
Forest Management and Nutrient Cycling in Eastern Hardwoods

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Abstract

The literature was reviewed for reports on nutrient cycling in the eastern deciduous forest, particularly with respect to nitrogen, and for effects of forest management on the nutrient cycle. Although most such research has dealt with conifers, a considerable body of literature relates to hardwoods. Usually, only those references that dealt quantitatively with nutrient cycling were cited.

The nutrient content of the forest stand is a relatively small part of the total nutrient pool contained in soil. Under the present practices of harvesting stem wood on a 50- to 100-year rotation, nutrient deficiency as a result of crop removal seems unlikely on most forest land. The probability of nutrient deficiency increases as the trend continues toward shorter rotations and more complete utilization of branchwood, thinnings, culls, and brush presently left on the site to nourish forest regeneration after cutting. Nutrient deficiencies that develop as a result of product harvest can be resolved by modifying cutting practices or by fertilization, or both.

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Figure 1.—Many observers see environmental ruin in a conventional clear-cut; wasted wood, depleted soil, and polluted streams. Actually, all marketable material had been harvested before this photograph was taken, including logs, pulpwood, and fence posts. (U.S. Forest Service)

Introduction

Theodore Roosevelt once said of forests, "Use them for grazing, for farming, for lumber, for whatever they are best adapted, but so use them that you will not destroy their usefulness for future generations" (49). Certainly the eastern deciduous forests have been used, some of them for more than three centuries, and sometimes with little regard for future needs. But today, Roosevelt's ethic is unacceptable to the prophets of environmental crisis, who argue that all but the most conservative forest cutting will lead to "pedological and ecological mayhem" (12). Others argue just as vehemently that our nation can ill afford to leave any mature trees uncut (fig. 1), and that the untended forest is an unbalanced ecosystem incapable of providing the goods and services expected from productive wildland (34). Foresters hold an uncomfortable middle ground between these idealistic extremes, under fire from one side as the compliant tools of forest industry, from the other as visionary preservationists.

Those who favor minimum cutting foresee soil sterility; those who favor maximum cutting foresee stand stagnation. Although the term seldom is used—indeed, the concept seldom is perceived—both sides tacitly hold that effective nutrient cycling will cease unless forests are managed as they advocate. As used in this paper, "nutrient cycling" means the continuing use and reuse of soil nutrients by forest vegetation. There has been much research pertinent to this subject; there are two good summaries of the older research (31, 39), but more recent papers (11, 45, and especially 43) provide better overviews of nutrient cycling as it relates to modern forest management.

Interest in nutrient utilization by forest trees is not new. The earliest American study known to us concerned ash analysis of wood, bark and twigs of selected old-growth hardwoods; it was reported by the U.S. Commissioner of Patents in 1850 (48). Both the pioneers and most modern students of nutrient cycling would probably accept cheerfully this qualitative statement of 36 years ago: "The amounts of essential mineral constituents in the soil and the amounts used by forest vege-

tation are such that even soils low in them contain an excess. Apparently, the exhaustion of essential mineral constituents by forest cropping seldom takes place" (47). This attitude prevailed until the "environmental crisis" of the past few years thrust into the vernacular such poorly understood catchwords as ecology, biodegradable, clearcutting, recycling, and pollution.

The Nitrogen Cycle

Ordinarily, no nutrient is more deficient in forest soils (20) or poses a greater pollution threat than nitrogen. Most abundant of the nutrients, nitrogen is essential for life, but some of its naturally occurring chemical forms can be harmful if present in high concentrations in drinking water (33). Although nitrogen is closely recycled in hardwood forests, tree eradication and conventional clearcutting have caused accelerated nitrate leaching from New Hampshire soils (37). Nitrate, a common form of soil nitrogen, is a freely diffusible ion in the soil solution and is easily lost by leaching. Because of its importance in the human as well as the forest environment, we will stress the role of nitrogen in nutrient cycling. Other minerals present lesser nutritive and pollution problems, and space does not permit dealing at equal length with them.

A model (fig. 2) provides one way to visualize the nitrogen cycle in forests. Cycles for other nutrients will differ considerably from this one. Note that the atmosphere, soil, and trees constitute sinks in the nitrogen cycle. The atmosphere is considered an inexhaustible reservoir for nitrogen which, in its elemental form, is entirely unavailable to trees. Gaseous nitrogen must be "fixed" in the soil (i.e., combined with oxygen or hydrogen) by any of several naturally occurring processes. Ordinarily, fixed nitrogen taken from the soil by trees is ultimately returned to the atmosphere or to the soil with little net change in the quantities available for tree growth. Fertilizing the forest and harvesting wood products are the usual means by which man modifies this balance; they provide our only important opportunities to influence nitrogen ingress into or egress from the cycle. Lesser nitrogen outgo may ac-

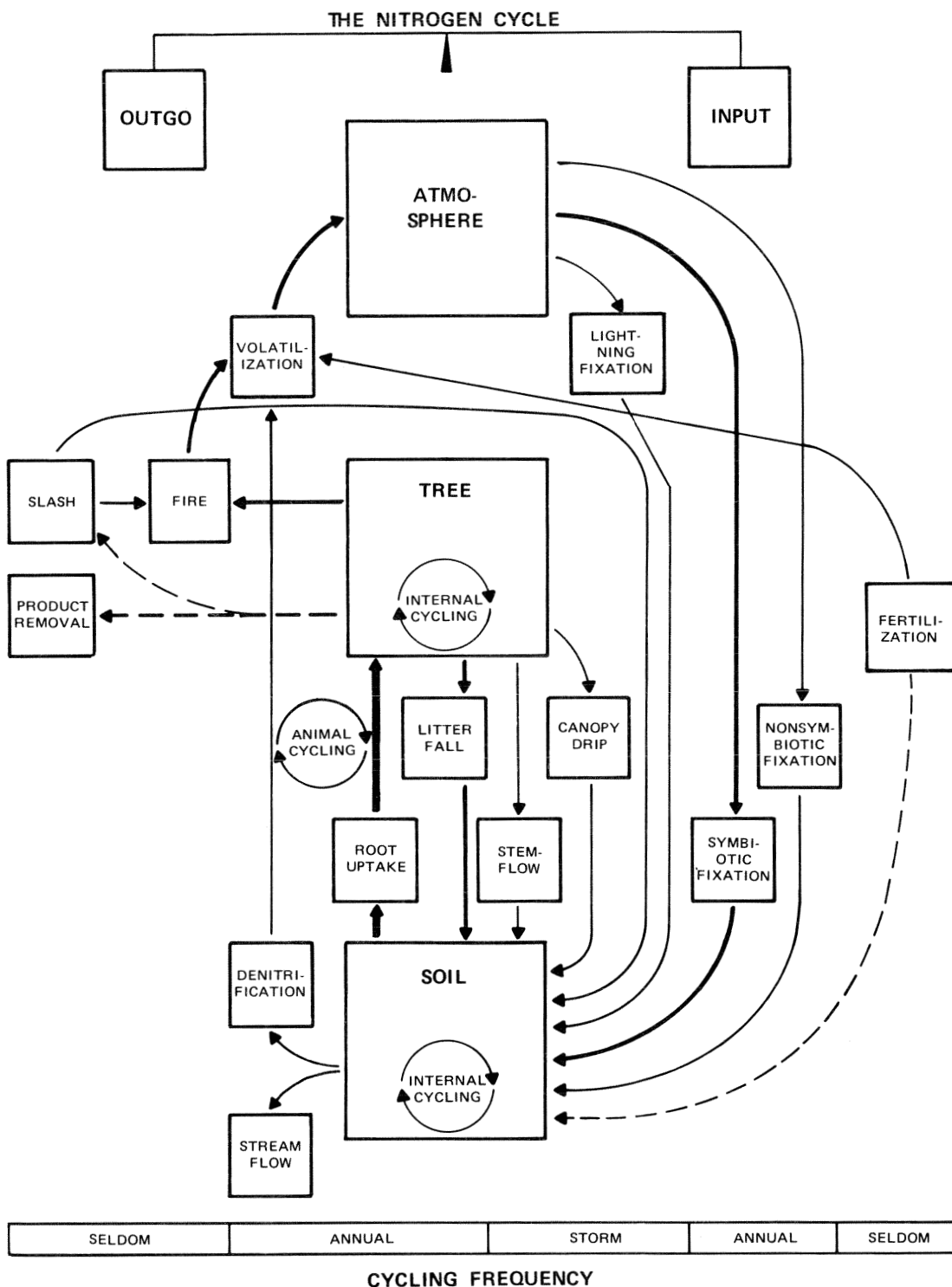


Figure 2.—The nitrogen cycle in the eastern deciduous forest. Several relationships are suggested nonquantitatively in this diagram. (1) The thickest lines imply the most important pathways. (2) Broken lines show nitrogen pathways subject to some control by forest managers. (3) Nitrogen pathways are "stacked" above cycling frequencies to show their recurrence rates. (4) Processes in the right half of the figure (nitrogen inputs to the soil-tree system) remain in long-term balance with processes on the left (nitrogen outgo from the soil-tree system).

company such cultural practices as thinning, controlled burning, or litter removal. Mismanagement, such as permitting repeated wildfire or accelerated erosion, may inadvertently open important avenues of nutrient escape from the cycle. In the future, legumes (either introduced or natural) may be more important as sources of fixed nitrogen, especially in light of the present energy crisis and the impact it may have on N fertilizer production.

Several subcycles of different frequencies make up the overall nitrogen cycle. During storms, modest inputs to the soil occur as stemflow, canopy drip, and washout from the atmosphere. Larger amounts of nitrogen are involved in a more or less continuous annual cycle; here litterfall and fixation by symbiotic and nonsymbiotic processes are the major inputs, while soil nitrogen is lost by root uptake, denitrification, and leaching to streamflow. The essential role of water in cycling nitrogen and any other nutrients must not be overlooked. Physically, water is the major vehicle of nutrient transport in the soil, the tree, and—to a large extent—the atmosphere. Man's major influence on the nitrogen cycle occurs at the "seldom" frequency in well-managed forests. Input by fertilization is especially important because any nutrient can be introduced into ecosystems at whatever time, place, and amount is deemed necessary. Wood product removal is the most common avenue of major nutrient loss from the cycle.

The supply of nitrogen withdrawn from forest soil by trees is replaced from several sources. Atmospheric washout adds from 2 to 10 kg/ha/yr (40) with lightning fixation accounting for 10 to 20 percent of this amount (25). Other significant sources of atmospheric washout in forests include nitrogen lost from agricultural land and from manufacturing. In agriculture, fixation by legumes ranges from 50 to 100 kg/ha/yr (34); however, rates are probably lower in forests, where legumes are relatively scarce. A net gain of 45 kg/ha/yr of fixed nitrogen was reported in a stand containing black locust (22). Over 300 species of non-leguminous nitrogen-fixing plants are known (6), these having fixative capabilities ranging from 50 to 100 kg/ha/yr (42). More recent studies report that the fixative capabilities of

nodulated American speckled alder are as high as 168 kg/ha/yr in thickets (13) and 85 kg/ha/yr on an abandoned mill pond where it was growing with red maple and paper birch (52).

Microorganisms transform important quantities of nitrogen. The blue-green algae are probably most important of the nonsymbiotic nitrogen-fixing microorganisms, with 20 such species known (17). However, their role in forest soils of the temperate zone is uncertain. The importance of nitrogen-fixing bacteria in forests is also unknown (17). Nitrifying bacteria increased in numbers 18- to 34-fold after forest cutting in New Hampshire and greatly increased humic nitrification (29). Russell (40) emphasized that biological nitrogen fixation appears to take place in agricultural soils only when the vegetation is not in equilibrium with the soil and climate, or when nitrogen compounds are being removed from the land. In these situations, continuing replacement of nitrogen in forest soils throughout the growing season seems probable.

Nutrients in the Unmanaged Ecosystem

Enormous amounts of nutrients are stored in forest soils (table 1). County soil surveys provide information specific to many locations and often will differ widely from the data in table 1. Such differences must be expected, not only because there is great variation among soils, but also because many different

Table 1.—Average total nutrient content of several forest soils of Connecticut. Adapted from Lunt (30)

Horizon	Horizon thickness	Total nutrients				
		N	P	K	Ca	Mg
	(cm.)	kg/ha/cm				
Organic	5	129	11	303	209	38
A	15	216	83	14	52	64
B	50	86	68	8	8	10
C	30	22	67	7	8	10
		kg/ha				
Profile	100	8836	6725	2334	2470	1967

For those readers unfamiliar with metric units, kg/ha can be regarded as about the same as pounds per acre. The actual conversion equation is lb/ac. x 1.12=kg/ha.

sampling and analytical techniques have been used. For example, forest soils of West Virginia (2) differ greatly from those of the Piedmont (14) and from those of Connecticut. Actually, the absolute amounts shown in table 1 are of little significance; they serve merely to illustrate the magnitude of nutrient supplies potentially available from one meter's depth of forest soil. Trees usually root profusely in the upper meter of forest soil and often extend much deeper (27).

Regolith weathering releases only a little nitrogen but it is a major source of other mineral nutrients. Its importance to trees on any given site is largely speculative. For example, a rate of 800 kg/ha/yr for weathering of silicate materials was calculated for New Hampshire, releasing about 4 kg/ha/yr of potassium, and about 8 of magnesium.¹ The whole-earth weathering rate for bedrock has been estimated at 270 kg/ha/yr (4). Apparently, there is little gain or loss of soil phosphorus in the deciduous forest (42). Some nutrients are released through slash decomposition and burning, although much of the nitrogen is released into the atmosphere in gaseous forms. Insects and disease organisms probably hasten the return of nitrogen and other nutrients to the soil, but effect little gain or loss to ecosystems. A variety of compounds are added to

soils by mortality of small roots, many of which probably live for no longer than a year (26). Other nutrients—organic and inorganic—are added by root exudation (44).

Forest trees contain far less nutrients than do the soils that support them (table 2). These data describe a carefully analyzed deciduous forest in Belgium; however, the amounts of phytomass and nutrients seem consistent with less thoroughly documented deciduous forests in the eastern United States. A few generalizations drawn from these data probably are applicable throughout the hardwood region: The harvested stem, about half of the forest phytomass, includes about one-third of the nutrients contained in forest trees. The remaining two-thirds of the mineral nutrients are contained in the unharvested half of the tree's phytomass, its extremities. Similar nutrient distribution has been observed in Maine (62) and in Canada (18). Bark is richer in nutrients than wood (61), branch wood more so than stem wood (7). The understory and other minor forest vegetation seldom comprise more than 5 percent of the phytomass (57) or nutrient content (15) of fully stocked mature stands on good sites. Stand age, species composition, and stage of succession also influence nutrient content (60). To generalize, conventionally unharvested tree parts are about twice as rich in nutrients as tree parts normally removed from the forest site.

The most comprehensive account known of nutrient cycling in an American deciduous for-

¹ Singer, M. and R. H. Rust. 1972. Phosphorus cycling in an east-central Minnesota deciduous forest. I. Biomass and phosphorus content of the natural system. Unpublished report, School of Forestry, University of Minnesota, St. Paul.

Table 2.—Nutrient distribution in tree components of a mature deciduous forest in Belgium. Adapted from Duvigneaud and Denaeyer-DeSmet (15)

Components	Phytomass	Nutrient Content					Ratio of nutrient content to phytomass
		N	P	K	Ca	Mg	
		— — — — — kg/ha — — — — —					
Stem wood	64,522	95	7	73	77	23	1:235
Stem bark	8,760	44	3	21	328	19	1:21
Branch wood	24,201	56	5	34	49	9	1:158
Branch bark	6,757	48	3	17	207	13	1:23
Twigs	4,947	40	3	13	79	6	1:35
Leaves	3,458	73	5	36	54	5	1:20
Roots	34,600	127	12	97	380	19	1:54
Totals	147,245	483	38	291	1174	94	

est (table 3) comes from North Carolina (56). These data suggest that yearly nutrient input is sufficient to replace all nutrients in the entire forest phytomass within 10 years. There are surprisingly large expanses (58) of nutrient-rich bark (1.5 to 2.8 m²/m² of ground surface) and of leaves (3 to 6 m²/m² of ground surface) from which nutrients can be washed as stemflow (19) or as canopy drip. Soil-nutrient input in North Carolina hardwoods substantially agreed with that in the Belgian forest; even though the former stand was a little older and somewhat less densely stocked, it had larger trees.

No published account is known of nutrient balance in an American deciduous forest; however, the following data for the deciduous forest in Belgium (table 4) probably are representative of American conditions. For nitrogen at least, this tabulated annual return (62 kg/ha) seems minimal because it did not, indeed could not, allow for nitrogen biologically fixed during the growing season. By the same token, the tabulated amounts for all other elements returned to the soil probably are con-

servative estimates because no quantities were allowed for mineral weathering. Thus, it is clear that forest trees actually retain only a rather modest portion of the nutrients taken from the soil.

Some Effects of Forest Management on Nutrient Cycling

As previously noted, fertilization (the deliberate addition of needed nutrients) is the only management technique by which man introduces large amounts of new nutrients into the forest cycle. Fertilization is done in many ways; the oldest measures used in forestry were biological and were celebrated thus in 1630 (46):

"The alder, whose fat shadow nourisheth,
Each plant set neere to him long flourisheth."

Nitrogen-fixing plants help bring about an astonishingly quick revegetation of extremely disturbed sites. For example, after glacial retreat in Alaska, alder quickly becomes established on newly exposed, sterile gravel, then is succeeded by Sitka spruce about 20 years later. After the leguminous tree, black locust, is established on strip mine spoil banks in the Ohio Valley, invasion by nonleguminous hardwoods follows within a few years (9). Despite their demonstrated value, such biological methods involve considerable time and labor and are seldom used in conventional forestry.

Sometimes a dual purpose is served when farm manure, certain factory wastes, or partially treated municipal sewage are spread on forest land. Sewage effluent, at least that containing low concentrations of heavy metals, can be so disposed of safely and without insult to the environment. Soil moisture is maintained at high levels, and forest growth is greatly stimulated by both the continuous water supply and the added nutrients. An experiment started in 1963 at the Pennsylvania State University thoroughly documents the disposal of secondary-treatment sewage and some of its effect on the nutrient balance of hardwood forests and the underlying soil (41). Many communities are taking a hard look at

Table 3.—Replenishment of soil nutrients in a North Carolina hardwood forest. Adapted from Wells, et al. (56)

Source	Nutrients (kg/ha)				
	N	K	P	Ca	Mg
Rainfall	3.53	0.28	0.88	3.42	0.72
Canopy drip	4.86	0.61	17.48	12.47	3.75
Stemflow	0.23	0.01	0.65	2.02	0.24
Litter	45.98	3.26	14.16	94.99	18.11
Annual input to soil	54.60	4.16	33.17	112.90	22.82

Table 4.—Annual nutrient balance of a mature deciduous forest in Belgium. Adapted from Duvigneaud and Denayer-De Smet (15)

Nutrient disposition	Nutrient				
	N	P	K	Ca	Mg
	— — — — — kg/ha/yr — — — — —				
Taken from soil by trees	92	6.9	69	201	18.6
Returned to soil in rain and litterfall	62	4.7	53	127	13.0
Retained in forest tree biomass	30	2.2	16	74	5.6

this possible solution to their sewage-disposal problems.

Unquestionably, aerial application of commercial fertilizers is the most efficient way to adjust the nutrient balance of forest ecosystems. Fertilization may also be helpful in preventing erosion on harsh sites and for enhancing wildlife habitat. Some biologic advantages of fertilization in terms of increased hardwood production have been reported (8, 24). Forest soils generally are deficient in nitrogen (20) but greatest tree growth often follows application of two or more nutrients (3). Moreover, different tree species often differ in their nutrient requirements and in their responses to fertilization (51). Existing knowledge of the ecological consequences of forest fertilization has been reviewed (5) but much remains to be learned. Greater economic incentives as well as more research are needed before large-scale fertilization is undertaken in eastern hardwoods.

To date, studies of nutrient cycling in fertilized hardwoods have not been comparable in numbers or in completeness to those in conifers. Some preliminary results, however, are available from a pioneer experiment in hardwood forest nutrient cycling at the Fernow Experimental Forest near Parsons, West Virginia. Nitrogen as urea was applied by helicopter on a calibrated watershed at a rate of 224 kg/ha. This rate was estimated to be the amount required to greatly increase tree growth without toxic effects. Estimates based on 643 water samples indicate that over 50 kg/ha of nitrogen, in both nitrate and ammonium form, were lost in streamflow during the first year after fertilization (1). This nitrogen loss was accompanied by increased concentrations of Ca, Mg and K in streamflow (1). Volatilization losses were sufficient to cause a distinct ammonia odor, but no attempt was made to quantify these losses. In Florida, less than 10 percent of a 100 kg/ha urea application was lost as gaseous NH_3 (53). Nitrogen content of the vegetation increased measurably but these data are insufficiently processed to report on an areal basis. Experience elsewhere suggests that much of the applied nitrogen has been incorporated more or less permanently into the ecosystem

and that losses to streamflow and to volatilization would have been less given lighter fertilization, different N sources, or different weather conditions.

Removing wood and bark from its site of growth accounts for most nutrient drain on forest land. The oft-told tale of reduced tree growth following centuries of litter removal in Germany (54) neatly illustrates how such problems can develop. Potassium deficiency in some northeastern soils is ascribed to the use of deciduous forests as a source of potash during Colonial times.² Nutrient deficiencies may accompany monocultures and type conversions, but management of this kind is rare in hardwoods. Severe forest grazing invites the same problems but this malpractice, as well as litter removal, is so rare in the deciduous forest as to pose a negligible nutrient drain. Fire, once considered a major agent of soil deterioration (47), now is regarded more as a determinant of species composition, in hardwood (10) as well as in coniferous forests. For example, burning has a relatively small effect on soil nutrient content in the southeastern coastal plain (55), whereas fire-caused mortality sets back young hardwood growth from 4 to 7 years (28). Road building and accelerated soil erosion undoubtedly provide another avenue of nutrient drain, but the amounts of such loss are not reported. While on this subject, we wish to emphasize that properly performed clearcutting of hardwoods causes no overland flow during heavy rain (36), therefore cannot cause accelerated soil erosion or the associated loss of soil nutrients (50). This point must not be confused with Pierce's (37) observations concerning mineral losses through, not across, the soil on clearcut land in New Hampshire.

The removal of wood products causes most nutrient loss from conventionally managed forest land. Actual measurement of products so harvested provided a real-life basis for estimating this loss (table 5). These data probably are representative of nutrient drain from most hardwood forest land as currently managed. They were obtained from several experi-

² Personal communication from G. W. Bengtson, Muscle Shoals, Alabama.

Table 5.—Estimated nutrient losses accompanying wood product removal from the Fernow Experimental Forest, Parsons, W. Va.

Practice	Cutting cycle ^a	Harvested phytomass	Nutrients ^b removed from soil ^c	
			per cycle	per year
	(yr.)		----- kg/ha -----	
Intensive selection (selected trees over 12.5 cm dbh)	5	10,323	98	20 ^d
Extension selection (selected trees over 27.5 cm dbh)	10	22,237	180	18
Diameter limit (all salable trees over 43 cm. dbh)	20	25,221	236	12
Commercial clear-cutting (all salable trees over 12.5 cm dbh)	75	51,030	473	6
Liquidation cutting (all salable trees branches and culls)	75	94,295	892	12

^a Frequency of recutting

^b N, P, K, Ca, Mg

^c Computed as 88 percent of the harvested phytomass as wood, 12 percent as bark; applying nutrient content to phytomass ratios for stemwood and bark as shown in Table 2.

^d Nutrients removed from soil per cycle ÷ years in cutting cycle.

mental watersheds in West Virginia, ranging in area from 14 to 36 ha. The stands consisted of 50- to 60-year-old second growth with residuals from a heavy cutting in 1905. Predominant species were oaks, maples, yellow-poplar, black cherry, and beech. Volumes ranged from 127 to 218 m³/ha with both sawtimber and pulpwood harvested. About half of the nutrients contained in above-ground phytomass of a mixed-oak stand were estimated to have been removed in commercial logs during clear-cutting in Pennsylvania (59).

Note that repeated light cuts tended to cause greater average annual nutrient drain than did a single cut per rotation. This greater drain was caused by harvesting the smaller and weaker trees that are likely to die in less intensively managed stands; their decay assures considerable nutrient return to the site. At present, economics dictates the desirability of less intensive management, aiming to produce a relatively few trees with high market value and thus posing no real threat to continuing site productivity. This situation will change if there is a profitable market for products now of no economic value and presently left in the woods. Then, more frequent cutting

and closer utilization with correspondingly greater nutrient drain must follow. For example, the use of presently noncommercial brush species for pulpwood will cause about the same nutrient drain as does the present harvest of commercial tree species (16). Increased utilization of boles, tops, and branches of hardwoods (fig. 3) is likely to double the present nutrient removal (7). These portions of harvested trees now are left on the ground to replenish soil nutrients, mostly because they have no other value—yet foresters are criticized for “wasting” this wood. Their critics do not believe that it is uneconomic to harvest such material, nor do they realize that, left in place, unharvested tree parts help to replenish soil fertility. Furthermore, slash removal from the forest raises other environmental questions. Intensive harvesting of small products could increase forest soil erosion and will concentrate nutrient-rich branch wood and bark near manufacturing centers already overloaded with wastes. A very close look at nutrient cycling and environmental problems is warranted if the concept of whole-tree harvest is applied on a large-scale, short-rotation basis in the eastern deciduous

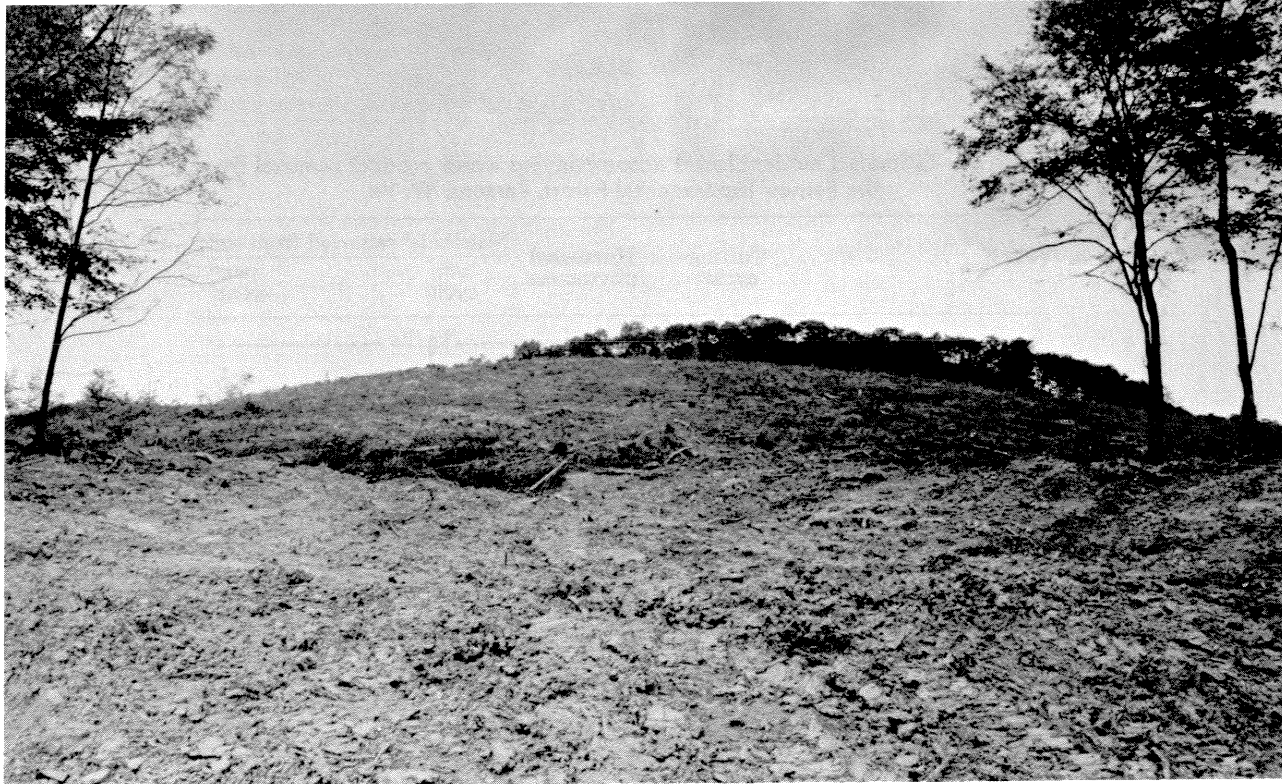


Figure 3.—The uncluttered look of this scene appeals to many observers. But despite its greater esthetic appeal, complete removal of slash and residue may lead to depletion of the soil as nutrients are removed from the cycle.

forest. Several such operations are already being successfully conducted on a pilot basis by industry and there is little doubt that whole-tree utilization will become a standard harvesting technique.

Discussion

There is a pronounced tendency in the literature to place more weight on nutrient outflow from forest soil than on its replacement, probably reflecting the common idea that man is the only disturbing element in an otherwise perfect forest scene. Disregarding the philosophical implications of this attitude, there may be good reason for such bias. Nutrient outflow is far more easily visualized than is nutrient replacement. Harvested wood not only is visible but is routinely measured. The accompanying nutrient loss is easily estimated—and deplored—from these figures. Natural nutrient replacement is a wholly invisible process. A related attitude contributes to this bias, the general belief that forest soils are low in fertility. True, many forest soils cannot meet

the exacting fertility needs of farm crops, but it hardly follows that further wood harvest will exhaust their store of nutrients. Nutrients available to trees in forest soils often have been underestimated, investigators having restricted their estimates of availability to the surface 15 cm of soil; but trees are widely known to root far deeper. Others have recognized the importance of such processes as the chemical breakdown of parent material and the bacterial transformations of nitrogen but few seek to quantify these less visible, less easily measured processes or to assess the stimulating effects of timber harvest on them.

There is another, related facet to this problem. The soil sometimes is envisioned as containing X amount of nutrients; timber harvest removes 0.5X; ergo, two timber harvests will exhaust the soil fertility. This concept of the nutrient supply, analogous to the water supply for flowers in a vase, is not only useless but needlessly alarming. It wholly fails to account for changing availability or continuing replenishment. Some nutrients (e.g., phosphorus) may be relatively abundant in an unavailable

form. When available phosphorus is depleted, natural conversion to an available form soon begins. For another example, nitrogen fixation is more rapid during nitrogen scarcity than when nitrogen is abundant in soil. Furthermore, nutrient use by trees does not proceed at a constant rate as soil fertility declines, but decreases gradually as nutrients are depleted. Nutrient stress does not develop without reduced growth rates and other warning signs, providing ample time to relieve the stress by fertilization or by modifying cutting practices. We do not dismiss the possibility of reduced forest soil fertility; we do not invoke much research and experience to assert that such problems are most unlikely to develop under rational forest management. To cite a single example: after centuries of intensive use, Germany's Black Forest continues to produce high yields of wood and otherwise provides ample justification for our optimism.

Above and beyond all of these technical matters, there is a general failure to appreciate the tremendous resilience that allows forest vegetation to survive many temporary derangements of a presumably constant nutrient supply. Here arises the concept of the steady state, heavily relied upon in many studies of nutrient cycling, but liable to over-literal interpretation. Most of the eastern deciduous forest has been cut over from one to several times. Much of it has been cleared at least once for agriculture. Much has burned from time to time and all of it is subject to windthrow, disease, and defoliation of varying severity. Superimpose on these recurring hazards the edaphic, microclimatic, and topographic irregularity of most forest land. Add the species and size diversity characteristic of the deciduous forest; then confound this complex picture with man's ubiquitous forest activities: a most unsteady state of nutrient cycling is easy to envision. Undeniably, the steady state is a useful concept; so is the average man, but one would be poorly advised to invest much time or money in quest of either one.

Forest occurs on the headwaters of most streams, especially in mountainous terrain, where yet another aspect of nutrient cycling, and of the steady state, merits comment.

Here, the variable source area concept of streamflow (21) pertains, in which watershed soil is seen as the ultimate origin of streams. Rain that infiltrates into hilly land moves downslope through the soil until, driven by gravity, it finally emerges in seeps and springs to form headwater streams. The implications of the source area concept on the nutrient cycle are great, because a mechanism is envisioned for nutrients dissolved upslope to nourish trees downslope, or if uptake by trees is precluded, ultimately to be flushed from the ecosystem. Since the extent of source areas and their drainage rates vary primarily with rainfall, their actual influence on nutrient distribution is virtually unmeasurable. Nevertheless, this movement probably accounts for the relative impoverishment of ridge soils and the relative richness of streamside soils. Furthermore, it suggests that the mineral composition of trees of the same species may differ according to their position, be it on a ridge or near a stream.

The Hubbard Brook study (37) embodies the most thorough and far-reaching research on nutrient cycling yet undertaken. But sometimes its results are misapplied (12), the accelerated outflow of soil fertility from a deforested watershed being interpreted as evidence that soil sterility would follow any but the most conservative of forest cutting. Actually, the Hubbard Brook results have little relation to nutrient outflow after conventional forest cutting elsewhere in the East, as the loss of nutrients appears to be negligible from podzol (50) as well as most nonpodzol soils (38).

Too little has been made of a far more useful outcome of the original Hubbard Brook study (29) which, in effect, removed the "tree sink" depicted in figure 1. By cutting the forest and preventing regrowth, we gained, for the first time, some insight into the enormous amount of nutrients available to a new generation of forest trees. The cutting and herbicide treatment was, in effect, a planned disaster. Consider the events that followed—greater soil moisture, increased soil temperature, better aeration, and increased chemical and biological activity in the freshly exposed forest floor. Fallen trees and foliage decomposed to augment nutrients also being released from decay-

ing litter. Given normal forest conditions, these events would provide optimal nutrition for seedling and sprout growth. But preventing regrowth with herbicides prevented all nutrient uptake and some of these decay-released materials were lost from the ecosystem via streamflow.

We interpret these results as evidence, not of damaging loss of soil fertility accompanying timber harvest, but of a survival mechanism to assure vigorous regrowth after disaster, whether man-caused or natural. When a pioneer stand finally was allowed to develop at Hubbard Brook, substantial loss of soil fertility ceased and nutrients were stored in pin cherry for subsequent use by the more permanent stand that followed (32). This experiment thus demonstrates a "shot-in-the-arm" effect following disaster, in which massive nutrient releases probably stimulate reforestation. Lesser nutrient releases probably stimulate regrowth similarly on land under more conventional forest management.

Conclusions

Obviously, much remains to be learned about nutrient cycling in the deciduous forest. The International Biological Program will help to meet this need, with a vast amount of new information even now being readied for publication. The following conclusions can be regarded as little more than tentative until they are refined in light of this new knowledge.

- I. It is unlikely that any conventional forest cutting poses an immediate threat to continued forest soil productivity.
- II. Presently unconventional practices, such as whole-tree harvest, can pose a threat to continuing forest productivity. Continuing assessment of tree nutrition should accompany shorter cutting rotations and more complete tree utilization.
- III. Nutrient release during periods of intermittent forest floor exposure provides an important mechanism for forest survival.
- IV. Should nutrient deficiencies develop, modern technology now permits their solution through a combination of fertilization, modified harvest practices, and regeneration methods.

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