Effect of snow-pack on oak-litter breakdown and nutrient release in a Minnesota forest

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With 2 figures

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1. Introduction

Decomposition of the leaves shed annually by deciduous trees, with the release of the nutrient elements contained in them, is critical to the continued productivity of forests. Decomposition is primarily a biological process and the rate at which it occurs is, therefore, dependent upon temperature. Additionally, the organisms which accomplish decomposition require free water, and their activity slows as moisture becomes limiting (Edwards 1970). Consequently, it has often been assumed that decomposition during winter at higher latitudes is negligible, due both to lower temperatures slowing metabolism of microorganisms and available water being tied up as ice. However, several studies have shown significant weight losses in litter when fall and spring standing crops have been compared. For example, Bleak (1970) placed litter bags containing grasses and forbs in the field prior to snowfall and recovered them following spring melt. Weight loss of litter in the bags averaged 30 to 50%.

Stark (1973) observed an over-winter weight loss of 9.0% in Jeffrey pine (Pinus jeffreyi) which was 85% of the annual loss.

At least two explanations can be given for the observed results. First, spring thaw is typically accompanied by rather widely fluctuating temperatures, yielding a cycle of freezing and thawing which can disrupt the soil surface. The freeze-thaw cycle may fracture leaves as well, and if particles formed are small enough to pass through mesh of litter bags, may constitute a mechanical breakdown of litter. However, snow is an effective insulator. Once a sufficient snow pack has accumulated to buffer the soil from extremes of air temperatures, the ground may thaw. Once the temperature of the litter zone rises above the melting point of water, decomposers should be initiated activity and, releasing heat in the process, maintain temperatures at or above 0°C. With a ready supply of water from melting snow, decomposition should proceed at a rate determined by litter-layer temperatures until temporarily halted by percolating waters and the freeze-thaw cycle during spring melt.

The primary objective of this study was to evaluate the alternate hypotheses of whether winter weight loss of mixed oak leaf litter is continuous and biological or episodical and mechanical. Additional objectives included estimation of biological activity, nutrient release, and C-substrate dynamics from the same litter materials.

2. Methods

Studies were conducted at the Cedar Creek Natural History Area, Minnesota (latitude 45°25'N, longitude 93°10'W). Native vegetation is oak savannah with an overstory of white oak (Quercus alba), northern pin oak (Q. ellipsoidalis), northern bur oak (Q. macrocarpa var. obovata), and northern red oak (Q. rubra) with an understory of perennial grasses. Fire had been excluded from the...
study site for several decades and the site was approaching canopy closure. Mean annual temperature is 6°C, with July being the warmest month (x = 22°C) and January the coldest (x = -11.5°C). Mean annual precipitation is 66 cm. The site is underlain by Nymore sand, an Entisol derived from glacial outwash sands of late Wisconsin age (Gintal et al. 1974).

Freshly fallen litter was collected during the autumns of 1974 and 1975 for placement in litter bags. Litter bags were constructed from 3-mm mesh nylon netting. Bags measured 25 cm x 25 cm and were filled with approximately 7.5 g (dry weight) of litter. Each bag was weighed before it was placed in the field and a water content correction was established by oven-drying extra bags which had received similar treatment up to that time.

In order to recover litter bags from under snow, wooden stakes were driven at 8-m intervals and 10 bags were tethered to each stake with monofilament nylon line. Recovery was then accomplished by digging through the snow to the base of the stake and following the lines out to the litter bags.

Enough bags were placed in the field the first year to permit recovery of 20 bags/month for up two years, and another year’s requirement was put out one year later. All data were pooled for analysis, however, because there were no significant differences in first-year weight loss regressions between the two sets. During the first year, 20 bags were collected each month. During the second year, 20 bags of first-year leaves and 20 bags of second-year leaves were collected each month.

Decomposer invertebrate populations and CO2 evolution rate (an index of microfungal activity) were assessed prior to, during, and following snow cover. To assess invertebrate populations, 10 each of first and second-year litter bags were placed on refrigerated, Tullgren funnels for three days. Animals were collected in 70% ethanol and identified and counted under a dissecting microscope. To measure CO2 evolution, three each of first and second-year litter bags were sealed in 5-liter chambers with a wide-mouth jar containing 10 ml of 0.1 N KOH. Measurements were taken in the field, at ambient temperature, for 0.5 hr. One chamber containing only KOH served as a control. Temperatures in the chambers were recorded and rates were standardized to 10°C using a Q10 = 2.

Weight loss was assessed by drying bags at 105°C for 24 hr., cooling to room temperature over a dessicant, and weighing on a platform balance. Litter was then removed from the bags and ground to pass a 2-mm mesh screen (~2-mm particles). Litter elemental analyses (N, P, K, Ca, Mg, Mn, Fe, Cu, B, Zn, Al) were done on bulked samples from 20 litter bags at the following sampling intervals: following snow-melt the first year litter was in field; after one year of decomposition; and following snow-melt the second year litter was in field. Nitrogen was analyzed by micro-Kjeldahl (Jackson 1938); all other elements were analyzed, following ashing at 500°C, by spark emission spectroscopy (Chaplin & Dixon 1974). Lignin, cellulose, and acid soluble fraction were analyzed using the methods of Van Soest (1963). Carbon-to-nitrogen ratios were estimated assuming C concentrations of approximately 50% of ash-free weight (Van Soest 1963).

3. Results

3.1. Weight Loss

As is common in litter-bag studies, there was an initial increase in the mean weight of litter bags after they were placed in the field (Fig. 1). The increases were not statistically significant (P > 0.05) but, nevertheless, affected the weight-loss parameters calculated by regression. A regression of the form Y = ae^xb was fitted to the data with the values of a and b calculated to be 104.3% and 0.0008 days^{-1}, respectively (r^2 = 0.70, P < 0.0001). The loss rate coefficient, b, describes an annual exponential weight loss of 29%. From that parameter, it is possible to predict how much time will be required for all of a year’s litterfall to be turned over. Dividing ln 2 by the loss rate, 0.0008, we determine that half of the litter remaining from a year’s litterfall is lost every 866 days or T_{1/2} = 2.37 years. After seven reductions by 50%, less than 1% of the original litter remains; that is, effectively all of the litter is lost after seven half-times. For these data, that point would be reached in approximately 16.6 years. Reiners & Reiners (1970) estimated turnover times of 15 years for oak litter at Cedar Creek by dividing the average litter pool size (all fractions) by the annual litter input. Regressions run on litter-bag data for oak forest in southern Wisconsin (Whittingham, unpublished data) estimated a turnover time of 13.3 years.

3.2. Biological Activity

Snow covers the ground for four to five months of each year, beginning approximately two months after litterfall is complete (Fig. 2). Approximately 55% of the first-year weight loss was coincidental with snow cover. Fungal mycelia were observed on leaves collected
Fig. 1. Weight loss from litterbags over a two-year period. The regression $y = 104.28 e^{-0.0008X}$ was significant at $P < 0.0001 (r^2 = 0.70)$.

Fig. 2. Snow depth during two winters within an oak forest at Cedar Creek Natural History Area, Minnesota.

from under snow in February of the first year, and spiders, fungus beetles, and oribatid mites were active in the litter bags, at least after they were brought into the laboratory. It was thought that biological activity was continuing under the snow while air temperatures ranged to as low as $-35$ °C. Consequently, biological activity was assessed during the second year (Table 1).

In order to facilitate comparisons, CO$_2$ evolution rates are standardized to comparable litter weights and temperatures. Prior to snowfall, microbial activity on fresh leaves was approximately twice that on year-old litter. With the establishment of a snow-pack, activity of first-year leaves increased by a factor of nearly seven. The nylon bags containing second-year litter had deteriorated to the point where they could not be retrieved intact from under the snow and comparable data were not collected. With the advent of melt, however, the activity on second-year litter was observed to have increased by a factor of 26 over autumn values while the activity on first-year litter remained virtually constant. Values declined as the litter dried following melt but remained above the pre-snow values, and the first-year litter remained above second-year litter by nearly a factor of two.

Faunal activity appeared to reflect an invasion phenomenon. Densities were quite low on new litter but doubled with snow-pack and remained relatively constant, as nearly as can be determined from the data, through melt and up to the second year's snow-pack. With the second year’s melt, faunal densities had increased by a factor of approximately 15. Melt was followed by a population decline.
Table 1. Decomposer activity at Cedar Creek Natural History Area, Minnesota, 1975—1976

<table>
<thead>
<tr>
<th></th>
<th>Pre-snow</th>
<th>Snowpack</th>
<th>Melt</th>
<th>Post-melt</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>CO₂</strong> (mg/g litter hr⁻¹ at 10 C)</td>
<td>0.0693ᵃ</td>
<td>0.4604</td>
<td>0.4966</td>
<td>0.3360</td>
</tr>
<tr>
<td><strong>Fauna</strong> (No./m²)</td>
<td>128ᵃ</td>
<td>315</td>
<td>258</td>
<td>260</td>
</tr>
<tr>
<td></td>
<td>285ᵇ</td>
<td></td>
<td>4195</td>
<td>715</td>
</tr>
</tbody>
</table>

ᵃ) First-year litter.
ᵇ) Second-year litter.

Table 2. Changes in weight, C constituent concentrations (% dry wt.), absolute amounts of C constituents (g) and C/N ratio in mixed oak leaf litterbags

<table>
<thead>
<tr>
<th></th>
<th>Fresh litter 0 days</th>
<th>First-year post-melt 165 days</th>
<th>First-year decomposition 375 days</th>
<th>Second-year post-melt 522 days</th>
<th>Exponenti loss rate, k (day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Weight (as-free)</strong></td>
<td>100</td>
<td>6.91</td>
<td>90.1</td>
<td>6.23</td>
<td>72.1</td>
</tr>
<tr>
<td><strong>Acid detergent soluble fraction¹</strong></td>
<td>61.6</td>
<td>4.26</td>
<td>53.4</td>
<td>3.30</td>
<td>49.6</td>
</tr>
<tr>
<td><strong>Cellulose¹</strong></td>
<td>16.2</td>
<td>1.12</td>
<td>16.9</td>
<td>1.07</td>
<td>16.1</td>
</tr>
<tr>
<td><strong>Lignin¹</strong></td>
<td>22.2</td>
<td>1.53</td>
<td>29.7</td>
<td>1.86</td>
<td>34.3</td>
</tr>
<tr>
<td><strong>Ash²</strong></td>
<td>1.0</td>
<td>-</td>
<td>1.9</td>
<td>-</td>
<td>5.0</td>
</tr>
<tr>
<td><strong>C/N ratio</strong></td>
<td>53</td>
<td>44</td>
<td>44</td>
<td>25</td>
<td>25</td>
</tr>
</tbody>
</table>

¹) All C fraction data recalculated as ash-free. Sum of C-fraction percentages equals 100.
²) Ash content remaining as percent of total weight following 72% H₂SO₄ digestion (Van Soest 1963)

Table 3. Changes in elemental concentrations (% ash-free dry weight) and in absolute amounts (mg) of elements in mixed oak leaf litterbags

<table>
<thead>
<tr>
<th></th>
<th>Fresh litter 0 days</th>
<th>First-year post-melt 165 days</th>
<th>First-year decomposition 375 days</th>
<th>Second-year post-melt 522 days</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>N</strong></td>
<td>0.95</td>
<td>11.14</td>
<td>2.02</td>
<td>1.77</td>
</tr>
<tr>
<td><strong>K</strong></td>
<td>0.60</td>
<td>41.10</td>
<td>0.22</td>
<td>0.17</td>
</tr>
<tr>
<td><strong>P</strong></td>
<td>0.12</td>
<td>7.7</td>
<td>0.06</td>
<td>0.09</td>
</tr>
<tr>
<td><strong>Ca</strong></td>
<td>1.08</td>
<td>74.6</td>
<td>1.17</td>
<td>1.45</td>
</tr>
<tr>
<td><strong>Mg</strong></td>
<td>0.1700</td>
<td>11.50</td>
<td>0.1600</td>
<td>0.1600</td>
</tr>
<tr>
<td><strong>Mn</strong></td>
<td>0.0900</td>
<td>6.00</td>
<td>0.1200</td>
<td>0.1100</td>
</tr>
<tr>
<td><strong>Fe</strong></td>
<td>0.0017</td>
<td>1.20</td>
<td>0.0360</td>
<td>0.0500</td>
</tr>
<tr>
<td><strong>Cu</strong></td>
<td>0.0010</td>
<td>0.07</td>
<td>0.0015</td>
<td>0.0012</td>
</tr>
<tr>
<td><strong>B</strong></td>
<td>0.0050</td>
<td>0.45</td>
<td>0.0030</td>
<td>0.0026</td>
</tr>
<tr>
<td><strong>Zn</strong></td>
<td>0.0060</td>
<td>0.42</td>
<td>0.0073</td>
<td>0.0075</td>
</tr>
<tr>
<td><strong>Al</strong></td>
<td>0.0200</td>
<td>1.34</td>
<td>0.0500</td>
<td>0.0700</td>
</tr>
</tbody>
</table>

3.3. Biochemical constituents

The acid soluble fraction (ASF) of litter was lost at a relatively constant rate which exceeded the general weight loss of litter (Table 2). The ASF includes those compounds, such as sugars and hemicelluloses, which are broken down relatively easily by the decomposer community. The exponential weight loss curve is explained by the initial, rapid movement of this fraction by decomposers with subsequent C replenishment through the breakdown of cellulose and further removal. After the first winter, the loss rate of cellulose was greater than the loss rate of ASF, as would be the case if the latter represented by-products of microbial utilization of cellulose (Table 2). The cellulose fraction was broken down little during
the first winter with \(< 5\%\) of the initial weight lost. Following snow melt, however, more rapid weight loss occurred, with approximately \(29\%\) of the original fraction being lost over a span of one year. Cellulose degradation is accomplished primarily by microflora (Kaarik 1974) which require time for establishment and which are further encouraged by faunal comminution of litter (Crossley & Witkamp 1964).

The lignin fraction increased by \(\sim 22\%\) over the initial weight during the first winter and remained at approximately the same level for the remainder of the study (Table 2). Since the increase is absolute and not due to relative loss of other fractions, it is interpreted as reflecting microbial processes such as fungal invasion, growth, metabolism, and turnover. A \(22\%\) increase is an absolute weight increase of approximately 330 mg lignin per litter bag. Fungi contain about 5 to 30\% lignin (Pugh 1974) and microbial decomposition processes result in formation of lignin-like humic materials (Allison 1973). Although the data do not permit discrimination between residual lignin from litter and microbial lignin, the actual formation rate of lignin and/or humic materials by microbes may have been greater than the approximately 330 mg per litter bag indicated.

Ash content increased throughout the study but most rapidly during the second winter. The results are not due to enrichment through removal of low-ash constituents because the increase was absolute. Rather, two sources are available, atmospheric fallout and faunal translocation, as will be discussed in the following section.

### 3.4. Elemental dynamics in litter

The transient behavior of the constituent elements of litter can conveniently be grouped into three classes: elements which are concentrated as litter disappears, elements which are lost more rapidly than litter, and elements which disappear more or less in proportion to litter loss rates. Aluminium, Fe, N, Zn, and Ca all accumulated relative to litter (Tab. 3); that is, concentrations increased over initial conditions and were never lower than the concentrations in fresh litter. Aluminum, Fe, and Zn are micronutrients with low biological activities, yet are abundant in soils. In the cases of at least Fe and Al, the enrichment results not only from being left behind as the litter breaks down but also from contamination of litter with soil. The latter process occurs in at least two ways: active transport by soil animals which enter the litter to feed and by atmospheric transport and fallout. Evidence for soil contamination can be seen in changes in the ash content of litter. Ash content of fresh litter was approximately 1.0\% of ash-free dry weight while the ash content of 18-month-old litter had risen to approximately 22\%. No attempt was made to isolate the contribution of soil from the increase due to differential breakdown of litter components, however.

The increase in Ca concentrations through time results from the fact that Ca loss rates from litter are less than the rate of weight loss (Cromack & Monk 1975). The conservation of Ca is considered to be the result of oxalate production by fungi (Graustein, Cromack & Sollins 1977). Calcium concentration increases were observed throughout the first year that litter was on the ground, with the rate of increase being greatest during the summer when higher temperatures produce higher metabolic rates. A 5\% decline was observed over winter in second-year litter.

Since initial concentrations of N in leaf litter are low, increases must result from fixation, translocation, or both. Both concentration and actual amount of N increased during the first year with the greatest increase during the summer. The decline over the second winter was also both in concentration and actual amount of N. The progressive increase of N during first-year decomposition would result in C: N ratios being decreased to where N-mineralization should have begun to occur (Jensen 1929).

Manganese, Cu, and Mg all fluctuated around the initial concentration (Table 3). Magnesium declined in absolute amount until the second-year snow melt, at which time there was a slight increase. Both Mn and Cu increased over the first winter and decreased over the following summer. During the second winter, Mn increased similar to Mg and Cu remained relatively constant.
Phosphorus, K, and B all were lost from litter more rapidly than the litter itself did, appeared (Table 3). Potassium is a highly mobile element and its concentration declined by 63% during the first winter, rose slightly over the summer, and declined by another 16% the second winter. Presumably, the loss coincided with snow melt and the loss was by leaching of soluble potassium. The pattern for loss of boron was sharply different. While the absolute amount declined during each season, the concentration declined only during the summer (∼48%) with virtually no change in concentration taking place during either winter.

Phosphorus concentration declined during the first winter that litter was on the ground, indicating that there was no conservation of the element. Thereafter, concentrations increased as the element was conserved. The initial loss was 52%, meaning that phosphorus was being lost almost twice as fast as overall litter weight loss.

4. Discussion

Breakdown of oak litter continues throughout the winter in the upper midwest although air temperatures may plunge to −30 °C or lower. The litter layer is buffered from temperature extremes by snow, although litter temperatures do not always remain above the freezing point. For example, during January 1975, air temperatures in the oak woodland ranged from −30 to +1.5 °C, while temperatures in litter ranged between −10 °C and +1 °C. It is thought that the litter is heated from below and is typically above air temperatures. During the month in the example, soil temperatures averaged 0.7 °C ± 0.03 (S.D.) at 4 cm depth and 1.8 °C ± 0.03 (S.D.) at 50 cm depth, which indicates that sufficient heat was available to warm the litter layer. Snow cover during the period averaged approximately 30 cm (Fig. 2).

While litter breakdown does proceed, the rate of breakdown implies that it may not be continuous throughout the winter. WITKAMP & OLSON (1963) reported a weight loss rate of 0.7028 year⁻¹ for confined litter in Tennessee with a mean annual temperature of 13.3 °C. In the present study, the loss rate was 0.2931 year⁻¹, with a mean annual temperature of 6.0 °C. Comparison of the two studies yields a Q₁₀ of 3.3, which implies that breakdown ceases for portions of the year in Minnesota. Since neither study continuously monitored litter temperatures, interpretations are better based on biological and chemical observations.

There is direct evidence for biological activity under snow in the CO₂ evolution rates (Table 1). The rate of CO₂ production on first-year litter was 6.6 times greater under snow than prior to snow fall, when corrected for temperature and weight differences, and invertebrate densities more than doubled. Melt produced an 18% decline in invertebrate densities but relative CO₂ evolution increased. While the critical snow-pack data are lacking for second-year litter, the melt data suggest greatly increased activity under snow during the second winter. This interpretation is supported by elemental analysis and ash data. Potassium declined rapidly during the first winter, both in concentration and absolute amount (Table 3), increased slightly in concentration over the summer, and again declined in both concentration and absolute amount over the second winter. Since K is so highly mobile, a loss of 13% of initial weight during the second year's melt would not necessarily require decomposition under snow. However, ash content increased dramatically during the same period and the ash was primarily added mineral soil, as evidenced by increases in Al, Fe, and Zn (Table 3). The primary route of mineral soil into the organic layer is via transport by invertebrates. Thus, the extremely high invertebrate densities present in second-year litter at snow melt (Table 1) are indicative of activity during the prior snow-pack.

Explaining the dynamics of N and P is somewhat speculative. Since the absolute quantity of N in litter increased during the first year on the ground, N fixation, translocation by fungi, or both, occurred. The decline over the second winter was both in concentration (from 2.0 to 1.8% of ash-free dry weight) and in total amount, because litter was also losing weight. However, biological activity was increasing during that period, (Table 1), so it is quite possible that the decline represents a flushing by snow melt. A similar flush did not occur during the first year because the litter was still experiencing fungal invasion and decomposition was not as well advanced.
The possibility of N increase due to fungal translocation is supported by the increase in both concentration and absolute quantities of lignin and/or humic materials resistant to 72% \( \text{H}_2\text{SO}_4 \); fungi are known to synthesize such C substrates (Allison 1973, Pugh 1974). Both N and Ca were immobilized in our litter bags. The same immobilization patterns for these two elements were observed for decomposing Douglas-fir fine roots (Sollins et al. 1978). These authors obtained direct evidence for fungal accumulation of N and Ca by separate analyses of fungal rhizomorph tissue growing into the roots.

It is interesting that P concentration continued to increase during the second winter, after having declined sharply with the first year's melt. The absolute quantities of P present declined significantly during the first winter, but remained relatively constant afterwards (concentration increased while litter weight was lost), indicating conservation of the element. A similar pattern of initial P loss, followed by fungal conservation was observed by Sollins et al. (1978) for decomposing Douglas-fir fine roots. Fungi have been found to contain approximately 0.24% P and decomposer invertebrates to contain about 1.1% (McBrayer 1977). Both fungal biomass and the biomass of 4200 invertebrates/m² could account for much of the conserved P. However, formation of relatively insoluble Fe and Al hydroxy phosphates resulting from contact with translocated soil may account for the majority of the immobilized P.

5. Conclusions

Litter breakdown does occur under snow in Minnesota, although it occurs rather slowly and is probably interrupted from time to time. Decomposer activity is thought to cease when air temperatures are cold enough to penetrate the snowpack and to restart when air temperatures rise and the litter layer is warmed from below. The critical air temperature is not known but it is well below 0°C and varies with snow depth. In addition to biological breakdown, freeze-thaw cycles may contribute mechanical disintegration. Snow melt does not appear to flush nutrients from the litter horizon, except for K and P, and the latter is flushed only from first-year litter. Colonizing microorganisms appear to play a significant role in transferring labile C substrates to resistant C substrates such as lignin and in immobilizing nutrients such as N and Ca.

6. Acknowledgements

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7. Summary · Zusammenfassung

Litter bags were used to study litter turnover in a Minnesota oak forest over a two-year period. Annual weight loss was 29%. Both microfloral and invertebrate decomposers were active under snow cover, but activity was thought to cease periodically when air temperatures fell below the insulation value of snow. Aluminium, Fe, Zn, Ca, and N were all concentrated as litter decomposed: concentrations of Cu, Mn, and Mg remained relatively constant; and P, K, and B were lost more rapidly than litter weight. Data are also presented on the turnover of lignin and cellulose in the litter-bag system.

Der Effekt der Schneedecke auf den Umsatz von Eichenstreuf und für die Nährstofffreisetzung in einem Minnesota-Forst

Um während einer 2jährigen Periode in einem Forst in Minnesota den Streunumsatz und die Nährstofffreisetzung zu studieren, wurden Streu-Beutel verwendet. Der jährliche Gewichtsverlust betrug 29%. Unter der Schneedecke waren sowohl die abbaubaren Mikroorganismen als auch Invertebraten aktiv; es wird jedoch angenommen, daß die Aktivität periodisch aufhört, wenn die Lufttemperaturen


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