

LEAF PROCESSING IN THE SANGAMON RIVER, ILLINOIS¹

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ABSTRACT

Changes in weight of leaves of *Platanus occidentalis* L. and *Acer saccharinum* L. were assessed during processing in the Sangamon River, which drains cropland in east-central Illinois. A processing coefficient of 0.0267 was obtained for leaf packs of maple and 0.0259 for sycamore. Processing coefficients calculated per unit area of leaf tissue remaining (leaf discs) were 0.0120 for maple and 0.0014 for sycamore. Maple leaves were extensively skeletonized and were processed more rapidly than those of sycamore. Sycamore leaves were not skeletonized and disappeared primarily by fragmentation. Leaves of sycamore and maple disappeared at rates similar to or higher than leaves in other lotic systems studied. The concentration of protein in leaves of both maple and sycamore increased, but in maple, absolute amounts decreased with increased time of submergence. In sycamore leaves, absolute amounts of protein increased to a maximum in 40 days and remained at about the same level throughout the study.

INTRODUCTION

Leaves of riparian origin are known to be an important source of fixed carbon for heterotrophic organisms living in streams (Hynes, 1963; Darnell, 1964; Cummins, et al., 1966; Coffman, et al., 1971; Cummins, et al., 1973). Leaves entering streams disappear in approximately one year due to leaching, mechanical fragmentation, direct grazing by stream invertebrates and use by microorganisms (Mathews & Kowalczewski, 1969; Kaushik & Hynes, 1971; Gosz, et al., 1973; Iverson, 1973; Anderson & Grafius, 1975; Boling, et al., 1975; Sedell, et al., 1975; Suberkropp, et al., 1976). Rates at which leaves disappear are affected by leaf type (Petersen & Cummins, 1974), leaf pack size (Reice, 1974), temperature (Reice, 1974), inorganic nutrient levels (Kaushik & Hynes, 1971), stream size (Sedell, et al., 1975) and substrate composition (Reice, 1974).

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Most field studies of leaf processing have been made in clear fast-flowing streams and springbrooks (Thomas, 1970; Krumholz, 1972; Iverson, 1973; Petersen & Cummins, 1974; Sedell, et al., 1975; Suberkropp, et al., 1976; Triska & Sedell, 1976) and in creeks and rivers (Mathews & Kowalczewski, 1969; Triska, 1970; Kaushik & Hynes, 1971; Paul, 1978). With the exception of an investigation of processing in a pastureland stream by Benfield, et al. (1977), there has been little study of leaf processing in streams and rivers in areas with small elevational differences and which drain primarily agricultural regions. It might be expected that slow flow rates, extremes in discharge, high levels of nitrates and phosphates, and high rates of sedimentation often associated with agricultural streams would affect organisms using leaves and hence the rates at which leaves are processed. The following study was undertaken in a river system in an agrarian area to determine whether processing of leaves occurs in a manner and at rates similar to those reported from other lotic systems.

STUDY SITE

The upper Sangamon River originates in east-central Illinois and flows south-westerly through wide flat valleys located in gently rolling to flat cropland. Although many of the tributaries, which originate from drainage tiles in cropland, are clearcut and channelized to facilitate drainage, much of the main artery of the river system is surrounded by floodplain vegetation. A sampling station was located on the upper Sangamon River 6.9 km NE of Mahomet, Champaign Co., Illinois ($40^{\circ} 15' 48''$ lat., $88^{\circ} 24' 30''$ long.). This corresponds to Site 1 in the study of physical and chemical characteristics of the upper Sangamon River made by Brigham (1975). The river at this station is bordered by floodplain vegetation with *Acer saccharinum* L. (silver maple) and *Platanus occidentalis* L. (American sycamore) as the predominant tree species. Considerable primary production in the clearcut drainage ditches and in the open areas of the river combined with smooth flow result in diurnal changes in D_0 , CO_2 and pH. The substrate is composed primarily of fine silt and sand with occasional patches of gravel or very large rocks.

Monthly averages and extremes of daily discharge rates for the period of study have been measured at Mahomet ($40^{\circ} 11' 30''$ lat., $88^{\circ} 24' 00''$ long.) by the U.S. Geological survey (1976, 1977). Discharges ranged from 0.145 to 144.045 with a mean of $9.7012 \text{ m}^3 \text{ sec}^{-1}$ during Study I and from 0.845 to 110.089 with a mean of $8.834 \text{ m}^3 \text{ sec}^{-1}$ during Study II. Maximum ranges in discharge and maximum discharges occurred in January and February during Study I and in February and March during Study II. Low mean discharges occurred in October, November, December and May during Study I and in October, November, January, May and June in Study II. Extreme ranges in discharge and depth result from the modification of the river system to facilitate drainage from cropland. During periods of high discharge, the river flows over its banks onto extensive floodplains where it entrains large quantities of fine silt and organic matter and deposits leaves and twigs.

The average velocities, calculated monthly from cross-sectional area and discharge, at Mahomet, Ill. for the duration of Study I ranged from 20.7 to 79.3 with a mean of 59.8 cm sec^{-1} and from 43.3 to 86.3 with a mean of 64.3 cm sec^{-1} for Study II (U.S. Geological Survey, 1976, 1977). The surface of the water is smooth with few riffle areas visible except at times of low discharge.

METHODS

1. Sampling Procedure

Two studies were made in successive years, 1974-75 (Study I) and 1975-76 (Study II). In Study I, fresh fallen leaves of maple and sycamore were collected along the banks of the Sangamon River during late October. Leaf packs were made by stacking ten maple leaves or five sycamore leaves and passing braided nylon fishing line through their centers several times. Whole leaves were cut into approximate fourths and placed in mesh bags. Leaf discs (1.5 cm diam) were cut from fresh fallen leaves with a cork borer and placed in nylon mesh bags (1 mm² pore size). Leaves and leaf discs used for dry weight determination were oven dried (80 C to constant weight) and weighed before they were submerged.

Because of large fluctuations in water level and high rates of siltation, the commonly used technique of tying leaf packs to bricks and placing them on the stream bottom was not feasible. Thus leaf packs and mesh bags were attached to a nylon rope anchored at one end by a cement block which in turn was attached by a nylon rope to a tree above flood level on the river bank. Leaves were submerged on 4 Nov 1974, and three samples were removed randomly at approximate two week intervals until 15 May 1975.

Leaf packs remained intact under the discharge regime of the river during Study I. Since mesh bags provide an unnatural protection to the leaf tissue and appeared not to be necessary, they were not used during Study II. Because of low flow rates at certain times, strings of leaf packs often rested on the river bottom and became partially covered with silt. Thus in Study II, leaf packs were attached to lines suspended by floats, which kept all the packs approximately 15 to 20 cm below the surface of the water regardless of water depth. Leaf packs were submerged on 15 Nov. 1975, and three samples were removed randomly from the river after one week and at approximate monthly intervals until 14 June 1976, except when the river was frozen.

2. Dry Weight Determination

Leaves and leaf discs were washed gently, dried (to constant weight at 80 C), cooled in a desiccator, weighed and ground in a Wiley Mill. Percent ash was determined by heating duplicate 50-100 mg samples at 550 C for 3 hr. Whole leaves in packs were separated and discs cut from them. These fresh-cut discs were then washed, dried, weighed, ground and ashed as above.

A processing coefficient (K) was estimated by a least squares fit of the mean ash-free dry weights at each sampling time to the exponential function $Y_t = Y_0 e^{kt}$. The fit of each weight-loss regression line to the exponential decay model was tested for significance by ANOVA. Processing coefficients were also calculated using initial and final ash-free dry weights according to the equation used by Petersen & Cummins (1974): $-K = \ln (\% \text{ remaining} \times 100) / \text{time}$. Differences between k-values from different treatments were tested for significance with a t-test.

3. Protein Measurement.

At each sampling in Study I, five discs each, from leaf packs, bagged leaves and precut discs, were gently washed with distilled H₂O, placed in 10 ml of 0.02 M glycine buffer (pH 7.8) at 100 C for exactly one minute, and cooled in an ice bath. The contents were homogenized by hand in a tissue grinder and frozen (-20 C) until time of assay. This material was then thawed and centrifuged. The amount of ATP present in the supernatant was determined by a modification of the method

described by Holm-Hansen (1973). Both the remaining supernatant and precipitate were washed onto a 0.45 μ m Millipore filter, dried and weighed. The leaf material was washed from the filter with 10 ml 0.1 N NaOH and extracted for protein by the method described by Kaushik and Hynes (1968). The protein content of triplicate aliquots was determined by procedures described by Lowry et al. (1951). When the supernatant from the ATP procedure was analyzed, no measurable protein was found, thus protein values were from analysis of the ppt only. During Study II, protein was determined from homogenized ground leaves rather than the precipitate from the ATP assay.

RESULTS AND DISCUSSION

I. Leaf Processing

During Study II, packs of sycamore leaves were processed more rapidly in the Sangamon River (Table 1) than in a pastureland stream in Virginia ($K = 0.0057$) (Benfield, et al., 1977). Paul (1978) found that processing coefficients of packs of sycamore leaves not in contact with the substrate varied considerably and generally were much higher than those obtained in other stream systems ($K = 0.0009$ to 0.0761). Enclosure of samples in a wire mesh container resulted in lower processing coefficients ($K = 0.0017$ for 20 g packs and $K = 0.0011$ for 10 g packs) than those observed for leaves in the Sangamon River.

Processing coefficients for leaf packs of silver maple in Study II were over twice as large as those reported for silver maple leaves placed in Augusta Creek, Michigan from December to May ($K = 0.0107$, $K = 0.0066$) (Petersen & Cummins, 1974). The difference between processing in the two systems could be due in part to different submersion techniques. Leaves in the Augusta Creek study were attached to bricks which may have provided support to the leaf packs, thereby reducing mechanical fragmentation. Of the processing coefficients reported for leaf packs of various other tree species, the processing coefficients of leaf packs of maple and sycamore were closest to those of *Tilia americana* L. ($K = 0.0234$) and *Carya glabra* (Mill.) Sweet ($K = 0.0305$) in Augusta Creek, Michigan (Petersen & Cummins, 1974).

Processing coefficients for maple leaves were significantly higher than those for sycamore in all instances except two (Table II). Differences were only weakly significant for discs cut from unbagged leaves in Study I, and were not significant for leaf packs in Study II. In Study II, at the end of 130 d, less than 10% of maple and 20% of sycamore packs remained (Fig. 1B). In contrast, loss of weight per unit area remaining (fresh-cut leaf discs) of sycamore leaves occurred much more slowly than in maple; after 130 d, 17.5% of the original maple tissue remained, while 89% of the original sycamore tissue remained (Fig. 1A). Observations of leaves during processing indicated clearly that leaves of the two species disappeared in different ways. Soon after submersion, the epidermal layers of maple leaves separated from the mesophyll layer, exposing the mesophyll to grazers and microbial activity. Almost total skeletonization of maple leaves occurred within 34 d after submersion during Study II. In contrast, the epidermis of sycamore leaves remained firmly attached to the mesophyll layer throughout the study and little skeletonization occurred. Loss of leaf tissue in sycamore occurred primarily by fragmentation of large pieces from the outer edges of leaves. Thus for leaf packs in Study II, processing coefficients for maple and sycamore leaves were similar (Table 1), but for

different reasons. In leaf packs, which were fully subjected to mechanical abrasion, no significant differences in the rate of processing between sycamore and maple leaves were discerned. When a technique was used which inhibited fragmentation (placing leaves in mesh bags), or when samples taken from tissue remaining were compared, distinct differences in the rates at which the leaf tissues of the two species were processed became apparent (Table II).

Occasional increases in percent ash-free dry weight remaining (Figs. 1A&B, 3A&B) were an interesting characteristic of several of the weight change patterns. The river system is heavily dependent on precipitation and drainage for water, and discharge and flow rates are greatly reduced at times of low precipitation. At such times, the system becomes more lentic than lotic and large numbers of leaves float gently downstream or accumulate in shallow water along the sides of the river. Low flow rates may have permitted extensive colonization of leaves by protozoans, algae, filamentous bacteria and fungi, all of which have been seen on the leaves either by direct microscopic examination or observation with SEM. Changes in weight of leaves at times of low flow probably reflect the activity of the biological community much more than the physical effects of flowing water. Thus during periods of low flow, maple leaves which appear to be used more extensively by invertebrates and microorganisms than sycamore leaves should disappear steadily while sycamore leaves which are colonized but not used extensively should disappear less rapidly, remain the same, or increase in weight. When leaves were submerged in Study II, they were first subjected to a period of low discharge; maple discs decreased while sycamore discs increased in weight (Fig. 1A). At this time, maple leaves were somewhat skeletonized but sycamore leaves were not. This period of low discharge was followed by one of fluctuating discharge (maximum—37 m³/sec) and a subsequent decrease in weight in both sycamore and maple leaves occurred. Then a period of low mean discharge and small fluctuations in discharge occurred, accompanied by a concomitant increase in weight of discs of both sycamore and maple. Park (1974) reported weight increases in cellulose filter paper contained in mesh bags submerged in the Inler River, Northern Ireland. The increases were greater in samples submerged in smooth flowing water with both slow and fast flow rates than in water with fast turbulent flow. Both this study and that of Park indicate clearly that measurement of changes in weight is not a highly reliable technique to use to determine rates of decomposition in rivers with smooth water flow.

In Study II, leaves were suspended from the surface and when the river froze, the leaves were also frozen in the ice. Changes in weight of leaf packs were markedly reduced during the time of ice cover but increased rapidly after the spring thaw (Fig. 1B). Probably the mechanical action of freezing and thawing on plant tissues followed by extremely high discharges, resulting from the spring thaw and rains, brought about large losses of leaf tissue. This was reflected in a rapid weight loss between 90 and 110 days of submersion, well before the temperature rose to above 5 C. In the Sangamon River, large quantities of leaves tend to float on or near the surface of the water and become bound in the ice. This material is unavailable to the system until the ice thaws.

Leaves located at or near the bottom of the river, as in Study I, were in a zone of slower water velocity and became more heavily covered with silt and detritus which could have resulted in reduced oxygen levels in leaf packs. Reduced water velocity, low oxygen levels and siltation are all factors which could have a detrimen-

tal effect on leaf shredders and microorganisms. During Study II, all samples were near the surface of the water where water velocity was greater and siltation reduced. The processing coefficient of discs cut from maple leaves was significantly greater in Study II than in Study I, while the processing coefficients of discs cut from sycamore leaves did not differ significantly between the two studies (Table II). Maple leaves, which were heavily skeletonized, appeared to be more affected by placement in the water column than sycamore leaves which were not skeletonized.

2. Protein Measurement

The protein content of leaves has been observed to increase with submersion time in streams (Kaushik & Hynes, 1971; Krumholz, 1972; Barlocher & Kendrick, 1974), thereby increasing the nutritional quality of the leaves. Nitrogen alone or N and P together added to leaves incubated in dishes resulted in an increase in protein of the leaves (Kaushik & Hynes, 1971). This suggests that nutrient levels in a stream might affect the degree of protein enrichment of leaves submerged in that stream. Since the Sangamon River receives extensive run-off from cropland fertilized with N and P, it might be expected that submerged leaves would show considerable protein enrichment. Protein increased, as percent of the ash-free dry weight, in both leaf species with increasing time of submersion (Fig. 2B, 4A&B). Protein increased more in sycamore than in maple leaves and the relative amount in sycamore leaves was twice as large at the end of both Studies I and II than at the beginning. These increases in protein are in line with those reported for leaves submerged in the Speed River, Canada (Kaushik & Hynes, 1971). Krumholz (1972) found, inexplicably, very little increase in protein of sycamore leaves submerged in Doe Run, Kentucky, even though the protein concentration of leaves of other species submerged at the same time increased.

The protein present as percent of the ash-free dry weight per unit area of leaf (Fig. 2A), reflects the differences in the way in which maple and sycamore leaves are processed. During Study II, the percent protein per unit area of maple leaves (Fig. 2A) declined initially as the leaves became skeletonized, then increased from December to February, but declined thereafter. The percent protein per unit area of sycamore leaves (Fig. 2A) increased initially, decreased briefly in December, increased during January and then decreased slowly thereafter. Although sycamore leaves became protein enriched, it appears that this material is not used directly by grazers to any large degree. Given the high quantity of lignin in sycamore leaves (Paul, 1978), it is possible that protein becomes complexed in phenolic-lignin compounds in sycamore and therefore is unavailable to heterotrophic organisms.

SUMMARY

As a result of extensive clearcutting and channelization of most of the tributaries of the upper Sangamon River, large fluctuations in temperature, inorganic nutrient levels, turbidity and discharge occur (Brigham, 1975). Small elevational differences along the river system result in generally smooth flow in the main channel of the river. It does not appear that physical and chemical conditions in the Sangamon River affect the processing of leaves adversely since they disappear at rates similar to or higher than leaves in other lotic systems studied. The rapidity with which leaves disappeared in February and March, when discharges were extremely high, suggests that the high discharges encountered in a system modified for water removal from croplands, may contribute to a short residency of leaves in

this type of river. During periods of high discharge, leaves may be washed downstream, fragmented into smaller pieces, which can then be carried downstream by slower flowing water, or deposited on the floodplain during over-the-bank floods. Leaf loss during high discharges can effectively reduce the food resources available to invertebrates. Since precipitation is unpredictable, the availability of one of the major food resources is also unpredictable. Thus the floodplain of the river, which serves as a continual source of leaves, may be very important in stabilizing food resources within the river.

Silver maple leaves were processed much differently than those of sycamore, but these differences were not detected by the standard technique of measuring changes in weight of leaf packs. Differences were detected, however, when changes in weight per unit area were compared. These two types of weight measurement, when applied to material being processed, provide more information about the way in which leaves are processed than either technique used alone. Although leaf packs of both species disappeared at the same rate, leaf tissue of maple was always processed more rapidly than that of sycamore. Maple leaves disappeared primarily through skeletonization and appear to be an important food resource in the Sangamon River. Sycamore leaves do not become skeletonized but disappear primarily through fragmentation. Although sycamore leaves do not seem to be used as a food resource, they may be important as sites of attachment for periphyton and as traps which filter benthic diatoms washed downstream from clear cut feeder streams.

The increases in ash-free dry weights, which were observed frequently, may result from a combination of colonization activities and trapping of algae and other organic materials. These increases may cause actual losses of weight of leaf tissues to be underestimated. Further studies of a different design are needed to sort out the respective effects of colonization and utilization on changes in ash-free dry weight of leaves in this type of river system.

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LITERATURE CITED

- Anderson, N. H. and Grafius, E. 1975. Utilization and processing of allochthonous material by stream Trichoptera.—*Verh. Int. Ver. Limnol.* 19: 3083-3088.
- Barlocher, F. and Kendrick, B. 1974. Dynamics of the fungal population on leaves in a stream.—*J. Ecol.* 62: 761-791.
- Benfield, E. E., Jones, D. R., and Patterson, M. E. 1977. Leaf pack processing in a pastureland stream.—*Oikos* 29: 99-103.
- Boling, R. H., Goodman, E. D., Van Sickle, J., Zimmer, J. O., Cummins, K. W., Peterson, R. C. and Reice, S. R. 1975. Toward a model of detritus processing in a woodland stream. *Ecology* 56: 141-151.
- Brigham, W. U. 1975. Physical and chemical limnology of the Sangamon River Basin. pp. 93-131. In: Bell, D. T. and Johnson, F. L. (eds.), *The upper Sangamon River Basin: Final report for the Springer-Sangamon Environmental Research Progr.*, Dept. Forestry and Ill. Agr. Exp. Sta., Univ. of Ill.
- Coffman, W. P., Cummins, K. W. and Wuycheck, J. C. 1971. Energy flow in a woodland stream ecosystem: I. Tissue support trophic structure of the autumnal community.—*Arch. Hydrobiol.* 68: 232-276.
- Cummins, K. W., Coffman, W. P. and Roff, E. A. 1966. Trophic relationships in a small woodland stream.—*Verh. Int. Ver. Limnol.* 16: 627-638.

- . Petersen, R. C., Howard, F. O., Wuycheck, J. C. and Holt, V. I. 1973. The utilization of leaf litter by stream detritivores.—*Ecology* 54: 336-345.
- Darnell, R. 1964. Organic detritus in relation to secondary production in aquatic communities.—*Verh. Int. Ver. Limnol.* 15: 462-470.
- Gosz, J. R., Likens, G. E. and Borman, F. H. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire.—*Ecol. Monogr.* 43: 173-191.
- Holm-Hansen, O. 1973. Determination of total microbial biomass by measurement of adenosine triphosphate.—pp. 73-89. In: Stevenson, L. H. and Colwell, R. R. (eds.). *Estuarine microbial ecology* Univ. South Carolina Press, Columbia, S. C.
- Hynes, H. B. N. 1963. Imported organic matter and secondary productivity in streams.—*Proc. XVI Int. Congr. Zool.* 3: 324-329.
- Iverson, T. M. 1973. Decomposition of autumn-shed beech leaves in a springbrook and its significance for the fauna.—*Arch. Hydrobiol.* 72: 305-312.
- Kaushik, N. K. and Hynes, H. B. N. 1968. Experimental study on the role of autumn-shed leaves in aquatic environments.—*J. Ecol.* 56: 229-243.
- and ———. 1971. The fate of the dead leaves that fall into streams.—*Arch. Hydrobiol.* 68: 465-515.
- Krumholz, L. 1972. Degradation of riparian leaves and the recycling of nutrients in a stream ecosystem.—*Univ. of Kentucky Water Resour. Inst. Res. Rep.* 57. pp 36.
- Lowry, O. H., Rosebrough, N. J., Farr, A. L. and Randall, R. J. 1951. Protein measurement with the folin phenol reagent.—*J. Biol. Chem.* 193: 265-275.
- Mathews, C. P. and Kowalczewski, A. 1969. The disappearance of leaf litter and its contribution to production in the river Thames.—*J. Ecol.* 57: 543-552.
- Park, D. 1974. Accumulation of fungi by cellulose exposed in a river.—*Trans. Br. mycol. Soc.* 63: 437-447.
- Paul, R. W. Jr. 1978. Leaf processing and the effects of thermal perturbation on leaf degradation in the New River, Virginia.—Ph.D. dissertation. Virginia Polytechnic Inst. and State Univ. Blacksburg, VA. 151 p.
- Petersen, R. C. and Cummins, K. W. 1974. Leaf processing in a woodland stream ecosystem.—*Freshwater Biol.* 4: 343-368.
- Reice, S. R. 1974. Environmental patchiness and the breakdown of leaf litter in a woodland stream.—*Ecology* 55: 1271-1282.
- Sedell, J. R., Triska, F. J., and Triska, N. S. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. Weight loss and associated invertebrates.—*Verh. Int. Ver. Limnol.* 19: 1617-1627.
- Suberkropp, K., Godshalk, G. L. and Klug, M. J. 1976. Changes in the chemical composition of leaves during processing in a woodland stream.—*Ecology* 57: 720-727.
- Thomas, W. A. 1970. Weight and calcium losses from decomposing tree leaves on land and in water.—*J. Appl. Ecol.* 7: 237-241.
- Triska, F. J. 1970. Seasonal distribution of aquatic hyphomycetes in relation to the disappearance of leaf litter from a woodland stream.—Ph.D. dissertation. Univ. of Pittsburgh. 189 p.
- and Sedell, J. R. 1976. Decomposition of four species of leaf litter in response to nitrate manipulation.—*Ecology* 57: 783-792.
- United States Geological Survey. 1976. Water Data Report IL-75-I.
- . 1977. Water Data Report IL-76-I.

Table I Level of significance of fit of weight-change data to an exponential decay model, processing coefficients (K), number of days required for loss of 50% of original weight and K calculated from % ash-free dry weight remaining at the end of each study.

Treatment	K	Level of Significance of Fit to the Equation $Y_t = Y_0 3^{-kt}$	No. of Days Required for 50% Weight Loss	K Calculated from $-K = \log_e (\% \text{ remaining} \times 100)/t$
<i>1974-75</i>				
Pre-cut maple discs	.0045	.005 > p > .001	152.4	.0087
Fresh-cut maple discs	.0036	p < .001	190.7	.0064
Pre-cut sycamore discs	.0011	.10 > p > .05	660.0	.0028
Fresh-cut sycamore discs	.0020	.05 > p > .025	354.2	.0020
Whole maple leaves, bagged	.0050	p < .001	139.1	.0079
Whole sycamore leaves, bagged	.0013	p < .025	535.8	.0020
<i>1975-76</i>				
Fresh-cut maple discs	.0120	p < .001	57.6	.0137
Fresh-cut sycamore discs	.0014	.005 > p > .001	505.3	.0010
Maple leaf packs	.0267	p < .001	26.0	.0272
Sycamore leaf packs	.0259	p < .001	26.8	.0283

Table II. Level of significance of the differences between leaf-processing coefficients for different types of measurements, different species of leaves and between the two years of study.

Comparison		Study	Level of Significance of Difference
Maple x Maple	Leaf Packs vs. Fresh-cut Discs	1975-76	.01 > p > .001
	Pre-Cut vs. Fresh-Cut Discs	1974-75	n.s.
	Fresh-Cut Discs	1974-75	
	vs. Fresh-Cut Discs	1975-76	p < .001
Sycamore x Sycamore	Leaf Packs vs. Fresh-cut Discs	1975-76	p < .001
	Pre-Cut vs. Fresh-Cut Discs	1974-75	0.4 > p > 0.3
	Fresh-Cut Discs	1974-75	
	vs. Fresh-Cut Discs	1975-76	n.s.
Maple x Sycamore	Fresh-Cut Discs	1974-75	0.2 < p < .1
	Pre-Cut Discs, Bagged	1974-75	p < .001
	Whole Leaves, Bagged	1974-75	p < .001
	Fresh-Cut Discs	1975-76	p < .001
	Leaf Packs	1975-76	n.s.

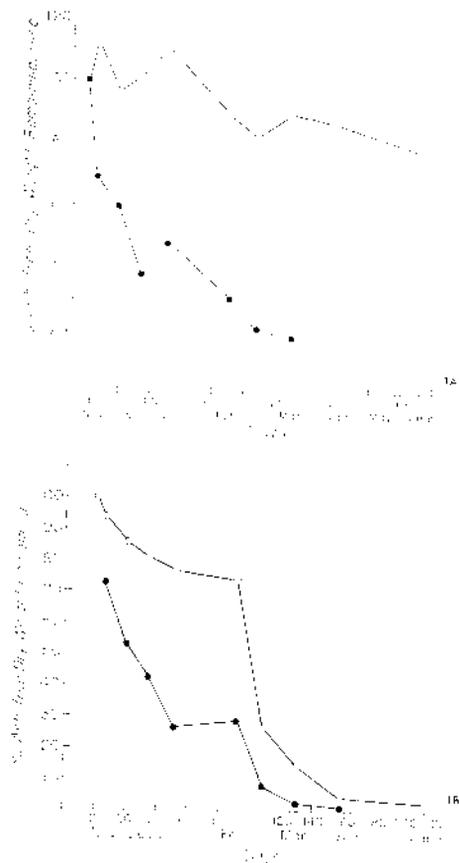


Figure 1. Percentages of the ash-free dry weight of sycamore ○-○ and maple ●-● leaves remaining during Study II for: A. discs cut from leaves in leaf packs; B. leaf packs.

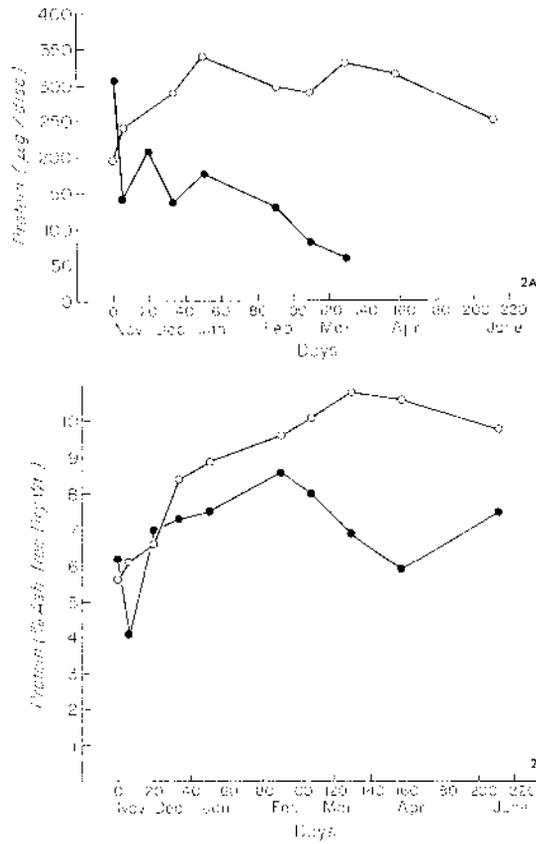


Figure 2. Changes in protein content of sycamore O-O and maple ●-● leaves during Study II: A. amount of protein per leaf disc B. protein as percent of ash-free dry weight.

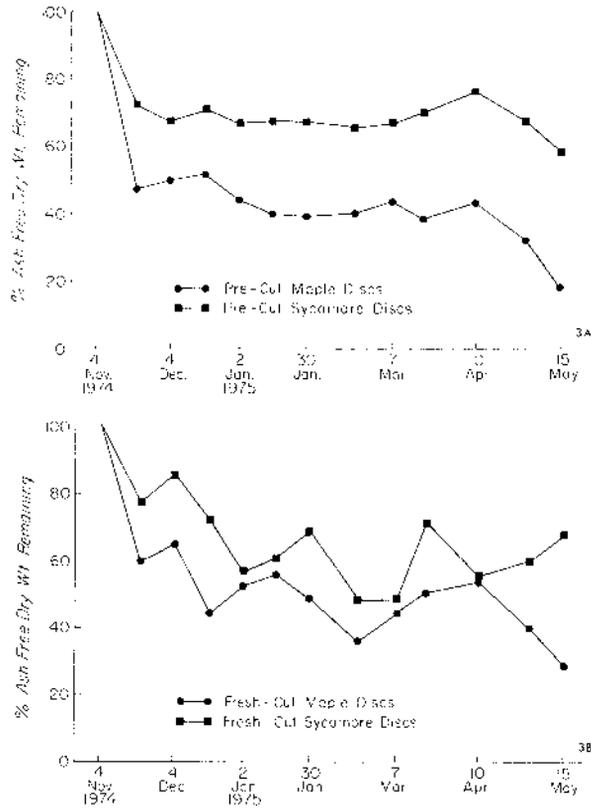


Figure 3. Percentages of ash-free dry weight of sycamore and maple leaves remaining during Study I for: A. pre-cut leaf discs contained in mesh bags; B. discs cut from leaves in leaf packs (fresh-cut).

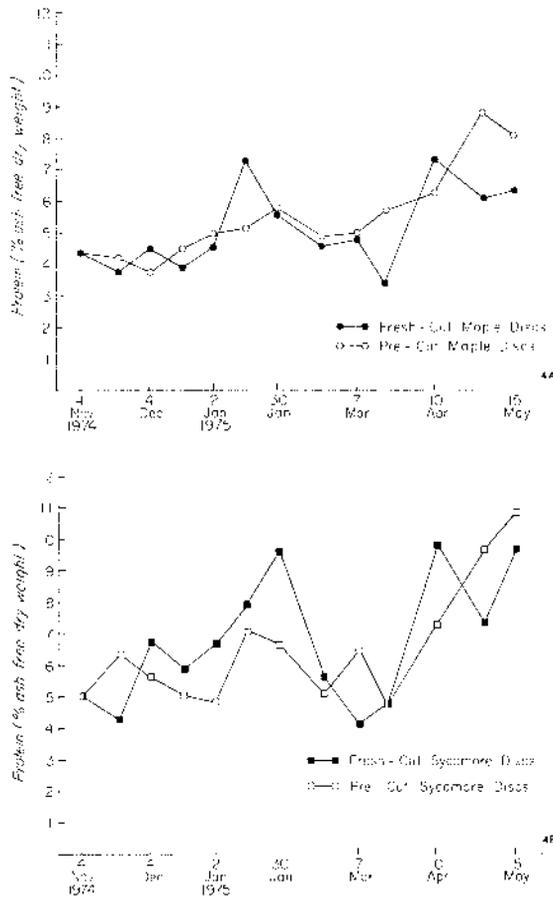


Figure 4. Changes in the the percent composition of protein of maple and sycamore leaves during Study 1 for: A. fresh-cut and precut maple discs; B. fresh-cut and precut sycamore discs.