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LEAF PROCESSING IN A
WOODLAND TROUT STREAM¹

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Introduction

As has been suggested by Hynes (1963) the dominant energy source of at least the rithron portion (Illies, 1961) of a stream is allochthonous input. The physical structure of stream benthos, flow dynamics, current velocity and shading although providing a suitable matrix for the concealment and attachment of many invertebrates does not allow the establishment of large primary production bases. As evidence of the lack of dependence of the stream community on primary production, Hynes (1961) reports that more than 2/3 of the species in a Welsh mountain stream completed their life cycle in the winter when the primary production would be expected to be of the least importance. Ross (1963) has shown that the Trichoptera have their dispersal associated with changes in the eastern deciduous biome. One of the reasons for this is the heavy autumnal fall of deciduous leaves into the stream every year.

This is not to say that primary production does not occur in streams. Odum (1956) has shown that substantial production does occur and especially in those streams recovering from organic pollution. The potamon stream-river may not compare energetically due to their lack of complete shade cover, generally higher temperature and lower current velocities. It is also doubtful that the large river system reflects true stream conditions due to the series of flood control impoundments which effectively produce a series of lentic environments (Starrett, 1972).

The quantitative measurement of this allochthonous input has been the focus of several investigations. These measurements have a high degree of similarity. For example Vannote (1970) estimates 3.00 gm

dry large particle detritus/ M^2 /day; Murless (personal communication, U. of Georgia) 420 gm/ M^2 /day; and Fisher (1971) 1.70 gm/ M^2 /day.

Mathews and Kowalczewski (1969) and Kowalczewski and Mathews (1970) estimate for the River Thames that .0489 gm/ M^2 /day is the allochthonous input. If only those portions of the river that are covered by riparian vegetation are used in the calculation the estimate becomes 4.35 g/M stream bank/day which compares to the small stream measurements.

Macfadyen (1971) points out that normal autotrophic terrestrial and freshwater communities which derive their energy from primary production have a net dry matter production of 1 kg/ M^2 /yr. This value also seems to apply to the quantity of allochthonous input to both soil and stream communities (Ovington, 1963; Ovington and Heitkamp, 1960).

Other investigations by Minshall (1967), Nelson and Scott (1962), Egglisshaw (1964), Triska (1970), and Fisher and Likens (1972) have investigated various aspects of the dependence of stream structure and function on the import of organic matter from the terrestrial environment. Other work concerns the processing dynamics of the allochthonous input in aquatic systems (Triska, 1971; Kormondy, 1968; Kowalczewski and Mathews, 1970; Mathews and Kowalczewski, 1969; Thomas, 1969, and Wallace et al., 1970). However, the topic of litter decay and the parameters which affect its processing dynamics have been extensively studied for many years by terrestrial soil ecologists.

Pioneer investigations by Waksman and Tenny (1927, 1928) and Melin (1930) demonstrated that the rate of decomposition depended on the type of organism, chemical nature of the material and the availability of nitrogen. Melin (1930) conceptualized this processing phenomenon into external and internal factors relating the effect of the environment

and chemical composition to the processing rate. More recent investigations have been concerned with extensions and modifications of these original concerns. Studies by Bocock and Gilbert (1957, 1960), Broadfoot and Pierre (1939), Coldwell and DeLong (1950), Crossley and Hogland (1962), and Edwards and Heath (1963) have been concerned with the disappearance of leaf litter under different experimental conditions. Witkamp (1963, 1966) and Hering (1967) have been concerned with the role of fungi and bacteria in the processing of leaf litter. The effect of temperature has been investigated by Ando (1970) and Nykvist (1959, 1961, 1962a, 1962b) and found to be of significant value to leaching and the metabolism of the microbial community.

Several techniques have been used in the terrestrial studies for holding the leaf material to be studied. Mesh bags of various sizes and weaves have been used to hold the material (Bocock and Gilbert, 1957; Shanks and Olson, 1961; Olson and Crossley, 1963; and Crossley and Hogland, 1962). Witkamp and Olson (1963) have investigated the difference in processing rates between litter in mesh bags and litter on strings. Even though they admit that strings may have given an overestimate due to the fact that large particles would not be accounted for and not have been totally decomposed, they concluded that although the mesh bags gave results with a lower variance, leaves on strings did not restrict invertebrates and were therefore a more accurate representation. It is clear from these studies that if complete degradation is to be measured, mesh bags will not allow the true effect of large invertebrates. It is for this reason that mesh bags were not used in the present study. Although other stream investigations have used bags (Mathews and Kowalczewski, 1969), the present

study has used 10 gm leaf packs tied to 2 lb. bricks to simulate the actual conditions. The loss of large fragments from the pack, although not fully decomposed represents a different set of measurements with a different set of processing rates and theoretical assumptions. In the present study the effect of large invertebrates has been unrestricted and the emphasis has been on whole leaf degradation.

Materials and methods, site description

Augusta Creek (TRS T.1S.-R.9W.) a hardwater, Brown trout stream rises in Barry County and follows a southerly course through Kalamazoo County to its confluence with the Kalamazoo River at Augusta. The course of the stream is one of numerous bends, riffles and pools, shaded by dense riparian shrubs or a canopy of mixed deciduous trees.

With the initiation of the study of leaf processing in Augusta Creek, an attempt was made to describe that portion of the water shed which made direct inputs of organic matter to the streams. The basin of Augusta Creek is composed of moist to wet muck or shallow peat soils with marshes, small depressions with slow drainage, and some agricultural development in drier sites.

Latitudinally, this soil type supports a climax growth of Black Ash, American Elm, and Red Maple. Recently Grimm (1961) described the Black Ash, American Elm, Red Maple forest association (Type 19) specific to Pennsylvania. The authors have modified Grimm's "Type 19" to apply to local conditions along Augusta Creek in southwestern Michigan (Table 1).

Forest types have long been described classically as climax or seral communities. Because man has caused great changes in forest

patterns throughout the world, because variations exist in local soils and climatic conditions, and because of possible intergrading between communities, it was required to define the forest association serving as the principal detrital input source to Augusta Creek.

Leaf pack construction

All leaves used in the study were collected from the tree prior to abscission and stored in containers until needed. Before each experiment, leaves were oven dried at 50^o C for 24 hours and weighed to 0.1 gm in 10.0 gm quantities. The leaves were then moistened and tied with nylon monofilament to a 2 lb. brick. At the conclusion of an experiment the leaves were thoroughly washed to remove any sediment and redried at 50^o C and reweighed. Several preliminary experiments with various methods of leaf handling showed that this method minimized breakage during handling and gave the most reliable results. Analysis of fall accumulations of natural leaf packs showed that 10 gm was an accurate representation of natural litter accumulations. The size is critical for insuring near natural investation of large detritivores. A smaller size pack tends to restrict the degradation process to fine particle feeders and microbial action. However, the lower size limit of leaf pack is not known at this time.

Preliminary investigations

A preliminary investigation with 7 species of riparian leaves was carried out in the Summer of 1970 at three sites in the Augusta Cr. drainage. Three leaf packs of each species composed of two leaves were incubated for 36 days, one pack per brick. The results are summarized

in Table 2. The results were calculated on a relative scale since the site and species effect was the primary concern. The results drawn graphically in Fig. 1 showed dramatic differences in site selection and species used. From this initial experiment the effect of the two sites, C Ave. and B Ave. were chosen as the major experimental sites for further study.

A second preliminary study was conducted in the Summer of 1971. In this experiment leaf packs of Carya glabra, Pignut Hickory, were constructed of 10 leaves, weighed and incubated in the stream for 30 days. Leaves were removed at 2, 4, 7, 9, 11, 14, 17, 21, and 30 days and reweighed. The results showed that there is constant fractional loss over time and at a rate that could be best described as an exponential loss model. The results of this preliminary experiment may be found in Table 7.

Exponential loss calculations

The use of exponential loss models to the disappearance of leaf litter has been proposed and used by several investigators (Jenny et al., 1949; Greenland and Nye, 1959; Olson, 1963 and Ando, 1970) and used in the aquatic system by Fisher (1971). The model assumes that for any amount of material X at any time t there is a constant fractional loss such that the rate of change of the total amount of X changes at a constant rate or:

$$\frac{dX}{dt} = -k X \quad (1)$$

where -k is the constant or rate coefficient, and X is the remaining amount. This particular model assumes that the income to the system during the interval t has been 0, since for the experiments conducted

in this study the concern is for the weight loss over time at a known initial amount it can be assumed that the income is zero. By integration (1) becomes, for the fraction remaining after time t from an initial amount X_0 :

$$\log_e \left(\frac{X}{X_0} \right) = -k \cdot t \quad (2)$$

The decay coefficient $-k$ can be estimated by statistical methods such as fitting of the data to a least squares fit to an exponential function. In the present study this is the method used. The degree of fit was estimated by the linear correlation coefficient of the $\log_e$ transformed dependent variable. The standard error of the decay coefficient was also estimated and a t -test for significance from zero carried out. Results in Tables 3-7 show the decay coefficients and supportive statistics.

If only two points are known, the initial and final weight of leaf material, then the conformance to an exponential decay model must be assumed. The decay coefficient can still be calculated from (2) where X_0 is the initial amount and X is the final amount. For the sake of comparison with published data values of final and initial weights were used in this way and are reported in Table 7.

Leaching experiments

As has been discussed by Nykvist (1961) the initial step in the processing of leaf litter is a massive and quick leaching of organic compounds out of the leaf and into the system. To define the rates of leaching several short-term experiments with various conditions of leaching were carried out. Leaf packs of 10 gm were placed in the stream at one of the sites and picked up after 6, 12, 18, and 24 hours.

Additional experiments carried the time out to 2, 3, 4, 5, and 6 days. The leaf packs were handled in the same manner as the regular leaf packs as explained above. Other experiments were conducted in the laboratory in 1 liter beakers held at different temperatures.

Experimental stream experiments

Two 11 m experimental streams (Cummins, 1971) were used to test the effect of large invertebrate detritivores on the decay of leaf material. Ten gm leaf packs of Quercus alba, White Oak, and Carya glabra were placed in each experimental channel, 500 gm of oak and 500 gm of hickory in each stream. After 6 days for microbial conditioning, stream 1 received 1065 large invertebrate detritivores. These invertebrates are large particle feeders and are the main functional processing group in the natural stream. They consisted of 594 Tipula sp., 419 Pycnopsyche spp. and 52 Pteronarcys sp. Stream 2 did not receive the large particle feeders. After 92 days the leaf packs were removed and reweighed.

Leaf pack experiments

The main experiment consisted of a long term study carried out in the Fall and Winter of 1970 at two sites on Augusta Cr. Leaf packs of selected species were prepared as above and placed in a random pattern at the site. During fall and winter, three packs of each species were removed at near monthly intervals and reweighed. Seven species were followed from September to December and 15 species from December to April.

Results and Discussion

In an analysis of the decomposition of leaf material in a stream, the first priority is to compartmentalize the various components of the degradation into a workable and easily conceptualized model. The term model is used to describe any set of connecting observations that can be linked into a nice story. The first procedure is to look for dramatic differences that can be used to separate the entire process into subparts. The first dramatic difference is the initial process of leaching and the slower long term degradation. This long-term phenomenon can then be partitioned into microbial and invertebrate processing. The invertebrate compartment can be partitioned into large particle feeders and fine particle feeders. This conceptual scheme has been proposed by Cummins (1971) and Kilmer and Cummins (personal communication, Michigan State University).

Leaching experiments

The 24-hour leaching experiments and subsequent daily monitoring for additional dramatic effects, have shown that the dominant leaching effect is within the first 24 hours. Using techniques of Riggs (1970) a log-normal plot of leaf decay shows two distinct decay functions with a decided break at 24 hours (Fig. 2). This result appears in the natural stream or in laboratory experiments using glass beakers to conduct the leaching. Comparing a 6 day experiment with measurements every day, with data for up to 143 days, does not show any additional severe break. This is a very similar observation to one made by Nykvist (1959, 1961) in which he found a rapid and pronounced loss of dry

weight during the first 24 hours with a long slow decay thereafter. The leaching rate dynamic conforms to an exponential loss model as shown by a least-squares fit to the observed data. The calculated leaching decay coefficients are presented for the 7 main species in Table 6 along with the % loss per day ($100 \times k$). The leaching coefficient is expressed on a daily basis as are all the decay coefficients.

Temperature effects

Temperature has been reported to be a major environmental variable controlling the rate of decomposition of leaf litter in soil systems (Ando, 1971; Witkamp, 1966). Witkamp's model of leaf litter decomposition ranks temperature as the major variable over moisture and bacterial density. Investigations by Nykvist (1959, 1961a, 1961b, 1962) have shown that temperature is important in the rate of leaching. In Table 9 Nykvist's data for Betula verrucosa are reproduced; the sizeable temperature effect is obvious. It is doubtful that temperatures in the range used by Nykvist are ever seen but the "tea bag" effect or the fact that tea leaches more in hot water than in cold can not be ignored. The temperature ranges during the fall in Augusta Cr. from about 15°C to 5°C . Not until late winter do temperatures get much below this. Since most leaching occurs in the fall, it is safe to assume that the temperature effect will have to be restricted to this range. For microbial activity the full fall-winter range will have to be used, $1^{\circ} - 15^{\circ}\text{C}$. The problem of temperature has been investigated two ways experimentally.

Results of leaf leaching at three temperatures from laboratory studies are shown in Fig. 3. There was no difference in the amount

leaching or the rate that the leaching occurred ($P < 0.05$) for the three temperatures. The reason is that the variance in estimating the % lost or remaining swamps out the estimate of the effect of the treatment. Leaf structures are not uniform. Differences in weight may not reflect absolute differences in the amount that has the ability to be leached or processed. Leaves may differ dramatically in chemical composition from tree to tree (Melin, 1930). All these factors lead to the inability to make small, accurate measurements, even though the precision with which these measurements are made is quite good. The second experimental approach to temperature problems concerns the long-term decay results.

Long-term decay

The results of the two long-term experiments carried out in Augusta Cr. are presented in Table 3-5. Comparing the two sites and the two seasons, no significant differences can be found. That is, the decay coefficients for the period of September to December and December to April are not significantly different for all species. Some species do have significantly higher decay coefficients at one site than at another but using a non-parametric test the two sites and the two time periods do not produce noticeable differences in the processing rates. There are, however, noticeable and dramatic differences between species of leaves. The significance of this depends on the functional definition of the decay coefficient.

Decay coefficients may be viewed as an index of the percent remaining at any particular time. The biological half life, a direct analog of radiotracer half life, may be used and calculated to indicate the time

it takes for half of the material to be degraded. The same calculation may be done to ask at what time 80% and 90% of the leaf would have been utilized by the environment. Since at no time will 100% of the leaf be processed due to the nature of exponential decay, the 80-90% utilization time may be a close approximation to the time at which the leaf has been effectively processed. The remaining portion will then consist of stems and petioles and other hard parts which are not functionally responding to the decay coefficients or to the microbial-animal community working at the measured decay coefficients. These parts then would become kinetically different and part of a different processing system. Fisher (1971) has functionally separated detrital input into two major groups based on leaves and twigs.

Table 10 summarizes the 7 species of leaves used in the main experiments. They are arbitrarily broken up into 3 processing ranges by their decay coefficients into slow (0.005), medium (0.005 - 0.010) and fast (0.010 - 0.015). The biological half life (t_{50}), eighty % life and ninety % life have been calculated. Leaves of Cornus and Fraxinus will be effectively consumed within 230 days or in 8 months. A leaf of these species entering the stream from September to November may not be expected to be found in a recognizable form much after April-June. For a medium species, a leaf entering in the fall months will not be present 8-15 months later. The slow species will take more than 15 months to have 90% of their material processed.

Another way of conceptualizing the meaning of decay coefficients is to calculate the percent of the leaf remaining after one year. If there is no net accumulation to detritus over time, then what is not

processed in one year's time must be in an effective export phase. The material is either being exported downstream to a terminal sink such as a lake or pond or the material is in a detritus sink in the stream and responds to a totally different set of decay parameters. Table 10 gives the % remaining after 1 year ($%R_{365}$), the ranges for the processing are again arbitrary. For most species of leaves used in the study no more than 16% of the leaf will be present after one year. This is without any loss due to export other than that export which reflects the original decay coefficient. The fast tract species will have less than 3% remaining after one year. The remaining represents the hard to decompose portions such as petioles and leaf midribs. These theoretical results are comparable to the raw data from Triska's (1971) work which is the only leaf processing study with values for an entire year. Fisher (1971) calculates a turnover time of about one year for the leaf detritus compartment and a much longer time for the twig branch compartment (4.2 years). The indication is that the processing rates for leaf litter, measured during the fall-winter months when microbial action may be expected to be at a minimum, can account for complete processing of the leaf material that is placed in it. The assumptions of this statement are that the system does not become overloaded and that the proportional loss model holds.

A third method of analyzing the decay coefficients is presented in Fig. 4. Here the leaf species are ranked in order of slow to fast instead of being grouped and the decay coefficients with 2 standard errors are plotted against this ranking. The result is a heirarchy of leaves along a continuum. The ecological significance, if any, is not

fully clear. Additional experiments will have to be carried out with other species from different forest associations with different climatic conditions.

Experimental stream studies

The results from the experimental stream study provides the only indication of the degree of partitioning of the long-term decay coefficient. From the above discussion, the first partitioning of the total decay is between the large physical leaching effect which is essentially a 24-hour process and the second, a long-term, up to a year, degradation. Several investigators of litter decay in the terrestrial system have directed their efforts to the partitioning of decay into microbial and invertebrate components (Kurcheva, 1960; Crossley and Hogland, 1962; Edwards and Heath, 1963; Lockheed and Chase, 1943; and Witkamp and Crossley, 1966). However, partitioning of these components has not been attempted in the stream system. Triska's (1971) data (Table 7) gives a good approximation of just microbial decomposition and the decay rates that may be expected. The experimental stream results in this study (Table 8) show a marked effect of the large particle, detritivorous invertebrates only on hickory leaves and not on oak. This difference is attributable to the much slower decay rate of the oak in the natural stream (Table 7). Oak tends to be one of the slowest leaves to be processed by the environment in both aquatic and terrestrial systems and the relatively short term of the experimental stream experiment, 92 days, did not allow the full effect of the invertebrates to be seen. From this experiment and for hickory, the contribution of the microbial community is about equal to the contribution in terms of

decay for the animal community. Kurcheva (1960) using a questionable technique of employing naphthaline to retard invertebrate activity shows a very small contribution to decay by the microbial component. Other investigators (Triska, 1971; Witkamp and Olson, 1963; and Melin, 1930) do not agree with Kurcheva's result. In these studies sizeable decay coefficients are obtained when the microbial component is analyzed. Further studies restricting invertebrates and using experimental manipulations will have to be conducted to fully understand the interaction and partitioning of the long-term decay component.

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Table 1. W. K. Kellogg Forest (Michigan State University)
 Black Ash - American Elm - Red Maple Association
 constructed to comply with dominant vegetation in the
 study site. Species used in the present study are indicated.

Dominant	Tree species	
	Black Ash	(<u>Fraxinus nigra</u>)
	American Elm	(<u>Ulmus americana</u>)
	Red Maple	(<u>Acer rubrum</u>) *
Associate	Tree Species	
	American Hornbeam	(<u>Carpinus caroliniana</u>) *
	Basswood	(<u>Tilia americana</u>) *
	Bur Oak	(<u>Quercus macrocarpa</u>)
	White Oak	(<u>Quercus alba</u>) *
	Red Oak	(<u>Quercus rubra</u>) *
	Yellow Birch	(<u>Betula lutea</u>)
	Silver Maple	(<u>Acer saccharinum</u>) *
	Tamarack	(<u>Larix laricina</u>)
	Quaking Aspen	(<u>Populus tremuloides</u>) *
	Green Ash	(<u>Fraxinus pennsylvanica</u> var. <u>lanceolata</u>) *
Shrubs		
	Silky Dogwood	(<u>Cornus amomum</u>)
	Red Osier Dogwood	(<u>Cornus Stolonicea</u>)
	Swamp (Marsh) Rose	(<u>Rosa palustris</u>)
	Buckthorn	(<u>Rhamnus carthartica</u>)
	Nannyberry	(<u>Viburnum lentago</u>)
	High Bush Cranberry	(<u>Viburnum trilobus</u>)
	Willow	(<u>Salix c. lucida</u>) *
	Whorled	
	Loosestrife	(<u>Decodon verticillatus</u>) *
	Thicket	
	Serviceberry	(<u>Amelanchier canadensis</u>)

Table 2. Winter processing rates Dec.-May of selected deciduous leaf species at B Ave. and C.Ave., Augusta Cr.

Species	B AVE				C AVE			
	-K ¹	α ²	r ³	S.E. ⁴	-K	α	r	S.E.
1. <u>Carpinus caroliniana</u>	.0028 ⁺	79.74	.7785	.0015	.0083	123.11	.9278	.0016
2. <u>Quercus alba</u>	.0056 ⁺	129.8	.7924	.0020	.0043	125.3	.9456	.0009
3. <u>Quercus rubra</u>	.0065	112.9	.9318	.0013	.0029 ⁺	89.3	.8771	.0008
4. <u>Juglans nigra</u>	.0070	105.3	.9972	.0003	.0072	111.9	.9085	.0016
5. <u>Carya glabra</u>	.0056 ⁺	83.83	.5746	.0034	.0081 ⁺	94.91	.8878	.0020
6. <u>Populus tremuloides</u>	.0035	78.66	.9241	.0007	.0058	76.16	.9945	.0004
7. <u>Populus grandidentata</u>	.0038	88.42	.9647	.0005	.0035 ⁺	92.98	.8118	.0012
8. <u>Salix lucida</u>	.0083 ⁺	61.41	.5977	.0068	.0119	95.38	.9685	.0015
9. <u>Acer saccharinum</u>	.0107	126.5	.9762	.0012	.0066 ⁺	100.3	.7883	.0024
10. <u>Acer rubrum</u>	.0093 ⁺	71.65	.6541	.0048	.0062	88.33	.9628	.0009
11. <u>Acer platanoides</u>	.0236 ⁺	301.6	.7638	.0093	.0076	109.2	.9758	.0009
12. <u>Tilia americana</u>	.0175	155.7	.9803	.0018	.0234 ⁺	234.8	.7452	.0097
13. <u>Cornus stolonifera</u>	.0127	111.2	.9518	.0020	.0106	99.18	.9707	.0013
14. <u>Decodon verticillatus</u>	.0083	92.16	.9663	.0011	.0086	111.7	.9975	.0003
15. <u>Fraxinus americana</u>	.0142	139.7	.9575	.0021	.0137 ⁺	141.6	.8083	.0047

1. Decay coefficient (regression coefficient of exponential decay)
2. Intercept; amount of leaf at time zero
3. Simple linear correlation coefficient
4. Standard error of regression coefficient, -K
5. +; rate coefficient -K not significantly different from zero.

Table 3. Decay coefficients and supportive statistics for selected leaf species during the fall and winter at B Ave, Augusta Cr.

SPECIES	FALL				WINTER				TOTAL			
	-K ¹	α ²	r ³	S.E. ⁴	-K	α	r	S.E.	-K	α	r	S.E.
1. <u>Quercus alba</u>	.0062	98.37	.9977	-- 5	.0056*	129.8	.7924	.0020	.0031*	91.99	.3619	.0020
2. <u>Carya glabra</u>	.0136	99.22	.8688	.0037	.0056*	83.83	.5746	.0034	.0070*	76.80	.3820	.0036
3. <u>Populus tremuloides</u>	.0059	75.47	.9202	.0010	.0035	78.66	.9241	.0007	.0030	67.76	.4570	.0012
4. <u>Salix lucida</u>	.0044*	69.61	.1480	.0053	.0083*	61.41	.5977	.0068	.0080*	76.74	.3074	.0045
5. <u>Cornus amomum</u>	.0098	73.40	.8794	.0021	.0127	111.2	.9518	.0020	.0102	79.98	.8698	.0015
6. <u>Decodon verticillatus</u>	.0133	105.4	.8997	.0026	.0083	92.16	.9663	.0011	.0088	86.74	.7833	.0017
7. <u>Fraxinus americana</u>	.0088*	75.57	.9198	.0026	.0142	139.73	.9575	.0021	.0108	93.91	.8654	.0019

1. Regression coefficient of exponential fit (decay coefficient)
2. Intercept of dependent variable (amount of leaf remaining at time zero)
3. Simple linear correlation coefficient
4. Standard error of regression coefficient
5. Calculation of error not possible
- *6. Decay coefficient not significantly different from zero $P < .05$

Table 4. Decay Coefficients and supportive statistics for selected leaf species during the Fall and Winter at C Avenue, Augusta Creek.

Species	FALL				WINTER				TOTAL			
	-K	α	r	S.E.	-K	α	r	S.E.	-K	α	r	S.E.
<u>Quercus alba</u>	.0048	92.60	.9295	.0005	.0043	125.3	.9456	.0009	.0029	92.48	.6463	.0007
<u>Carya glabra</u>	.0084	87.16	.8894	.0011	.0081	94.91	.8878	.0020	.0074	86.71	.9224	.0006
<u>Populus tremuloides</u>	.0030**	73.76	.5882	.0008	.0058	76.16	.9945	.0004	.0024	73.44	.5198	.0007
<u>Salix lucida</u>	.0064**	76.97	.5653	.001	.0119	95.38	.9685	.0015	.0088	80.49	.7638	.0014
<u>Cornus amomum</u>	.0127	76.06	.8833	.0016	.0106	99.18	.9707	.0013	.0096	73.88	.7932	.0014
<u>Decodon verticillatus</u>	.0103	91.27	.9558	.0007	.0086	111.7	.9975	.0003	.0080	88.62	.8657	.0009
<u>Fraxinus americana</u>	.0113	89.32	.9645	.0008	.0137	141.4	.8083	.0047	.0105	90.75	.9448	.0008

¹Decay coefficient (regression coefficient of exponential fit by least squares)

²Intercept - Amount of leaf remaining at time zero

³Simple linear correlation coefficient

⁴Standard error of decay coefficient

** Winter decay coefficient significantly $P < .05$ higher than Fall

Table 5. Approximate evaluation of leaf loss after 36 days in Augusta Creek (May 19 - June 24) at three sites in Augusta Creek. Based on three leaf packs, composed of two leaves of each of seven species (or a total of 14 leaves) sewn together with nylon leader and feathered to bricks (one pack per brick) at each location.*

Site	Sample	Number (out of two) of leaves recognizable, and estimated % remaining per leaf										Totals							
		Red oak		White oak		Dogwood		Black Cherry		Sassafras				Walnut (leaflet)		Maple		Undet.	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	Amt.
B Ave.	1	2	.50 .25	2	.20 .10	1	.10	-	-	-	-	-	-	-	-	5	(3).05 (2).10		
	Sample tot.	2	.75	2	.30	1	.10									5	.35	10	1.5
	2	-	-	2	.20 .85	-	-	-	-	-	-	-	-	-	-	8	(7).05 (1).10		
	Sample tot.			2	1.05											8	.45	10	1.5
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	(7).05		
	Sample tot.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	.35	7	.35
Site totals and $\bar{X}$'s		2	.75	4	1.35	1	.10	-	-	-	-	-	-	-	-	20	1.15	27	1.15
C Ave.	1	2	.50 .75	2	.80 .10	2	1.0 .10	1	.50	2	.95 .85	2	.95 .40	2	.50 .95	1	.10		
	Sample tot.	2	1.25	2	.90	2	1.10	1	.50	2	1.80	2	1.35	2	1.45	1	.10	14	8.45
	2	2	.80 .60	-	-	2	.80 .60	2	.10 .10	1	.75	1	.25	2	.20 .20	2	.50 .50		
	Sample tot.	2	1.40			2	1.40	2	.20	1	.75	1	.25	2	.40	2	1.00	12	5.40
	3	2	.75 .50	1	.20	2	.60 .75	1	.25	2	.75 .20	1	.50	2	.10 .10	3	(2).05 (1).10		
	Sample tot.	2	1.25	1	.20	2	1.35	1	.25	2	.95	1	.50	2	.20	3	.20	14	4.90
Site totals and $\bar{X}$'s		6	3.90	3	1.10	6	3.85	4	0.95	5	3.50	4	2.10	6	2.05	6	1.30	40	6.00

Kellogg Forest	1	1 .75	1 .60	1 .75	2 .60 .40	1 .60	2 .60 .50	- -	6 (2).05 (1).10 (3).20	
	Sample tot.	1 .75	1 .60	1 .75	2 1.00	1 .60	2 1.10	- -	6 .80	14 5.6
	2	- -	- -	2 .40 .50	- -	1 .75	- -	1 .20	4 (2).05 (2).10	
	Sample tot.			2 .90		1 .75		1 .20	4 .30	8 2.1
	3	1 .10	- -	1 .60	2 .75 .40	2 .30 .60	1 .25	- -	4 .05	
	Sample tot.	1 .10	- -	1 .60	2 1.15	2 .90	1 .25		4 .20	11 3.2
Site totals and $\bar{X}$'s										
	2	.85	1 .60	4 2.25	4 2.15	4 2.25	3 1.35	1 .20	14 1.30	33 3.4

* Amount remaining given as per cents expressed as decimals; numbers in parentheses are the number of leaves estimated to have a given per cent remaining in multiple counts (undetermined). The total amount is expressed as sum of decimal per cents (possible total = 14.0).

Table 6. 24 hour leaching coefficients and % loss for selected leaf species.

Species	$-K_L$	% Loss
Quercus alba	0.0530	5.16
Carya glabra	0.1095	10.37
Populus tremuloides	0.2127	19.20
Salix lucida	0.2580	22.74
Cornus amomum	0.3175	27.20
Decodon verticillatus	0.1234	11.61
Fraxinus americana	0.1145	10.82

Table 7. Comparison of decay coefficients from some published studies on leaf processing.
Both terrestrial and aquatic literature combined and arranged taxonomically.¹

Species	Season or Temperature	Duration of Study Days	Decay Coefficient		Experimental Conditions	Author
			-K	S.E.		
Salicales						
Salicaceae						
<u>Populus tremuloides</u> Michx.	Fall-Spring	---	.0046 ²	.0008	stream	present study
<u>Populus grandidentata</u> Michx.	Dec.-May	146	.0038	.0005	stream	present study
" "	25 °C	120	.0030	---	lab microbial	Melin, 1930
<u>Salix nigra</u> Marsh	Nov.-Nov.	365	.0062	---	stream microbial	Triska, 1970
<u>Salix lucida</u> Muehl.	Fall-Spring	---	.0078 ²	.0015	stream	present study
Juglandales						
Juglandaceae						
<u>Juglans nigra</u> L.	Dec.-May	146	.0070	.0003	stream	present study
<u>Carya glabra</u> (Mill.) Sweet	Fall-Spring	---	.0089 ²	.0002	stream	present study
	5 °C	92	.0072	---	experimental stream ³	"
	5 °C	92	.0032	---	experimental stream ⁴	"
	Summer	30	.0305	---	stream	"
Fagales						
Betulaceae						
<u>Betula lutea</u> Michx.	Nov.-Nov.	365	.0116	---	stream microbial	Triska, 1970
<u>Betula papulifera</u>	25 °C	120	.0050	---	lab microbial	Melin, 1930
<u>Betula papyrifera</u>	25 °C	120	.0066	---	lab microbial	Melin, 1930
<u>Carpinus caroliniana</u> Walt.	Dec.-May	146	.0083	.0016	stream	present study
<u>Alnus glutinosa</u> (L.) Gaertn.	Nov.-Nov.	365	.0075	---	stream microbial	Triska, 1970
Fagaceae						
<u>Fagus grandifolia</u> Ehrh.	25 °C	120	.0025	---	lab microbial	Melin, 1930
<u>Quercus borealis</u> var. ⁵ maxima (Marsh.) Ashe	Nov.-Nov.	365	.0027	---	stream microbial	Triska, 1970
<u>Quercus alba</u> L.	Fall-Spring	---	.0052 ²	---	stream	present study
" "	5 °C	92	.0022		experimental stream ³	" "
" "	5 °C	92	.0020		experimental stream ⁴	" "
" "	Dec.-April	150	.0013	.0001	Pine stand ⁶	Witkamp and Olson, 1963
" "	" "	"	.0019	.0001	Oak stand ⁶	" "

¹Taxonomy based on Grimm, 1961

²Value obtained as a mean of two sites through two seasons

³Experimental stream enriched with large particle detritivores

⁴Experimental stream not enriched with large particle detritivores

⁵Referred to by Triska (1970) as Quercus rubra, Eastern red Oak

⁶Leaves were placed in fiberglass bags with lumm openings

⁷Leaves were tied to nylon cord and exposed

decay represents microbial action without animal activities

Table 7 Continued

Species	Season or Temperature	Duration of Study Days	Decay Coefficient		Experimental Conditions	Author
			-K	S.E.		
<u>Quercus alba</u> L. (cont.)	Dec.-April	150	.0019	.0002	Maple stand ⁶	Witkamp and Olson, 1963
" "	June-March	300	.0030	.0001	Pine stand ⁷	" "
" "	" "	300	.0046	.0003	Oak stand ⁷	" "
" "	" "	300	.0055	.0003	Maple stand ⁷	" "
<u>Quercus robur</u> L.	Summer	140	.0057		soil	Kurcheva, 1960
" "	" "	"	.0007		soil microbial	" "
" "	Nov.-June	240	.0044		stream	Mathews and Kowalczewski, 1969
Urticales						
Ulmaceae						
<u>Ulmus americana</u>	10 °C	56	.0028	.0005	lab microbial	Kaushik, pers. comm., Univ. of Waterloo
	10 °C	56	.0059	.0007	" " enriched	" "
	21 °C	56	.0045	.0005	" " "	" "
	21 °C	56	.0091	.0015	" " "	" "
Sapindales						
Aceraceae						
<u>Acer saccharum</u>	25 °C	120	.0033		lab microbial	Melin, 1930
<u>Acer saccharinum</u>	Dec.-May	146	.0107	.0012	stream	present study
<u>Acer rubrum</u> L.	25 °C	120	.0041	---	lab microbial	Melin, 1930
" "	Dec.-May	146	.0062	.0009	stream	present study
<u>Acer platanoides</u>	Dec.-May	146	.0076	.0009	stream	present study
<u>Acer pseudoplatanus</u> L.	Nov.-June	240	.0110	---	stream	Mathews and Kowalczewski, 1968
Malvales						
Tiliaceae						
<u>Tilia americana</u>	Dec.-May	146	.0175	.0018	stream	present study
Cornales						
Cornaceae						
<u>Cornus amomum</u>	Fall-Spring	---	.0115 ^a	.0007	stream	present study
Myrtales						
Lythraceae						
<u>Decodon verticillatus</u>	Fall-Spring	---	.0101 ^a	.0012	stream	present study
Gentianales						
Oleaceae						
<u>Fraxinus americana</u>	Fall-Spring	---	.0120	.0012	stream	present study

Table 8. Leaf weight loss in experimental channels over a 92-day period (Feb. 16-May 19) at a mean temperature of 5 °C. Stream 1 received 1065 large particle feeders 6 days after introduction of 1 kg (dry wt.) of leaves to each stream (500 gm hickory, 500 gm oak).

Stream	Leaf Species	#Leaf Packs	% wt. loss		% Leached	% Processed	-K*
			$\bar{x}$	SD			
1	Hickory	25	53.58	± 9.26	10.37	43.21	.0072
2		23	33.04	± 3.62	10.37	22.67	.0032
1	Oak	24	23.27	± 4.01	5.16	18.11	.0022
2		24	21.58	± 2.82	5.16	16.42	.0021

* $K = \text{Log}_e (\% \text{ Leaf wt. final} / \% \text{ Leaf wt. initial}) / 92 \text{ days}$

Table 9: Calculated decay coefficients for 24 hour leaching from Nykvist (1961a, 1962) showing the effect of temperature and species differences.

Species	Temp °C	-K	\$ loss/day
<u>Betula verrucosa</u>	3	0.0833	8.33
" "	20	0.1165	11.65
" "	40	0.1508	15.08
" "	60	0.1684	16.84
" "	80	0.2046	20.46
<u>Alnus glutinosa</u>	25	0.1278	12.78
<u>Fagus silvatica</u>	25	0.0408	4.08
<u>Quercus robur</u>	25	0.1803	18.03

Table 10. Processing groups of selected leaf species and calculated time for 50%, 80% and 90% to be processed at the coefficient rate range. Time in days

Group I "FAST"	-K	50 ¹	80 ²	90 ³	% R ₃₆₅
1. <u>Cornus amomum</u>					
2. <u>Fraxinus americana</u>	>.010	<46	<107	<230	
		<46-69	<107-161	<154-230	<1 -3

Group II "MEDIUM"

1. <u>Carya glabra</u>					
2. <u>Salix lucida</u>	.005-.010	69-138	161-322	230-461	3-16
3. <u>Decadon verticillatus</u>					

Group III "SLOW"

1. <u>Quercus alba</u>					
2. <u>Populus tremuloides</u>	<0.005	138	322	461	16

1. $t_{50} = .693/K$ (also referred to as the biological half life)
2. $t_{80} = 1.609/K$
3. $t_{90} = 2.303/K$

AUGUSTA CREEK

Fig. 1 Results of preliminary experiment with 7 species of riparian vegetation from 3 sites in the Augusta Cr. drainage.

Fig. 2 Log-normal plot of percent remaining of leaf over short periods of time. Decay consists of a double exponential, a 24 hour leaching process and a long term leaf decay.

Fig. 3 Effects of temperature on the short term loss of dry weight by leaves of *Carya glabra*. Mean of three leaves with 1 S.D. are plotted. The three curves are not different; $P < 0.05$.

Fig. 4 Plot of mean decay coefficient of two sites during two seasons, Fall and Winter, with 2 S.E., for ranked species, showing heirarchy.