/(ha yr) in the first 3 years following disturbance (Table 6). The amount of P loss, however, remained small, totalling 0.18 kg P/ha over 3 years.

Table 4
Nutrients removed by whole-tree and stem-only clearcutting

	Harvest removal (kg/ha)		Harvest removal ratio
	Whole-tree	Stem-only	
Biomass	205,000	50,000	2.7
P	50	6	5.4
N	445	74	3.9
K	216	40	3.5
Ca	578	107	3.5
Mg	51	11	3.0
S	56	13	2.8

The Harvest Removal Ratio shows how much more biomass or nutrient was removed in whole-tree than in stem-only harvest.
Whole-tree harvest removals for W-5 were calculated by T.G. Siccama (pers. comm.) and include a correction for growth between the diameter survey in 1982 and the harvest in 83–84.
Stem-only harvest removals are for W-4 (Hornbeck, 1986), which was harvested in strips from 1970 to 1974.
Harvest Removal Ratios were adjusted to account for the difference in initial biomass between the two logging treatments.

3.3. Change in ecosystem P cycling

Aboveground living biomass in Watershed 5 two years after whole-tree harvest contained only 1.7 kg P/ha, one-thirtieth as much as the pre-harvest forest (Fig. 1). Litterfall contained 0.13 kg P/ha in the first year and 0.24 kg P/ha in the second year after harvest, averaging about one-twentieth as much P as

Table 5

Dissolved nutrient export in streamwater from the reference (REF) and the whole-tree harvested (WTH) watersheds

Water	Water flux (mm)		Nutrient export (kg/ha yr)									
Year	REF	WTH	N (NO_3)		N (NH_4)		Ca		K		P	
			REF	WTH	REF	WTH	REF	WTH	REF	WTH	REF	WTH
1982–1983	770	813	1.1	0.9	0.10	0.09	7.7	8.6	1.7	1.4	0.008	0.007
1983–1984	1003	955	0.6	0.5	0.13	0.15	8.4	11.0	2.3	4.1	0.013	0.023
1984–1985	670	800	0.6	29.2	0.08	0.17	6.2	21.0	1.5	9.6	0.009	0.014
1985–1986	913	931	0.9	29.7	0.15	0.20	8.0	21.1	1.9	9.5	0.021	0.020
1986–1987	837	791	1.6	5.1	0.18	0.18	7.6	11.6	2.1	5.1	0.023	0.028

The whole-tree harvest was conducted during the latter part of the 1983–1984 water year.

The water year runs from June 1st to May 31st.

Data were provided by Don Buso, Institute for Ecosystem Studies.

litterfall in the mature forest. Phosphorus uptake, calculated as the sum of above and belowground accumulations and losses, averaged 1.1 kg P/(ha yr), which was 12% of the rate of P uptake in the 70-yr old forest.

Losses from the forest floor totalled 2.1 kg P/(ha yr): leaching loss of P from the forest floor increased to 1.0 kg P/(ha yr), and P uptake averaged 1.1 kg P/(ha yr). The calculated leaching loss applies to areas of forest floor unaffected by mechanical disturbance; mixing of the forest floor with mineral soil during the harvest operation was widespread and quantitatively important (Ryan et al., 1992), contributing further to the loss of P from the forest floor in the watershed as a whole. The rate of change in forest floor P content shown in Fig. 1 is therefore probably a conservative estimate of the average P loss from the forest floor in the watershed as a whole.

Table 6

Phosphorus export in particulate matter in the first three years following whole-tree harvest from the reference (REF) and the whole-tree harvested (WTH) watersheds

Interval	Mass (kg/ha)		P (kg/ha)	
	REF	WTH	REF	WTH
7/83–6/84	27.0	56.1	0.018	0.035
6/84–6/85	3.3	17.4	0.003	0.012
6/85–6/86	18.3	224.2	0.014	0.132
Total	48.6	297.7	0.035	0.180
Average/year	16.2	99.2	0.012	0.060

Net P mineralization in the forest floor of the undisturbed forest was calculated as the excess of phosphate exported from the forest floor over the amount received, assuming the storage of mineralized P in the forest floor to be constant. Applying the same calculation to the post-harvest forest floor gives a net P mineralization of only 1.6 kg P/(ha yr), compared to 5.6 kg P/(ha yr) in the undisturbed system (Yanai, 1992). This calculation, like the leaching loss from the forest floor, applies to areas of forest floor not mechanically disturbed by harvesting.

4. Discussion

4.1. Direct and indirect P removals

When compared to ecosystem stores of P in all forms, organic and mineral, the loss by all mechanisms of P in whole-tree harvest was slight. The amount of P exported in streamwater and particulate matter was negligible (Tables 5 and 6). The amount of P removed in whole-tree harvest, although much higher (50 kg P/ha, Table 4), was still only 3% of total ecosystem P stores (1700 kg P/ha; Yanai, 1992). Calculations of nutrient losses from six sites in the eastern United States, including this site, showed removals of P, K, and Mg by whole-tree harvest to be ≤ 3% of total ecosystem stores (Federer et al., 1989). The fraction of N lost was somewhat greater (4% to 8%), and Ca losses were as high as 13% and 19% in two forests containing oak and

hickory (Federer et al., 1989). These values include accelerated streamwater export. Streamwater export of Ca was especially high (Table 5), making this element the most likely to be depleted by repeated forest harvest (Tritton et al., 1987; Mann et al., 1988; Federer et al., 1989).

Although the total amount of P in the ecosystem, which includes the soil fraction < 2 mm, is large compared to the amounts removed in harvest, much of this P is not readily available to support the regrowth of the forest. Most P is in the mineral soil, which cycles P only very slowly (turnover rates are 0.33%/yr, compared to 7%/yr in the forest floor, Yanai, 1992). Moreover, an unknown fraction of the 4 kg P/(ha yr) supplied from the mineral soil in the mature forest (Fig. 1) is input from mineral weathering, rather than recycled from secondary mineral and organic P pools. Weathering rates are difficult to estimate in natural conditions, and measurements specific to P have not been made at HBEF. Wood (1980) estimated a rate of P release from soil minerals of 1.5 kg P/(ha yr), based on the denudation rate of Ca (Likens et al., 1977) and the Ca:P of the parent material (Johnson et al., 1968). This rate agrees with the rate of P denudation of the mineral soil (1.47 kg P/ha yr, Fig. 1). More recent estimates of Ca weathering, however, are an order of magnitude lower (Likens et al., 1996), because Ca, like P, may be supplied from soil stores during forest growth by other processes than primary mineral weathering. Neither the rates nor the relative availability of these P sources is well understood, which makes it difficult to predict the maximum sustainable rate of P removal.

Above- and belowground biomass and the forest floor, which cycle P more rapidly, together contained about 157 kg P/ha before the harvest. Thus the whole-tree harvest removed 32% of the most readily available P stock. When viewed in this light, the fact that whole-tree harvest removed five times as much P as the adjacent stem-only strip cut suggests that the intensity of logging removal may affect the rates or pathways of P supply to the regenerating forest. To restore living biomass to its pre-harvest state would require a P supply equivalent to 58% of the P remaining in the forest floor and in stumps and roots in the case of whole-tree harvest but only 4% in the case of stem-only harvest.

Phosphorus removal in stem-only harvest as a fraction of P removal in whole-tree harvest ranged from 17 to 87% in a study of 11 forest stands across the United States (Mann et al., 1988). Most values fell between 30 and 60%. At some of the sites, mechantable stem biomass was considerably less than total stem biomass, as was the case for the strip cut at HBEF (Tables 3 and 4). This experimental whole-tree harvest, in contrast, included steep areas of the watershed that would not have been commercially logged. In a commercial whole-tree harvest, the amount of biomass and P removal could be less than that reported here.

The low rates of erosional losses in the first 2 years after this whole-tree harvest are typical of the region (Martin and Hornbeck, 1994). Erosion rates are highly variable, probably due to large storm events (Bormann et al., 1974; Martin and Hornbeck, 1994). Had there been a heavy rain during the time that the watershed was essentially bare of vegetation, P loss through erosion might have been much larger. The amount of P in particulate matter was so small, however, that even a several-fold increase in losses would have little effect on the total P output.

Dissolved P in streamwater remained low after whole-tree harvest disturbance, in contrast to other nutrient elements (Table 5). Soils in the White Mountains of New Hampshire are prone to nutrient leaching following clearcutting (Pierce et al., 1972) perhaps because these Spodosols have little capacity to retain the excess of ions mineralized in the overlying organic horizon (Reinhart, 1973). Phosphorus, however, is strongly retained by these ecosystems (Zhang and Mitchell, 1995), presumably due to the high P sorption capacity of the mineral soil (Wood, 1980). Even after clearcutting, leaving all biomass on site to decompose, and preventing regrowth for 3 years with herbicides, the concentration of dissolved P in streamwater did not increase (Hobbie and Likens, 1973). Other studies have also shown greater losses of N, K, and Ca than of P in streamwater or leachate following forest harvest (Mann et al., 1988). Sulfate, in contrast, often decreases following forest disturbance, because decreasing pH creates more positive charge on variable-charge adsorbing surfaces (Nodvin et al., 1988). This process did not appear to affect P concentrations in soil solutions in this study (Yanai, 1991).

4.2. Biomass and P accumulation

Biomass and P content of regrowing vegetation in the first few years after forest harvest vary widely across sites and studies (Table 7). Some of the variation may be due to differences in harvest method. Whole-tree harvest of upland hardwoods in Tennessee resulted in greater seedling abundance but reduced stump sprouting compared to bole-only harvest (Mann, 1984). Greater biomass accumulation after whole-tree harvest than bole-only harvest was reported in a northern mixed forest (Hendrickson, 1988) and in a Sitka spruce plantation in Wales (Fahey et al., 1991). Whole-tree harvest of fir and

birch produced greater biomass and P accumulation than bole-only harvest followed by slash burning (Outcault and White, 1981a,b).

Regrowth following the whole-tree harvest of W-5 at HBEF was slower than that following the bole-only clearcut of the adjacent W-4, but the amount of harvest removals was not the only important difference between these studies. First, species composition was different in W-4, which was strip cut to favor birch regeneration (Martin and Hornbeck, 1989). Second, W-4 was sampled at the end of the growing season, while W-5 was sampled in July. Finally, W-5 suffered more extensive soil disturbance than did W-4 (C.W. Martin, personal commu-

Table 7
Biomass and P content of aboveground living vegetation 1 to 4 years after clearcutting by whole-tree harvest (WTH) or conventional harvest (CH) in temperate forests

Age	Location; dominant vegetation	Biomass (kg/ha)		P content (kg P/ha)		Source
		WTH	CH	WTH	CH	
1	Hubbard Brook, NH; Raspberry		286			Whitney (1982)
	Beddgellert, UK; Graminoids	730	270			Fahey et al. (1991)
	Bartlett, NH; Pin cherry		796			Marks (1974)
	Hubbard Brook, NH; Mixed hardwoods	990		1.3		Mou et al. (1993)
	H.J. Andrews, OR; Residual shrubs		1211		0.9	Gholz et al. (1985)
	Hubbard Brook, NH; Mixed hardwoods		1450[a]			Bicknell (1979)
	Coweeta, NC; Mixed oak, cove hardwood sprouts		1725		2.5	Boring et al. (1981)
	Oak Ridge, TN; Herbs and hardwood sprouts	1837	1765			Mann (1984)
	Coweeta, NC; Scarlet oak, mountain laurel		2371		3	Boring (1982)
	Clemson, SC; Herbaceous plants	3130	2456	2.6	1.9	Cox and Van Lear (1985)
2	Beddgellert, UK; Graminoids	1350	720			Fahey et al. (1991)
	H.J. Andrews, OR; Residual shrubs		1633		1.5	Gholz et al. (1985)
	Hubbard Brook, NH; Pin cherry	1720		1.7		this study
	Cloquet, MN; Mixed hardwoods	4181	2604[b]	7.9	5.8	Outcault and White (1981a,b)
	Hubbard Brook, NH; Raspberry		3768			Whitney (1982)
	Hubbard Brook, NH; Mixed hardwoods		3970[a]			Bicknell (1979)
	Hubbard Brook, NH; Mixed hardwoods	4148		4.4		Mou et al. (1993)
	Clemson, SC; Herbaceous plants	5800	3510	4.4	2.7	Cox and Van Lear (1985)
	Coweeta, NC; Scarlet oak, mountain laurel		5909		6	Boring (1982)
	Coweeta, NC; Mixed oak, cove hardwood sprouts		8200		9	Boring (1982)
3	H.J. Andrews, OR; Residual shrubs		2596		3.3	Gholz et al. (1985)
	Beddgellert, UK; Graminoids	3120	1510			Fahey et al. (1991)
	Hubbard Brook, NH; *Rubus*		5879			Whitney (1982)
	Hubbard Brook, NH; Pin cherry		6290			Bicknell (1979)
	Hubbard Brook, NH; Mixed hardwoods	8716		5.5		Mou et al. (1993)
	Coweeta, NC; Mixed oak, cove hardwood sprouts		11,452		9	Boring (1982)
4	Beddgellert, UK; Graminoids	6960	3910			Fahey et al. (1991)
	Bartlett, NH; Pin cherry		7064		4.3	Safford and Filip (1974)
	Hubbard Brook, NH; *Rubus*		7457			Whitney (1982)
	Ontario: Hardwood sprouts	9438	7879			Hendrickson (1988)
	Hubbard Brook, NH; Pin cherry		15,548			Bicknell (1979)
	Hubbard Brook, NH; Mixed hardwoods	11,970		6.9		Mou et al. (1993)
	Hubbard Brook, NH; Pin cherry		19,694			Marks (1974)

[a] Includes belowground biomass.
[b] Slash burning.

nication), as is common for whole-tree harvesting (Martin, 1988), and vegetation recovered more slowly in highly disturbed areas.

In addition to the intensity of harvest removal, differences in revegetation rates reflect other factors such as the type of harvesting equipment used, the degree of soil disturbance, the timing of harvest (Outcault and White, 1981a; McMinn, 1985), vegetation type, and soil fertility (Hendrickson, 1988). Initially, vegetation accumulation may be favored by whole-tree harvest due to less shading by slash (Fahey et al., 1991; Mann, 1984). The effect of reduced nutrient capital resulting from intensified biomass removal may not be expressed until later in stand development, if at all.

An independent study of vegetation regrowth on W-5 (Mou et al., 1993) estimated biomass and nutrient accumulation to be more than twice as rapid as that reported in this study. This difference may be partly due to disturbance: the study by Mou and coworkers involved intensive measurement on eight large plots which were protected from logging disturbance, whereas this study used 100 small plots randomly located and including severely disturbed sites. Clearly, variation in experimental design can contribute differences as large as the treatment effects in comparisons of measured revegetation rates.

4.3. Decomposition and P mineralization

The increased export of N in streamwater following whole-tree harvest implies that N mineralization exceeded uptake by vegetation by more than before the harvest. If the same were true of P, then the lack of P in streamwater could be attributed to the high P sorption capacity of the mineral soil (Wood, 1980). Alternatively or additionally, mineralization of P may not exceed P uptake to the same degree as for other nutrients. The effect of disturbance on P mineralization can be assessed through budgetary calculations, at least in the forest floor, where P sorption is negligible (Wood et al., 1984).

According to these P budgets (Fig. 1), plant uptake of P from the forest floor declined by over 4 kg P/(ha yr), from 5.9 kg P/(ha yr) in the undisturbed forest to at most 1.1 kg P/(ha yr) in the first 2 years after whole-tree harvest (some of the 1.1 kg P/(ha yr) came from mineral soil). If net P mineralization

in the forest floor had remained constant, then P leaching should have increased by the amount that uptake declined, 4.8 kg P/(ha yr). But P leaching increased by only 0.7 kg P/(ha yr). In effect, estimated net P mineralization in the forest floor declined from 5.6 kg P/(ha yr) in the undisturbed forest to 1.6 kg P/(ha yr) in the first 2 years after whole-tree harvest.

In more disturbed sites, P loss from the forest floor may have been substantially greater than the leaching loss measured in undisturbed sites. Lysimeter sites were established before harvesting and protected from vehicular traffic; soil solution chemistry, therefore, characterizes mechanically undisturbed soil. In vegetation surveys, on the other hand, the watershed was sampled widely and at random locations, avoiding only the streambed. Net P mineralization, which is essentially the sum of P uptake and P leaching, is probably underestimated for areas with undisturbed soil, where growth was greater than the watershed average. In disturbed areas, on the other hand, this method cannot be used to calculate net P mineralization because the mixture of mineral soil into the forest floor by logging disturbance may increase the P adsorption capacity of the forest floor such that some mineralized P may be neither taken up by plants or microbes nor leached into lower soil horizons. It is an assumption of this method of calculating net P mineralization that change in storage of mineralized P in the forest floor can be neglected.

Net P mineralization in the forest floor for undisturbed sites can be estimated using rates of P accumulation measured by Mou et al. (1993) in the same whole-tree harvested watershed. Applying the same budgetary calculations to P accumulation on these plots, which were protected from disturbance, gives a P uptake rate of 3.0 kg P/(ha yr) in the first 2 years of growth, compared to 1.1 kg P/(ha yr) calculated for the watershed average (Fig. 1). The decline in uptake from the forest floor is still much greater than the increase in P leaching, even assuming all of the uptake in the first 2 years comes from the forest floor. The estimate of net P mineralization using the higher growth rate is 3.4 kg P/(ha yr), which still represents a decrease of 40% compared to the undisturbed forest.

The effect of disturbance on organic matter de-

composition and nutrient mineralization rates has been the subject of considerable research. Increased temperature, moisture, and nutrient availability following logging have usually been assumed to cause increased forest floor decomposition (Witcamp, 1971; Covington, 1981; Bormann and Likens, 1979; Houghton et al., 1983). In some cases, however, drying of the forest floor after canopy removal has reduced decomposer activity (Abbott and Crossley, 1982; Whitford et al., 1981). In this study, during the first 2 years after whole-tree harvest, the rate of decomposition of forest floor blocks incubated on site was 5% per year (Johnson et al., 1995), which is less than the rate reported for the undisturbed forest (12% per year, Gosz et al., 1976). The reduced rate of mass loss reflects reduced rates of litterfall as well as any change in decomposition rates per unit substrate.

Rates of nutrient loss from the forest floor may differ from rates of organic matter loss, because of variations in mineralization and immobilization across elements. Gross mineralization rates may differ in heterogeneous material because the substrate is not uniformly decomposed. Even in homogeneous material, gross mineralization rates may differ by element due to the specificity of degradative enzyme systems (McGill and Cole, 1981). Additional variation in net mineralization rates may accrue from differential microbial immobilization of different elements.

Nitrogen mineralization has been observed to accelerate following disturbance in many forest types (Vitousek and Matson, 1985; Matson and Boone, 1984; Gordon and Van Cleve, 1983; Matson et al., 1987; Frazer et al., 1990). Nitrogen is presumably mineralized in excess of N demand in the process of C catabolism (McGill and Cole, 1981). Phosphorus mineralization, in contrast, should be more responsive to plant and microbial demand: phosphatase production depends on microbial demand for P (Nannipieri et al., 1978; Tabatabai, 1982), and end-product inhibition makes phosphatase kinetics sensitive to the concentration of phosphate in soil (Juma and Tabatabai, 1978; Spiers and McGill, 1979). Thus, the rate of P mineralization per unit substrate might well be expected to decrease following a disturbance that raises the concentration of phosphate in soil solution. Concentrations of P in soil solution in the forest floor averaged 248 ± 68 μg/l in whole-tree harvested sites and 67 ± 12 μg/l in undisturbed sites in the 2-year period of this study (Yanai, 1991).

In addition to effects that could reduce the rate of mineralization per unit substrate, whole tree harvest disturbance reduces the supply of organic P to the forest floor per unit land area. The rate of litterfall, throughfall, root litter and root exudation were reduced from a sum of 8.3 kg P/(ha yr) in the undisturbed forest to only 0.3 kg P/(ha yr) in the first 2 years after harvest (Fig. 1). Logging debris contained only about 2 kg P/ha, and this P would be released over a period of years. Decomposition of tree roots killed in harvest might amount to 0.8 kg P/(ha yr) in the forest floor (Yanai, 1990, based on Fahey et al., 1988). These inputs fall short of compensating for the reduction in above- and below-ground nutrient return by the vegetation.

Increased microbial immobilization of P may also be responsible for part of the calculated decline in net P mineralization. Microbial P has not been measured at HBEF, but in a mature Appalachian hardwood forest, 31 to 35% of forest floor organic P was microbial (Walbridge, 1991). Acid organic soil in the North Carolina coastal plain had from 37 to 56% of soil organic P in the microbial fraction (Walbridge et al., 1991). The degree to which microbial storage of P in forest soils can vary with disturbance or even seasonal changes is unknown. If one-third of the 61 kg P/ha in soil organic matter in the Hubbard Brook forest floor is in microbial mass, this mass would have to increase only 20% to account for a 4 kg P/(ha yr) decrease in net P mineralization.

In sites without soil disturbance, leaching losses of P from the forest floor are low, whether due to reduced decomposition, reduced phosphatase production and activity, increased microbial immobilization, or reduced supply of organic matter to the forest floor. Phosphorus in the forest floor can be more readily recovered by plants than P in the mineral soil. Thus, although whole-tree harvest removes a major portion of 'actively cycling' organic P stores, the P remaining in dead wood and the forest floor is retained in a more available form than if P mineralization and leaching to the mineral soil were greatly accelerated. This P retention may contribute to the capacity of the ecosystem to recover from disturbance.

Acknowledgements

References

Abbott, D.T., Crossley, D.A. Jr., 1982. Woody litter decomposition following clear-cutting. Ecology 63, 35–42.

Bicknell, S.H., 1979. Plant succession in a revegetating northern hardwood ecosystem. PhD Thesis, Yale University, p. 218.

Boring, L.R., Monk, C.D., Swank, W.T., 1981. Early regeneration of a clearcut southern Appalachian forest. Ecology 62, 1244–1253.

Boring, L.R., 1982. The role of black locust (*Robina pseudoacacia*) in forest regeneration and nitrogen fixation in the southern Appalachians. PhD Thesis, University of Georgia, Athens.

Bormann, F.H., Likens, G.E., 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York.

Bormann, F.H., Likens, G.E., Eaton, J.S., 1969. Biotic regulation of particulate and solution losses from a forest ecosystem. BioScience 19, 600–610.

Bormann, F.H., Siccama, T.G., Likens, G.E., Whittaker, R.H., 1970. The Hubbard Brook Ecosystem Study: Composition and dynamics of the tree stratum. Ecol. Monogr. 40: 373–388.

Bormann, F.H., Likens, G.E., Siccama, T.G., Pierce, R.S., Eaton, J.S., 1974. The effect of deforestation on ecosystem export and the steady-state condition at Hubbard Brook. Ecol. Monogr. 44, 255–277.

Covington, W.W., 1981. Changes in forest floor organic matter content following clearcutting in northern hardwoods. Ecology 62 (1), 41–48.

Cox, S.K., Van Lear, D.H., 1985. Biomass and nutrient accretion on Piedmont sites following clearcutting and natural regeneration of loblolly pine. USDA Forest Service Gen. Tech. Rep. SO-54, pp. 501–506.

Fahey, T.J., Hill, M.O., Stevens, P.A., Hornung, M., Rowland, P., 1991. Nutrient accumulation in vegetation following conventional and whole-tree harvest of Sitka spruce plantations in North Wales. Forestry 64, 271–288.

Fahey, T.J., Hughes, J.W., Mou, P., Arthur, M.A., 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. For. Sci. 34, 744–768.

Federer, C.A., Hornbeck, J.W., Tritton, L.M., Martin, C.W., Pierce, R.S., Smith, C.T., 1989. Long-term depletion of calcium and other nutrients in Eastern US Forests. Environ. Manage. 13, 593–601.

Frazer, D.W., McColl, J.G., Powers, R.F., 1990. Soil nitrogen mineralization in a clearcutting chronosequence in a northern California conifer forest. Soil Sci. Soc. Am. J. 54, 1145–1152.

Gholz, H.L., Hawk, G.M., Campbell, A., Cromack, K. Jr., Brown, A.T., 1985. Early vegetation recovery and element cycles on a clear-cut watershed in Western Oregon. Can. J. For. Res. 15, 400–409.

Gordon, A.M. Van Cleve, K., 1983. Seasonal patterns of nitrogen mineralization following harvesting in the white spruce forests of interior Alaska. In: Wein, R.W., Pierce, R.R., Methven, I.R. (Eds.), Resources and Dynamics of the Boreal Zone. Association of Canadian Universities for Northern Studies, Sault Sainte Marie, Ontario, Canada, pp. 119–130.

Gosz, J.R., Likens, G.E., Bormann, F.H., 1976. Organic matter and nutrient dynamics of the forest and forest floor in the Hubbard Brook forest. Oecologia 22, 305–320.

Hendrickson, O.Q., 1988. Biomass and nutrients in regenerating woody vegetation following whole-tree and conventional harvest in a northern mixed forest. Can. J. For. Res. 18, 1427–1436.

Hobbie, J.E., Likens, G.E., 1973. Output of phosphorus, dissolved organic carbon, and fine particulate carbon from Hubbard Brook watersheds. Limnol. Oceanogr. 18, 734–742.

Hornbeck, J.W., 1986. Nutrient cycles and forest productivity. In: Smith, C.T., Martin, C.W., Tritton, L.M. (Eds.), Proceedings, Symposium Productivity of Northern Forests Following Biomass Harvesting. University of New Hampshire, Durham, pp. 23–27.

Houghton, R.A., Hobbie, J.E., Melliro, J.M., Moore, B., Peterson, B.J., Shaver, G.E., Woodwell, G.M., 1983. Changes in the carbon content of terrestial biota and soils between 1860 and 1980: a net release of CO_2 to the atmosphere. Ecol. Monogr. 53, 235–262.

Hughes, J.W., 1987. Maintenance of floristic patterns in a disturbed northern hardwood forest: regeneration strategies and forest history. PhD dissertation, Cornell University.

Hughes, J.W., Fahey, T.J., 1994. Litterfall dynamics and ecosystem recovery during forest development. For. Ecol. Manage. 63, 181–198.

Hughes, J.W., Fahey, T.J., Brown, B., 1987. A better seed and litter trap. Can. J. For. Res. 17, 1623–1624.

Huntington, T.G., Ryan, D.F., Hamburg, S.P., 1988. Total soil carbon and nitrogen in a northern hardwood forest ecosystem. Soil Sci. Soc. Am. J. 52, 1162–1168.

Johnson, C.E., Johnson, A.H., Huntington, T.G., Siccama, T.G., Hughes, J.W., 1995. Carbon dynamics following clearcutting

of a northern hardwood forest ecosystem. In: Kelly, J.M., McPhee, W.W. (Eds.). Carbon: Forms and Function in Forest Soils. American Society of Agronomy, Madison, WI, pp. 463–488.

Johnson, N.M., Likens, G.E., Bormann, F.H., Pierce, R.S., 1968. Rate of chemical weathering of silicate minerals in New Hampshire. Geochem. Cosmoch. Acta 32, 531–545.

Johnson, P.L., Swank, W.T., 1973. Studies of cation budgets in the southern Appalachians on four experimental watersheds with contrasting vegetation. Ecology 54, 70–80.

Juma, N.G., Tabatabai, M.A., 1978. Distribution of phosphomonoesterases in soils. Soil Sci. 126, 101–108.

Likens, G.E. (Ed.), 1985. An Ecosystem Approach to Aquatic Ecology: Mirror Lake and its Environment. Springer-Verlag, New York.

Likens, G.E., Bormann, F.H., 1970. Chemical analyses of plant tissues from the Hubbard Brook Ecosystem in New Hampshire Bull 79. Yale University School of Forestry, New Haven, CT.

Likens, G.E., Bormann, F.H., Pierce, R.H., Eaton, J.S., Johnson, N.M., 1977. Biogeochemistry of a Forested Ecosystem. Springer-Verlag, New York.

Likens, G.E., Driscoll, C.T., Buso, D.C., 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. Science 272, 244–246.

Mann, L.K., 1984. First year regeneration in upland hardwoods after two levels of residue removal. Can. J. For. Res. 14, 336–342.

Mann, L.K., Johnson, D.W., West, D.C., Cole, D.W., Hornbeck, J.W., Martin, C.W., Riekerk, H., Smith, C.T., Swank, W.T., Tritton, L.M., Van Lear, D.H., 1988. Effects of whole-tree and stem-only clearcutting on postharvest hydrologic losses, nutrient capital and regrowth. For. Sci. 34, 412–428.

Marks, P.L., 1974. The role of pin cherry (*Prunus pennsylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecol. Monogr. 44, 73–99.

Martin, C.W., 1988. Soil disturbance by logging in New England —review and management recommendations. North. J. Appl. For. 5, 30–34.

Martin, C.W., Hornbeck, J.W., 1989. Revegetation after strip cutting and clearcutting in northern hardwoods: a 10-year history. USDA Forest Service Res., Pap. NE-625.

Martin, C.W., Hornbeck, J.W., 1994. Logging in New England need not cause sedimentation of streams. North. J. Appl. For. 11, 17–23.

Matson, P.A., Boone, R.D., 1984. Natural disturbance and nitrogen mineralization: wave-form dieback of mountain hemlock in the Oregon Cascades. Ecology 35, 1511–1516.

Matson, P.A., Vitousek, P.M., Ewel, J.J., Mazzarino, M.J., Robertson, G.P., 1987. Nitrogen transformations following tropical forest felling and burning on a volcanic soil. Ecology 68, 491–502.

McGill, W.B., Cole, C.V., 1981. Comparative aspects of cycling of organic C N S and P through soil organic matter. Geoderma 26, 267–286.

McMinn, J.W., 1985. Whole-tree harvesting affects pine regeneration and hardwood competition. South. J. Appl. For. 9, 81–84.

Mou, P., 1991. Biomass and nutrient accumulation following large-scale disturbance of a northern hardwood ecosystem. PhD Dissertation, Cornell University, Ithaca, New York.

Mou, P., Fahey, T.J., Hughes, J.W., 1993. Effects of soil disturbance on vegetation recovery and nutrient accumulation following whole-tree harvest of a northern hardwood ecosystem. J. Appl. Ecol. 30, 661–675.

Nannipieri, P., Johnson, R.L., Paul, E.A., 1978. Criteria for measurement of microbial growth and activity in soil. Soil Biol. Biochem. 10, 223–230.

Nodvin, S.C., Driscoll, C.T., Likens, G.E., 1988. Soil processes and sulfate loss at the Hubbard Brook Experimental Forest. Biogeochemistry 5, 185–200.

Outcault, K.W., White, E.H., 1981a. Phytosociological changes in understory vegetation following timber harvest in northern Minnesota. Can. J. For. Res. 11, 175–183.

Outcault, K.W., White, E.H., 1981b. Understory biomass and nutrients 2 years after timber harvest in northern Minnesota. Can. J. For. Res. 11, 305–308.

Pierce, R.S., Martin, C.W., Reeves, C.C., Likens, G.E., Bormann, F.H., 1972. Nutrient loss from clearcuttings in New Hampshire. In: Proc. Natl. Symp. on Watersheds in Transition. Am. Water Resour. Assoc., Urbana, IL, pp. 285–295.

Reinhart, K.G., 1973. Timber-harvest clearcutting and nutrients in the Northeastern United States. USDA Forest Serv. Res. Note NE-170.

Ryan, D.F., Huntington, T.G., Martin, C.W., 1992. Redistribution of soil nitrogen, carbon and organic matter by mechanical disturbance during whole-tree harvesting in northern hardwoods. For. Ecol. Manage. 49, 87–99.

Safford, L.O., Filip, S.M., 1974. Biomass and nutrient content of 4-year-old fertilized and unfertilized northern hardwood stands. Can. J. For. Res. 4, 549–554.

Schlesinger, W.H., 1991. Biogeochemistry: an analysis of global change. Academic Press, San Diego.

Siccama, T.G., 1991. Watershed 5: Hubbard Brook NH Nutrient and biomass data. Ecological Data Exchange EDEX 4-2-1-2-3. Yale School of Forestry and Environmental Studies, New Haven, CT.

Siccama, T.G., 1992. Chemistry of WS-5 plant material. Ecological Data Exchange EDEX 4-2-1-4. Yale School of Forestry and Environmental Studies, New Haven, CT.

Siccama, T.G., Hamburg, S.P., Arthur, M.A., Yanai, R.D., Bormann, F.H., Likens, G.E., 1994. Corrections to allometric equations and plant tissue chemistry for Hubbard Brook Experimental Forest. Ecology 75, 246–248.

Smith, W.H., 1976. Character and significance of forest tree root exudates. Ecology 57, 324–331.

Spiers, G.A., McGill, W.B., 1979. Effects of phosphorus addition and energy supply on acid phosphatase production and activity in soils. Soil Biol. Biochem. 11, 3–8.

Stark, N., Jordan, C.F., 1978. Nutrient retention by the root mat of an Amazonian rain forest. Ecology 59, 434–437.

Tabatabai, M.A., 1982. Soil Enzymes. In: Methods of Soil Analysis: Part 2. Chemical and Microbiological Properties-Agronomy Monograph, no. 9, 2nd edn., pp. 903-947.

Tritton, L.M., Martin, C.W., Hornbeck, J.W., Pierce, R.S., 1987. Biomass and nutrient removals from commercial thinning and

whole-tree clearcutting of central hardwoods. Environ. Manage. 11, 659–666.

Vitousek, P.M., Matson, P.A., 1985. Disturbance, nitrogen availability and nitrogen losses in an intensively managed loblolly Pine plantation. Ecology 66, 1360–1376.

Walbridge, M.R., 1991. Phosphorus availability in acid organic soils of the lower North Carolina coastal plain: estimation and control of P availability and plant response. Ecology 72, 2083–2100.

Walbridge, M.R., Richardson, C.J., Swank, W.T., 1991. Vertical distribution of biological and geochemical phosphorus subcycles in two southern Appalachian forest soils. Biogeochemistry 13, 61–85.

White, E.H., 1974. Whole-tree harvesting depletes soil nutrients. Can. J. For. Res. 4, 530–535.

Whitford, W.G., Meentemeyer, V., Seastedt, T.R., Cromack, K. Jr., Crossley, D.A. Jr., Santos, P., Todd, R.L., Waide, J.B., 1981. Exceptions to the AET model: deserts and clear-cut forest. Ecology 62, 275–277.

Whitney, G.G., 1982. The productivity and carbohydrate economy of a developing stand of *Rubus ideaus*. Can. J. Bot. 60, 2697–2703.

Whittaker, R.H., Bormann, F.H., Likens, G.E., Siccama, T.G., 1974. The Hubbard Brook Ecosystem Study: forest biomass and production. Ecol. Monogr. 44, 233–254.

Whittaker, R.H., Likens, G.E., Bormann, F.H., Eaton, J.S., Siccama, T.G., 1979. The Hubbard Brook Ecosystem Study: forest nutrient cycling and element behavior. Ecology 60, 203–220.

Witcamp, M., 1971. Soils as components of ecosystems. Ann. Rev. Ecol. Syst. 2, 85–110.

Wood, T., Bormann, F.H., Voigt, G.K., 1984. Phosphorus cycling in a northern hardwood forest: biological and chemical control. Science 223, 391–393.

Wood, T.E., 1980. Biological and chemical control of phosphorus cycling in a northern hardwood forest. PhD dissertation, Yale University, New Haven, CT.

Yanai, R.D., 1990. The effect of disturbance by whole-tree harvest on phosphorus cycling in a northern hardwood forest ecosystem. PhD dissertation, Yale University, New Haven, CT.

Yanai, R.D., 1991. Soil solution phosphorus dynamics in a whole-tree harvested northern hardwood forest. Soil Sci. Soc. Am. J. 55, 1746–1752.

Yanai, R.D., 1992. The phosphorus economy of a 70-year old northern hardwood forest. Biogeochemistry 17, 1–22.

Zhang, Y., Mitchell, M.J., 1995. Phosphorus cycling in a hardwood forest in the Adirondack Mountains, New York. Can. J. For. Res. 25, 81–87.