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The processing of conifer and hardwood leaves in two coniferous forest streams: II. Biochemical and nutrient changes[1]

F. J. Triska, J. R. Sedell and B. Buckley

With 6 figures and 2 tables in the text

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Introduction

Since TEAL (1957), numerous workers have confirmed the role of allochthonous debris as a major energy input to forest stream communities (NELSON & SCOTT 1962; HYNES 1963; EGGLISHAW 1964; MINSHALL 1967; FISHER 1971; FISHER & LIKENS 1972). Following the general acceptance of the heterotrophic nature of small woodland streams, recent investigations have centered on processing of such debris and its relationship to the biotic community (KAUSHIK & HYNES 1968, 1971; HYNES & KAUSHIK 1969; TRISKA 1970; CUMMINS et al. 1972, 1973; IVERSEN 1973; SEDELL et al. 1974; BARLOCHER & KENDRICK 1973 a, b; PETERSON & CUMMINS 1974). PETERSON & CUMMINS (1974) have summarized much processing data to date and speculated on the possibility of error in extrapolating processing data from cold, fast flowing woodland streams, to warm, slow moving, open river systems. SEDELL et al. (1975) in a previous paper compared weight loss of leaf detritus in two streams of different size in the Oregon Cascades. Their data indicated that total processing of four leaf species occurred faster in Mack Creek, the larger stream, compared to Watershed 10, the smaller stream. The relationship of mean insect weight to microbial conditioning was also discussed. In this paper, litter conditioning in two different sized streams will be considered in terms of certain chemical and biological parameters, more specifically: (1) nutrient concentration, (2) decomposition and carbon quality, and (3) microbial respiration.

Materials and methods

Nutrient analysis

Leaf material was collected at abscission, formed into leaf packs, dried, weighed, and incubated in Mack Creek and Watershed 10, two different sized streams in the same drainage. A detailed explanation of methodology and site description may be found in SEDELL et al. (1975). Following collection, leaf material was dried at 50 °C and ground to 40 mesh on a Wiley mill. Nutrient analyses were conducted as follows:

1) Nitrogen concentration is expressed as total nitrogen and was measured by the KJELDAHL method.
2) Phosphorus analysis is in the form of total phosphorus and was measured on a Jarrell-Ash Model 750 spark emission spectrophotometer.
3) Carbon content was determined on a Burrell Carbotrane carbon analyser.
4) Carbon quality was assessed by the acid detergent method of VAN SOEST (1963).

Microbial respiration

Microbical respiration of decomposing leaf detritus was measured on all four species of leaves outlined in the previous study (SEDELL et al. 1975): alder, *Alnus rubra;* vine maple, *Acer circinatum;* bigleaf maple, *Acer macrophyllum;* and conifer, *Pseudotsuga menziesii.* Measurements were undertaken on leaf litter collected in the autumn of 1973, dried at 50 °C, placed into litterbags of 1 mm mesh, and incubated in Mack Creek and Watershed 10 during November, 1973. Three bags each of all four species were collected after 15, 50, 78, 121, 143, 163, and 202 days in place. Leaf material was returned to the laboratory where insect larvae were removed by hand. Leaf detritus was cut into disks and placed in a 14 station Gilson respirometer. Respiration was measured at ambient stream temperature.

Results and discussion

Nutrient concentration

Studies to date of water quality (FRIEDRICKSON 1972) and leaf tissue decomposition indicate if any nutrient is biologically limiting it would be nitrogen, phosphorus, or carbon. Nitrogen, an essential nutrient for both microbial and invertebrate protein, is present in low concentration (< 1 %) in all leaf substrates except alder (Fig. 1). As a result, two interesting phenomena may be observed as leaf detritus decomposes through time.

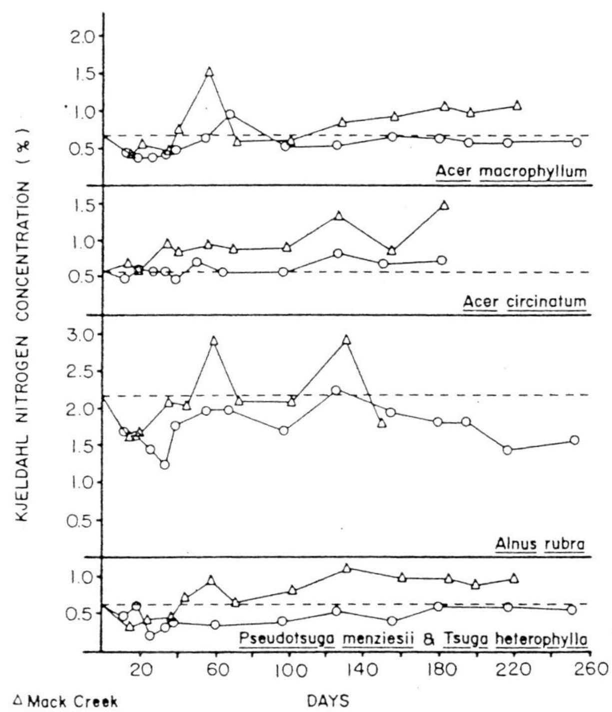

Fig. 1. Nitrogen concentration of decomposing leaf litter in Mack Creek, a large stream, and Watershed 10, a small stream, in the H. J. Andrews Experimental Forest.

First, as decomposition proceeds, nitrogen concentration increases following initial leaching. The observed increase is probably the result of microbial immobilization of nitrogen as carbon is mineralized to CO_2. Nitrogen immobilization has commonly been observed in agricultural research (RICHARDS & NORMAN 1931; WAKSMAN & GERRETSEN 1931; BREMNER 1955; ALEXANDER 1961). Similar increases in nitrogen concentration or immobilization have also been observed for many species of leaf litter and wood in soil studies (MELIN 1930; COLDWELL & DELONG 1950; SAITO 1957; IVARSON & SOWDEN 1959; BOCOCK et al. 1960; GILBERT & BOCOCK 1960; ALLISON & KLEIN 1961; BOCOCK 1963, 1964; SWIFT 1973). In fact, GILBERT & BOCOCK (1960) and BOCOCK (1964) have reported absolute increases in nitrogen content as litter decomposes. In streams, previous studies by KAUSHIK & HYNES (1968, 1971) and HYNES & KAUSHIK (1969) in Canada, indicate an increase in protein content as litter decomposition proceeds. MATHEWS & KOWALCZEWSKI (1969) reported increases in nitrogen concentration throughout decomposition, and absolute nitrogen increases during initial stages of decomposition of willow and sycamore litter in coarse

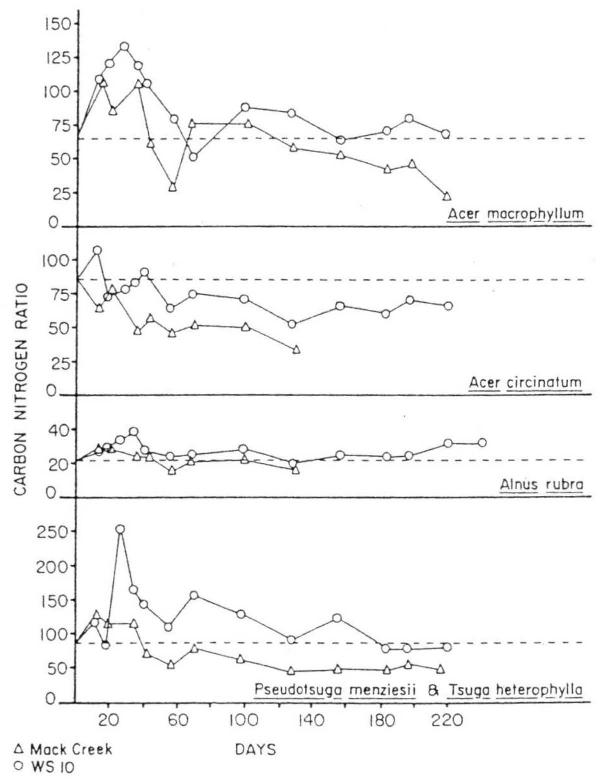

Fig. 2. Carbon-nitrogen ratio of decomposing leaf litter in Mack Creek and Watershed 10, a large and small stream in the H. J. Andrews Experimental Forest.

mesh bags. Iversen (1973) has also found both absolute increase and increase in concentration of nitrogen in beech leaves incubated in a Danish stream.

Secondly, the nitrogen concentration is virtually always higher in Mack Creek than in Watershed 10, the smaller stream. As a result, litter material from Mack Creek provides a better nitrogen source than initial unconditioned litter (dashed line). In Watershed 10, however, litter of bigleaf maple, alder, and Douglas-fir represents a poorer nitrogen source than initial unconditioned litter, while vine maple is only marginally better.

Some of these data may be better represented by conversion into carbon-nitrogen (C/N) ratios (Fig. 2). C/N ratios have commonly been used as an index of decomposition, although rates of decay may be dependent on many other factors (e.g., activity of bacteria, fungi, or actinomycetes as major decomposers, anaerobic or aerobic decomposition, and carbon quality). As a general rule, however, a C/N ratio of approximately 10:1 would be considered optimal for decomposition of organic debris (Alexander 1961). As the C/N ratios increase nitrogen gradually becomes limiting, while at lower C/N ratios carbon can become limiting to decomposition and nitrogen is mineralized. In this

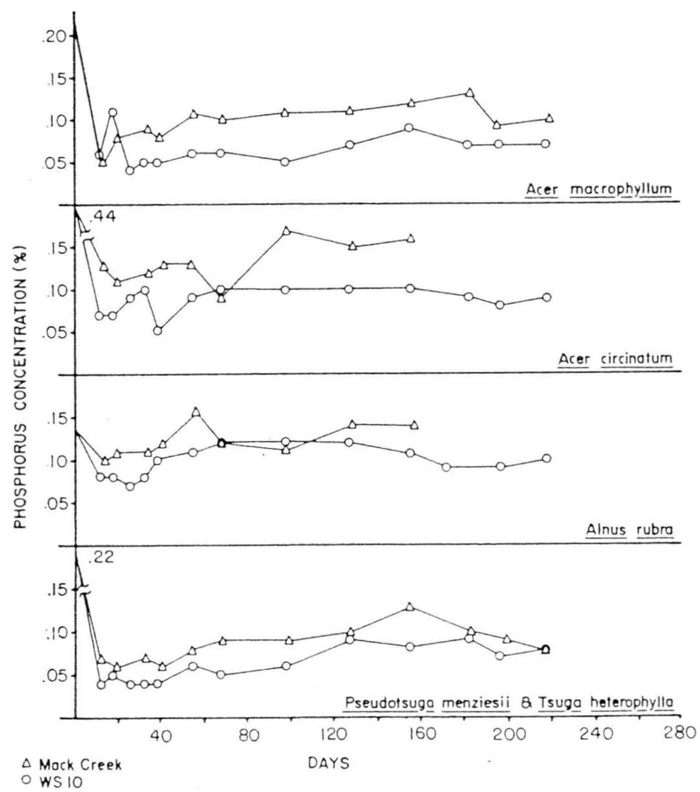

Fig. 3. Change in phosphorus concentration as decomposition proceeds in Mack Creek and Watershed 10 of the H. J. Andrews Experimental Forest.

study, leaf litter at no time during decomposition approached a C/N ratio of 10 : 1. Alder with its higher initial N content came closest at approximately 20 : 1, while the other three litter species maintained a C/N ratio of 50 : 1 to 100 : 1. Although C/N ratios tended to decrease slightly with time, which is consistent with the soil studies of HAYES (1965), nitrogen concentration was theoretically limiting to decomposition in both streams for the fall decomposition period. As a result, decomposing litter from Mack Creek with its lower C/N ratio both decomposed faster and was a superior N source for aquatic invertebrates that consume litter detritus as a food source.

Phosphorus, an essential nutrient in cellular energy transfer, is also present in low concentration in decomposing leaf detritus (Fig. 3). The major loss of phosphorus occurred as leaching during the first few days. Following initial leaching, P concentration stabilized and increased slightly as decomposition proceeded. As with N, concentrations of phosphorus were higher in Mack Creek than Watershed 10. ALEXANDER (1961) has indicated that carbon/phosphorus (C/P) ratios greater than 300 are favorable to P immobilization. All of the leaf types decomposed in Mack Creek and Watershed 10 had C/P ratios greater

Tab. 1. Carbon-phosphorus ratios of decaying laef detritus in two Cascade streams.

	Mack Creek	Watershed 10
Acer circinatum	361	395
Alnus rubra	420	492
Acer macrophyllum	487	749
Pseudotsuga menziesii	613	900

than 300 (Tab. 1). Theoretically, both N and P were, therefore, limiting to carbon mineralization. Higher P concentrations in Mack Creek provided further indirect evidence of faster detrital processing in the larger stream. The ability of the microbial community to more rapidly colonize leaf detritus in the larger stream affected not only the rate of decomposition, but may have also influenced the role of decomposing litter as a nutrient source for detritus feeding invertebrates.

Carbon quality

Carbon, at least in quantity of particulate organic matter, does not appear limiting to either decomposition or insect growth, since a significant quantity of carbonaceous organic debris is present on a year round basis in both streams. Most of the carbon present, however, may not be available in readily utilizable forms for either invertebrates or microbes, since it consists of highly lignified residues such as wood and bark, and fine particulate organic matter of high lignin content. In terms of leaf detritus, carbon content remains remarkably constant (mean value ± 3 %) throughout the decomposition period. These results are consistent with those of ANDERSON (1973) in a study of litter breakdown on forest soils.

Although carbon content is constant, carbon quality may vary significantly as decomposition proceeds. PEEVY & NORMAN (1948), PINCK, ALLISON & SHERMAN (1950), and ALEXANDER (1961) have indicated from terrestrial studies that changes in lignin composition may provide a good relative prediction of litter decomposition rates. CROMACK (1973), working in a wet hardwood forest and white pine plantation, found the rate of change of lignin content the best single criterion of litter decay rates. In terms of initial carbon quality, this was

Tab. 2. Determination of acid detergent cell wall (ADCW), cellulose (C), lignin (L) and ash (A) prior to decomposition.

	% ADCW	% L	% C	% A
Alnus rubra	80.6	9.5	9.0	1.0
Acer circinatum	78.9	8.5	14.7	2.9
Acer macrophyllum	64.8	17.3	16.3	1.6
Pseudotsuga menziesii	59.4	24.2	14.5	1.9

also true in our studies (Tab. 2). The acid detergent cell wall (ADCW) fraction consists of the most labile constituents, including soluble carbohydrates, soluble protein, organic acids, nonprotein nitrogen, hemicellulose, and additional soluble organic material. *Alnus rubra* and *Acer circinatum*, the litter species that decompose most rapidly, are those characterized by the highest ADCW component and lowest concentration of lignin. *Acer macrophyllun* and *Pseudotsuga menziesii*, characterized by higher lignin content and smaller ADCW fraction, are more slowly decomposed. As leaf detritus undergoes decomposition, a gradual shift to more refractory residues is evidenced.

Absolute decline in acid detergent cell wall (ADCW) and lignin as detritus is decomposed can be compared assuming an initial leaf pack weight of 10 grams. For both vine maple and alder, ADCW constitutes the major carbon fraction even after the initial leaching period (Fig. 4). Leaf pack weight loss occurs primarily by decomposition of ADCW, while lignin is more slowly decomposed. Similar results using different methodology were reported by MINDERMAN (1968) in a forest study. Most important, the rate of ADCW loss was faster in Mack Creek than in Watershed 10. More rapid decline of both ADCW and lignin in the larger stream was observed for both leaf species. For the slower decomposing leaf detritus, bigleaf maple and Douglas-fir, lignin concentration is higher in relation to ADCW, particularly after initial leaching (Fig. 5). Yet, as in the faster decomposing species, loss rates of both fractions were higher in Mack Creek than Watershed 10. Such data provide additional indirect evidence for faster processing rates in the larger stream.

Microbial respiration

Although evidence for faster processing in Mack Creek, on the basis of mineral immobilization and carbon quality has been consistent, a more direct method of determining microbial processing rates in the two streams was desired. As a

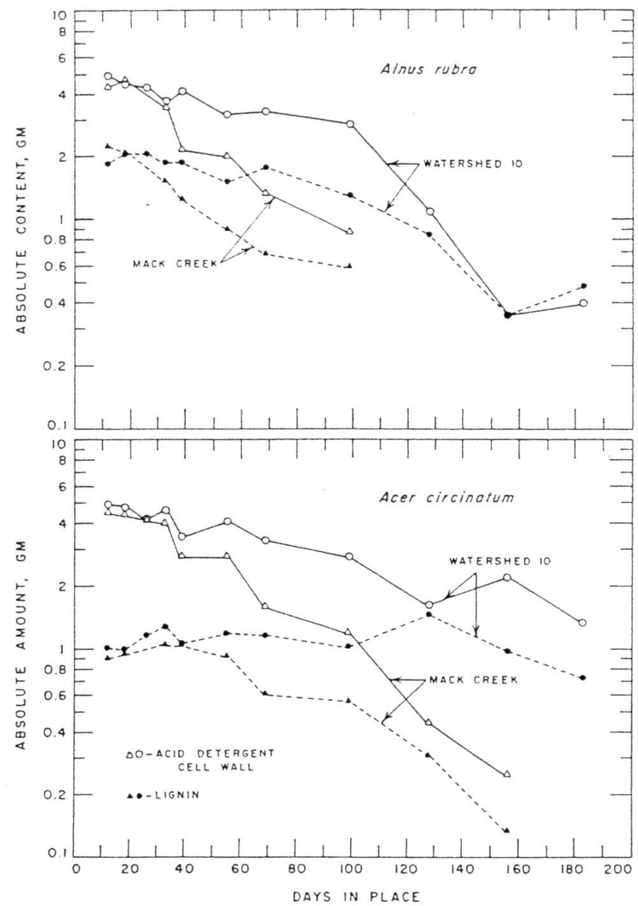

Fig. 4. Absolute decline of acid detergent cell wall (ADCW) and lignin, for a standard 10 gram leaf pack of alder, *Alnus rubra*, or vine maple, *Acer circinatum*, in two streams of different size.

result, measurements of microbial respiration were undertaken the following year (Fig. 6). The general pattern for respiration was a bimodal curve influenced by temperature and carbon quality. During the first phase temperature was falling but litter quality was high, and respiration rates rose. As litter quality fell and temperature remained low, respiration also declined. As water temperature increased in the spring, respiration rates also increased. Overall, microbial processing occurred faster in Mack Creek, the larger stream, on the basis of oxygen consumption.

Summary and conclusions

Leaf material, as it entered the stream, underwent leaching and microbial colonization. This process, called conditioning, rendered allochthonous debris palatable to stream invertebrates. The conditioning process also resulted in increased concentration

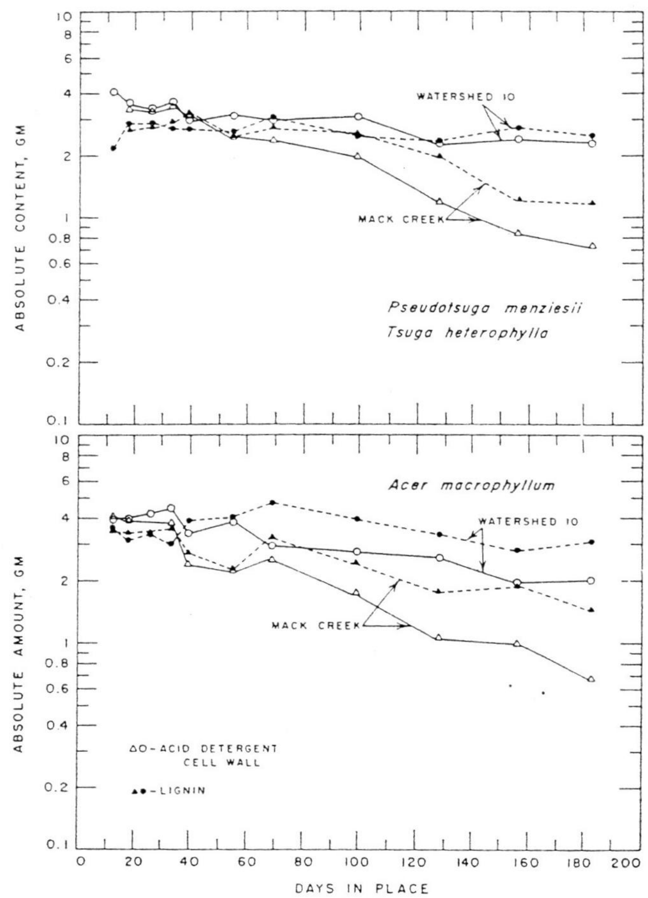

Fig. 5. Absolute decline of acid detergent cell wall (ADCW) and lignin, for a standard 10 gram leaf pack of conifer, *Pseudotsuga menziesii* and *Tsuga heterophylla*, or bigleaf maple *Acer macrophyllum*, in two streams of different size.

of certain essential nutrients such as N and P. Concentration increases were highest in the larger stream with the more active microbial flora. The cost of conditioning was some qualitative deterioration of carbon quality for detritus-consuming invertebrates. Such conclusions are consistent with the observations of Kaushik & Hynes (1968), Triska (1970), Makay (1972), and Barlocher & Kendrick (1973 a, b), who found microbial colonization, particularly by fungi, and important intermediate step in the consumption of detritus by invertebrates. Fenchel (1970), in studies on the detritus feeding amphipod *Parhyalella whelpleyi* maintained that these organisms digested only the microorganisms on detritus while the plant residue remained undigested.

Faster leaf processing was observed in Mack Creek, the larger stream, when compared to Watershed 10 by all measured parameters, weight loss, nutrient immobilization, carbon quality, and microbioal respiration. The mechanism for faster microbial processing remains obscure. Such data indicate the need for a more thorough examination of the physical, chemical, and biological properties of the soil-water interface. Sedell et al. (1975) considered the role of such physical factors as substrate mobility and water

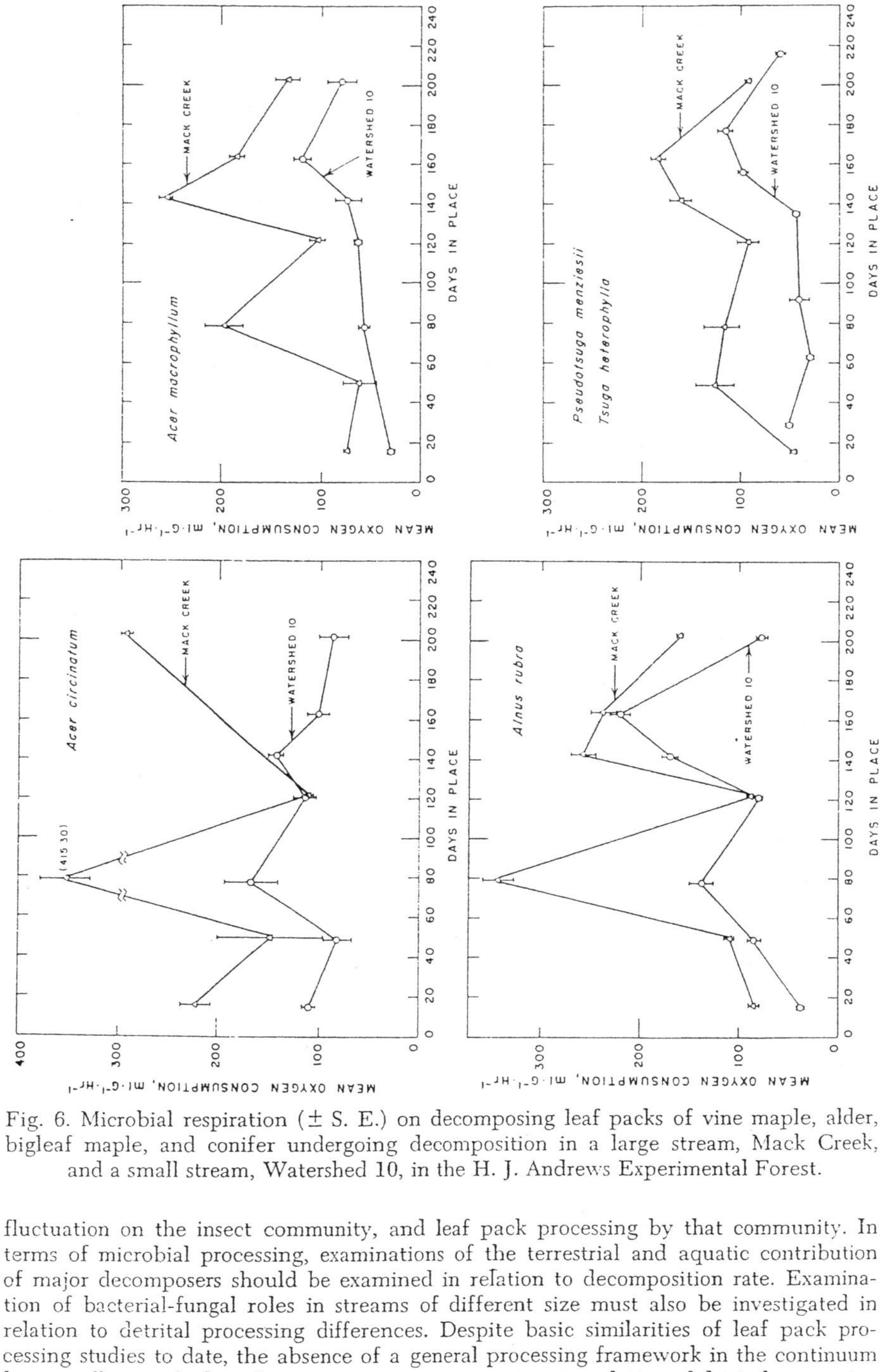

Fig. 6. Microbial respiration (± S. E.) on decomposing leaf packs of vine maple, alder, bigleaf maple, and conifer undergoing decomposition in a large stream, Mack Creek, and a small stream, Watershed 10, in the H. J. Andrews Experimental Forest.

fluctuation on the insect community, and leaf pack processing by that community. In terms of microbial processing, examinations of the terrestrial and aquatic contribution of major decomposers should be examined in relation to decomposition rate. Examination of bacterial-fungal roles in streams of different size must also be investigated in relation to detrital processing differences. Despite basic similarities of leaf pack processing studies to date, the absence of a general processing framework in the continuum from small watersheds to large river systems, prevents extrapolation of detrital processing data at this time.

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Discussion

MEEYR: What are the concentrations of dissolved nitrogen and phosphorus in the two streams?

TRISKA: Dissolved nitrate and phosphate concentrations are presented in Tab. 1 of the previous paper (SEDELL et al. 1975). Dissolved organic nitrogen concentrations for WS-10 is approximately 0.03 mg/l. In Mack Creek dissolved nitrogen levels are slightly higher. Studies conducted by us on replicate experimental streams did not reveal decomposition differences when nitrate concentration were raised almost five times above base level to .130 mg/l.

THAYER: Do you attribute the differences between Mack Creek and Watershed 10 to "largeness" or "smallness" of stream size or to differences in stream slope (45 vs 25 ⁰/₀) or sediment?

TRISKA: Basic differences in decomposition rate are related to activity of the microbial community. One possibility is differences in the microbial flora. For example, the presence of a large component of terrestrial fungi, operating in the aquatic habitat of a small stream may result in slower decomposition rates, than processing by better adapted aquatic fungi. Physical factors such as silt load could effect colonization in this way. Slope differences do not appear to be important at this time.