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Patterns of nitrogen uptake and loss in relation to litter disappearance and associated invertebrate biomass in six streams of the Pacific Northwest, U. S. A.

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With 5 figures and 2 tables in the text

Introduction

In 1968, KAUSHIK & HYNES first demonstrated protein increases in litter undergoing decomposition in a lotic ecosystem. Since that time, numerous studies have indicated conditioning of litter by the microbiol community is an important prerequisite to invertebrate consumption (TRISKA 1970; MAKAY & KALFF 1973; BARLOCHER & KENDRICK 1973 a, b, 1975; IVERSEN 1973; ANDERSON & GRAFIUS 1975). Rates of leaf processing of various leaf species in a single stream have also been determined (MATHEWS & KOWALCZEWSKI 1969; THOMAS, 1970; TRISKA 1970; IVERSEN 1973, 1975; PETERSON & CUMMINS 1974; SEDELL et al. 1975; HODKINSON 1975). Proposed mechanisms of microbiol conditioning in conjunction with decomposition include such factors as leaf texture, protein and nutrient increase, partial cellulose hydrolysis and polyphenolic leaching, to name a few.

In streams of the Cascade Mountains (Oregon, U. S. A.) previous studies have led to the conclusion that if any nutrient is limiting to the biota associated with litter it is N. As a result, a study of N change during litter decomposition was undertaken in six different streams using identical litter substrates. The study had four specific objectives:

1) to ascertian the decay coefficient (PETERSON & CUMMINS 1974) of identical litter debris over a wide range of stream habitats.
2) to observe both qualitative and quantitative changes of the N pool of litter undergoing decomposition in a wide variety of habitats.
3) to determine the extent to which leaf litter might act as a N sink for the stream ecosystem and as a source to the invertebrate community.
4) to determine the response of invertebrates to changes in the N pool.

The overall goal was to define properties of litter processing common to the six streams by using a single leaf species over a wide variety of habitat types, rather than using many leaf species in a single stream as has most often been the case in previous litter studies.

Site description

To accomplish the objective and overall goal listed above, six diverse sites were selected from three different regions of Oregon and Washington, U. S. A. (Fig. 1, Table 1). Two streams were selected from each of three major areas, the Coast Range, the Cascade Range and the Experimental Spring site. The coast streams were characterized by sedimentary deposits with a large proportion of fine mineral particulates. The riparian vegetation was primarily deciduous dominated by alder (*Alnus rubra*) and salmonberry (*Rubus spectabilis*). Beyond the riparian zone vegetation was dominated by a 130-year-old Douglas-fir (*Pseudotsuga menziesii*) forest at Flynn Creek and a 10-year-old clearcut at Needle Branch Creek. At the Experimental Spring site (Washing-

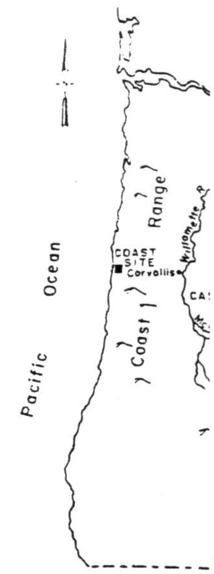

Fig. 1. Location of the thr

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experimental spring strea
0.4 m/sec. The mineral
4 cm diameter. Riparian

Table 1. Physical-chemical

	Stream order
Coast Range	
1. Flynn	3
2. Needle Br.	2
Experimental Spr	
3. Nitrate input	N. A.
4. Control	N. A.
Cascade Streams	
5. Mack	3
6. WS 10	1

Environmental ch
Coast Range: Sedimentary
rains; old-growth forests
Experimental Spring Strea
precipitation 300 cm; cl
Cascade Range: Volcanic
rains and spring snow m

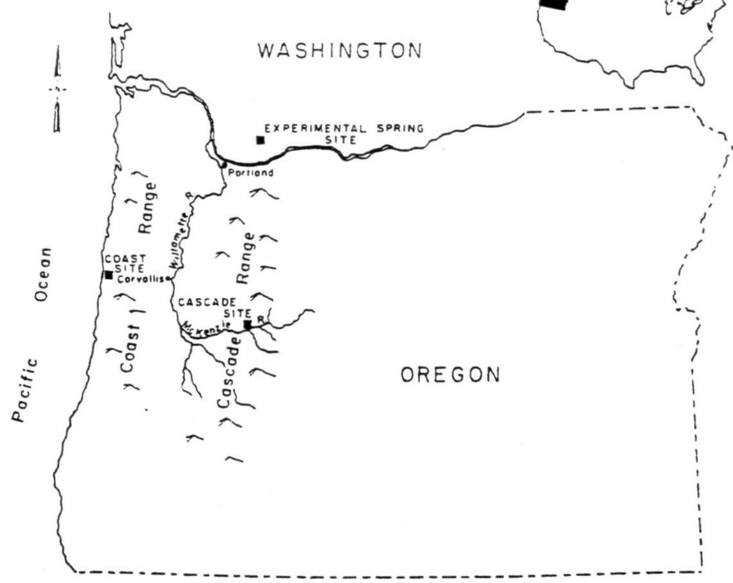

Fig. 1. Location of the three study sites in the Pacific Northwest, U. S. A.

ton, U. S. A.) channels are man made replicates whose source is a large spring. Both experimental spring streams are 1.2 m wide with a current velocity between 0.3 and 0.4 m/sec. The mineral substrates consist of smooth washed gravel between 2 and 4 cm diameter. Riparian vegetation was completely removed exposing the streams to

Table 1. Physical-chemical characteristics of six Oregon sites.

	Stream order	Drainage area (km^2)	Stream (m)	Altitude (m)	Gradient (%)	NO_3 conc. (mg/l)	Temp. range (° C)
Coast Range							
1. Flynn	3	2.02	3	209	2.5	1.15	3—16
2. Needle Br.	2	0.70	1.5	200	1.4	.17	3—16
Experimental Spring Stream							
3. Nitrate input	N. A.	N. A.	1.2	367	1.5	.14	6±0.5
4. Control	N. A.	N. A.	1.2	367	1.5	.04	6±0.5
Cascade Streams							
5. Mack	3	6.50	5	830	20	.03	2—15
6. WS 10	1	0.10	1	430	45	N. D.	2—18

Environmental characteristics:

Coast Range: Sedimentary rock; 3600 degree days/yr.; precipitation 250 cm as fall-winter rains; old-growth forests = 130 years.

Experimental Spring Stream: Washed river gravel (4—6 cm DIA.): 2200 degree days/yr.; precipitation 300 cm; cleared of vegetation.

Cascade Range: Volcanic rock; 2700 degree days/yr.; precipitation 220 cm as fall-winter rains and spring snow melt; old-growth forests = 450 years.

full sunlight. Finally at the Cascade site (Oregon, U. S. A.) streams flowed over substrates of volcanic basalt. The surrounding forest, primarily Douglas-fir approximately 450 years old, formed a dense canopy over the streams.

Order of the six streams (STRAHLER 1964) varied from springs to third order streams. Drainage area varied from 0.10 to 6.5 km², and in width from 1—3 m. Site elevation varied from 200—830 m. The lowest stream gradient was 1.4 % and the highest 45 %. Nitrate concentration ranged from nondetectable levels to 1.15 mg/l. Temperatures varied from 2—18 °C annually, except for the experimental spring streams which had a constant temperature of 6 ± 0.5 °C. Within this diversity of geological physical and chemical parameters a decomposition study was conducted using needle litter of Douglas-fir.

Material and methods

Needle litter was collected at abscission, dried at 50 °C and strung on monofilament nylon line to form 5—15 gram packs. Needle litter offered many advantages over faster decomposing leaf litter since events which mark the general history of decomposition are more readily observed within longer sampling intervals. In addition, each pack consisted of hundreds of needles which dampened potential variation between needles in fiber or nutrient content. Leaf packs were preweighed, tied to bricks and placed in the streams so the pack rested against the face of the brick. Leaf packs were collected at approximately tri-weekly intervals and returned to the laboratory where they were gently rinsed. Insects and ancillary debris were removed by hand. Associated invertebrates were dried and weighed on samples from the Coast and Cascade sites. Leaf packs were again dried and weighed to estimate weight loss. The series of weight loss data was fitted to the exponential decay model of PETERSON & CUMMINS (1974):

$$Y_t = Y_0 e^{-kt}$$

Lines were fitted by linear regression and logarithmetic transformation. The slope of the regression, k, served as an index of decomposition. After packs had been reweighed, the litter was ground on a Wiley mill (40 mesh) and analysed for nitrogen using the microkjeldahl technique.

Results

Significant differences in weight loss were observed between the six streams. Decay coefficients (Table 2) indicated a five-fold range in weight loss rates from 0.18 to 1.0 %/day. Both the lowest (WS 10) and highest (Mack Creek) rates of weight loss were observed in Cascade streams. The two experimental spring streams exhibited approximately equal disappearance rates despite the artificially elevated concentration of nitrate (100 ppb) in the N input stream (TRISKA & SEDELL 1976). The two Coast streams also had similar decay rates despite large differences in the nitrate concentration of the water (0.17 vs. 1.15 mg/l).

Since weight loss rates varied widely, N changes were examined to define properties common to the decomposition of litter in streams. In all six streams, N concentration increased with the passage of time following losses due to leaching (Fig. 2 a, b). Initial N concentration (0.53 %) decreased by almost half within two days in the N input and control stream, the only streams where short term leaching data were available. Following leaching, a dramatic increase in N concentration was observed on litter from five of the six streams (Fig. 2 a). Within 40 days, needle litter from these five streams exhibited N concentrations higher than that observed in the initial litter. N concentrations peaked at a level almost twice as high as litter prior to incubation except for WS 10, the only true first

Table 2. Weight loss data

1. Flynn	
2. Needle Br.	
3. Nitrate Input	
4. Control	
5. Mack	
6. WS 10	

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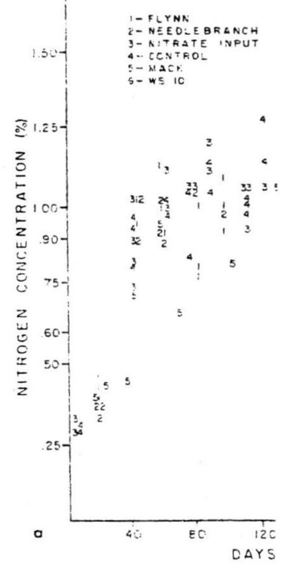

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Table 2. Weight loss data (1973—74) for needle litter of Douglas-fir from six streams.

	Decay coefficient (k)	Regression equation	r
1. Flynn	.0083	LN(Y) = 4.2552—0.0083X	.75
2. Needle Br.	.0089	LN(Y) = 4.3318—0.0089X	.66
3. Nitrate Input	.0041	LN(Y) = 4.503 —0.0042X	.91
4. Control	.0045	LN(Y) = 4.4735—0.0046X	.82
5. Mack	.0100	LN(Y) = 4.8102—0.0100X	.75
6. WS 10	.0018	LN(Y) = 4.3456—0.0019X	.82

order stream. Qualitatively, similar results were observed in all six streams in terms of N concentration, namely, large leaching losses followed by a larger increase in N concentration. Quantitatively, however, increased N concentration above zero time levels in WS 10 were only observed after 180—200 days in place, compared to 40—60 days for the other five streams.

Loss of N due to leaching also dramatically altered carbon : nitrogen ratios since N losses were greater than carbon losses from leaching, and because C concentrations varied little as decomposition continued. Prior to incubation, C/N ratio of needle litter was 93, but rose to as high as 250 in WS 10. Within 60 days C/N ratios fell, again to a range between 40—60 and remained within this range as decomposition proceeded in the first 5 streams (Fig. 3 a). In WS 10 (Fig. 3 b), decomposing needle litter never exhibited a C/N ratio below 80, while the minimum C/N ratio was between 45 and 50 for the other five streams. The

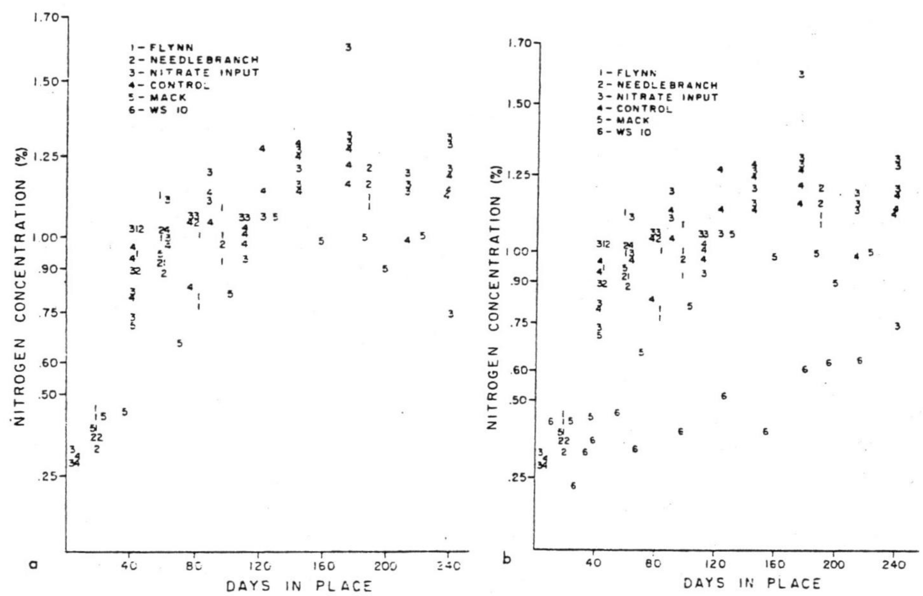

Fig. 2. Change in N concentration as decomposition proceeds on litter of Douglas-fir. (a) Pattern of N change in streams 1—5. (b) Pattern of N change with the addition of data from stream 6 (WS 10). Initial N concentration was 0.53 %.

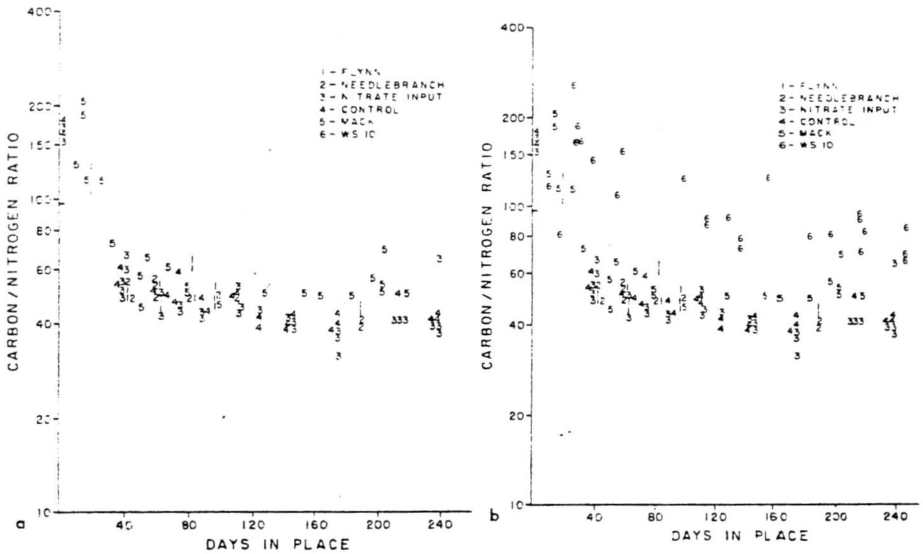

Fig. 3. Decrease in C/N ratio as decomposition proceeds on litter of Douglas-fir. (a) Pattern of C/N ratio decrease in streams 1—5. (b) Pattern of C/N ratio decrease with addition of data from stream 6 (WS 10). Initial C/N ratio was 93.

minimum C/N ratio was also attained at a far later date in WS 10 than in the other five streams.

Since both N concentration and C/N ratio provide only relative indices, absolute N content (capital) was also calculated based on a theoretical starting weight of 10 grams (Fig. 4). A ten gram leaf pack had a N capital of about 53 mg N prior to incubation. Initial leaching lowered the N capital to approximately 20 mg during the first few days. Thus, while total weight loss due to leaching amounted to 20 %, loss of N capital exceeded 50 %. From this base of approximately 20 mg, N capital increased rapidly as decomposition continued. N capital was greatest between 40—60 % weight loss for the first five streams and between 30—50 % in WS 10. At some stage of decomposition an absolute increase in N capital above zero time levels was observed in all six streams. The increase in N capital was least at WS 10. After N capital peaked it declined steadily as carbon was mineralized.

If N is a major factor of conditioning, the food quality should be optimal near the time of lowest C/N ratio and some invertebrate response might be expected. To observe this potential effect, the C/N ratio of litter was plotted against invertebrate biomass associated with leaf packs (Fig. 5). Watershed 10, which had the least gain in nitrogen concentration or capital, and the highest C/N ratio, also had the least invertebrate biomass associated with needle packs. Maximum invertebrate biomass (11.2 mg/g leaf pack) was found at the time of lowest C/N ratio (80). In Mack Creek, the lowest (C/N ratio was approximately 50 and occurred about 3 weeks before maximum invertebrate biomass was observed on the litter. Once discovered by

Fig. 4. Absolute N cap
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Fig. 5. Invertebrate bio
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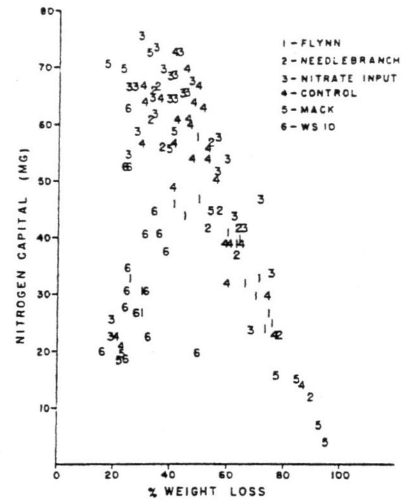

Fig. 4. Absolute N capital (mg) in relation to weight loss for leaf packs of Douglas-fir undergoing decomposition in six different streams.

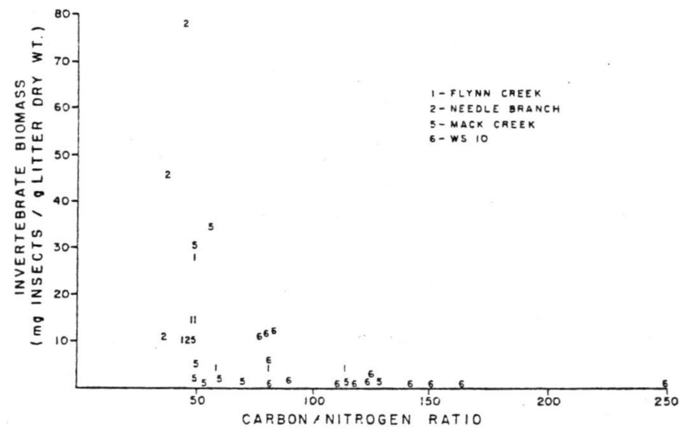

Fig. 5. Invertebrate biomass in relation to C/N ratio on litter of Douglas-fir from four different streams.

the invertebrate community a maximum of 35 mg invertebrate biomass occurred/gram of needle pack. This compares favorably with Flynn Creek where a maximum of 28 mg invertebrate biomass/g needle pack was collected at a C/N ratio of 49. Highest invertebrate biomass was associated with litter packs at Needle Branch Creek which also reached the lowest C/N ratio (42). In that stream, highest invertebrate biomass was 76 mg invertebrates/g of needle pack, on a sample with a C/N ratio of 50.

Discussion

One major drawback of using decay coefficients as decomposition parmeters is the effect of abiotic processes as leaching or physical abrasion or biotic parmeters such as insect consumption which might result in significant weight loss.

In addition, other factors such as temperature regime and sediment size (siltation) may also effect litter disappearance rates. Thus, for streams of approximate size, geology, and gradient such as in the Coast sites (Flynn and Needle Branch Creek) or the Experimental Spring site (control and N input), decay coefficients were similar despite differences in the dissolved nitrate concentration of the water. In the Cascades, where physical differences in stream width, gradient, and elevation were large, differences in decay coefficient were likewise large. Thus, within similar watersheds of a region, decay coefficients may be a valid index of decomposition. However, across regions, gradient and size of drainage established decay coefficients may not apply even for identical litter.

While decay coefficients may not apply over a wide variety of physical habitats, certain decomposition processes were found in common. Large amounts of N were leached from needle litter, yet an absolute gain in N capital was eventually observed in all six streams. Similar gains in absolute N content have previously been reported in the literature for lotic ecosystems (MATHEWS & KOWALCZEWSKI 1969; IVERSEN 1973; HODKINSON 1975; TRISKA & SEDELL 1976). This gain in N capital demonstrates the capacity of the microbial flora to colonize leached litter. This colonization in turn determines the speed and extent to which litter is conditioned for consumption by invertebrate consumers. Although this gain is mediated by microbial colonization, IVERSEN (1973) estimated only 1—3 % of total litter N can be accounted for by microbial biomass. He postulated the remainder came from microbial secretion. This idea is also supported by data of MORTON & BROADBENT (1955) who observed secretion of short chain refractory polypeptides in culture by *Scopulariopsis brevicaulis* from a variety of N sources. Therefore, the source of N for microbial secretion may be tissue N, dissolved organic N from the water, and even inorganic N from the water or sediments (NICHOLS & KEENEY 1973). Once captured by the microbial community, subsequent secretions may be complexed to refractory fibrous tissue of litter debris (SUBERKROPP & KLUG 1976; SUBERKROPP et al. 1976; TRISKA unpubl. data). Although the mechanism is complex and not well established, the gain in N capital does demonstrate how leaf litter and, perhaps, detritus in general may serve as a N sink for the stream ecosystem. The magnitude of this sink, however, is ultimately dependent on the capacity of the channel itself to capture and store organic material.

Summary and conclusions

Decay coefficient varied over a five-fold range in the six streams studied. Despite this large difference in disappearance rate a qualitatively similar pattern of N uptake and release was observed in the six streams studied. The pattern was characterized by a large physical loss due to leaching followed by a N gain presumably related to microbial colonization. Quantitatively, this pattern was similar for five of the six streams. The exception was WS 10, a first order forested stream. All streams exhibited an absolute N gain sometime during decomposition. This N gain was presumably mediated by microbial colonization. Whatever the source, the absolute gain in N capital results in a N sink for the ecosystem and a source to litter consuming invertebrates. In addition, an invertebrate response was observed in relation to the C/N ratio of decomposing needle litter. Highest invertebrate biomass was found associated with litter packs when C/N ratio was lowest. Needle Branch Creek, where needle litter had the lowest C/N

ratio, had the highest associated invertebrate biomass. Thus, the capacity of litter microflora to mediate N uptake and release may directly influence the production of litter consuming invertebrates in lotic ecosystems.

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