

Leaf Decomposition Rates of Five Species in a North Temperate Stream

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ABSTRACT

The decomposition rates of leaves of sugar maple, speckled alder, red-stem dogwood, sweet gale, and eastern hemlock were studied experimentally in a north temperate stream, Tenderfoot Creek, in Gogebic Co., Michigan. The study was conducted over a six-week period from June 3 to July 15, 1992. Fresh leaves of each species were dried and weighed into packs of about 5g each. They were then each placed in mesh pouches, tied to bricks with rubber bands, and placed in a riffle area of the stream in a randomized block design. Four packs of each species were sampled and weighed after 48 hours and after two, four, and six weeks.

The 48-hour period, which measured mostly leaching effects, accounted for dry mass loss ranging from about 7% in hemlock to 40% in maple. All of the leaf species decomposed considerably after six weeks. Maple and dogwood lost 99.5% of the original mass, while speckled alder lost 97% of mass. These three species with the highest decomposition rates were leafy deciduous trees. Sweet gale lost about 80% of mass and hemlock lost about 50% of mass after six weeks. Hemlock, a conifer, probably was not as readily colonized by microorganisms because of its tough cuticle and presence of secondary chemicals. Sweet gale, though leafy like the deciduous species, may contain compounds similar to those in hemlock. In general, decay rates (-k) were fast when compared with rates of similar species in previous studies.

INTRODUCTION

Organic matter from the canopy of riparian vegetation is an essential component of the energy budget of woodland streams (Anderson and Sedell 1979, Cummins et al. 1973, Reice 1974). Leaves that fall and are retained in the stream are an important external, or allochthonous, source of organic matter for the system (Anderson and Sedell 1979, Cummins et al. 1973, Cummins et al. 1989, Lamberti and Gregory 1989, Reice 1974). Minshall (1967) stated that leaf litter was the most important food for stream macroinvertebrates, although he later acknowledged the energetic importance of in-stream primary production (Minshall 1978). Plants growing in the stream, such as algae, constitute a different category of organic energy known as autochthonous production (Lamberti and Gregory 1989).

Leaves that enter streams must be retained in the stream, and then processed to release the energy for use by the biota in the aquatic environment. Processing involves the microbially mediated breakdown of the organic material as well as the conversion of the large leaf fragments to smaller particles (Petersen et al. 1989, Short and Maslin 1977).

The first stage in leaf processing involves leaching of soluble organic compounds (Petersen et al. 1989, Reice 1974, Short and Maslin 1977). This leaching, much of which occurs in the first 48 hours in the water (Anderson and Sedell 1979, Reice 1974, Short et al. 1980), may result in loss of as much as 40% of the leaf dry mass (Cummins et al. 1989). Next, the remaining organic matter is colonized by microorganisms, such as bacteria and fungi (Cummins et al. 1989, Lamberti and Gregory 1989, Petersen et al. 1989). These microorganisms "condition" the leaves by making them nutritionally acceptable to macroinvertebrates, often called shredders, which accelerate the leaf processing (Reice 1974, Short and Maslin 1977). The shredders feed on any properly conditioned leaf litter (Cummins et al. 1973), whereas microorganisms colonize and grow more rapidly on certain species of leaves (Short et al. 1980). Leaf decomposition rates depend greatly on this selective colonization (Cummins et al. 1989). Current velocity has been shown to have relatively less effect than biotic processes on the rate of decomposition (Reice 1977).

The leaves must be in an aerobic environment to maximize microbial growth and to allow the shredders to feed (Anderson and Sedell 1979, Cummins et al. 1989). The *in situ* leaf pack method of sampling has been used extensively to study leaf decomposition rates (Anderson and Sedell 1979, Benfield and Webster 1985, Cummins et al. 1989, Gurtz and Tate 1988, Reice 1974). The leaves of each species generally are grouped together and placed in the stream, sometimes in a mesh container that maintains an aerobic environment, allows for passage of invertebrates, and also holds the leaf pack secure in the stream (Benfield and Webster 1985).

The objectives of my study were to determine the decay rates of native species from the riparian zone of a northern Michigan stream and to compare these rates with those of the same or similar species in previous studies.

MATERIALS AND METHODS

Tenderfoot Creek is a medium-sized stream in Michigan's Upper Peninsula, which flows north from its origin in Tenderfoot Lake and eventually empties into Lake Superior. The study site was a riffle area 3 km downstream from Tenderfoot Lake with about a 15m wide wetted channel. The riparian zone was dominated by small trees and shrubs that provided only a slight canopy. Average depth was about 30-40cm in midchannel. The mean daytime water temperature for June and July, 1992, was 18C.

Leaves of five species of trees were studied: 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.). Aquatic decomposition rates were measured based on dry mass loss. The leaves were collected before abscission from trees along a 20m reach of the riparian zone of Tenderfoot Creek. The leaves were then dried at 40C for 24 h to remove excess moisture. Because the needles of hemlock became very brittle with oven drying, they were instead air-dried for 48 hours. Leaves were then arranged into packs of approximately 5g each, weighed on a Sartorius top-loading balance (± 0.01 g), and then carefully re-wet with water until soft to prevent crumbling when placed in the stream (Reice 1974). The leaves were then placed into a 10cm x 15cm pouch of 10mm mesh gutter-guard material and secured at the ends with a twist-tie weaved in and out of the mesh. This secured the leaves in the pack while allowing invertebrates access to them. Each pack was individually labelled to show species name and pack number. One hundred packs, twenty for each species, were constructed, including four extra for each species in case packs were lost. Each pack was secured to a brick with rubber bands. The packs were placed in three groups (randomized block design) in the middle of Tenderfoot Creek, and oriented parallel to the current. The location of each pack was recorded on a map.

Four random packs of each leaf species were removed after 48 h, 2 weeks, 4 weeks, and 6 weeks in the stream. The 48-hour sample was used to measure loss due to leaching. The samples taken at two week intervals thereafter measured long-term decomposition.

After removal, the leaves were rinsed in a 250 micron sieve to separate leaves from debris and macroinvertebrates that had colonized the packs. Remaining leaf material was dried at 40C for 24 h and weighed to the nearest 0.01g. Macroinvertebrates from each pack were preserved in 80% ethanol. These macroinvertebrates were retained for later analysis of densities and taxonomic composition.

Leaf decomposition was fit to a negative exponential decay model of the form $Y_f = Y_o e^{-kt}$, as has been used in many previous studies (Benfield and Webster 1985, McArthur and Barnes 1988, Sedell et al. 1975, Short et al. 1980). Y_f is the final dry mass, Y_o is the starting dry mass, $-k$ is the decay coefficient, and t is the time variable, measured in days (Short et al. 1980).

RESULTS

After 48 hours in the stream, all leaves lost substantial mass, except for only small losses for hemlock (Table 1). Mass lost in 48 h ranged from 40% for sugar maple to only 7% for hemlock. Dogwood, alder, and sweet gale were intermediate in 48 h mass loss.

The 2-14 d period showed a large decrease in mass among the more leafy deciduous species, i.e. maple, dogwood, and alder. Dogwood decomposed at a very fast rate over this period, surpassing the decay rate of sugar maple. Hemlock and sweet gale had lower rates of decomposition. All five species displayed relatively distinct decomposition rates (Table 2).

During the 14-28 d period, dogwood and maple lost nearly all of the remaining mass (over 95% total decay). Hemlock continued to decompose slowly, with over 60% of the original mass remaining (Table 3). Sweet gale and speckled alder remained intermediate in decay rate.

After 6 weeks of decomposition, hemlock, with 50% mass remaining, was the only species with more than 25% of the original mass remaining in the stream (Table 4). Only traces, mostly stems, of the dogwood and sugar maple were found in the leaf packs after six weeks, with their final decomposition being about 99.5% of the original mass. Speckled alder maintained a steady mass decline to a final decomposition of over 95%. The final mass of sweet gale (about 20%) remained considerably higher than those of the other deciduous species.

Figure 1 compares the overall decomposition of each leaf species. The standard deviation (S.D.) and standard error (S.E.) for the means are given in each table. The decay coefficient $-k$ was calculated for each leaf species in order to compare results with other studies (Table 5).

DISCUSSION

All five species of leaves had higher decay rates than those observed in previous studies, with the exception of alder (Table 5). *Alnus rhombifolia* had a decay rate of more than double that of *Alnus rugosa* of my study. However, this rate is an estimate from data presented in that article (Hart and Howmiller 1975). Stout et al. (1985) studied *Alnus rugosa* (the same species in my study) and observed a much slower decay rate than in Tenderfoot Creek.

Losses due to leaching ranged from about 7% of dry mass for eastern hemlock to about 42% in sugar maple. This range is consistent with previous studies (Cummins et al. 1989, Reice 1974, Short et al. 1980). McDowell and Fisher (1976) studied leaching in sugar maple and found that it accounted for at most about 30% loss of dry mass. Anderson and Sedell (1979) found leaching in alder to account for 27% dry mass loss, while Short et al. (1980) found 28.6% dry mass loss due to leaching in alder. These two studies are consistent with the average 27% dry mass loss of alder due to leaching in my study.

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Because this study was conducted over a relatively short period of time, full decomposition of the leaves (in the case of the dogwood, maple, and alder) was surprising. Most previous studies took place over more than 100 days (Cummins et al. 1989, McDowell and Fisher 1976, Reice 1974, 1977, Short et al. 1980), and leaves did not always fully decompose within the time frame of those studies. The short decomposition time in my study was unusual considering that the leaves normally must be conditioned by bacteria before shredders will consume them (Cummins et al. 1989, Lamberti and Gregory 1989, Petersen et al. 1989). High numbers of invertebrates were present in the leaf packs during the last three sampling periods, which probably accelerated leaf decay. Macroinvertebrates were dominated by midge larvae (Diptera) and caddisflies (Trichoptera). Invertebrate samples are currently being analyzed.

As in previous studies, the coniferous eastern hemlock decomposed more slowly than the deciduous species (Anderson and Sedell 1979, Cummins et al. 1989, Sedell et al. 1975, Short et al. 1980). Sweet gale was a particularly interesting species to study because it is a common species in northern Michigan riparian zones, often directly overhanging the water. However, we could find no previous information on its decay rate. I predicted that, as a relatively leafy plant, sweet gale would decompose readily in the stream. However, the leaves of this plant emit an odor similar to evergreens when they are rubbed or broken. My study showed that sweet gale had a decomposition rate intermediate between those of the deciduous trees and the conifer, suggesting that secondary chemical compounds may inhibit decay.

Previous studies suggest mechanisms that may explain the rapid decay that was seen in our study. Shredding stoneflies have been shown to prefer alder and dogwood leaves over many other species, with pine the least preferred food (Wallace et al. 1970). In my study the alder and dogwood also had fast decay rates. The condition of leaves (fresh versus fallen) also is a factor in the decay rate. The midge *Brillia flavifrons* has been shown to prefer fresh speckled alder leaves over those collected after abscission (Stout and Taft 1985). Stout et al. (1985) found that the decay rate of fresh alder leaves was double that of abscissed leaves. Hart and Howmiller (1975) reported that fresh alder leaves fully decomposed in 34 days.

Leaf decay often is fastest in the summer (Reice 1974, Short and Smith 1989, Smock and MacGregor 1988), and temperature is a major factor in decomposition (Iversen 1975, McArthur and Barnes 1988). Most studies have been done in the fall and early winter after the leaves have fallen (Table 5). In contrast, my study was run from early June to mid-July and had the relatively highest water temperature (18C). With the exception of Hart and Howmiller (1975), the other studies were conducted in the fall when water temperatures were cooler. Hart and Howmiller (1975) reported that alder leaves decomposed in 34 days in early summer when water temperatures were about 14C. Anderson and Sedell (1979) observed relatively decay of conifer needles ($-k = 0.018$) in a stream at 15C. Stout et al. (1985) also studied *Alnus rugosa* in two Michigan streams. That study was begun in late August and run through the fall, with a mean water temperature of about 10C. *Alnus rugosa* decomposed at a much slower rate under these conditions than did *Alnus rugosa* in Tenderfoot Creek in the summer. This suggests that

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temperature plays an important role in leaf processing, possibly by affecting microbial metabolism and invertebrate activity.

A combination of the above factors may explain why the decay rates in our study were faster than those in other studies. The timing of the leaf inputs (summer) probably had the largest influence on the processing rate due to the high water temperature. The high numbers of macroinvertebrates may also have accelerated decay, although shredders densities are not yet known. Finally, the use of fresh leaves picked directly off the trees, as opposed to autumn abscised leaves, most likely affected the decay rates.

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Leaf Decomposition in a Stream

Table 1. Starting and ending masses of leaves after 48 hours (June 5, 1992).

Sugar Maple #	Starting Mass (g)	Final Mass (g)	% Remaining
12	5.03	3.22	64.0
14	4.98	2.98	59.8
18	4.97	2.64	53.0
20	4.98	2.79	55.8

Mean = 58.1%
S.D. = 4.2
S.E. = 2.1

Dogwood

06	4.97	3.60	72.4
07	4.97	3.35	67.4
15	5.00	3.46	69.2
16	5.01	3.43	68.5

Mean = 69.4%
S.D. = 1.9
S.E. = 0.9

Speckled Alder #

12	5.02	3.73	74.3
13	5.00	3.67	73.4
18	5.01	3.48	69.5
19	5.02	3.72	74.1

Mean = 72.8%
S.D. = 2.0
S.E. = 1.0

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Sweet Gale #

02	4.95	3.84	77.8
07	5.00	4.00	80.0
16	4.99	4.06	81.4
17	4.98	4.03	80.9

Mean = 80.0%
S.D. = 1.5
S.E. = 0.7

E. Hemlock #

01	4.95	4.49	90.7
12	4.94	4.76	96.4
13	4.96	4.68	94.4
14	4.94	4.41	89.3

Mean = 92.7%
S.D. = 2.8
S.E. = 1.4

Leaf Decomposition in a Stream

Table 2. Starting and ending masses of leaves after 14 days of decomposition

(June 17, 1992)

Sugar Maple	Starting Mass (g)	Final Mass (g)	% Remaining
04	4.96	1.27	25.6
07	4.96	1.54	31.0
11	5.02	1.38	27.5
16	4.97	0.88	17.7

Mean = 25.5%
S.D. = 4.9
S.E. = 2.4

Dogwood #

02	4.96	1.37	27.6
04	5.00	1.34	26.8
08	4.96	0.89	17.9
11	4.98	0.76	15.2

Mean = 21.9%
S.D. = 5.4
S.E. = 2.7

Speckled Alder #

04	5.01	1.80	35.9
06	5.01	1.60	31.9
14	4.97	1.72	34.6
16	5.00	2.26	45.2

Mean = 36.9%
S.D. = 5.0
S.E. = 2.5

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Sweet Gale #

03	4.96	3.00	60.4
09	5.01	2.81	56.1
10	4.98	3.23	64.9
12	5.02	3.25	64.7

Mean = 61.5%
S.D. = 3.6
S.E. = 1.8

E. Hemlock #

06	5.03	4.01	79.7
15	4.95	3.55	71.7
17	4.97	4.08	82.0
19	4.95	4.16	84.0

Mean = 79.4%
S.D. = 4.7
S.E. = 2.3

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Table 3. Starting and ending masses of leaves after 28 days of decomposition

(July 1, 1992)

Sugar Maple #	Starting Mass (g)	Final Mass (g)	% Remaining
01	4.98	0.04	0.8
02	4.97	0.04	0.8
09	4.98	0.21	4.2
17	4.96	0.09	1.8

Mean = 1.9%
S.D. = 1.4
S.E. = 0.7

Dogwood #	Starting Mass (g)	Final Mass (g)	% Remaining
05	4.98	0.12	2.4
09	4.98	0.04	0.8
10	4.98	0.18	3.6
13	5.00	0.07	1.4

Mean = 2.1%
S.D. = 1.1
S.D. = 0.5

Speckled Alder #	Starting Mass (g)	Final Mass (g)	% Remaining
08	5.02	1.11	22.1
10	5.03	1.28	25.4
11	4.99	0.43	8.6
20	4.98	0.88	17.7

Mean = 18.5%
S.D. = 6.3
S.E. = 3.2

Leaf Decomposition in a Stream

Sweet Gale #

04	4.96	1.60	32.3
08	4.97	1.52	30.6
11	4.97	1.88	37.8
19	5.00	1.78	35.6

Mean = 34.1%
S.D. = 2.8
S.E. = 1.4

E. Hemlock

04	4.98	3.01	60.4
08	5.03	3.06	60.8
09	5.01	2.72	54.3
10	5.07	3.40	67.1

Mean = 60.7%
S.D. = 4.5
S.E. = 2.3

Leaf Decomposition in a Stream

Table 4. Starting and ending masses of leaves after 42 days of decomposition

(July 15, 1992)

Sugar Maple #	Starting Mass (g)	Final Mass (g)	% Remaining
05	4.98	0.01	0.2
06	4.96	0.05	1.0
15	4.98	0.03	0.6
19	4.96	0.01	0.2

Mean = 0.5%
S.D. = 0.3
S.E. = 0.2

Dogwood #

03	5.02	0.01	0.2
14	4.96	0.01	0.2
17	5.00	0.06	1.2
20	5.01	0.03	0.6

Mean = 0.5%
S.D. = 0.4
S.E. = 0.2

Speckled Alder #

01	4.99	0.10	2.0
02	4.99	0.15	3.0
05	4.96	0.33	6.7
07	4.99	0.11	2.2

Mean = 3.5%
S.D. = 1.9
S.E. = 0.9

Leaf Decomposition in a Stream

Sweet Gale #

13	4.99	0.92	18.4
14	4.98	1.03	20.7
15	4.96	0.37	7.6%
18	4.98	1.92	38.6

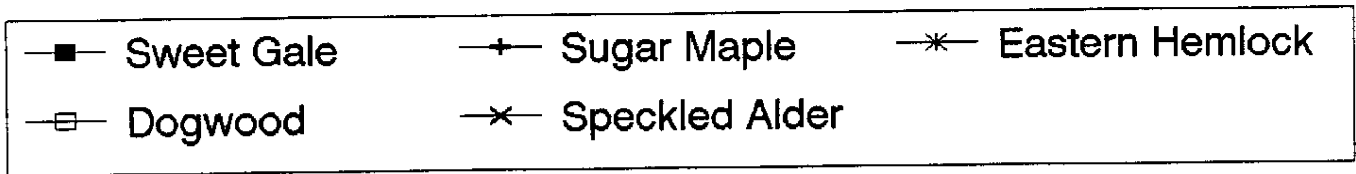
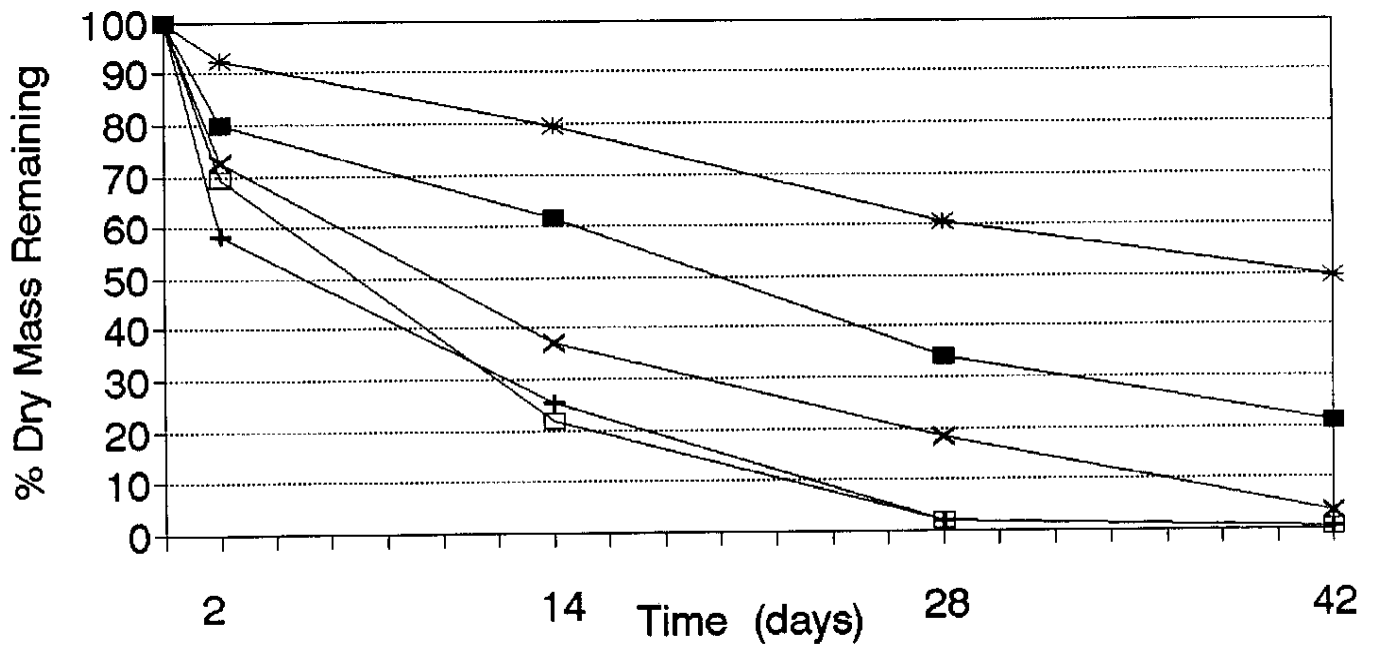
Mean = 21.3%
 S.D. = 11.2
 S.E. = 5.6

E. Hemlock #

03	4.95	2.02	40.8
07	5.06	2.56	50.6
16	5.06	2.59	51.2
18	4.98	2.78	55.8

Mean = 49.6%
 S.D. = 5.5
 S.E. = 2.7

Figure 1
Decomposition During Six Week Period



Leaf Decomposition in a Stream

Table 5. Comparison of decay rate constants (-k) from several studies.

Leaf	Species	-k	Location	Temp.	Study
Maple	<i>A. saccharum</i>	0.127	Michigan	18C	1
	<i>A. circinatum</i>	0.020	Oregon	8C	2
	<i>A. macrophyllum</i>	0.011	Oregon	8C	2
	<i>A. rubrum</i>	0.014	Virginia	11C	3
	<i>A. negundo</i>	0.039	Utah	9C	4
	<i>A. negundo</i>	0.024	Utah	3C	5
Dogwood	<i>C. sericea</i>	0.129	Michigan	18C	1
	<i>C. florida</i>	0.025	N. Carolina	13C	6
	<i>C. florida</i>	0.022	Virginia	11C	3
Alder	<i>A. rugosa</i>	0.073	Michigan	18C	1
	(fresh) <i>A. rugosa</i>	0.017	Michigan	10C	7
	(fallen) <i>A. rugosa</i>	0.009	Michigan	10C	7
	<i>A. tenuifolia</i>	0.038	Colorado	0C	8
	<i>A. rhombifolia</i>	0.183	California	13C	9
	<i>A. rubra</i>	0.017	Oregon	8C	2
Gale	<i>M. gale</i>	0.038	Michigan	18C	1
Hemlock	<i>T. canadensis</i>	0.017	Michigan	18C	1
	<i>T. heterophylla</i>	0.013	Oregon	8C	2

¹ present study, ² Sedell et. al. (1975), ³ Benfield and Webster (1985), ⁴ Oberndorfer (1984),

⁵ McArthur and Barnes (1988), ⁶ Webster and Waide (1982), ⁷ Stout et. al. (1985),

⁸ Short et.al. (1980), ⁹ Hart and Howmiller (1975)