LITTER DECOMPOSITION BENEATH DEEP SNOW IN TEMPERATE CLIMATES

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The pattern of leaf litter decomposition and associated nutrient release, of critical importance to the nutrition of forest ecosystems, is complicated in temperate biomes by the imposition of long cold winters. Decomposition is a microbially mediated process, so sub-zero temperatures and loss of free water to ice for 4-6 months each year could create a significant check on the rate of litter decay and hence retard the rate of nutrient release. On the other hand, snow is an effective insulator, and soil surface temperatures beneath a winter snowpack are often mild (+1 to -3°C) and relatively independent of air temperatures. Cold-adapted microbes can actively grow under these conditions.

The period of snow melt in early spring may be especially important, because then water becomes available to stimulate decomposition, while subnivean temperatures remain stable. Simultaneously there is a flux of available nutrients, particularly N and S, from the snowpack. Conversely, acidic meltwater may depress decomposer activity, and leach nutrients and soluble organic matter from the litter.

This study examined patterns of litter decomposition under deep snow in a sub-alpine balsam fir forest north of Quebec City, where the ground is completely covered with snow for 5-6 months each year.

The catchment of Lac Laflamme is a small ($0.68\ km^2$) basin on the Precambrian Shield (elevation 777-884 m), about 80 km north of Quebec City. The basin supports a climax boreal forest dominated by balsam fir, with some white spruce and paper birch. Ground cover is mostly *Sphagnum* and soil is a strongly acidic (pH 3.7-4.2 in organic layers) ferro-humic podzol. Climate is humid continental, with long, cold, snowy winters. Temperatures extend below the freezing point on average 234 d each year, and mean January temperature is -16°C. Continuous snow cover usually extends from December to late May, and accumulations > 1.5 m are common. The snow cover effectively insulates the litter layer from extreme temperature fluctuations: temperatures at the litter-snowpack interface vary between 0 and -2°C.

On 19 November 1987, as the first winter snow fell, 1-g, pre-dried samples of senescent birch leaves, fir needles and arboreal lichens, confined in fibreglass bags (1 mm mesh) were pinned to the ground within a 10 x 10 m plot in the forest. Small twigs (< 3 mm diameter) were tagged and pinned directly to the ground. Five replicates of each litter type were collected every month or 2 months until snow cleared in May, and again in June. Respiration on needles and leaves was measured by confining the bags in sealed plastic containers under the snow for 24-48 h and then measuring accumulated CO_2 in a gas chromatograph. After drying and weighing, samples were ground and analyzed for total N and S.

By late February, snow had accumulated to a depth of 1.5 m, and depth changed little until melt began in early April. Most snow was gone by mid-May. Decomposition of most substrates continued at a slow and more or less steady pace throughout the winter; there were no discontinuities in the patterns of mass loss to suggest a more rapid decay rate during snow melt in April or May (Fig. 1). Surprisingly, the mass loss rate for fir needles was greater than that for birch leaves ($p < 0.001$), quite the reverse of the result

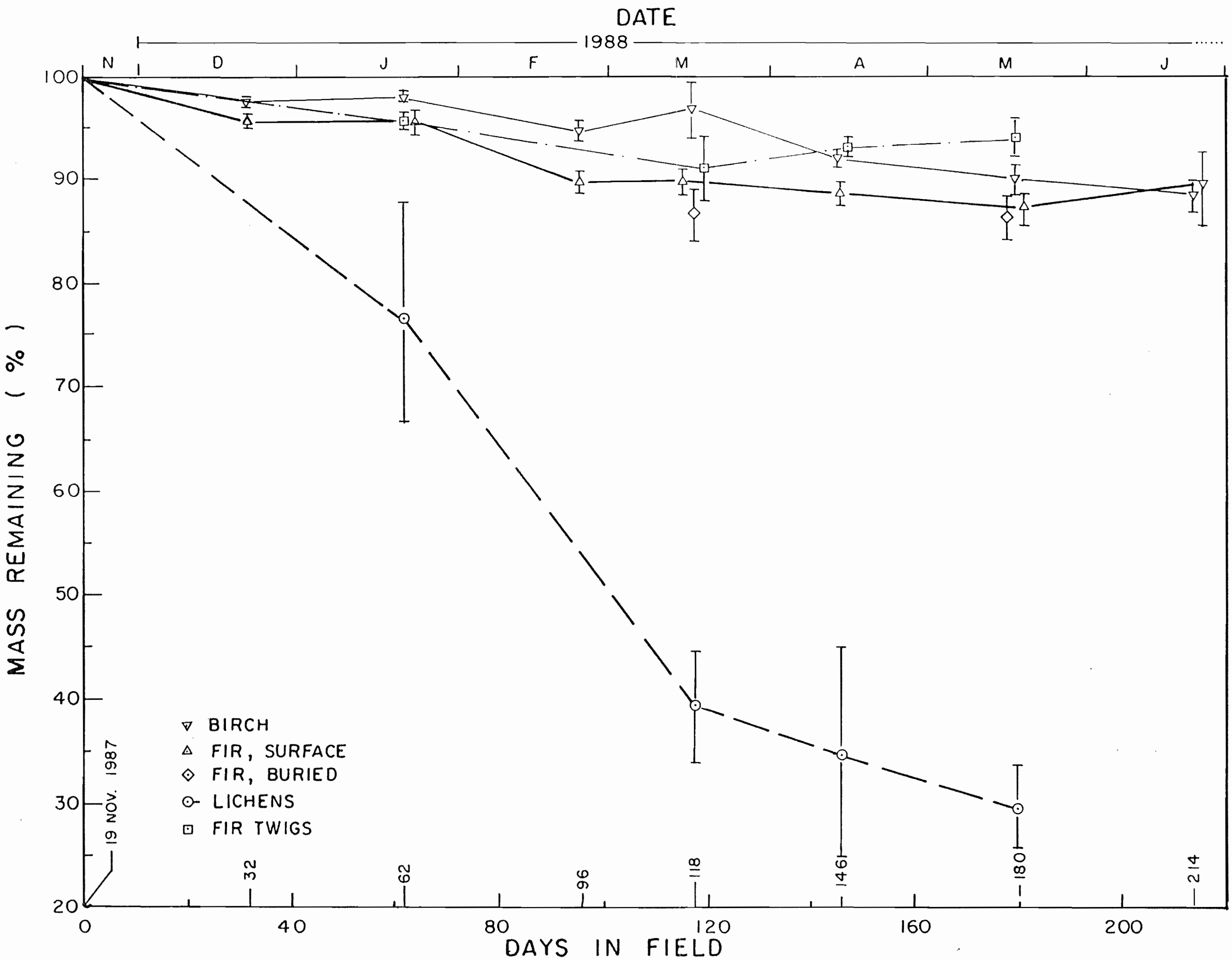

Figure 1: Decomposition rates (mass remaining) of various litter types under snow at Lac Laflamme, winter of 1987-1988.

universally found at higher temperatures. Mass losses for needles buried under the moss layer, and thus out of contact with the snowpack, were not significantly different from those of needles on the surface. Mass losses from twigs were erratic and very small (6%). In contrast, lichens decomposed extremely quickly throughout winter, and by May only 30% of original mass remained (Fig. 1).

In situ respiration rates increased steadily from about 1 mg CO_2 g^{-1} d^{-1} in February to 3-5 mg g^{-1} d^{-1} in May, but were always lower than in the summer. There was no significant difference in respiration rate between birch leaves and fir needles, again in contrast to the usual result for the snow-free seasons. Adjustment of respiration rates to a common temperature of 10°C removes much of the seasonal trend, which implies that by late winter microbial communities were well established and any subsequent increases in respiration rates were due to warmer temperatures, not continued growth of microbial populations.

There was a significant increase in N concentration of all litter types except twigs over the course of the winter (Fig. 2). However, N content, calculated as concentration times mass remaining, showed a more complex behaviour. N content of fir needles did not change over winter, while that of birch leaves declined, probably due to leaching, and then rose during spring melt (Fig. 2). Rapidly decomposing lichens lost a third of their N content, all of it before spring melt began. Hence, the behaviour of nitrogen was different for each kind of litter; only birch leaves (and occasionaly fir needles) assimilated N from the environment, which could include melting snow. Patterns of sulphur accumulation and release generally paralleled those for N.

It is possible to estimate the total nutrient uptake by fresh litter over winter, based on data in Fig. 2 and previous estimates of litterfall. For leaves and needles combined, the estimated over-winter uptake of N is 50 mg/m^2, and of S, 7.5 mg/m^2. By comparison, concentrations of inorganic N and S in the snowpack just before spring melt were 270 mg/m^2 and 310 mg/m^2, respectively, roughly 5.4 times (N) and 40 times (S) larger than these generous estimates of uptake by decomposing litter.

It is clear from this preliminary experiment that decomposition does proceed beneath the snowpack at Lac Laflamme. Further, microbial metabolism, not just leaching, must be responsible for some of this decay: first, the observed mass losses exceed the contents of water soluble material in all the litter types; second, microbial respiration was evident on needles and leaves throughout winter, even when temperatures above the snowpack were well below zero; third, fungal mycelia were visible to the naked eye on needles and lichens; fourth, there was active retention or accumulation of N and S beyond that which could be explained by leaching.

How do these results compare with those in other regions? Table 1 summarizes a literature review of decomposition under deep snow in a range of cool temperate forests. To render the data more comparable, mass losses were standardized to a uniform winter of 6 months duration. Naturally, estimates obtained in this way are prone to widely varying accuracy. Nevertheless, a few generalizations are possible:

(1) Significant decomposition under snow has been observed in all regions and with all litter types; it may or may not contribute a large part of the annual mass loss.

(2) First-winter mass losses vary according to the proportion of soluble or labile material in the litter, from 5% or less in twigs and needles, to as much as 40% in herbaceous plants. Both leaching and microbial metabolism are implicated in this mass loss.

(3) In contrast, mass losses in second and subsequent years are small (5%), remarkably uniform across the whole range of litter types, and depend entirely upon microbial degradation of resistant substrates such as lignocellulose.

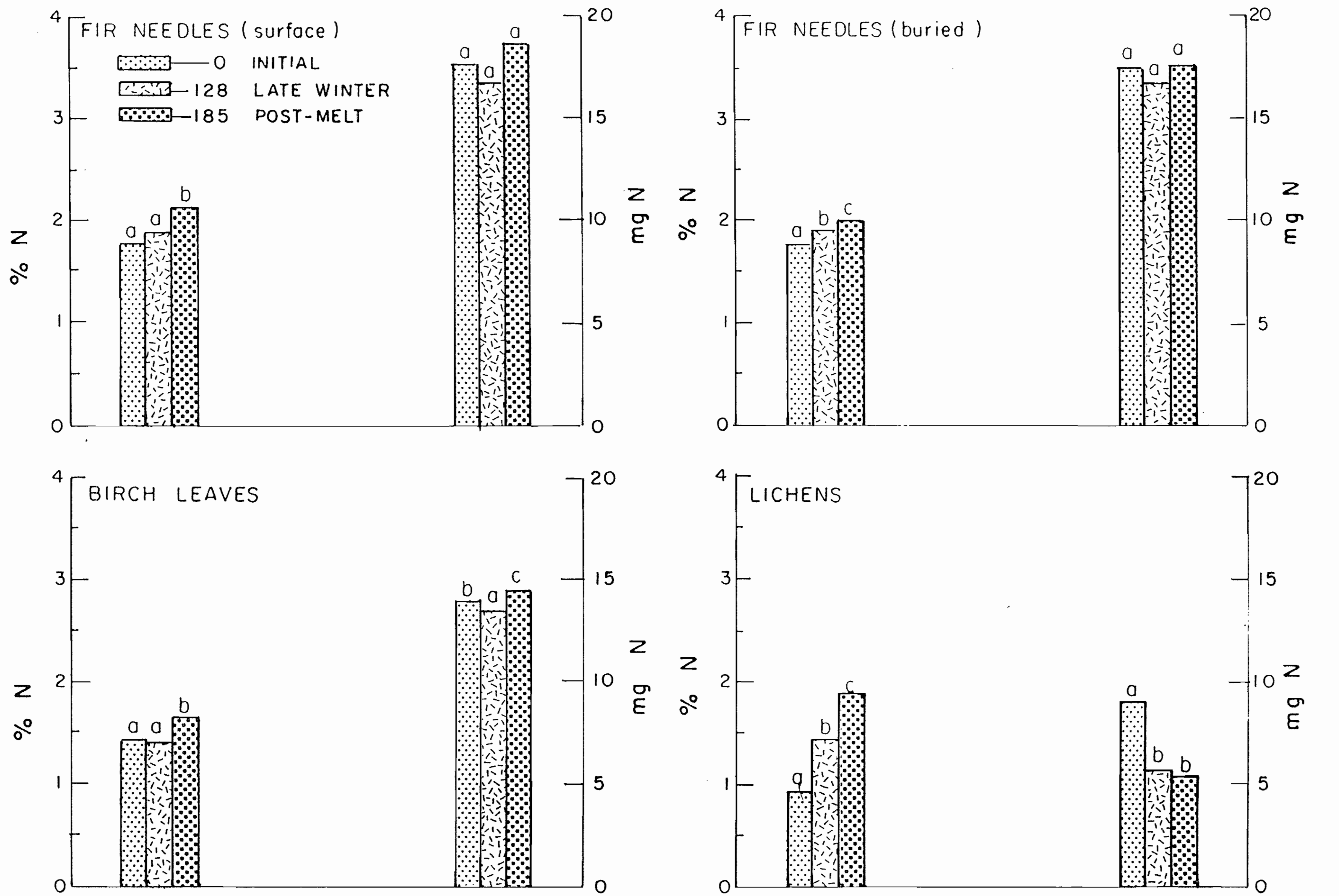

Figure 2: Changes in N concentration (left) and N content (right) in litter decomposing under deep snow at Lac Laflamme.

TABLE 1

Estimated over-winter mass losses from different types of litter decomposing under deep snow in cool temperate biomes

LITTER TYPE	% MASS LOSS (6-MONTH WINTER)			SOURCES
	Median	Range	N*	
FIRST YEAR				
TWIGS	5.7	2.0 - 14.9	8	7, 13, 17
CONIFER NEEDLES	10.0	1.3 - 15.3	10	2,3,4,6,13, 15,16,17
DECIDUOUS LEAVES	15.6	2.4 - 32.1	22	1,4,7,8,9, 10,11,12,13, 14,16,17,18
GRASS	21.0	11.4 - 30.3	5	5,19
FORBS	39.0	31.0 - 44.0	4	5,19
SECOND YEAR				
ALL TYPES	5.0	0 - 9	10	

* Number of species or sites considered.

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