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Degradation of Riparian Leaves and the Recycling of Nutrients in a Stream Ecosystem

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ABSTRACT

Leaves collected at 4 stations in the upper 5 km of Doe Run, Meade County, Kentucky, indicated an annual accumulation within the stream of 354 g/m^2/year (17,700 kg). Leaves of sycamore (23.6%), red oak (21.7%), sugar maple (9.7%), beech (9.6%), white oak (7.1%), and hickory (6.0%) trees were most abundant, and leaves from 14 other kinds made up the remaining 22.3%. About a third of the annual leaf fall occurred during the last half of October and about two-thirds in the last 3 months of the year.

Calorific equivalents for different kinds of leaves ranged from 3,789 cal/g dry weight for hickory to 4,417 cal/g for red oak. It is estimated that allochthonous leaf material made an annual contribution of about 70 million kcal of energy to the upper 5 km of Doe Run.

Protein, carbohydrate, and lipid contents of leaves varied independently of seasons with average values of about 52, 79, and 32 mg/g dry weight, respectively. In leaves submersed in the stream experimentally, carbohydrates leached rapidly, lipids leached slowly, and there was an apparent increase in protein content.

Indigenous amphipods preferred hickory, red elm, sugar maple, beech, red oak, and sycamore leaves as food in that order.

Key Words: VI-G Ecologic impact of water development

Ecology
    RT Aquatic Habitats

Detritus
    RT Decomposing organic matter
       Degradation (decomposition)

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Special gratitude is offered Dr. Charles R. Liston for the many hours spent in the field and laboratory collecting samples, making analyses, and compiling data. It was largely through his efforts that the study was completed. During his tenure as a graduate student, Dr. Liston received assistance as a National Science Foundation Trainee, and was supported in large part through Annual Allotment funds from the Office of Water Resources Research. His enthusiasm for the project is documented in these pages. The efforts of Harry H. Woodward deserve special mention. He assisted greatly in the collection and identification of plants in the Doe Run area, particularly those along the stream's edge. Specimens of all kinds of plants collected are in the P. A. Davies Herbarium at the University of Louisville.

We take this opportunity to thank Kay Craig, Sharon Pierce, Patti Vick, and especially Shirley Viers for typing the many revisions of the manuscript.

This research is part of a long-range study on Doe Run which commenced in 1959 as a continuing study that would provide insight into the functioning of the stream as an ecosystem. None of that work could have been accomplished without the consent and cooperation of Messrs. Curtis L. Brown and Albert Holsten who allow continuing access to their properties along the stream. We are extremely grateful for their cooperation.

INTRODUCTION

Primary production in streams is utilized, as in all ecosystems, by two general routes: (1) the grazing food chain where living organisms serve as food, and (2) the detritus food chain where remains of dead organisms are consumed (Odum 1963). Hynes (1963) stated that in running water much of the initial organic production takes place elsewhere, and likened streams to the bottoms of lakes and deep oceanic areas where major sources of energy are imported. In an earlier study, Minckley (1963) reported that allochthonous detritus was at least as important as primary production within Doe Run, especially in areas some distance downstream from the source. Similarly, Minshall (1967), in a study of Morgan's Creek, a spring brook about 6 miles from Doe Run, found that allochthonous leaf materials provided the main source of energy for primary consumers, and indirectly for the entire benthic fauna. Minshall further reported that periphyton contributed much less to the economy of the stream than did the leaf detritus.

With this information in mind, and having studied other biological, chemical, and physical characteristics of Doe Run for more than 10 years, a detailed study of leaves from riparian plants that entered Doe Run was undertaken. The objectives of the study were: (1) to determine the kinds and amounts of riparian leaves entering Doe Run, Meade County, Kentucky, (2) to determine the calorific equivalents of the different kinds of leaves entering the stream and to document whatever seasonal differences occur within species, (3) to determine the amounts of protein, carbohydrate, and lipid materials present in the different kinds of leaves and to note seasonal changes in those amounts, and (4) to determine the rates of loss of protein, carbohydrate, and lipid materials from leaves submersed in the stream over extended periods of time. In addition to these stated objectives, some quantitative and qualitative relationships between the streambank vegetation and the species composition of the leaves entering Doe Run were studied. Also, preliminary studies were made of the preference of different kinds of leaves by the indigenous amphipod *Gammarus bousfieldi*.

MATERIALS AND METHODS

Minckley (1963) has provided a detailed and comprehensive description of Doe Run, and Krumholz (1967) gave a shorter description of the physical, chemical, and biological characteristics of the stream. Doe Run flows through a relatively narrow valley that is underlain with Mississippian limestone. It is a spring-fed stream with an average width of about 10 m that rises at 175 m above mean sea level near Ekron, Kentucky, and flows north-northeast for 15.5 km to enter the Ohio River at Ohio River Mile 642.2 at 114 m msl. Parts of the valley floor have been cultivated from time to time, but most of the stream is heavily shaded by riparian trees most of the summer. Water temperatures at the source of Doe Run are consistently between 14 and 14 C. Downstream, water temperatures gradually warm during the summer and cool during the winter especially in the lower reaches of the stream. At the lowest portion of the stream included in this study (5 km from the source), water temperatures ranged between 6.1 C in March 1961 and 20.0 in August 1960. The discharge at the source of Doe Run undergoes extreme variation seasonally depending on precipitation. Maximal discharge usually occurs during the spring (up to 600 cfs) whereas minimal discharges are in the later summer or early fall (as little as 7 cfs).

Dissolved oxygen in Doe Run was consistently between 8 and 9 ppm (usually at least 75% of saturation and frequently more than 100%); pH at the source deviated only slightly from 7.0, but generally increased downstream to more than 8.0; total alkalinities ranged from 150 to 250 mg/l throughout the stream; and nitrate nitrogen ranged from 0.25 to slightly more than 2.1 mg/l.

Stations for leaf collections were near the permanent sampling stations of previous studies (Mickley 1963, Krumholz 1967, Prins 1968) (Fig. 1) and their descriptions have been enhanced by detailed surveys of the riparian vegetation in the contiguous 1000 m^2. Station I was about 75 m downstream from the source of Doe Run, Station II was about 2.7 km downstream from the source, Station IIA about 3.8 km downstream from the source, and Station III about 4.9 km from the source (for a detailed analysis of the vegetation see Liston 1972).

Leaves from riparian plants were collected at weekly intervals for 15 months in trays having an area of 0.87 m^2, with sides of 1 x 10-inch fir and bottoms of 0.5-inch hardware cloth. A set of 5 such trays was placed across the stream at each of the 4 stations with a tray fitted tightly into each bank of the stream and 3 trays suspended over the open water. All leaves were taken from the trays each week, sorted to species, dried at 80 C for 24 hours, and weighed to the nearest tenth of a gram. Calorific equivalents for each species were determined seasonally with a Parr adiabatic calorimeter. Other samples of leaves were used to determine concentrations of proteins, carbohydrates, and lipids. Proteins were determined by the methods of Kaushik and Hynes (1968) and Lowry et al. (1951); total sugars and related substances were determined colorimetrically using the method of Dubois et al. (1956); and lipids were determined following the procedures of Bleigh and Dyer (1959).

Samples of the 6 most abundant kinds of leaves were submersed in nylon net bags near the source of Doe Run to determine the rates of loss

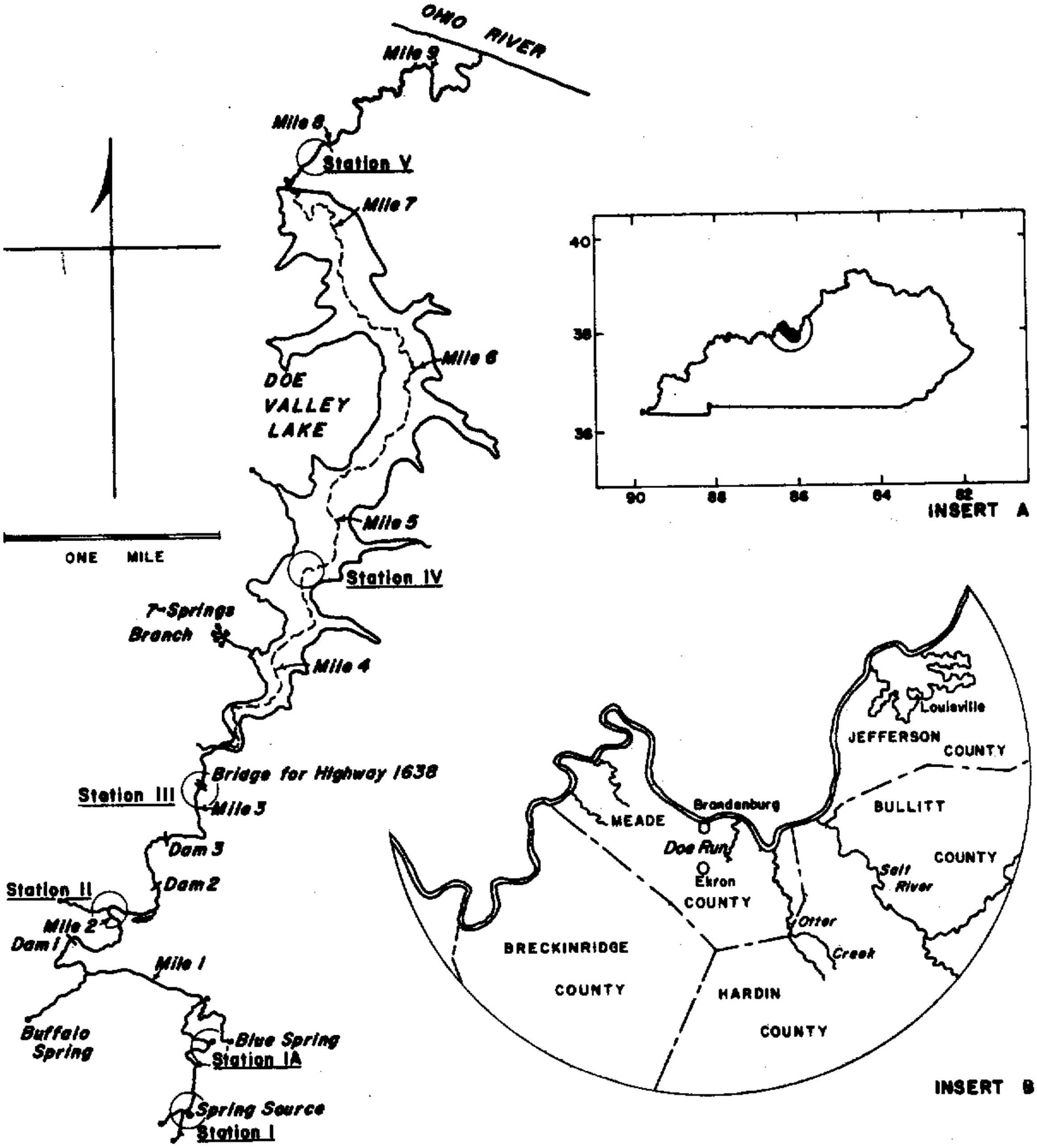

Fig. 1. Map of Doe Run, Meade County, Kentucky, indicating locations of collecting stations, dams, stream miles, and extent of Doe Valley Lake, Station IIA is immediately downstream from Dam 2 (after Krumholz 1967).

of organic materials and to determine how rapidly the leaves disintegrated. Samples were analyzed each 2 weeks over 8-week periods in the spring and in the fall.

Sample quadrats, 0.1 hectare in area, 0.05 ha on each side of the stream at each of the 4 stations were used to determine the extent of the canopy and whatever relationship it might have with the numbers and kinds of leaves taken from the trays. Sizes and heights of trees were estimated using standard forestry procedures. The 500-m^2 quadrats were divided into 10 x 10-m sections and all trees greater than 2 cm at breast height were measured. From these data, relative dominance, relative abundance, relative frequency, and importance value for each species of trees were calculated following the method of Cox (1967). On this basis, the riparian vegetation of 4% of the total streambank in the upper 5 km of Doe Run was sampled. The scientific terminology for all plants referred to here follows Gray's Manual of Botany (Fernald 1950).

In addition to the contributions of the riparian leaf material to the stream, a series of preliminary feeding experiments were performed to determine the preference of the amphipod *Gammarus bousfieldi* for the different kinds of leaves. That amphipod is indigenous to Doe Run and was provided an opportunity to feed on 6 different kinds of leaves under experimental conditions. The amounts of leaf material consumed were determined on the basis of dry weights of leaves before and after having been offered to the amphipods. Leaves were leached for 1 week prior to the experiment to minimize loss in weight through loss of soluble materials. Disks were punched from the leaves with a No. 11 cork borer, dried, and stored. In each experiment, 12 trays were used, 8 containing water from Doe Run, amphipods, and disks, and 4 containing only water and disks.

AMOUNTS AND KINDS OF LEAVES ENTERING DOE RUN

During the 15-month study period, leaves from 19 different kinds of leaves taken in the trays could be identified (Table 1). Of those, leaves of sycamore and red oak trees were by far the most abundant, and, together with the 10 other most abundant kinds, made up 93.7% of the total annual collections. No other kind of leaf contributed as much as 1.0% of the total dry weight; identifiable leaves in the trays made up 96.8% and the unidentifiable fragments 3.2% of the total dry weight. Different kinds of leaves did not fall uniformly at all stations, nor was the total dry weight taken in the trays similar. However, it is believed that collections at the 4 stations are representative of the upper 5 km of the stream and that the average dry weight of leaves per square meter of tray surface was approximately 355 g per year. Since the average width of Doe Run is about 10 m, the total annual weight of leaves that entered the stream was estimated to be about 18,570 kg (19.5 tons). In all probability, that figure is minimal since the verdancy of the foilage was rather sparse because the rainfall during the first 3 months of the year was less than three-quarters (9.50 inches, 74.9%) of the normal precipitation (U.S. Department of Commerce, Climatological Data, Irvington, Kentucky, 1969). The previous year the precipitation was less than half (6.30 inches, 49.7%) the normal.

Leaves did not enter Doe Run at a uniform rate throughout the year. Maximum leaf fall occurred during the last half of October, tapered off during the winter, rose to a lesser peak in March, and was minimal in spring and summer. The lesser peak of deposition in March is traceable to the fact that some trees, such as some beeches and white oaks, hold their leaves during the winter, and they do not fall until new buds begin to swell in the spring. The data in Table 1 also indicate that there were marked differences

Table 1. Total weights in grams of leaves from riparian trees taken in trays at each of 4 stations in Doe Run, Meade County, Kentucky, arranged in order of decreasing total weight for all stations, together with the estimated weights in kilograms of leaves that entered the upper 5 km of the stream in 1 year.

	Station Number				Total in	Total in
	I	II	IIA	III	trays (g)	stream (kg)
Sycamore	569	199	451	180	1,399	4,184
Red oak	875	343	33	35	1,286	3,846
Sugar maple	146	207	2	217	572	1,711
Beech	204	366	--	--	570	1,705
White oak	270	149	1	1	421	1,259
Hickory	275	79	5	--	359	1,074
Chinquapin oak	11	17	69	182	279	834
Red elm	118	19	8	64	209	625
Ash	12	25	4	128	169	505
Grape	57	3	18	41	119	356
Dogwood	41	5	38	15	99	296
American hornbeam	1	26	25	7	59	176
Black cherry	19	5	--	25	49	147
Redbud	--	2	5	31	38	114
Basswood	32	--	--	1	33	99
Black walnut	13	3	14	1	31	93
Ohio buckeye	--	25	--	--	25	75
American elm	1	8	--	--	9	27
Pawpaw	--	5	--	--	5	15
Other	49	55	24	59	187	559
Total	2,693	1,541	697	987	5,918	17,700

in the abundances of different kinds of leaves at each station: at Station I, leaves of red oak, sycamore, hickory, and white oak trees were most abundant in the trays in that order; at Station II, the most abundant leaves in the trays were beech, red oak, sugar maple, and sycamore; at Station IIA, sycamore leaves were more abundant in the trays than all other kinds combined and were followed in order by chinquapin oak, dogwood, and red oak; at Station III, leaves of sugar maple, chinquapin oak, sycamore, and ash trees were collected in the trays in that order. The single most abundant kind of leaf made up 32.5, 23.8, 64.6, and 22.0% of the total, respectively, at Stations I, II, IIA, and III.

Even though sycamore was the most abundant kind of leaf only at Station IIA, it was most abundant in the total collected at all stations, and was the only kind represented among the 4 most abundant kinds at all stations (Table 1). Similarly, red oak was the most abundant kind of leaf in the trays only at Station I, but was second in overall abundance. These 2 kinds of leaves made up 45.4% of all leaves taken in the trays. The other 17 kinds listed in Table 1 made up 51.5%, but no single species of that group made up as much as 10% of the annual total. The 3.2% listed as "other" consisted of unidentifiable fragments.

Other riparian plants that may have contributed to the allochthonous leaves entering Doe Run, but not identified in the trays at any of the stations, were identified in the analysis of vegetation in the 100-m^2 plots contiguous to the sampling stations. In addition to the 19 species listed in Table 1, the following kinds of plants were collected and identified (arranged in order of decreasing relative dominance): spicebush, red cedar, persimmon, honey locust, black gum, viburnum, red mulberry, indian cherry, hackberry, hophornbeam, black willow, bladdernut, smooth sumac, silver maple, sassafras, fragrant sumac, buttonbush, hydrangea, leatherwood, tulip poplar, and wahoo. Of these, only the spicebush was of importance, largely because of relatively heavy concentrations of plants at Stations IIA and III where they ranked eighth in relative dominance.

In summarizing the data on riparian trees from the 100-m^2 plots at each station and for the stream as a whole, we followed the recommendation of Bray and Gorham (1964) in using the relative dominance of the plant in the community as the best indicator of litter production. Although importance values (Cox 1967) are quite useable in descriptive vegetational analysis, they are not as accurate for indicating litter production. A comparison of the data on the amounts of leaves collected in the trays with the relative dominance of the plants in the riparian forest, indicates that the material taken from the trays is a fair representation of the availability of the leaves, especially among the 12 most abundant kinds (Table 2). The relative dominance of grapevines in the forest is difficult to assess because of the growth form of the plants. The leaves of black walnut are alternate pinnate and relatively large and heavy and usually remain where they fall. Most of the other kinds of leaves taken in the trays may be easily windblown when dry.

There also was close correlation between the amounts of leaves in the trays and the density of the riparian forest. At Station I, where the greatest amounts of leaves were taken in the trays, the total basal area of all trees was greater than at any other station, and was dominated by dogwood, sycamore, sugar maple, white oak, beech, and black walnut. The reason red oak leaves were so abundant in the trays but not dominant in the forest is easily explained by the terrain. The east slope of the bank at Station I is very steep and high and the dominant trees on the top are red oaks. However, those trees were largely outside the 100-m^2 plot at that station and caused that discrepancy in our data. At Station II, where the second highest weight of leaves was collected in the trays, the combined basal area of all trees ranked second among

Table 2. Comparison between total weights of leaves collected in the trays and the relative dominance of trees in the riparian forest, Doe Run, Meade County, Kentucky.

	Accumulation in trays		Relative dominance	
	Weight	Rank	Value	Rank
Sycamore	1399	1	43.9	1
Red oak	1286	2	7.0	4
Sugar maple	572	3	9.4	2
Beech	570	4	5.0	5
White oak	421	5	3.0	8
Hickory	359	6	2.1	9
Chinquapin oak	279	7	1.0	13
Red elm	209	8	8.2	3
Ash	169	9	4.0	6
Grape	119	10	--	--
Dogwood	99	11	1.6	12
American hornbeam	59	12	2.0	10
Black cherry	49	13	0.5	15
Redbud	38	14	2.0	11
Basswood	33	15	0.01	16
Black walnut	31	16	3.6	7
Ohio buckeye	25	17	0.9	14
American elm	9	18	--	--
Pawpaw	5	19	--	--

the stations. There, sycamore, red oak, American hornbeam, and sugar maple were the dominant trees. At Station IIA, where the total amount of leaves in the trays was least among the stations, the number of trees and their total basal area were the lowest recorded at any station. Sycamores comprised about 70% of the total basal area at Station IIA. At Station III, the diversity and number of trees were greater than at any other station, but the total basal area ranked third, as did the total amount of leaves in the trays. The most numerous tree at Station III was the red cedar, but those trees were not close to the bank and the leaves are not easily blown about by the wind. The dominant trees, however, were the sugar maple and the sycamore.

Another method of comparison was between the kinds of trees taken in the trays and the kinds identified in the 100-m^2 plots. At Station I, 16 kinds of leaves were identified in the trays, and 17 kinds were identified in the 100-m^2 plots. There were hackberry, black gum, spicebush, viburnum, and red mulberry in the plots that were not collected in the trays, and leaves of basswood, American elm, and chinquapin oak were collected in the trays but were not recorded in the plots. At Station II, leaves from 17 kinds of trees were taken in the plots, leaves of black gum, sassafras, and red cedar were not taken in the trays. None of those trees were common in the forest. At Station IIA, leaves from only 12 kinds of trees were collected in the trays, but 18 kinds of trees were represented in the forest plots. Those present on the plots but not collected in the trays were spicebush, black cherry, hackberry, honey locust, persimmon, hydrangea, red cedar, and red mulberry, whereas those found in the trays but not in the plots were white oak and hickory. At Station III, leaves from 14 kinds of trees were collected in the trays but 31 kinds of trees were identified in the 100-m^2 plot. Those trees not represented by leaves in the trays were red cedar, spicebush, Biltmore ash, indian cherry, bladdernut, persimmon, hackberry, black willow, Ohio buckeye, hophornbeam, red mulberry, viburnum, fragrant sumac, silver maple, buttonbush, leatherwood, smooth sumac, hickory, tulip poplar, and wahoo. Leaves of white oak, basswood, and American elm leaves were taken in the trays but their total combined weight amounted to 1.5 g for the entire year.

All together, 41 different kinds of trees were identified in the plots contiguous to the sampling trays but no more than 31 occurred at any single station. In addition to the leaves of those trees, leaves from grapevines made a measurable contribution to the allochthonous leaf fall entering Doe Run. Of those, only 18 kinds, along with grape leaves, were taken in the trays. Thus it is apparent that our estimate of 19.5 tons of allochthonous leaf fall for the uppermost 5 km of Doe Run is minimal. Furthermore, because of the limited rainfall during the first 3 months of the year we believe the verdancy of the riparian forest was below average and would have been much greater had the precipitation been normal.

As an addendum to the present study, a rather comprehensive list of the flora of the drainage basin of Doe Run (see Liston 1972) is in preparation for publication. That list includes 174 species referable to 67 families of plants. In that list are included 29 species not included in the plants of Meade County either by Braun (1943) or by Davies (1955).

CALORIFIC EQUIVALENTS OF LEAVES

Within the past few years there has been increasing interest in the energy contributions of allochthonous detritus to the economy of the stream ecosystem. An integral part of the present study is the assessment of the calorific equivalents of the leaves from riparian trees that enter Doe Run throughout the year. On the basis of the abundance of leaves taken in the sampling trays and the total area of the stream under consideration, it is possible to estimate the calorific input to the stream from those leaves.

The calorific values of the kinds of leaves taken in the trays (Table 1) from 2,885 calories per gram, dry weight, for some hickory leaves to 4,875 cal/g for some sycamore leaves (Table 3). The averages for the 14 most abundant leaves ranged from 3,789 cal/g for hickory to 4,417 cal/g for red oak. Using the total weights of leaves listed in Table 1 and the average calorific equivalents for each species (Table 3), along with the estimated area of the uppermost 5 km of Doe Run as 5 hectares, the total energy contribution to the stream by leaves from riparian vegetation was nearly 74 million kilocalories (Table 3).

Although there was variation in the calorific values of the different kinds of leaves, it is difficult to discern meaningful trends in those variations. On a year-round basis of sampling of sycamore leaves, a minimum of 3,583 cal/g, dry weight, was found in April and a maximum of 4,873 cal/g was found in January; it was only in April that the monthly average fell below 4,200 cal/g. There were no demonstrable seasonal changes in calorific equivalents for any of the kinds of leaves tested. Obviously, the greatest calorific input was at Station I where the greatest numbers of leaves were collected and where the forest canopy was densest, and the least input was at Station IIA where the stream sides were flat and there was only a fringe of trees.

SEASONAL VARIATIONS IN LEAF NUTRIENTS

Just as important as the energy contributed to Doe Run by the leaves from riparian vegetation are the kinds and amounts of organic nutrients provided by those leaves. The three principal nutrients considered here are the carbohydrates, lipids, and proteins, which are the most important in the minds of other workers as well (Kaushik 1969, Kaushik and Hynes 1971). In addition, an attempt was made to determine at which seasons of the year the greatest contribution was made by each nutrient, and how rapidly the nutrients were lost

Table 3. Calorific equivalents, in calories per gram, dry weight, of the 14 most abundant kinds of leaves taken in trays at 4 stations in Doe Run, Meade County, Kentucky, together with estimates of the total kilocalories of energy contributed to the upper 5 km of the stream.

	Calories per gram		Total in stream (kcal)
	Range	Mean	
Sycamore	3,583-4,873	4,405	18,430,520
Red Oak	3,322-4,673	4,417	16,987,782
Sugar maple	3,540-4,215	3,882	6,642,102
Beech	3,094-4,508	3,909	6,664,845
White oak	3,327-4,444	3,979	5,009,561
Hickory	2,885-4,192	3,789	4,069,386
Chinquapin oak	3,839-4,590	4,083	3,405,222
Red elm	3,772-4,264	3,998	2,498,750
Ash	3,935-4,591	4,332	2,187,660
Grape	3,474-4,385	4,012	1,428,272
Dogwood	3,537-4,237	3,938	1,165,648
American hornbeam	3,672-4,483	4,054	713,504
Black cherry	3,046-4,661	4,125	606,375
Redbud	3,898-4,529	4,202	479,028
All other		4,080	3,537,360
Total	2,885-4,873	4,080	73,826,015

when leaves were submerged in the stream.

Extensive studies on the amounts of carbohydrates and proteins contained in leaves of sycamore, beech, and red elm leaves that had fallen into the trays indicate that the average protein content of sycamore leaves ranged from 42 to 71 mg/g with an annual average of 52.3 mg/g, with no apparent seasonal relationship. While freshly fallen leaves were being added to the stream (June through November), the protein content ranged from 42 to 60 mg/g, but in November and December the values increased from about 42 mg/g early in November to more than 70 mg/g in mid-December. During the rest of the year, the values remained near 50 mg/g. In beech leaves, the protein content ranged from 65.5 mg/g in early November to more than 90 mg/g in mid-October with an annual average of 78.6 mg/g. Here, there was no apparent relationship with seasons. In red elm leaves, the protein content ranged from 25.8 mg/g in September to 45.4 mg/g early in December with an annual average of 32.4 mg/g. The data for red elm leaves is too scanty to indicate whether or not there were any seasonal relationships.

The concentrations of sugars and related carbohydrates in sycamore leaves showed extreme variations throughout the year from a low of 13 mg/g in April to a high of 72.6 mg/g in August. Carbohydrate concentrations usually were high when freshly fallen leaves were accumulating in the stream from June through November but remained low and relatively constant the rest of the year. In beech leaves, concentrations of carbohydrates ranged from about 60 mg/g in October for freshly fallen leaves to about 20 mg/g in April for leaves that had been on the ground over winter. Similarly with leaves from red elm trees, freshly fallen leaves in September contained 65.5 mg/g whereas those that had remained on the ground until early December contained only 21.6 mg/g.

These limited data show that there is a wide divergence in amounts of nutrients in different kinds of leaves. For the kinds of leaves analyzed here, the best value for proteins is most likely that of the freshly fallen leaves because the increases recorded after they had been exposed to the natural degradation processes probably are traceable to the increases caused by accumulations in the saprotrophs (bacteria and fungi). Similarly, the values for carbohydrates in freshly fallen leaves are the truest ones since those materials are readily leached by rainfall. The longer they remain on the ground, the more the soluble carbohydrates are leached from the leaf material. There appears to be a close correlation between amount of precipitation and loss of carbohydrates from fallen leaves.

When the leaves of sycamore, beech, red oak, white oak, sugar maple, and red elm leaves were submerged in Doe Run, for 8 weeks, there was a net gain in the relative amounts of protein in all species. However, the net gain in protein content was greatest in red elm leaves and least in that of sycamore leaves (Figs. 2 and 3). With carbohydrates, there was a rapid initial loss in all kinds of leaves studied followed by what appeared to be a gradual leveling off to less than a third of the original concentrations. For lipids, the material was lost gradually either through leaching or through biological decomposition. During submergence, all kinds of leaves studied, gradually disintegrated but accurate measurements of weight loss were hampered by difficulty in separating small sand grains and marl deposits from the leaf fragments. Still, it was obvious that red elm leaves lost weight and underwent decomposition more rapidly than any of the other kinds. During the 8-week period of submergence, red elm leaves lost about 40% of their original weight, white oak and sycamore leaves lost between 20 and 30%, red oak and sugar maple leaves lost about 20%, and beech leaves about 10%.

On the basis of these limited data, it is possible to make preliminary estimates of the total contributions of those 6 kinds of leaves so far as

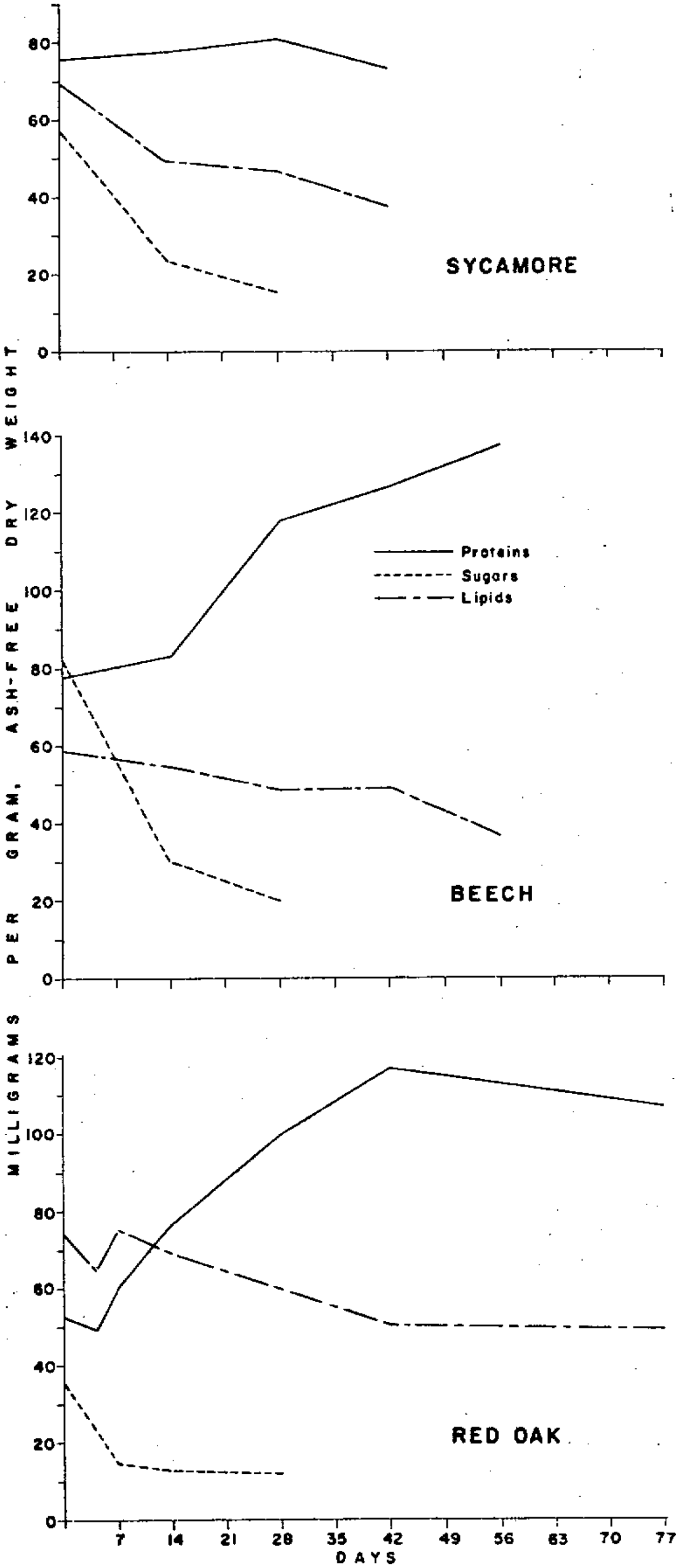

Fig. 2. Changes in amounts of proteins, carbohydrates, and lipids in leaves of sycamore, beech, and red oak trees during submergence in Doe Run, Meade County, Kentucky.

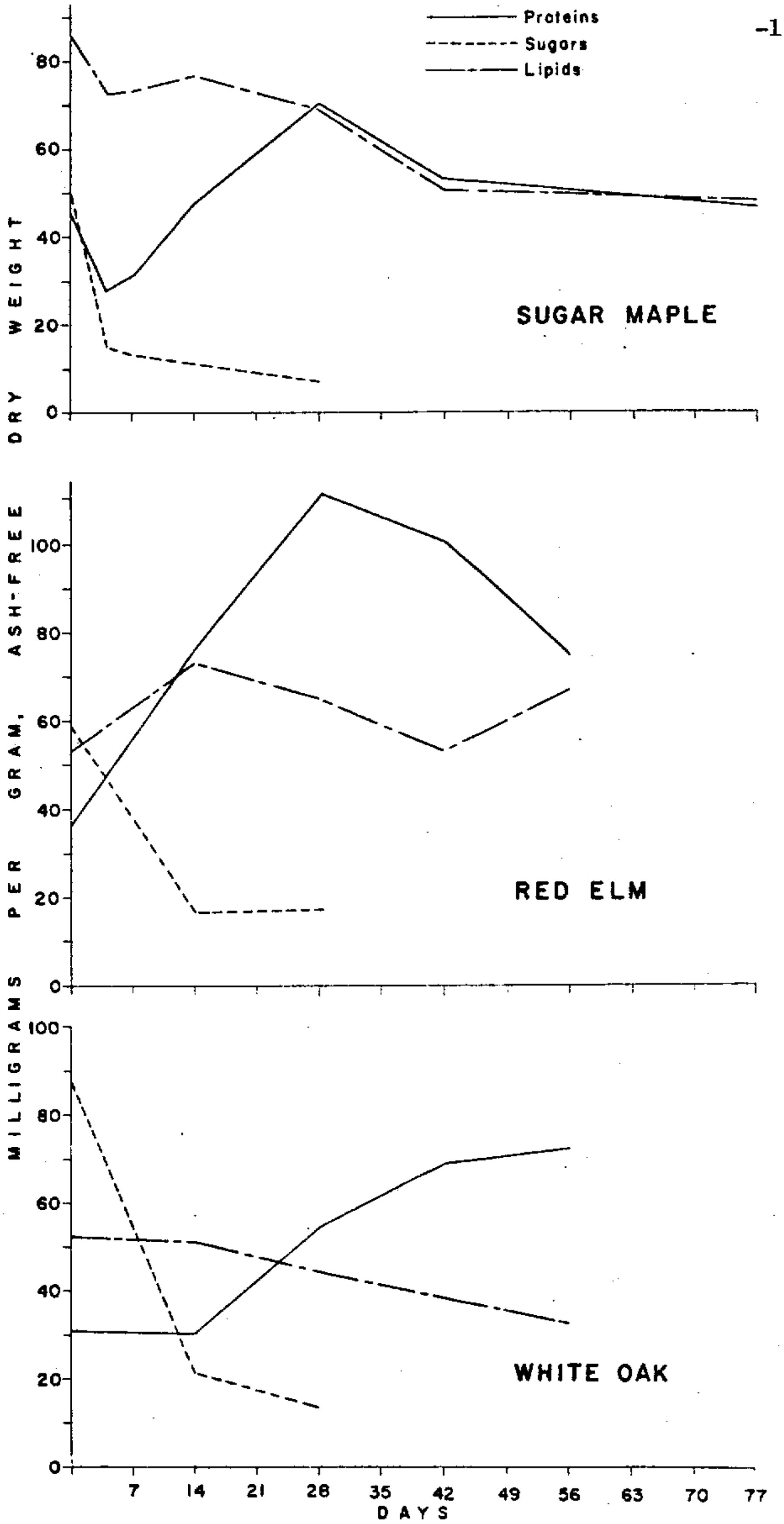

Fig. 3. Changes in amounts of proteins, carbohydrates, and lipids in leaves of sugar maple, red elm, and white oak trees during submergence in Doe Run, Meade County, Kentucky.

proteins, fats, and carbohydrates are concerned. Using the initial figures at the time of submergence, for each nutrient for each of the 6 kinds of leaves at each station, and an average of those values for all other leaves collected in the trays, it is estimated that leaves in the trays would have contributed 340.7 g of sugars and related carbohydrates, 404.4 g of lipids, and 340.0 g of proteins to the stream ecosystem (Table 4). Again, assuming that the samples in the trays are representative of the upper 5 km of Doe Run (Table 1), there were 1,019 kg of carbohydrates, 1,209 kg of lipids, and 1,017 kg of proteins for a total of 3,245 kg of those nutrients released into the stream during the year under study.

LEAVES AS FOOD FOR AMPHIPODS

Individuals of the indigenous amphipod *Gammarus bousfieldi* were offered a choice of sycamore, beech, red elm, red oak, and sugar maple leaves for 14 days, and showed a marked preference for red elm and sugar maple of which they consumed 29.7 and 10.8%, respectively, of the total weight offered. Those two kinds of leaves also decomposed more rapidly than the others when submerged in Doe Run. Of the other kinds of leaves offered, the amphipods consumed 5.4% of the sycamore, 4.9% of the red oak, and 3.9% of the beech.

When given a choice of the 3 least preferred kinds of leaves for 14 days, the amphipods consumed 6.2% of the beech, 4.4% of the sycamore, and 3.4% of the red oak. Concurrent observations in the laboratory indicated that hickory leaves were readily skeletonized by the amphipods, and when offered a choice of hickory and red elm leaves for 12 days, they consumed 18.8 and 12.5%, respectively. Here, again, it was demonstrated that red elm leaves decomposed more rapidly than hickory leaves when not exposed to the depredations of amphipods. These experiments were a preliminary attempt to understand more about the role of allochthonous leaf fall as a direct source of food rather than in the role solely of supplying nutrients to the stream ecosystem.

Table 4. Amounts in grams of carbohydrates (sugars and related substances), lipids, and proteins estimated to have been released annually from leaves of riparian trees into Doe Run, Meade County, Kentucky, together with estimates of amounts in kilograms released into the upper 5 km of the stream.

	Amounts of nutrients released						Total nutrients (kg)
	In Trays (g)			In Stream (kg)			
	Sugars	Lipids	Proteins	Sugars	Lipids	Proteins	
Sycamore	76.9	97.4	104.6	230.1	291.2	312.9	834.2
Red oak	46.3	95.2	67.1	138.4	284.6	200.7	623.7
Sugar maple	31.5	49.1	25.8	94.1	146.9	77.1	318.1
Beech	48.4	33.5	44.3	144.9	100.2	132.4	377.5
White oak	35.8	22.0	13.1	107.0	65.8	39.0	211.8
Red elm	11.5	11.2	7.7	34.4	33.6	23.1	91.1
All others	90.3	96.0	77.4	270.0	287.0	231.6	788.6
Total	340.7	404.4	340.0	1,018.9	1,209.3	1,016.8	3,245.0

DISCUSSION

Few attempts have been made to measure the contributions of allochthonous organic detritus to the economy of stream ecosystems even though their importance has long been recognized (Lindeman 1942). In the present study, efforts have been confined to the contributions of leaves from riparian plants and have not taken into account the contributions from woody materials, dead animals, animal wastes, and other dissolved substances that are carried into the stream either on a seasonal basis or as a result of flooding. Hynes (1963, 1970) pointed out some of the difficulties incurred in trying to separate the contributions of each of those materials. Of particular concern are the contributions from agricultural fertilizers, wastes from feed lots for cattle, swine, and other animals used as food by man, effluents from sewage disposal facilities, especially those with only primary treatment, and a great many lesser sources.

Darnell (1964) reported that organic detritus was heavily utilized as food by fishes and invertebrates in headwater streams, in brackish estuaries, and in littoral marine environment. As already mentioned, Minckley (1963) pointed out that allochthonous detritus was at least as important, if not moreso, as primary production to the overall economy of Doe Run, especially in areas some distance downstream from the source. He further stated that in streams such as Doe Run, fallen leaves contributed the greatest mass of detrital material. As the floating leaves settle out in pools and eddies of the stream course, "leaf packets" (Badcock 1954) form against obstructions in riffles where they undergo decomposition and release nutrients into the water. Minckley examined the guts of many kinds of primary consumers and showed that organic and inorganic detritus was a major food source. Minshall (1967, 1968) reported that the most important source of food for the entire benthic fauna of Morgan's Creek, Meade County, Kentucky, was allochthonous leaf material which occurred as suspended material in the water, as a component of materials attached to the streambed, and as whole leaves and fragments of leaves. He further showed that such materials made up more than 90% of the diet of the most abundant invertebrate in the stream, *Gammarus minus*. From the fundamental role of allochthonous leaf material as a major source of energy, he showed that its importance permeates the entire ecosystem. Nelson and Scott (1962) stated that primary consumers in a riffle of the Middle Oconee River, Georgia, derived two-thirds of their energy from allochthonous organic material. Still, those authors made no attempt to determine the energy contribution of that detritus to the stream ecosystem. Coffman et al. (1971), in a detailed study of a riffle area in a Pennsylvania woodland stream, reported that of the 75 most common species of macroconsumers, only 5 (4 dipterans and a mayfly) received more than half their caloric intake from detritus. However, they found that all but 1 of the 75 species utilized at least small amounts of detritus during some stages in their life cycles, and that there was a general pattern for young individuals to feed largely on detritus and to change over to algae and other animals as they grew older.

The amounts of leaf litter in Doe Run differ from those of other studies. Mathews and Kowalczewski (1961) reported the input into the Thames River, England, to be about 23.2 g/m^2/year by measuring litter fall along the shoreline. But Murless (University of Georgia, pers. comm. to Liston) stated that about 5.4 times the litter fall from a known area of riparian forest entered an equivalent area of woodland stream in Georgia. Annual averages for Doe Run ranged from about 80 g/m^2/year in trays suspended over the stream at Station III to about 1,118 g/m^2/year in trays affixed to the bank at Station I. In the present study, no more than about 29% of the total leaves collected from trays were taken in those suspended over the stream; the average for all stations was 23%. From these data it is obvious that the major portion of allochthonous leaf fall entering Doe Run was windblown.

The average values for all stations was 354 g/m^2/year for Doe Run, about 17,700 kg for the upper 5 km of the stream for the entire year. Murless (pers. comm.) reported an average litter input of about 1,700 g/m^2/year for a small stream in Georgia, and McConnell (1968) estimated that about 750 g/m^2 of litter entered Penna Blanca Lake, Arizona, during 1959 but that only about 50 g/m^2 entered the lake in 1965 and again in 1966. Also, Bray and Gorham (1964) reported that litter production in the same forest can vary from year to year because of climatic variations. These data corroborate our findings that litter input varies considerably from year to year at a particular locality and that the value of those measurements lie primarily in their applicability to the particular body of water under consideration. It has been pointed out earlier that the amount of rainfall during the winter may have had a marked effect on the verdancy of the forest and hence on litter production. When our data from October 1968 through 24 November 1969 are assembled into annual periods beginning at intervals of 2 weeks (Table 5), it is apparent that there is a difference of 249 g/m^2/year among the 5 annual totals, a deviation of 18.6% from the mean.

In temperate zones of the world, greatest accumulation of litter occurs in Autumn; about 80% of the annual accumulation in Doe Run took place from early September through November, with by far the greatest portion falling in October. Similar results have been reported from Missouri (Bray and Gorham 1964) where 60% of the annual leaf fall occurred from September through November, and in New Hampshire, where 80% of the mixed angiosperm litter falls in October. Such a sudden influx of organic material is known to have drastic effects on water quality, especially in small streams. In

Table 5. Differences in annual leaf fall, in grams per square meter, at two-week intervals at each of 4 stations in Doe Run, Meade County, Kentucky, together with the total leaf fall in the trays for each period.

	Station No.				Total
	I	II	IIA	III	
10/1/68-9/30/69	644	369	167	236	1416
10/15/68-10/14/69	663	407	173	255	1498
10/29/68-10/28/69	553	327	143	231	1254
11/11/68-11/10/69	534	342	146	227	1249
11/25/68-11/24/69	532	351	144	234	1261
Average	585	359	155	237	1336

Doe Run (Minckley 1963), accumulations of leaves in the fall were sufficient to block riffles in the downstream areas where they caused oxygen deficits in pools at night or on cloudy days in spite of the relatively swift nature of the stream. "Black waters" have been caused by leaf accumulations in streams (Schneller 1955, Slack 1955, Larimore et al. 1959) with concurrent deoxygenation of the water to levels at which much of the fauna dies or is forced to leave the area. Slack and Feltz (1968) reported that the solute load in a small stream in Virginia was altered rapidly by allochthonous leaves, and that the water quality parameters most influenced by submerged litter were dissolved oxygen, pH, specific conductance, iron, manganese, bicarbonate, and color of the water. Also, they pointed out that there is a direct correlation between rates of leaf fall and changes in water quality at low discharge rates.

The oxygen demand of decomposing maple leaves is equivalent to about 75% of their weight whereas oak leaves and pine needles have an oxygen demand of about 50% of their weight (Chase and Ferullo 1957). If the demand for oxygen by the nearly 20 tons of leaves that enter Doe Run each year is in the range of 50% of the weight, it is readily apparent why such accumulations can cause critical levels of dissolved oxygen in streams, particularly in the fall when discharges frequently are minimal. Schneller (1955) pointed out similar conditions in Salt Creek, Indiana, as did Minckley (1963) for Doe Run.

The calorific values for different kinds of leaves were slightly higher (Table 3) for most kinds than those reported by Golley (3,902 cal/g, 1961), but were lower than those reported by Triska (1970: 4,757; 4,918; and 4,352 for sugar maple, red oak, and American elm, respectively) but our values for ash were higher than his (4,286 cal/g). In a more recent study, Cummins and

Wuycheck (1971) tabulated mean values for calorific equivalents for organisms in different trophic levels, and pointed out that there may be marked differences within species as well as among species. In the present study, the ranges in calorific values within species was as little as 492 cal/g for red elm and as great as 1,615 cal/g for black cherry (Table 3). The overall range among species was from a low of 2,885 cal/g in some samples of hickory leaves to a high of 4,873 cal/g for some sycamore leaves, a total range of 1,988 cal/g. Still, there was no obvious relationship between calorific values and season of the year. It is important to note, however, that standard values should be based on freshly fallen leaves since there may be considerable leaching during rainfall, and values will change as biological degradation takes place. Similarly, values from the same kinds of trees in different parts of the country are likely to be different, as shown by the values reported by Triska (1970) and Cummins and Wuycheck (1971) for Pennsylvania, Golley (1961) for Georgia, and Kaushik (1968), Hynes and Kaushik (1969), and Kaushik and Hynes (1971) for Ontario. As pointed out much earlier by Cummins (1966), the energy from autochthonous detritus is not sufficient to support the total stream biota, and that many workers in different parts of the continent have recognized the importance of the energy from allochthonous detritus, especially riparian leaf materials, as a specific requirement for the proper functioning of the stream community. Still, we believe that variations in calorific equivalents, however great they may be, are small enough that the potentially available energy from each kind of leaf can be estimated from dried leaf material and that a single value for energy content is all that is needed.

So far as Doe Run is concerned, much of the nearly 74 million kilocalories of energy derived from riparian leaves may be transported out of the ecosystem, not having been used in the trophic aspects of the stream community, but there is no estimate for that figure. It is known that much of the leaf detritus is reatined in the mill ponds as the leaves become waterlogged and decompose in those impoundments. However, the released nutrients may or may not be used before leaving the stream. With the construction of the dam for Doe Valley Lake in 1961 (see Fig. 1), it is believed that most of the nutrients released into the upper 5 km of Doe Run from allochthonous detritus never reach the Ohio River, but may well be used in primary or secondary production in the areas upstream from the dam.

The protein contents of freshly fallen leaves determined in this study lie within the range of those reported in the literature. In a study of water-insoluble protein of 9 species of autumnal leaves, Melin (1930) reported values that ranged from 2% for pitch pine (*Pinus rigida*) to 11% for paper birch (*Betula papyrifera*). His estimates for sugar maple and beech were 4.13 and 3.0% respectively, compared with our estimates of 4.5 and 7.8%. Kaushik and Hynes reported protein percentages of 7.7 and 6.5%, respectively, for white oak and American elm, whereas our estimates were 3.1 and 3.7%, for white oak and red elm leaves, respectively. Any comparison of such studies of leaf analysis is fraught with danger because of the likely differences in soil nutrients in different geographic areas. Although Daubenmire (1953) demonstrated that differences in nutrient content are primarily species related, Ovington (1956) mentioned reports of earlier workers who showed that the composition of tree leaves is not constant, but changes while the leaves remain on the trees, and that chemical composition can differ in successive years and can vary with crown position. Lutz and Chandler (1946) reported that such soil conditions as pH, nitrogen, potassium, and phosphorus concentrations can affect the chemical composition of tree leaves.

In all leaves submerged in nylon net bags in Doe Run with the exception of sycamore leaves, there was an increase in protein content. Kaushik and Hynes (1968) reported an increase in the protein content of submerged American elm leaves but not in those of alder or white oak. Also, Odum and de la Cruz (1967) reported an increase in decomposing leaves of *Spartina alternifolia* in a Georgia salt marsh with increased time of submergence and decreased size of detritus particles. Kaushik (1969) reported that leaves of American elm, alder, white oak, beech, and sugar maple increased in protein and nitrogen content when allowed to decompose in nutrient enriched water in a natural stream, particularly in the elm and maple leaves. In the present study, red elm leaves underwent a more rapid increase in protein content than any of the other species studied, and had an increase of 20% of the original weight in 28 days. Goldman (1961) reported that nitrogen drainage from shore lined with alder trees contributed about 15% of the average nitrogen content of Castle Lake, California, from June to October.

The relative increase in protein in submerged leaves may be due in part to the leaching of water-soluble non-nitrogenous substances, but it is believed that there is also an actual addition of protein to the leaves while decomposition progresses. Kaushik (1969) reported actual increases in all kinds of leaves studied, and Mathews and Kowalczewski (1969) reported similar increases in oak, willow, and sycamore leaves that had been submerged in the Thames. It was concluded by Kaushik (1969) that the growth of fungi was the primary cause of the increase in protein. This was demonstrated earlier by Kaushik and Hynes (1968) when they incubated elm leaves in the presence of a bacteriocide and recorded an increase, but recorded a consistent decrease in protein when such leaves were incubated in the presence of a fungicide. Triska (1970) also observed that when leaves were submerged in the presence of antibiotics the fungi were primarily responsible for oxygen consumption and leaf decomposition. The most abundant leaf in Doe Run (sycamore) showed little overall change in protein content when submerged for 42 days (Fig. 2) but had shown an increase during the first 4 weeks. All other kinds showed changes in protein content during submergence (Figs. 2 and 3) but there was a marked overall increase in each.

The different kinds of leaves that entered Doe Run lost from 55 to 80% of the sugars and related carbohydrates during 2 weeks of submergence (Figs. 2 and 3). Coldwell and DeLong (1950) also reported an early rapid loss of sugars, starches, and nitrogenous substances during initial stages of leaf decomposition. Nykvist (1963) reported similar results from his studies and noted that leaves of European beech (*Fagus sylvatica*) lost 6.2% and ash (*Fraxinus excelsior*) lost 20.8% of those materials, in a single day. The rapid loss of carbohydrates from weathering leaves along the banks of Doe Run, as well as from the leaves that enter the stream, undoubtedly have a major effect on the overall energy regime. When it is considered that those materials leach readily from the leaves it seems likely that the input of carbohydrates is increased markedly during the late fall and winter rains. Those materials would enhance the growth of the saprotrophs in the leaf litter which in turn could be used directly by organisms in the stream. McConnell (1968) reported that newly hatched *Xenopus* larvae increased significantly in weight when fed on the bacterial biomass that grew on the soluble extract from oak leaves, and Fredeen (1964) reported that blackfly (*Simulium*) larvae are able to convert bacterial biomass into body tissue. Adams (1970) reported that carbohydrates, when added to artificial ponds at warm temperatures, were utilized an an energy source by algae, and that the numbers of saprotrophs increased very rapidly. Also, Warren et al. (1964) reported a dramatic increase in growth of cutthroat trout (*Salmo c. clarki*) when concentrations of dissolved sucrose were maintained at 2-4 ppm in the hatchery waters.

The amounts of lipids in the various kinds of leaves studies here ranged from about 52 mg/g of leaf material in freshly fallen beech leaves to about 86 mg/g in sugar maple leaves (Figs. 2 and 3), and were next to proteins in total nutrient content in such leaves. In initial content, they outranked proteins in 4 of the 6 species studied, and in red oak and sugar maple leaves they were higher than either proteins or carbohydrates. It has been reported by Doby (1965) that plant fats are present in relatively small amounts in all parts of the plant except for certain storage organs as seeds and fruits. Odum and de la Cruz (1967) reported about 4% by weight of fats in marsh grass, and that there was only a slight loss on standing in water. It may well be that saprotrophs are responsible for the breakdown and release of lipids. McConnell (1968) reported only slight traces of lipids in water extracts from oak litter, suggesting that those substances are not water soluble.

The results of our feeding experiments with amphipods are in general agreement with the findings of Hynes (1963, 1970), Hynes and Kaushik (1969), Kaushik and Hynes (1968), Kaushik (1969), Wallace et al. (1970), and others. Although those workers used isopods, insect larvae, and other invertebrates as well as amphipods in their studies, the findings agree that some leaves serve directly as food and that there was a distinct preference for certain kinds of leaves over others. It was reported by Wallace et al. (1970) that nymphs of the stonefly *Peltoperla maria* usually avoided leaves of sycamore, beech, and white oak trees but readily ate elm, sourwood, alder, and dogwood leaves. Also, in Europe, Levanidov (1949) and Bölling (1962) have shown that there is food preference among aquatic invertebrates for deciduous tree leaves, especially elm and alder, over others.

The fact that in this study the amphipods preferred the hickory leaves over all other kinds offered and that they largely avoided leaves of sycamore, red oak, and beech trees indicates that the preferences are not related solely to the rapid degradation of the leaves. The red elm leaves decomposed most rapidly and the hickory leaves most slowly when submerged in the stream, yet each was preferred over other kinds. Still, it may be that the availability of leaves as food depends on the length of submergence. With leaves being blown by the wind into the stream throughout the winter, leaf detritus usually is available in all stages of decomposition and in great variety. In such a situation there is assurance of a degree of stability in energetics available throughout the trophic structure of the stream. In any event, the role of allochthonous detritus in the energy regime of flowing waters in deciduous temperate forests is a major one. Such materials serve directly as food for many kinds of organisms and the nutrients released during decomposition are widely utilized in primary and secondary production.

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