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American Midland Naturalist, Vol. 133, No. 1 (Jan., 1995), 184-195.

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Rapid Decomposition of Summer-input Leaves in a Northern Michigan Stream

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ABSTRACT.—Processing of leaves of five riparian plant species [sugar maple (*Acer saccharum*), speckled alder (*Alnus rugosa*), eastern hemlock (*Tsuga canadensis*), red-stem dogwood (*Cornus sericea*) and sweet gale (*Myrica gale*)] was studied during the summer in a northern Michigan stream. In June 1992, dried green leaves (~5 g) of each species were placed into coarse-mesh bags and tethered in a riffle. Mass loss and macroinvertebrate colonization were measured after 2, 14, 28 and 42 days. In general, decay rates were fast ($k = 0.017 - 0.134$), with most species losing >80% of mass within 28 days. The order of decomposition (in declining rate) was: maple = dogwood > alder > sweet gale = hemlock. Macroinvertebrate numbers in the leaf packs were highest at 14 days, but densities per unit remaining mass increased steadily during the experiment. Midge larvae (Diptera: Chironomidae) and net-spinning caddisflies (Trichoptera: Hydropsychidae) comprised 54% and 44%, respectively, of the macroinvertebrates, which generally lacked typical shredder taxa. Of several measurements of leaf chemistry, toughness and morphology, leaf surface area per unit mass was the best predictor of processing rate. Hemlock and sweet gale may contain secondary compounds that inhibit decomposition. Leaf processing rates were among the highest observed for any North American stream, which may be related to high microbial activity at summer water temperatures, good nutritional status of fresh leaves, and abundant macroinvertebrates. Summer inputs of leaves to woodland streams are transient but possibly important energy resources for some stream organisms.

INTRODUCTION

Studies of leaf processing in temperate-zone streams have focused on the breakdown and decomposition of leaves abscised during the autumn, the normal peak of leaf input (*e.g.*, Cummins *et al.*, 1973; Reice, 1974; Anderson and Sedell, 1979; Cummins *et al.*, 1989). However, some leaf input from riparian vegetation and floodplains occurs year-round in temperate streams, in particular from coniferous species (Webster, 1983; Gregory *et al.*, 1991). Leaves that enter streams during summer months, when allochthonous matter is scarce, may provide important energetic resources for lotic organisms. For example, stream macroinvertebrates that are generalists in their food preferences may use these patchy but high-quality food items.

In deciduous forest streams of the midwestern United States, significant quantities of leaves can enter streams during the summer (Stout *et al.*, 1985). Major means of input include: (1) felling of trees by beaver (*Castor canadensis* Kuhl); (2) natural dieback of tree or shrub branches followed by leaf shed; (3) windstorms that break branches or blow litter from stream banks into streams; and (4) floods that transport stored material from floodplains or inundate streamside plants. These four mechanisms can deliver to streams both fresh green leaves and also dried green leaves, which have different nutritional characteristics than autumn-abscised leaves (Boulton and Boon, 1991). In the Upper Peninsula of Michigan, streams receive summer inputs of leaves from all of these sources. Riparian vegetation along these streams typically is composed of a diverse array of shrubs, deciduous trees and conifers, which contribute a variety of leaf types for lotic processing.

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We studied the summer leaf processing of five plant species in a northern Michigan stream that received inputs of summer leaves from the sources described above. Our objectives were to: (1) quantify summer processing rates and compare those rates to those obtained from autumn studies of abscised leaves of the same or similar species; (2) determine if certain leaf features, including elemental (C, N) composition, surface area and leaf toughness, influenced summer processing rates; and (3) quantify macroinvertebrate colonization patterns of leaf packs during a season when shredders typically are absent or in low abundance (Cummins *et al.*, 1989). We postulated that favorable summer conditions, including higher water temperature and nutrient content of leaves, should accelerate decomposition rates, but that the lack of shredding macroinvertebrates could reduce processing. Thus, leaves should be processed rapidly during the summer if physical and microbial degradation dominated, but slowly if macroinvertebrate shredding was most important.

MATERIALS AND METHODS

Study site.—The study was conducted in Tenderfoot Creek, located in the western half of the Upper Peninsula of Michigan (46°13'N, 89°32'E; elev. = 500 m). The stream begins as the outflow of Tenderfoot Lake, flows N through the University of Notre Dame Environmental Research Center and then joins the Ontonagon River, which empties into Lake Superior. Tenderfoot Creek has a low gradient (3 m/km) and a summer baseflow of ca. 2.0 m³/sec. The study site was a riffle 3 km downstream from Tenderfoot Lake. The stream channel was ca. 8 m wide and average water depth in midchannel was 35 cm. Substrate was dominated by cobble and gravel in about equal proportions. Mean midday water temperature for June and July 1992 was ca. 18 C.

The second-growth riparian zone of Tenderfoot Creek was dominated by young trees and shrubs that provided a limited canopy. We studied the processing of leaves from five native plants common in the riparian zone: sugar maple (*Acer saccharum* Marsh.), speckled alder (*Alnus rugosa* Clausen), eastern hemlock (*Tsuga canadensis* Carr.), red-stem dogwood (*Cornus sericea* L.) and sweet gale (*Myrica gale* L.). Fresh leaves of each species were collected on 25–29 May 1992 from plants along a 20-m reach of the riparian zone of Tenderfoot Creek. Care was taken to pick only healthy leaves and, for hemlock, needles of approximately the same age. The leaves were then dried at 40 C for 24 h to remove excess moisture. Because hemlock needles became very brittle with oven-drying, they were instead air-dried for 48 h.

Experimental design.—We enclosed leaves within litter bags of coarse mesh, which is a common method used to study leaf decomposition (Webster and Benfield, 1986) but may impart some artifacts associated with leaf containment (Boulton and Boon, 1991). Leaves were arranged into packs of approximately 5 g each, weighed to the nearest 0.01 g, and then carefully rewetted with water until soft to prevent crumbling when placed in the stream (Reice, 1974). The leaves were placed into 10 cm × 15 cm pouches of 1-cm mesh, gutter-guard material and secured at the ends with a twist-tie weaved in and out of the mesh. These bags secured the leaves in the pack while allowing invertebrates access to them (Benfield and Webster, 1985). Twenty packs of each species were secured to the tops of bricks with rubber bands. On 3 June 1992, the packs were placed in a randomized block design (to minimize position effects) in midchannel of the riffle in Tenderfoot Creek, oriented parallel to the current. After 2, 14, 28 and 42 days in the stream, four random packs of each leaf species were removed into a 250- μ m mesh net held downstream and sealed in plastic bags. The 2-day sample was used to measure loss in mass due to leaching, whereas samples taken thereafter measured longer-term decomposition.

Sample processing.—After removal from the bag, the leaves were gently rinsed into a 250-

μm sieve to separate leaves from debris and macroinvertebrates that had colonized the packs. Macroinvertebrates from each pack were preserved in 80% ethanol. Remaining leaf material was dried at 40 C for 24 h and weighed to the nearest 0.01 g. Leaf processing rates were measured based on dry mass loss.

Macroinvertebrates in leaf packs from the 14-, 28- and 42-day sampling periods were sorted and counted. Because of disturbance imparted by initial placement of leaf packs in the riffle (e.g., invertebrate dislodgement by our activities), macroinvertebrates taken with the 2-day sample were deemed incidental and not sorted. Macroinvertebrates were identified to genus except for Chironomidae, which generally were early instars and were not identified further.

Several physical and chemical measurements were made for each leaf species. Leaf surface area, before decay, was determined by photocopying three leaves of each species and using a computer digitizer to measure surface area (Tank *et al.*, 1993). Surface area was related to the dry mass of the leaf to generate an area-to-mass ratio. Elemental composition of leaves was determined with a Perkin-Elmer 2400 Series II CHNS/O Analyzer. Three dried leaves of each species were ground with mortar and pestle; samples of ca. 2 mg were weighed to the nearest 1 μg ($n = 3$) and analyzed for C and N content.

A penetrometer similar to that described by Feeny (1970) was used to measure leaf toughness, defined as the force required to penetrate the leaf cuticle. Four leaves of each species were soaked for 24 h to match the original preparation of the leaf packs. The penetrometer was passed through an area of each leaf that contained no major veins. To determine the penetrance force (toughness) of each leaf species, the mass in grams required to penetrate the leaf (x) was fit into the equation of Gallardo and Merino (1993):

$$\text{penetrance force in kPa} = \frac{x}{13.8 \text{ mm}} \times \frac{9.8 \text{ kPa}}{1 \text{ "gram force"/mm}^2}$$

Data analysis.—Leaf processing rates were calculated as the rate coefficient (k) for dry mass loss. The coefficient k was estimated for each leaf species by regressing leaf dry mass (g) against time (days) in the stream using the exponential decay model: $M_t = M_0 e^{-kt}$, where M_0 is initial mass and M_t is mass remaining at time t . This model, first applied to leaf processing by Petersen and Cummins (1974), has been used in many subsequent decay studies (Webster and Benfield, 1986) and, of the models tested, most closely fit our decomposition patterns.

We used analysis of covariance (ANCOVA), with time as the covariate, to test the null hypothesis that the processing rate k was not different among plant species (Zar, 1984). Tukey's HSD test was then used to determine where specific differences among processing rates resided. Differences among species in leaf chemistry and surface area were analyzed with one-way analysis of variance (ANOVA) followed by post-hoc Tukey's tests (Zar, 1984).

Macroinvertebrate colonization rates of leaves similarly were compared with ANCOVA followed by Tukey's tests. Macroinvertebrate community structure on leaves of different species was compared by calculating the Euclidean distance between communities on different leaf types. Euclidean distance is a unitless dissimilarity measure whose value increases as two samples become less similar (Krebs, 1989). Euclidean distance can vary from zero (identical communities) to infinity. Macroinvertebrates from all sampling dates were pooled for each plant species before calculating Euclidean distance.

Stepwise multiple regression was used to determine which factor or factor combination was the best predictor of processing rate k . As independent variables in the multiple regression, we used leaf C:N ratio, penetrance (kPa), surface area-to-mass ratio (SA:M) and macroinvertebrate abundance.

TABLE 1.—Decay coefficient (k), elemental composition (%C, %N), carbon to nitrogen ratio (C:N), toughness (kPa), and surface area per unit mass (SA:M) of different leaf species used in decomposition study (standard error in parentheses). Data were analyzed with ANCOVA (k) or ANOVA (all others) followed by Tukey's HSD test ($\alpha = 0.05$). For each column, measurements followed by a different superscript letter are significantly different from one another

Species	k	%C	%N	C:N	kPa	SA:M
Maple	0.134 (0.008) ^a	44.7 (0.08) ^a	1.78 (0.01) ^a	25.1 ^a	176.1 (4.4) ^a	509.6 (18.5) ^a
Dogwood	0.133 (0.007) ^a	45.7 (0.08) ^b	1.79 (0.01) ^a	25.5 ^a	149.1 (12.9) ^a	268.3 (21.7) ^b
Alder	0.077 (0.005) ^b	47.6 (0.14) ^c	2.28 (0.01) ^b	20.9 ^b	157.8 (15.2) ^a	226.0 (15.8) ^b
Sweet gale	0.039 (0.004) ^c	50.5 (0.05) ^d	2.35 (0.02) ^b	21.5 ^b	172.9 (9.0) ^a	201.9 (13.7) ^b
Hemlock	0.017 (0.001) ^c	49.6 (0.08) ^a	0.93 (0.02) ^c	53.3 ^c	164.1 (5.9) ^a	87.8 (9.1) ^c
F-statistic	$F_{4,94} = 25.3$	$F_{4,15} = 576.1$	$F_{4,15} = 1349.4$	$F_{4,15} = 546.0$	$F_{4,14} = 1.9$	$F_{4,10} = 60.4$
P-value	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P = 0.165$	$P < 0.001$

Due to nonlinearity of regressions, all data subjected to ANCOVA or multiple regression were transformed by computing the natural logarithm of $x + 1$ prior to analysis. Data subjected to ANOVA were transformed only if heterogeneity in variances was detected with Bartlett's test. Analyses were conducted using the MGLH module of SYSTAT (Wilkinson, 1990). An alpha level of 0.05 was applied to all analyses.

RESULTS

Leaf processing rates.—Processing rate k differed significantly among the five plant species ($P < 0.001$), ranging from 0.017 (day^{-1}) for hemlock to 0.134 for maple (Table 1). Tukey's test recognized three significantly different groups based on k : maple and dogwood had the fastest decomposition rates, alder was intermediate in decay, and sweet gale and hemlock were the slowest leaves to decompose (Fig. 1).

During their first 48 h in the stream, all leaves except hemlock lost substantial mass (Fig. 1), ranging from 20% for sweet gale to 42% for sugar maple. Hemlock needles lost 7% of their mass in the first 2 days. The leaves of maple, dogwood and alder declined rapidly in mass from 2–14 days. Dogwood and maple lost nearly all of their remaining mass from 14–28 days (>95% total decay). After 42 days of decomposition, only hemlock, with 50% remaining mass, retained more than 25% of the original mass. Only traces of sugar maple and dogwood (mostly stems) were found in the leaf packs after 42 days and a small amount of speckled alder (5%) remained. Sweet gale had considerably more mass remaining after 42 days (21%) than did the other deciduous species.

Factors affecting decomposition.—Carbon and nitrogen contents of leaves were not good indicators of summer processing rate. The dry mass of all species was about 50% C (Table 1); small, significant differences probably were not biologically meaningful. The four deciduous species all had ca. 2% N content by mass (Table 1); of these, the two fastest decomposers (maple and dogwood) had significantly lower N. The coniferous species, hemlock, had less than 1% N content and also was the slowest decomposer. Multiple regression analysis indicated that C:N ratio was not a significant predictor of decay rate. However, slowly decomposing hemlock needles had a much higher C:N ratio than the other species. There were no significant differences among species in leaf toughness.

Leaf surface area per unit mass (SA:M) differed significantly among species, with maple having the highest ratio and hemlock the lowest (Table 1). SA:M was the best predictor of processing rate in the multiple regression, explaining 76% of the variation in k (Table 2).

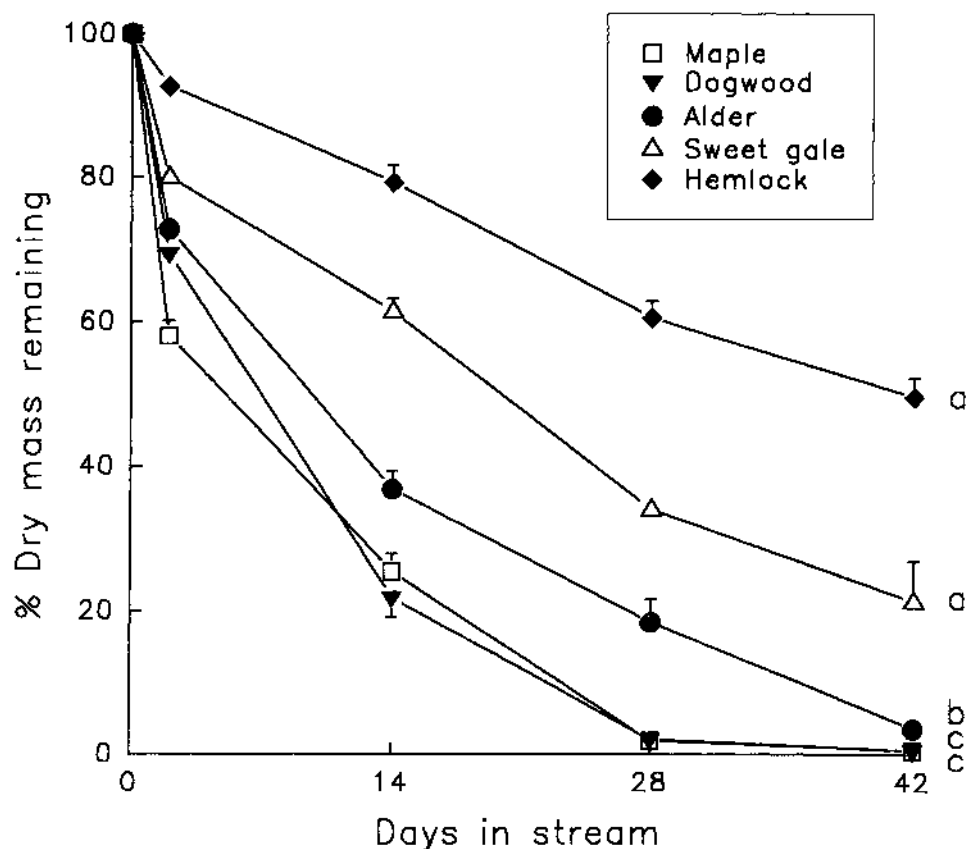


FIG. 1.—Decomposition of different leaf species over 42 days. Different lower-case letters to right of lines indicate significantly different processing rate k (Tukey's $P < 0.01$). Error bars represent 1 SE.

Thus, high surface area was associated with rapid processing. The exception was sweet gale, which had moderate SA:M but decomposed slowly.

Macroinvertebrate colonization of leaf packs.—Macroinvertebrates in the leaf packs were dominated by midge larvae (Diptera: Chironomidae) and net-spinning caddisflies (Trichoptera: Hydropsychidae), which represented 54% and 44%, respectively, of the total macroinvertebrates collected (Table 3). Only a few invertebrate genera found in the leaf packs

TABLE 2.—Results of stepwise multiple regression of decomposition factors on processing rate k . Only surface area to mass ratio (SA:M) and invertebrate abundance per leaf pack (Inverts) were significant predictors of k . Overall analysis of variance was: $F_{2,2} = 49.8$; $P = 0.02$

Factor	Coefficient	Standard error	Cumulative r^2	F-statistic	P-value
Constant	0.806	0.236	—	11.6	0.076
SA:M	0.066	0.008	0.759	71.2	0.014
Inverts	-0.125	0.026	0.980	22.5	0.042

TABLE 3.—Average number of macroinvertebrates of different genera per leaf pack over all three sampling periods

Taxon	Maple	Dogwood	Alder	Sweet gale	Hemlock
Ephemeroptera					
Baetidae					
<i>Baetis</i>	1.3	1.0	0.6	1.1	0.8
Heptageniidae					
<i>Heptagenia</i>	0	0.1	0	0	0
Ephemerellidae					
<i>Ephemerella</i>	0	0.3	0	0	0.1
<i>Serratella</i>	12.4	5.9	5.9	7.6	9.4
Plecoptera					
Perlidae					
<i>Acroneuria</i>	1.3	1.0	3.8	2.3	3.8
Coleoptera					
Elmidae					
<i>Optioservus</i>	0	0	0.1	0	0
Diptera					
Simuliidae					
<i>Simulium</i>	0.2	0.2	0.6	0	0.6
Chironomidae	288.9	284.7	356.0	614.3	271.7
Trichoptera					
Philopotamidae					
<i>Chimarra</i>	0.8	0.3	0.2	0.4	0.4
Polycentropodidae					
<i>Polycentropus</i>	0	0	0.1	0	0
Hydropsychidae					
<i>Cheumatopsyche</i>	68.1	34.1	36.0	50.7	66.9
<i>Hydropsyche</i>	274.1	201.9	269.6	209.8	268.3
Brachycentridae					
<i>Brachycentrus</i>	0.3	0.8	0.3	2.3	1.3
Helicopsychidae					
<i>Helicopsyche</i>	0	0	0	0.1	0
Leptoceridae					
<i>Oecetis</i>	0.7	0.9	0.8	1.0	0.4
Amphipoda					
Gammaridae					
<i>Gammarus</i>	0.1	0.2	0	0.1	0.4
Totals	648.2	531.4	674.0	889.7	624.1

were considered shredders according to the classification of Merritt and Cummins (1984), although midges were not identified to genus. Presumably, many macroinvertebrates in the leaf packs were feeding on material other than leaves (*e.g.*, microbial biofilm, seston, fine particulate organic matter or other macroinvertebrates).

Absolute numbers of macroinvertebrates in the leaf packs were highest on day 14, declined from 14–28 days for all leaf species, and remained relatively stable from 28–42 days (Fig. 2A). ANCOVA indicated significant differences among leaf types ($F_{4,39} = 3.1$, $P = 0.03$), but Tukey's tests revealed only one difference: sweet gale had higher absolute num-

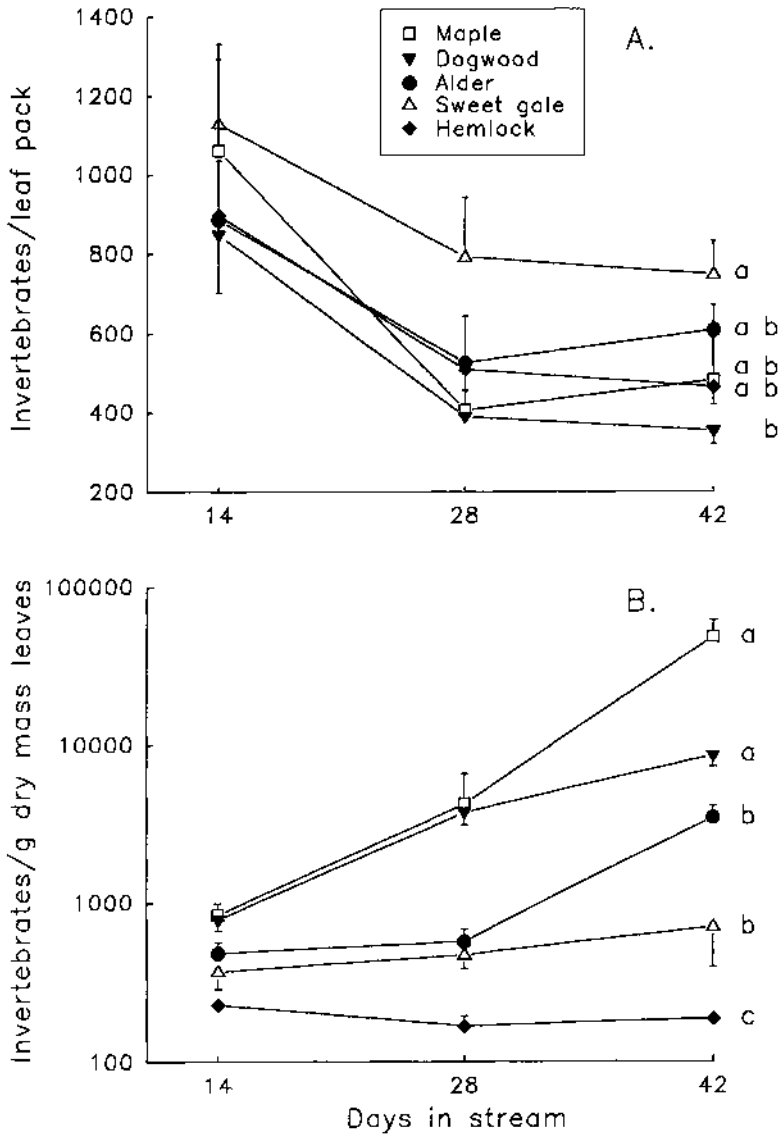


FIG. 2.—Macroinvertebrate abundance in leaf packs. A. Number of macroinvertebrates per leaf pack at each sampling date. B. Number of macroinvertebrates per unit mass of remaining leaves (note logarithmic y-axis). Different lower-case letters to right of lines indicate significantly different macroinvertebrate abundances (Tukey's $P < 0.01$). Error bars represent 1 SE

bers of macroinvertebrates than dogwood. Multiple regression analysis indicated that invertebrate abundance over the entire period was the second best predictor of processing rate, explaining an additional 22% of the variation in k (Table 2).

The number of macroinvertebrates per unit leaf mass generally increased over time and

TABLE 4.—Matrix of Euclidean distances comparing macroinvertebrate communities found in leaf packs of different species

	Maple	Dogwood	Alder	Sweet gale	Hemlock
Maple	0				
Dogwood	181	0			
Alder	168	221	0		
Sweet gale	748	743	598	0	
Hemlock	42	169	202	783	0

as mass declined (Fig. 2B). Significant differences existed among leaf types (ANCOVA $F_{4,99} = 31.1$, $P < 0.001$). Tukey's test revealed three distinct groups: maple and dogwood had the highest number of macroinvertebrates per unit remaining mass, alder and sweet gale were intermediate and hemlock had the fewest invertebrates.

Similar macroinvertebrate communities based on Euclidean distance were found on most leaf packs, except that invertebrates associated with sweet gale were substantially different from all other species (Table 4). Chironomid larvae were about twice as abundant on sweet gale as on the other leaf types. Hydropsychid larvae were most numerous on maple and hemlock but did not recruit as rapidly to sweet gale. Invertebrate communities associated with maple and hemlock were most similar.

DISCUSSION

High processing rates in Tenderfoot Creek.—The summer input and processing of fresh leaves has received relatively little attention from stream ecologists, probably because of the overwhelming autumn pulse of abscised leaves (Cummins *et al.*, 1989). However, limitations in allochthonous organic matter are more likely to occur in summer when leaves are scarce than in autumn when leaves are abundant. Our study simulated the processing of dried fresh leaves during the summer, whose input can occur during various disturbance scenarios such as tree death or damage (*e.g.*, Lamberti *et al.*, 1991). Under these conditions, the cuticle may be broken by drying, which would make readily available the high summer nutrient content of leaves (Crawley, 1983). Higher summer water temperatures also should accelerate decay rates, whereas the absence of shredding macroinvertebrates could reduce processing. Based on these criteria, we postulated that leaves would be processed rapidly during the summer if physical and microbial degradation dominated, but slowly if macroinvertebrate shredding was most important.

Summer processing rates of leaves in Tenderfoot Creek indeed were very high when compared to the autumn decomposition of abscised leaves of the same or similar species in other systems (Table 5). Webster and Benfield (1986) computed an overall mean processing rate for leaves in bags as $k = 0.0054$, which is lower than any single rate in our study. Processing categories developed by Petersen and Cummins (1974) would place all of our species in the "fast" ($k > 0.010$) category. In the study most pertinent to ours, Stout *et al.* (1985) compared the processing of summer-fresh and autumn-abscised leaves of speckled alder (*Alnus rugosa*) in a northern Michigan stream. Processing rates were much lower ($k = 0.006$ – 0.017) than for alder in Tenderfoot Creek ($k = 0.077$). They observed that initially (26 days) fresh leaves decomposed more slowly than abscised leaves, which they attributed to the waxy cuticle that delayed leaching and microbial colonization. Later rates of breakdown were higher for fresh than abscised leaves, which they speculated was related to higher nutrient content of fresh leaves. Regardless, the near complete decomposition of

TABLE 5.—Comparison of decay rate coefficients (k) from several lotic studies of leaf decomposition. NR = not reported

Leaf	Species	k	Location	Mean temp. (C)	Duration (d)	Study*
Maple	<i>Acer saccharum</i>	0.134	Michigan	18	42	1
	<i>A. circinatum</i>	0.020	Oregon	8	~220	2
	<i>A. macrophyllum</i>	0.011	Oregon	8	~220	2
	<i>A. rubrum</i>	0.014	Virginia	NR	207	3
	<i>A. negundo</i>	0.039	Utah	4	57	4
	<i>A. negundo</i>	0.024	Utah	3	175	5
Dogwood	<i>Cornus sericea</i>	0.133	Michigan	18	42	1
	<i>C. florida</i>	0.022	N. Carolina	10.5	~200	6
	<i>C. florida</i>	0.022	Virginia	NR	207	3
Alder	<i>Alnus rugosa</i>	0.077	Michigan	18	42	1
	<i>A. rugosa</i> (fresh)	0.013–0.017	Michigan	12	115	7
	<i>A. rugosa</i> (abscised)	0.006–0.009	Michigan	9	115	7
	<i>A. tenuifolia</i>	0.031	Colorado	0	112	8
	<i>A. rubra</i>	0.017	Oregon	8	~220	2
Hemlock (and other conifers)	<i>Tsuga canadensis</i>	0.017	Michigan	18	42	1
	<i>T. heterophylla</i>	0.013	Oregon	8	~220	2
	<i>Pinus ponderosa</i>	0.004	Colorado	0	168	8
	<i>Pseudotsuga menziesii</i>	0.013	Oregon	8	~220	2

* ¹Present study; ²Sedell *et al.* (1975); ³Benfield and Webster (1985); ⁴Oberndorfer *et al.* (1984); ⁵McArthur and Barnes (1988); ⁶Webster and Waide (1982); ⁷Stout *et al.* (1985); ⁸Short *et al.* (1980)

maple, dogwood and alder in the relatively short duration (42 days) of our study was striking. Most autumn studies last more than 100 days (*see* reviews by Webster and Benfield, 1986; Boulton and Boon, 1991), and leaves sometimes do not fully decompose.

Interspecific variation in processing.—Interspecific differences in processing rate were evident in our study. The coniferous species decomposed more slowly than the four deciduous species, as observed in previous studies (reviewed by Webster and Benfield, 1986). This pattern has been attributed variously to low nutritive quality, presence of secondary chemicals or high toughness of conifer needles. In our study, the low decay rate of eastern hemlock was associated with low (<1%) N content and low surface area to mass, which may have restricted biofilm development. Considering all species, however, leaf nitrogen content, C:N ratio and toughness were not good predictors of decay rate. In future studies, it may be advisable to examine phytochemicals that deter breakdown, such as condensed tannins (Stout, 1989), along with the absolute quantities of nutrients.

Sweet gale is a particularly interesting species because it is a common shrub in northern Michigan riparian zones around both streams and lakes, often directly overhanging the water. However, we could find no previous information on its decomposition. We expected that, as a relatively broadleaved plant with high nitrogen content, sweet gale would decompose rapidly in the stream. However, sweet gale had a decomposition rate that was substantially slower than those of the other deciduous species and similar to that of hemlock. Sweet gale may contain defensive phytochemicals related to those of conifers; we noted that crushed leaves and needles emitted similar chemical odors. A related species, bayberry

(*Myrica cerifera* L.), contains chemicals in its bark (e.g., myricic acid) that are used medicinally as astringents and emetics to induce vomiting in humans (Budavari, 1989). This information suggests that secondary chemicals may inhibit decay of sweet gale. Chironomid larvae, however, apparently were attracted to sweet gale and may have been able to mine into the fleshy leaves. Further study of the chemistry of sweet gale and other leafy riparian shrubs is warranted.

Factors contributing to decay.—Previous studies suggest mechanisms that may explain the rapid decay of leaves in our study. Temperature is a major factor in decomposition (Iversen, 1975; McArthur and Barnes, 1988), and higher temperatures may accelerate leaf decay in the summer (Reice, 1974; Short and Smith, 1989; Smock and MacGregor, 1988). Speckled alder leaves placed in two Michigan streams in autumn at 9–12 C (Stout *et al.*, 1985) decomposed at a much slower rate than did the same species at 18 C in Tenderfoot Creek. This suggests that temperature is important in leaf processing, possibly by increasing microbial degradation and macroinvertebrate activity.

Macroinvertebrates in the leaf packs were dominated by larvae of chironomid midges and hydropsychid caddisflies. Few shredder taxa were found consistently on any leaf species, perhaps due to the season (summer) compared to the typical period of highest shredder abundance (autumn). In general, we observed higher macroinvertebrate densities but lower taxonomic diversity than in previous studies. In our study, densities on day 14 exceeded 50,000/m² on all leaf species compared with typical maximum densities ranging from 3000/m² (Reice, 1977) to 30,000/m² (Hax and Golladay, 1993). However, most leaf packs in our study contained less than 16 macroinvertebrate taxa, compared to 19–36 taxa reported by others (Sedell *et al.*, 1975; Reice, 1977; Short *et al.*, 1980; Hax and Golladay, 1993).

As a lake-outflow stream with abundant plankton-derived seston, Tenderfoot Creek was dominated by filter-feeding macroinvertebrates. Filter-feeders and chironomid larvae rapidly colonized our leaf packs; because most stream invertebrates are omnivorous during their life cycle (Power *et al.*, 1988), they may have hastened leaf decomposition. Stout and Taft (1985) reported that the midge *Brillia flavifrons* preferred fresh alder leaves to abscised ones, possibly related to the higher nitrogen content of the fresh leaves. These results suggest that "typical" autumn assemblages of shredding invertebrates are not essential for rapid decomposition of leaves. The high densities of summer invertebrates present in our leaf packs within 14 days, which probably included facultative shredders, may have contributed to rapid processing.

Summer processing of leaves appears different from autumn decomposition, in terms of rates, limiting factors, and macroinvertebrate colonization. Rate of decomposition was positively associated with the surface area to mass ratio, suggesting that decomposition is accelerated by increased surface area for biofilm development (*see also* Hax and Golladay, 1993). The development of productive biofilms on leaf surfaces also may recruit nonshredder taxa (e.g., grazers) to summer leaf packs (Stout *et al.*, 1985), which then disrupt leaf surfaces and accelerate decomposition. However, plant species that exhibit unique chemical or morphological features, as perhaps sweet gale does, defy generalizations and may provide insight into the specific factors controlling processing and use of leaf litter in streams.

Acknowledgments.—Support for this research was provided by the National Science Foundation (BSR-8907968) and the Bernard J. Hank Family Endowment. We thank Martin Berg for advice on study design, Barbara Hellenenthal for assistance with plant identification, and Mark Lavery and Patrice Charlebois for technical assistance.

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SUBMITTED 10 MAY 1994

ACCEPTED 26 SEPTEMBER 1994