CHANGES IN FOREST FLOOR ORGANIC MATTER AND NUTRIENT CONTENT FOLLOWING CLEAR CUTTING IN NORTHERN HARDWOODS

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Abstract. A secondary succession sequence of 14 northern hardwoods stands was sampled for forest floor organic matter and nutrient content. During the first 15 yr following clear cutting, the forest floor decreased by 30.7 Mg/ha, a decline of over 50%. The decrease in the forest floor and slash (logging residue) may be greater than the increase in the living biomass. During the next 50 yr the forest floor increased by 28.0 Mg/ha and by year 64 was within 5% of an asymptote of 56.0 Mg/ha.

Nutrients were analyzed in 6 of the 14 stands. Magnesium, potassium, and nitrogen concentrations showed no successional pattern. However, calcium concentrations were significantly higher in the stands in which forest floor mass was low.

The initial decrease in forest floor mass is attributed to lower leaf and wood litter fall and to more rapid decay resulting from higher temperature, moisture content, and nutrient levels and to early successional litter being more easily decomposed. The recovery of the forest floor is explained primarily as resulting from the rapid increase in the quantity and diameter of wood litter fall. JABOWA, the northern hardwood forest growth simulator, predicts a maximum rate of increase in woody litter by years 10--20 with a leveling off by years 30--50.

An apparent asynchrony in function of the forest floor and slash as nutrient sources may be important to the recovery process. During the first 15 yr the forest floor is a major source of nutrients, releasing a net amount of approximately 800 kg/ha of nitrogen. During this period nitrogen immobilization in the decay of slash may account for as much as one-half of the nitrogen released from the forest floor. After year 15 the forest floor is no longer a source but a sink for nutrients as nutrients and organic matter accumulate. By year 15 the slash probably shifts in function from a sink to a source, providing nitrogen for the continuing rapid nitrogen accumulation in vegetation beyond year 15.

Key words: clear cutting; northern hardwoods; nutrient cycling; organic matter; secondary succession.

INTRODUCTION

The forest floor is an important structural and functional component of the northern hardwood forest ecosystem. It is a major storage of organic matter and nutrients (Dominski 1971, Gosz et al. 1976) and plays an important role in recovery after disturbance. While the forest floor of old-growth northern hardwoods apparently is not increasing in depth (Lull 1959, Leak 1974), it is not a closed system. It remains constant because inputs (above and below ground death of living tissues, dissolved and particulate organic matter in stemflow and throughfall, and root exudates) are balanced by outputs (decomposition, export to mineral soil, and export in stream flow). Upon disturbance such as clear cutting this balance is radically altered; forest floor nutrient and organic matter storages decrease (Dominski 1971, Pierce et al. 1972, Bormann et al. 1974). Bormann et al. (1974) have suggested that the rate of nutrient mobilization from the forest floor may regulate recovery after vegetation by insuring the availability of essential elements during recovery.

Several early studies (Morey 1942, Sartz and Hutinger 1950, Trimble and Lull 1956) found that forest floor depth continued to decline for one to two decades after clear cutting, far beyond the 3--4 yr period by the end of which leaf area and thus leaf fall are thought to have substantially recovered (Marks 1974, Covington and Aber 1980). This paper presents the results of an analysis of changes in forest floor organic matter and nutrient content during secondary succession following clear cutting in northern hardwoods.

METHODS

Other than stand age, the major factors influencing forest floor accumulation in northern hardwoods are soil drainage, topographic position, site quality, slope, and elevation (Sartz and Hutto 1950, Trimble and Lull 1956, and Gosz et al. 1976). To minimize these site differences I selected stands with generally similar elevation (420--700 m), slope (5--30%), topographic position (middle slopes), and site quality (intermediate site quality, as judged by United States Forest Service timber surveys). Stands with a high density of aspen were excluded since aspen is indicative of poor drainage (Leak et al. 1969). To restrict the variation in forest floor organic storage caused by physical disturbance by logging activities, I excluded stands with an abundance of paper birch, which often develop after such scarification (Marquis 1965, Leak et al. 1969).

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Table 1. Northern hardwood stands in the White Mountains, New Hampshire, used in this study. Age since clear cutting, as of 1974 (sampling year).

<table>
<thead>
<tr>
<th>Stand age (yr)</th>
<th>Elevation (m)</th>
<th>Dominant tree species (in order by percentage of total leaf fall contributed by each)</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>570-630</td>
<td>pin cherry, striped maple, birch</td>
<td>Hubbard Brook Forest, Watershed 101</td>
</tr>
<tr>
<td>4</td>
<td>480-540</td>
<td>pin cherry, sugar maple, birch</td>
<td>D.O.C. watershed of Pierce et al. (1972)</td>
</tr>
<tr>
<td>7</td>
<td>480-510</td>
<td>sugar maple, birch, striped maple</td>
<td>Bartlett Forest, Compartment 36</td>
</tr>
<tr>
<td>11</td>
<td>420-450</td>
<td>sugar maple, pin cherry, birch</td>
<td>Bartlett Forest, Compartment 34</td>
</tr>
<tr>
<td>18</td>
<td>450-510</td>
<td>beech, sugar maple, striped maple</td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>540-600</td>
<td>beech, birch, sugar maple</td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>540-570</td>
<td>sugar maple, birch, red maple</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>450-510</td>
<td>sugar maple, birch, ash</td>
<td></td>
</tr>
<tr>
<td>35</td>
<td>480-540</td>
<td>sugar maple, beech, birch</td>
<td>D.O.C. uncut watershed of Pierce et al. (1972)</td>
</tr>
<tr>
<td>40</td>
<td>570-600</td>
<td>sugar maple, beech, birch</td>
<td></td>
</tr>
<tr>
<td>44</td>
<td>480-540</td>
<td>sugar maple, beech, birch</td>
<td>Hubbard Brook Forest, Watershed-6</td>
</tr>
<tr>
<td>49</td>
<td>540-580</td>
<td>sugar maple, ash, birch</td>
<td></td>
</tr>
<tr>
<td>57</td>
<td>600-690</td>
<td>sugar maple, beech, birch</td>
<td></td>
</tr>
<tr>
<td>200</td>
<td>600-630</td>
<td>sugar maple, beech, birch</td>
<td>The Bowl Natural Area</td>
</tr>
</tbody>
</table>

These stand selection criteria should have restricted site differences so that time since cutting should be the major variable influencing differences in forest floor accumulation among the selected stands.

First I located potential study sites in the United States Forest Service Timber Management Atlases and then located them on United States Geological Survey topographic maps to determine approximate elevation and aspect. In this manner, I narrowed possible sites to a total of 40. From these, I selected 14 which were relatively evenly distributed with respect to age, which were readily accessible (within 3 km of an all-weather road), and which met the above criteria. The selected stands ranged in age from 3 yr to a presumed virgin stand (Table 1) dominated by trees >200 yr old. All stands were located in the White Mountains of New Hampshire, USA, within 80 km of the Hubbard Brook Experimental Forest.

It was virtually impossible to locate stands older than 60 yr which met my stand selection criteria and had a known history. In this regard, most of the stands had been harvested to a greater or lesser extent in the late 1800s and early 1900s. Thus all but the oldest stand (200+ yr) had been cut twice. However, forest floor depth 50-60 yr after cutting appears to be comparable to that of old growth stands (Morey 1942, Trimble and Lull 1956, Leak 1974). Thus, residual effects of cutting on forest floor organic matter storage after 50-60 yr should be negligible.

The one old-age stand I did locate was preserved from cutting by its inaccessibility (Leak and Graber 1974). In this stand disturbance seems primarily due to the death of individual trees or windthrow in localized areas. My study area in this uncut forest was dominated by large (70-100 cm) sugar maple and yellow birch and slightly smaller (60-70 cm) beech. Age-diameter relations in the Northeast (Bormann and Buell 1964) suggest a stand age of >200 yr.

Forest floor samples

The sampling technique was a line point method in which five transects, 50 m each, were randomly located perpendicular to a 100-m baseline which was approximately parallel to the slope. As far as possible I avoided areas disturbed by logging operations and areas which were obviously poorly drained or which contained abnormal gaps in the canopy. In this regard, I avoided in both the 18- and 40-yr-old stands several large residual (precutting) beech trees.

At six random points along each transect I used a template to cut out and extract a forest floor sample, yielding a total of 30 samples per stand. To reduce variation, I excluded sample points:

1) in water courses,
2) where rocks, roots, or wood (>2 cm diameter) were within 5 cm of the surface,
3) where horizonation was abnormal (any sequence other than L, F, H),
4) on windthrow mounds or depressions.

The exclusion of pits and mounds and of sampling areas which had little or no forest floor would tend to make my results an overestimate of forest floor organic matter content on an areal basis.

At each sampling point a 10 x 10 cm wooden template was used to extract a forest floor core to the mineral soil including any mineral soil mixed with the H-layer. Steel skewers were inserted through holes drilled around the border of the block through the forest floor material, thus stabilizing the core. I used a knife to cut around the template, scraped away the extraneous forest floor material and removed the core. Then I scraped off any mineral soil adhering to the bottom of the H-horizon. In some cases the lowermost H-layer was mixed with very fine mineral soil which was then included in the forest floor sample.
The sample was dried (72 h at 80°C) and sieved (2-mm sieve). A size 14 rubber stopper was used to crumble leaves and partially decomposed wood, facilitating their passage through the sieve. Live roots, stones, or dead wood which did not pass through the sieve with modest pressure were discarded.

For all 30 samples from each of the 14 stands, organic matter content was determined as loss on ignition (Dominski 1971, Gosz et al. 1976). I selected six stands (aged 4, 19, 22, 40, 57, and 200 yr) distributed throughout the time sequence and analyzed samples from them for N, Ca, Mg, and K using procedures of Likens and Bormann (1970). I selected the 19- and 22-yr stands to be representative of the forest floor near its minimum in organic matter storage. N was determined by the Kjeldahl technique. Nutrient concentrations were expressed on an ash-free dry mass basis (i.e., as a percentage of organic mass).

As part of this study, JABOWA, a stochastic simulator that successfully reproduces the dynamics of a northern hardwood forest (Botkin et al. 1972a and b), was used to predict woody litter fall. In JABOWA, growth of each tree is computed from general characteristics such as its age, diameter, and height, and relationships between growth rate and light intensity, elevation, soil depth, and soil moisture. Biomass regressions of Whittaker et al. (1974) and Likens and Bormann’s (1970) chemical analyses have been incorporated into JABOWA so that it can be used to predict DBH, biomass, or nutrient content by species and plant part (D. Botkin and J. Aber, personal communication).

**RESULTS**

*Forest floor organic matter*

I used a nonlinear regression program (No. BMDP3R [Dixon 1975]) to fit a least squares curve (Fig. 1) to the organic matter mass data using a “gamma” function:

$$Y = AX^\alpha e^{CX^\alpha} + E$$

where $Y$ is the forest floor organic matter content (megagrams per hectare), $X$ is the time since clear cutting (years), and $A$, $B$, $C$, $D$, and $E$ are regression coefficients ($E$ is the asymptote). I chose the “gamma” function as the simplest ecologically reasonable representation of how the forest floor behaves following clear cutting. With $A$ and $C$ negative and the others positive, this function describes a curve which decreases exponentially for a period and then returns asymptotically to its initial value ($E$). The early part of the curve is strongly influenced by the power function ($AX^\alpha$) which, with $A$ negative, approaches negative infinity with increasing age (at age 100, $AX^\alpha = -1386$), as might occur when decomposition exceeds litter input. By year 10 the second half of the gamma function ($e^{CX^\alpha}$) takes over and $Y$ approaches an asymptote as this half of the equation approaches zero ($e^{CX^\alpha} = 0.00017$ at age 100). Although there is no unique solution for the regression coefficients, because they strongly interact in controlling the shape of the curve, the predicted curve and its asymptote essentially are unique.

The important points are:

1) the asymptote (86.75 Mg/ha) is estimated from the data, not established a priori;
2) the predicted minimum of 39.2 Mg/ha occurs at year 15;
3) by year 64 the predicted value is 82.6 Mg/ha which is within 5% of the asymptote.

Thus the degrading phase lasts from years 0–15 while the rapidly aggrading phase occurs between years 15 and 64, a period of 49 yr.

*Forest floor nutrient concentration*

Nutrient concentrations for six of the stands are presented in Table 2. The N concentration in the forest floor of Hubbard Brook Watershed-6 (57-yr-old stand) was 2.58%, which is in close agreement with Dominski’s (1971) estimate of 2.48% for nearby Watershed 1 and Watershed 3. I found no significant change in forest floor N concentration with stand age. Similarly I can discern no major successional trend in Mg or K concentration.

There may be a significant successional trend in forest floor Ca concentration (Table 2). The Ca concentrations of the 19- and the 22-yr-old stands are significantly higher than the others. This increased Ca concentration coincides with the low point in organic matter content for the successional sequence (Fig. 1) and the correlation is significant ($P = .01$). This result can be readily explained by the fact that the major decrease in forest floor organic matter is most likely from the H-layer, which has a considerably lower Ca concentration (0.296%) than does the F-layer (0.634%).
TABLE 2. Forest floor nutrient concentrations as percentage of organic matter. Data are mean and one-half the 95% confidence interval for six representative stands.

<table>
<thead>
<tr>
<th>Stand age (yr)</th>
<th>Ca</th>
<th>Mg</th>
<th>K</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>0.612 (.096)</td>
<td>0.132 (.023)</td>
<td>0.126 (.018)</td>
<td>2.61 (.09)</td>
</tr>
<tr>
<td>19</td>
<td>0.936 (.159)</td>
<td>0.092 (.011)</td>
<td>0.132 (.017)</td>
<td>2.49 (.14)</td>
</tr>
<tr>
<td>22</td>
<td>0.898 (.081)</td>
<td>0.124 (.016)</td>
<td>0.129 (.010)</td>
<td>2.69 (.14)</td>
</tr>
<tr>
<td>40</td>
<td>0.447 (.067)</td>
<td>0.107 (.017)</td>
<td>0.203 (.024)</td>
<td>2.75 (.17)</td>
</tr>
<tr>
<td>57</td>
<td>0.483 (.102)</td>
<td>0.097 (.025)</td>
<td>0.173 (.029)</td>
<td>2.58 (.14)</td>
</tr>
<tr>
<td>200</td>
<td>0.499 (.063)</td>
<td>0.056 (.010)</td>
<td>0.097 (.015)</td>
<td>2.69 (.09)</td>
</tr>
</tbody>
</table>

Grand mean | .646 | .101 | .143 | 2.63 |

or the L-layer (0.790%) (Table 5 of Gosz et al. 1976). The lack of similar trends for Mg, K, and N is due to their less steep concentration gradients.

Wood litter fall prediction from JABOWA

JABOWA predicts low input of woody litter (twigs, branches, and boles) to the forest floor during the first several years following clear cutting (Fig. 2). By years 10–20, it is increasing at its greatest rate, leveling off by years 30–50. Much of the wide variation in wood litter fall occurring after year 30 is due to the death of increasingly larger individuals.

DISCUSSION

The dynamics of forest floor organic matter are controlled by a complex interaction of factors which change during succession: decomposition rate, leaf litter input, wood litter input, and decomposability. The early decline in forest floor organic matter content might be attributed in part to accelerated rates of decomposition. Numerous authors (e.g., Lutz and Chandler 1946, Moller 1954, Hart 1961, Ovington 1968, Witkamp 1971, Marks and Bormann 1972, Bormann et al. 1974) have speculated that devegetation of forest lands leads to higher rates of decomposition caused by increased soil temperature and moisture content. Increased nutrient availability, and in general decreased competition between vegetation and decomposers for water and nutrients may also be important. The importance of these increases in decomposition should be limited to the first few years immediately following forest cutting, for, as Marks (1974) has pointed out, the attainment of full occupancy, which he estimates to occur within 4 yr for densely stocked pin cherry stands, should cause microclimatic conditions at the soil surface to approach those in undisturbed forests. Wiegert and Monk (1972) used similar logic in suggesting that once a closed canopy is attained, decomposition rates should approach steady state values. My data suggest that the explanation is not so simple.

By year 4 leaf tissue production approached that of the mature forest (Covington and Aber 1980). This was followed by a 20% decline by year 11 and then a gradual recovery to precutting levels by year 30. Shading, transpiration, and nutrient uptake by the vegetation (and hence soil temperature, moisture, and nutrient availability) might follow these trends in leaf tissue production. Thus while canopy closure data suggest that temperature, moisture, and nutrient conditions in the forest floor may approach precutting values within 4 yr, one would infer from the leaf production pattern that these factors might not stabilize until much later. However, the major changes in microclimate are probably restricted to the first 3–4 yr, during which time the leaf biomass increases from near zero to within 5–20% of precutting levels.

Changing inputs of woody litter may also influence forest floor organic matter dynamics. Marks (1974) found that mass of dead branch storage (still attached to live stems) increased steadily with increasing age from year 1 through year 14. Rodin and Bazilevich (1967) suggested that for immature deciduous forests the amount of wood litter input is strongly dependent upon stand age, reaching a maximum between years 25 and 40. The age at which trunk fall due to natural thinning becomes intense seems to determine whether maximum litter input is reached earlier or later (Rodin and Bazilevich 1967).

Covington and Aber (1980) suggest that a major dieoff of pin cherry may occur between years 4 and 11 associated with reduced nitrogen availability; another period of intense natural thinning may occur between years 30 and 35 when pin cherry reaches its maximum longevity. Interestingly, the former would coincide with the point of inflection at which the curve for forest floor organic matter content slows its decline and bends upward. The latter (years 30-35) increase in nat-

FIG. 2. Wood litter fall predicted by northern hardwoods growth simulator (JABOWA) of Botkin et al. (1972a). Each point represents the average of 50 plots in the JABOWA simulation. Data from D. B. Botkin and J. D. Aber, personal communication.
ural thinning would coincide with the period of most rapidly increasing forest floor organic matter content (Fig. 1). Whittaker et al. (1974) suggest that stem and branch production in northern hardwoods reaches steady state values approximately 30 yr after clear cutting. Whether stem and branch litter fall attains steady state rates contemporaneously with this is uncertain, although one would expect some time lag.

The general trend in wood litter production predicted by JABOWA (Fig. 2) has some interesting implications for forest floor organic matter dynamics. During the first several years when the forest floor mass is rapidly declining, wood litter input is low. By years 10–20, it is increasing at its greatest rate, which would coincide with the turnaround in the curve for forest floor organic matter content. Dead biomass production (predicted by JABOWA) seems to level off by years 30–50. However, the trend in secondary succession should be from a fairly uniformly distributed and easily decomposed wood litter fall during the first few decades to a more highly localized wood litter fall composed of a higher proportion of less easily decomposed, larger diameter wood. Notably, much of the predicted wide variation in wood litter fall occurring after year 30 is due to the localized death of increasingly larger diameter individuals. Nye (1961) has recognized this as a major difficulty in constructing organic matter budgets for forest ecosystems and observed that wood litter fall over small areas is very erratic and difficult to measure, since it is greatly influenced by the fall of a single large tree. Such localized input of large-diameter trees would not appear immediately as an input to the forest floor due to the long delay in breakdown.

Since bark is richer in nutrients than sapwood or heartwood (Likens and Borrmann 1970), and since smaller diameter wood has a higher bark-to-wood mass ratio, the nutrient concentration of a piece of wood should be inversely related to its diameter. Thus nutrient concentration may enhance the structural factors that make early successional wood litter more decomposable than that of later stages. However, factors other than nutrient concentration and size also control the decomposability of wood litter. While the bark of sugar maple, red maple, and beech decays fairly rapidly compared to their wood, the bark of pin cherry, paper birch, and yellow birch remains identifiable long after the wood begins to disintegrate.

The leaves which fall during the first few years are probably more easily decomposed than those of later stages. Cromack (1973) studied and reviewed the factors known to control the rate of decay of fallen litter and concluded that decomposability increased with increasing nutrient concentrations (especially N) and decreased with increasing fiber content (especially lignins). Since leaf nutrient concentrations are often highly correlated with nutrient availability (Mitchell 1936, Mitchell and Chandler 1939, Scott 1955) and since nutrient availability is high during the first few years following clear cutting, the leaf fall of early stages should be higher in nutrients and hence more easily decomposed than that of later stages. Chemical analyses of plant tissues at Hubbard Brook suggest that tissues of pin cherry are generally higher in nutrient concentration than those of later successional species (sugar maple and beech) (Likens and Borrmann 1970). It is unclear what proportion of this higher nutrient concentration is due to higher nutrient availability in disturbed sites and what proportion is attributable to physiologic differences among the species involved.

Unit area estimates of forest floor organic matter dynamics

Evaluation of budgetary effects of forest floor dynamics requires the estimation of areal changes. To reduce the number of samples needed for establishing the shape of the curve describing behavior of the forest floor during secondary succession, I used a restricted sampling design (see Methods). A random sample of Hubbard Brook Watershed-6 (my 57-yr-old stand) by Gosz et al. (1976) resulted in an estimate of 46.8 Mg/ha of organic matter in the forest floor, in close agreement with Dominski's (1971) estimate of 45.9 Mg/ha for Watershed-1 and Watershed-3, which are similar in cutting history to Watershed-6. My restricted sampling produced a higher estimate of 72.5 Mg/ha for Watershed-6 (Fig. 1), due to undersampling of areas of the watershed low in forest floor organic matter. Multiplying by the ratio of Gosz's estimate to mine, reduces the asymptote (Fig. 1) to 56.0 Mg/ha of organic matter and the minimum at year 15 to 25.3 Mg/ha. Thus assuming a forest floor at or near the predicted steady state at the time of cutting, my results suggest a decrease of 30.7 Mg/ha (a decrease of over 50%) during the degrading phase (years 0-15). During the first several years of this phase the rate of decrease in organic matter storage in the forest floor and in the slash undoubtedly exceeds the rate of increase in organic matter storage in the living biomass, thus giving a negative net annual increment. During the rapidly aggrading phase (years 15-64) the forest floor should increase by 28.0 Mg/ha. Thereafter the rate of increase is slow and by year 200 the forest floor should be close to its predicted asymptote, having increased by a total of 2.7 Mg/ha, or approximately 20 kg·ha⁻¹·yr⁻¹ during the period from year 64 to year 200.

My results agree well with those of Dominski (1971). He found a 10.8 Mg/ha decrease in forest floor organic matter during the 1st 3 yr following the experimental devegetation (cutting and herbicide application) of Hubbard Brook Watershed-2. My empirically derived regression equation (Fig. 1) predicts an areal decline of 10.75 Mg/ha at year 3 following a commercial clear cut.
TABLE 3. Nutrient increment of the forest floor during secondary succession in northern hardwoods. In kg/ha. Data are total change for each phase.

<table>
<thead>
<tr>
<th>Phase</th>
<th>Ca</th>
<th>Mg</th>
<th>K</th>
<th>N</th>
<th>Organic matter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Degrading phase (years 0–15)</td>
<td>-35</td>
<td>-31</td>
<td>-44</td>
<td>-808</td>
<td>-30 700</td>
</tr>
<tr>
<td>Rapidly aggrading phase (years 15–64)</td>
<td>22</td>
<td>28</td>
<td>40</td>
<td>738</td>
<td>28 000</td>
</tr>
<tr>
<td>Slowly aggrading phase (years 64–200)</td>
<td>13</td>
<td>3</td>
<td>4</td>
<td>70</td>
<td>2700</td>
</tr>
</tbody>
</table>

Forest floor nutrient dynamics

Using my results for forest floor nutrient concentrations (Table 2) and the predicted changes in forest floor organic matter storage (Fig. 1), I calculated the forest floor’s nutrient dynamics during secondary succession following clear cutting. The only successional trend in nutrient concentration of the forest floor was a higher concentration of calcium for stands which were near the minimum in forest floor organic matter storage. Therefore, I used the average of the three oldest stands analyzed for nutrients (40-, 57-, and 200-yr-old stands) for the calcium concentrations of the forest floor at year 0 and year 64 since these two ages have near maximum forest floor organic matter accumulations. For year 15, I used the average calcium concentration of the two stands nearest in age (the 19- and 22-yr-old stands). For the concentrations of all other nutrients (potassium, magnesium, and nitrogen), I used the average for all six stands analyzed for nutrients (stands aged 4, 19, 22, 40, 57, and 200 yr). Concentrations were multiplied by organic matter accumulation to obtain estimates of nutrients in the forest floor at four ages. The results of these calculations are presented in Table 3.

To discuss the relative importance of the forest floor’s nutrient dynamics during secondary succession I must first differentiate the biotic compartments from which there is a probable net release of nutrients from those which serve as nutrient sinks. During succession, biotic sources may fluctuate considerably in magnitude or even switch from a source to a sink or vice versa. Biotic sources and sinks with a fairly simple behavior, i.e., varying in magnitude only, are nitrogen fixation (source), denitrification (sink), vegetation (sink), and stream flow (sink). The remaining sources and sinks (forest floor, slash, other dead wood, and mineral soil) exhibit a more complex behavior. I will refer to these latter compartments collectively as the dead organic matter compartment. During secondary succession, a large nutrient drain is placed upon nutrient sources by nutrient sinks, especially by uptake by vegetation and stream flow. Apparently increased output of nutrients in stream flow is important only during the 1st 3-4 yr (Pierce et al. 1972, Bormann et al. 1974, Bormann and Likens 1979). The increased output in stream flow for experimentally devegetated Hubbard Brook Watershed-2 during the 1st 4 yr was found to be 266 kg/ha of Ca, 53 kg/ha of Mg, 130 kg/ha of K, and 389 kg/ha of N. For commercial clear cuts, nutrient losses are less than half of this amount (Pierce et al. 1972, Likens and Bormann 1976, Bormann and Likens 1979).

To this increased transfer of nutrients from the dead organic compartment to the stream output sink must be added the increased nutrient transfer in the living biomass sink. The period of increased nutrient transfer into living biomass is much longer than that of increased output in stream flow. In fact, Whittaker et al. (1974) have suggested that living biomass increases exponentially for the first 30–40 yr following clear cutting and may continue to increase for several centuries.

Approximately 800 kg/ha of nitrogen are released from the forest floor during the degrading phase (Table 3). Thus increased nutrient output in stream flow might account for at most ≈100–200 kg/ha of N (Bormann and Likens 1979). Nutrient accumulation by the vegetation during this 15-yr period might account for another 160 kg/ha of N (J. D. Aber and D. B. Botkin, personal communication). Thus these two sinks can account for at most less than one-half of the N released from the forest floor during the degrading phase.

A considerable portion of this unaccounted-for N might be immobilized in the decomposition of the slash during the degrading phase. Fresh trunk wood of sugar maple, beech, and yellow birch has an N content of 0.092% to 0.120% (Likens and Bormann 1970). Well-decayed wood in red spruce-yellow birch forests has an N concentration of 1.09% (McFee and Stone 1966), a ten-fold increase in concentration. The absolute amount of N increases during wood decay (Gosz et al. 1973, Williams and Gray 1974). This N apparently comes from a combination of throughfall, absorption of nitrogen mobilized from the forest floor (Gosz et al. 1973), and N fixation.

The pattern of slash decay has some important implications for nutrient dynamics during the degrading phase. It is improbable that all of the nutrients in the slash are released by year 15. Spaulding and Hansbrough (1944) describe the sequence of hardwood slash decay in the White Mountains, New Hampshire. Generally within 5–8 yr the nutrient-rich, fine slash (twigs and branches 4 cm diameter) and the sapwood of the larger diameter wood is well decayed. By year 15 most of the larger slash is falling apart, so long as it is not waterlogged. However, McFee and Stone
(1966) report that some large-diameter stems may retain their identity for many decades after falling.

The decay of the nutrient-rich twigs and small branches and bark during the first 5–8 yr suggests a nutrient release from the dead wood during the first several years after clear cutting. The larger diameter wood, however, is very low in nutrient content, especially N (Likens and Bormann 1970, Williams and Gray 1974). A net immobilization of N probably occurs during its first 10–15 yr of decomposition, after which a net mineralization might begin. Thus slash may behave both as a source and a sink for nutrients during the degrading phase.

During the rapidly aggrading phase (years 15–64) the forest floor (and presumably the mineral soil) may no longer be a net source of nutrients but instead a sink. Conversely, the slash probably changes in function from an N sink to a source during the rapidly aggrading phase, as the nitrogen in the decaying wood reaches the concentration at which a net mineralization may occur. This implies an important function for slash (and presumably for dead wood in a naturally occurring disturbance such as a blow down). During the 1st 15 yr or so the slash may act as an N sink, taking up perhaps more than 50% of the N mobilized from the forest floor. During the ensuing years a net mineralization of N from the slash probably occurs; thus slash may serve as a major source of N during this period (years 15–64). It appears, then, that not only the forest floor but also the slash plays an important role in the homeostasis of the northern hardwoods forest ecosystems.

Living biomass accumulation might be substantially different if no dead wood remained after devegetation. Perhaps a higher rate of living biomass accumulation and N leakage in stream flow would occur due to the absence of slash as an N sink during the 1st 15 yr, but a slower rate of biomass accumulation during the period after year 15 might occur due to the absence of N mineralized from the slash during this time. An important question is whether the final accumulations of living biomass would be equivalent. The current trend toward increasingly intensive forest management including full tree logging and stump removal (e.g. Pearce and Stenzel 1973, Weetman and Webber 1972, Koch 1974) warrants more research into the role of slash in recovery after disturbance.

Acknowledgments

John D. Aber worked on a canopy dynamics study on these stands at the same time this study was being completed. Without his help and encouragement this study would have been more difficult and hardly as much fun.

I would like to thank my doctoral committee: D. B. Botkin, D. M. Smith, and G. K. Voigt for their encouragement and criticisms. Finally I wish to acknowledge my gratitude for the guidance, encouragement, and criticisms of my doctoral advisor, F. H. Bormann. This research was supported by a National Science Foundation grant to F. H. Bormann, and a Yale University Graduate Fellowship.

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