

Natural and constraint-induced factors influencing the breakdown of dogwood and oak leaves

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Received 23 January 1991; in revised form 1 August 1991; accepted 22 August 1991

Key words: dogwood, oak, leaf colonization, leaf breakdown rates, constraint techniques

Abstract

Breakdown rates and microbial colonization patterns of dogwood and oak leaves were measured between November and June of 1987–88 and 1988–89. Leaves were placed in artificial streams loose (unconstrained), in bags, or in packs. Discharge was maintained at approximately 0.25 l s^{-1} , and no shredders were present in the streams. Average microbial biomass as ATP, for all species and treatments, increased from near 0 mg g^{-1} AFDW in November to over 8 mg g^{-1} AFDW in June. Microbial respiration increased from about $0.01 \mu\text{g glucose respired hr-g}^{-1}$ AFDW in November to about $0.03 \mu\text{g hr-g}^{-1}$ AFDW in June. Microbial biomass and activity were significantly greater on dogwood leaves than on oak leaves. Dogwood and oak leaf breakdown rates were fastest when unconstrained, -0.0034 and $-0.0027 \text{ degree-day}^{-1}$ respectively. Breakdown rates of dogwood leaves were faster in bags ($-0.0025 \text{ degree-day}^{-1}$) than in packs ($-0.0015 \text{ degree-day}^{-1}$) while rates of oak leaves were not significantly different between bags and packs (-0.0014 and $-0.0018 \text{ degree-day}^{-1}$ respectively). Breakdown rates of dogwood and oak leaves obtained in this study were much slower than those obtained by other investigators either in the presence or absence of shredders. A comparison of results from this study with results from other studies revealed that dogwood leaves may be affected more by turbulence, while oak leaves may be influenced more by shredder activity.

Introduction

In forested headwater streams, leaf inputs are the major source of organic carbon (e.g. Minshall, 1967; Fisher & Likens, 1973). Timing, conditioning rates, and time of disappearance of leaf inputs from the stream are important factors governing macroinvertebrate populations as well as secondarily influencing higher trophic levels (Cummins, 1989). After leaves enter the stream they are bro-

ken down by physical processes such as leaching and abrasion, and biological processes such as microbial degradation and invertebrate feeding (Kaushik & Hynes, 1968; Kaushik & Hynes, 1971; Cummins, 1974; Petersen & Cummins, 1974). A wide range of leaf breakdown rates have been observed. Previous studies have shown that leaves from herbaceous plants (Petersen & Cummins, 1974) and labile leaves such as dogwood (Benfield & Webster, 1985), black locust (Meyer

& Johnson, 1983), and tulip-poplar (Thomas, 1970) breakdown rapidly. More refractory leaf species such as oak (Petersen & Cummins, 1974) generally have slower breakdown rates.

Species-specific breakdown rates have been shown to be influenced by both internal and external factors. Internal factors include leachability of dissolved organic components (Suberkropp *et al.*, 1976), nitrogen content (Kaushik & Hynes, 1971), and amount of structural polymers such as lignin and cellulose (Cromack & Monk, 1975; Godshalk & Wetzel, 1978). External factors include nutrient concentration of the water (Rosset *et al.*, 1982), current velocity (Chergui & Pattee, 1988), temperature (Hauer *et al.*, 1986), and invertebrate shredders (Cummins *et al.*, 1973; Wallace *et al.*, 1982; Kirby *et al.*, 1983; Rounick & Winterbourn, 1983; Cuffney *et al.*, 1984; Mutch & Davies, 1984; Benfield & Webster, 1985; Smith, 1986).

Most information on breakdown has been obtained by placing leaves in mesh bags or by stacking the leaves on top of one another and loosely sewing them together into packs (Peterson & Cummins, 1974; Benfield *et al.*, 1979; Brock *et al.*, 1982; Iverson *et al.*, 1982). Results from these studies have not been consistent. Some studies indicated that breakdown rates obtained from leaves in bags and packs were similar (Webster & Waide, 1982; Mutch *et al.*, 1983), while others found that leaves in packs broke down faster than leaves in bags (Cummins *et al.*, 1980). Bags have been shown to reduce gas exchange and render leaves less vulnerable to leaching and physical abrasion (Peterson & Cummins, 1974). Packs may also limit gas exchange but should not protect the leaves from abrasion or interfere with leaching.

One exception to the previous methodologies is a study by Cummins *et al.* (1980). They compared breakdown rates of unconstrained basswood leaves with breakdown rates of basswood leaves in bags (1 mm mesh) and packs. Breakdown rates of loose leaves were calculated with the use of a length-weight regression developed using the dry basswood leaves before they were placed in the stream. They determined that packs provided a

good representation of decomposition rates of loose leaves but that small mesh bags did not.

We suggest that these studies obtained a variety of results because one of the primary impacts of constraint technique is to decrease exposure to physical and microbial processing. Accordingly, the extent to which constraint method influences breakdown will vary from species to species depending upon leaf physical rigidity. A constraint technique that is acceptable for one species may be unacceptable for another. This study was designed to determine how constraint technique alters natural factors that influence breakdown of leaves such as dogwood and oak, which differ in structural rigidity. We hypothesized that tough leaves should be affected less by constraint technique than more fragile leaves.

Methods

Dogwood and oak leaves were collected just prior to abscission in the fall of 1987 and 1988. Leaves for all 3 treatments (unconstrained, packs, bags) were air dried for several weeks and weighed dry. Leaf bags of each species were made by placing 10 g of dry leaf material into plastic pecan bags (5 mm mesh openings). Leaf packs of each species were made by weighing 10 g of dry leaf material, soaking the leaves in water until softened, and loosely sewing the leaves together with fishing line (6 kg test).

The study streams consisted of lengths of plastic drain pipe 15 m long, 20 cm wide, with a 2% slope. Each stream was partially filled with 5–10 cm of gravel. Water was piped from a natural stream through a headbox with a series of faucets (1987–88) or v-notches (1988–89) so that the streams had a discharge of approximately 0.25 l s^{-1} . During certain times of the year, debris partially blocked the water intake pipe resulting in fluctuating discharges throughout the study. Macroinvertebrates did not colonize the artificial streams through the intake pipe, and throughout the study no macroinvertebrates were found in the streams. In November 1987 (year 1) and

November 1988 (year 2) leaf bags (year 1), or leaf packs and unconstrained leaves (year 2), were placed in the streams.

Periodically, between November and June of both years, three bags or packs of each leaf type were removed from the streams to determine leaf breakdown rates, total kjeldhal nitrogen (TKN), total phosphorus (TP), and percent ash. Leaf disks (1.5 cm diameter) were cut from randomly selected leaves in each pack to determine microbial biomass and microbial activity. Area to dry weight conversions of leaf disks were calculated so that microbial biomass and activity could be determined on a per gram and per area basis. Analyses on each pack were done in triplicate. Between November 1988 and June 1989, this procedure was repeated with leaf packs and loose leaves. At the end of the 1989 sampling period, all loose leaves were removed from the streams, dried, and ashed to determine the breakdown rate of loose leaves.

Leaf packs or bags (with disks removed) were dried (60 °C) and weighed. Leaf material was ground in a Wiley mill (1 mm mesh) and then three 0.25 g sub-samples from each bag or pack were ashed at 550 °C for 30 min. to determine ash free dry weights (AFDW). Post leaching AFDW of leaf material remaining and days or degree days were log transformed and regressed to determine breakdown rates. To determine TKN, ground leaf material was digested with H₂SO₄, and ammonium was measured using a cyanurate-salicylate reaction (Reynolds & Deal, 1986). To determine TP, ground leaf material was digested with perchloric acid, and TP was measured as soluble reactive phosphorus (SRP) (Reynolds & Deal, 1986). Chemical analyses of digested material were done on a Technicon autoanalyzer II.

Microbial biomass was estimated as ATP content according to Suberkropp *et al.* (1983). ATP was extracted from each disk by placing it in 5 ml of cold 1.2N H₂SO₄ plus 5 ml of tris buffer. The ATP was then brought to a pH of 7.5 with NaOH frozen at -4 °C. At a later date, three subsamples of each extract were analyzed photometrically with a Lab-Line photometer (model 9140). Lu-

ciferin luciferase (0.4 ml) was added to a 0.1 ml aliquot of each sample and ATP was determined as a function of the amount of florescence produced.

Microbial activity of leaf material was estimated by measuring ¹⁴C glucose respiration (Williams & Askew, 1968; Peters *et al.*, 1989). Individual leaf disks (1 cm diam.) were placed in 25 ml incubation flasks containing 5 ml of sterile water. Labeled ¹⁴C (specific activity 304.7 mCi mole⁻¹) was added to the water to obtain a concentration of 0.5 µg-glucose l⁻¹ and flasks were sealed with rubber septa. Filter paper treated with phenethylamine was suspended in the flasks to capture ¹⁴C respired (Hobbie & Crawford, 1969). In preliminary experiments, flasks were incubated from 1 to 4 hours to determine the incubation time that minimized isotopic dilution (i.e. recycling of ¹⁴CO₂, King & Berman, 1984). An incubation time of 3 hours was determined to be sufficient. Therefore, flasks were incubated at ambient stream temperatures for 3 hours. At the end of the incubation period, respiration was stopped by adding 2N H₂SO₄ and the filter paper was removed from the flask and placed in a scintillation cocktail for later analysis on a Beckman Model LS-3105T Scintillation Counter.

During the second year of the study, penetrance (i.e. pressure that must be applied to push a metal rod through the leaf) was used as a measure of leaf conditioning (Feeny, 1970; Suberkropp & Klug, 1981). Three leaves were selected from each pack. Each leaf was held firmly between two plexiglas plates and the mean weight (3 replicates per leaf) required to push a metal rod (5 mm diam) through the leaf was determined. Care was taken to avoid major veins.

Statistical analyses were conducted using main-frame SAS software procedures for ANOVA, t-test, and Pearson's correlations (PEARSON). Two sets of ANOVA's, t-tests, and correlations were run. For each variable of interest data was (1) grouped by leaf type with all dates combined to get an overall significance value, or (2) grouped by leaf type with each sample date evaluated separately to determine significant differences on a monthly basis. Significance values noted in the

text are for analyses conducted with all sample dates combined. Asterisks denoted on the figures indicate significance on a particular date. Correlations were based either on individual samples and dates or grouped by sample date.

Results and discussion

Water temperature in the artificial streams ranged from a low of 1 °C in December to a high of 14 °C in June (Fig. 1). Velocity increased from approximately 0.06 m s⁻¹ at the onset of the experiment to about 0.12 m s⁻¹ in June as leaf material in the streams broke down.

When leaves were placed in the streams, in either bags or packs, dogwood leaves lost more weight due to leaching of soluble components during the first 3 days in the stream than oak leaves. Dogwood leaves had a 30% weight loss while oak leaves lost only about 20% of their initial weight. In addition to leaching more soluble material than oak leaves, dogwood leaves contain less fiber (Benfield, unpublished data).

Dogwood leaves in bags broke down significantly faster than oak leaves in bags (*t*-test, *p* < 0.05) based on days and degree-days⁻¹. When leaves were constrained as packs there was no difference between dogwood and oak breakdown rates (Fig. 2). Differences in microbial activity and biomass may at least partially explain

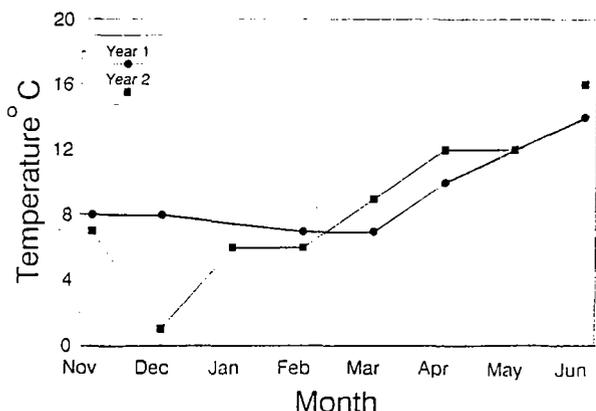


Fig. 1. Mean monthly water temperature (°C) in the artificial streams during year 1 (1987-88) and year 2 (1988-89).

differences in dogwood and oak breakdown rates. Microbial biomass and activity were greater on dogwood leaves than on oak leaves during most months. Over all months, microbial activity was significantly higher on dogwood leaves (*t*-test, *p* < 0.05), however, microbial activity was variable so that significant differences on a monthly basis were spotty. Microbial biomass was significantly greater on dogwood leaves than oak leaves (*t*-test, *p* < 0.05) during all months except June. Penetrance data, collected only during year 2, showed that oak was typically tougher than dogwood and significantly tougher on an overall basis (*t*-test, *p* < 0.01) (Fig. 3), illustrating that oak leaves have more structural rigidity than dogwood leaves and that dogwood leaves were conditioned more effectively than oak leaves (*sensu* Suberkropp & Klug, 1981).

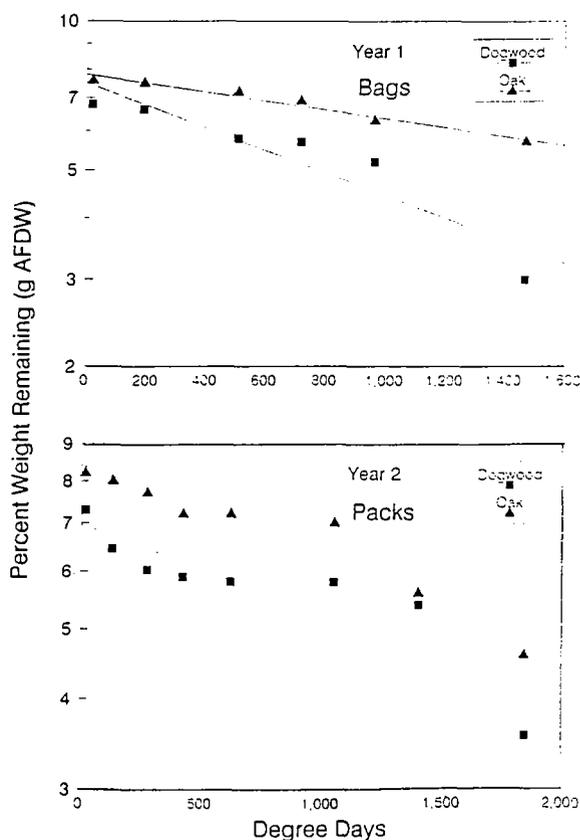


Fig. 2. Dogwood and oak leaf biomass remaining in bags (year 1) or packs (year 2) as a function of degree-days. Initial biomass = 10.0 g.

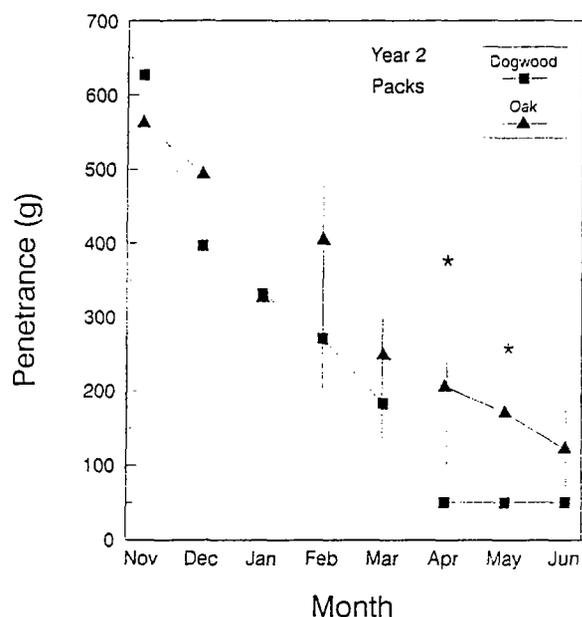


Fig. 3. Mean penetrance of leaf material as mg pressure ($n = 3$) during year 2 (1988-89). Asterisk denotes significance at $p < 0.05$ (t -test).

Although bags and packs were placed in the stream during different years, calculation of breakdown rates based on degree days allowed for direct comparison. There was no difference-

between the breakdown rates of oak leaves in bags and packs. In contrast, dogwood leaves decomposed faster in bags than in packs (t -test; $p < 0.05$) (Fig. 4). For both species, loose leaves decomposed much more quickly than leaves in bags or packs (Table 1) (t -test).

Differences in breakdown rates of constrained and unconstrained leaves may also be partially explained by differences in microbial biomass and activity on the leaves. For both species, microbial biomass (Fig. 5) and activity (Fig. 6) increased from November, when the leaves were placed in the streams, to June, when the study was terminated. During year 1, when the leaves were in bags, dogwood leaves broke down more faster than in year 2 when they were in packs and also had significantly higher levels of microbial activity (t -test, $p < 0.05$). Oak leaf breakdown rates were not different between the two years, nor was microbial activity on oak leaves.

In addition to differences in microbial activity, dogwood leaves were softer than oak leaves (i.e. less force is required to penetrate the leaf matrix). Perhaps as a result of this softness, dogwood leaves may be affected more by constraintment than tougher leaf species such as oak. Dogwood leaves in packs, even when loosely tied, stacked

Table 1. Leaf breakdown rates¹

Treatment	Leaf breakdown degree-day ⁻¹		Discharge (ls ⁻¹)	Source
	Dogwood	Oak		
Artificial streams-No shredders				
Bags	-0.0025Aa	-0.0014Ba	0.25	This study
Packs	-0.0015Ab	-0.0018Ba	0.25	
Loose	-0.0034Ac	-0.0027Bb	0.25	
1st Order Streams-No Shredders				
Bags	-0.0106 A	-0.0040 B	1.0-2.0	Wallace <i>et al.</i> , 1982
Moderate Velocity-Shredders				
Bags	-0.0169 A	-0.0108 B	1.0-2.0	
2nd Order Streams-Shredders				
Bags	-0.023 A	-0.008 B	17.7	Webster & Waide, 1982
Packs	-0.012 A	-0.008 B	17.7	

¹ Upper case letters indicate a significant difference between leaf type at $p < 0.05$ with ANOVA. Lower case letters indicate a significant difference between treatment at $p < 0.05$ with ANOVA.

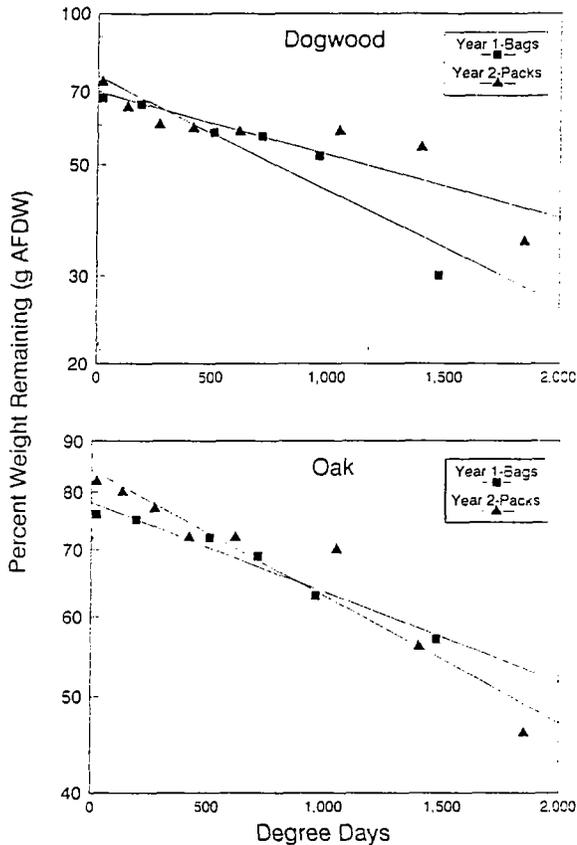


Fig. 4. Comparison of dogwood biomass remaining in bags (year 1) and packs (year 2) and oak biomass remaining in bags (year 1) and packs (year 2) as a function of degree-days. Initial biomass = 10.0 g.

closely on one another. Consequently, microbial activity of dogwood leaves in packs was less than activity on dogwood leaves in bags. Visual observation of dogwood leaf packs revealed that inner leaves were less damaged than outer leaves. In bags, the leaves were more spread out and were less likely to have other leaves on both sides. Microbial activity of oak leaves was not related to constraintment method.

Nutrient content of the leaf material may also have influenced microbial biomass and thereby leaf type and constraintment related breakdown rates. Both dogwood and oak leaves supported levels of microbial activity and biomass that continued to increase for 9 months at these slow rates of decomposition. However, dogwood leaves contained more TP than oak (2.3 mg g^{-1}

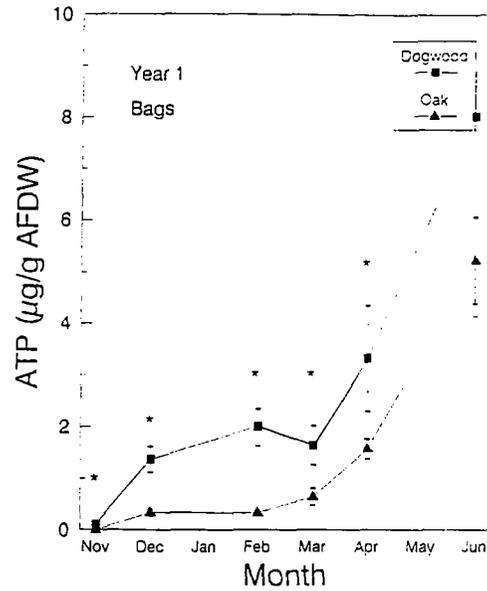


Fig. 5. Microbial biomass ($\text{ATP } \mu\text{g g}^{-1} \text{ AFDW}$) of dogwood and oak leaves during year 1 (1987-88). Asterisk denotes significance at $p < 0.05$. (t -test).

AFDW and $1.1 \text{ mg g}^{-1} \text{ AFDW}$ respectively) (t -test, $p < 0.0001$) during both years of the experiment and typically had a higher TKN content ($10.5 \text{ mg g}^{-1} \text{ AFDW}$) than oak leaves ($9.2 \text{ mg g}^{-1} \text{ AFDW}$) though this difference was significant only during the second year of the study (t -test, $p < 0.001$). Because dogwood leaves only contain about half the lignin of oak leaves (Webster & Benfield, 1986) they also have a much lower lignin to nitrogen ratio than oak leaves. Melillo *et al.* (1982) showed that leaves with lower lignin to nitrogen ratios breakdown more quickly than leaves with higher ratios. And Triska *et al.* (1982) suggested that leaves with a higher TKN content support higher levels of microbial activity and breakdown more quickly than leaves with less abundant microbial communities.

Comparisons with other studies revealed that water velocity and feeding by invertebrates also impacted dogwood and oak leaves to different extents. Natural streams at Coweeta Hydrologic Laboratory, North Carolina, have higher discharges than the artificial streams we used. Discharge and velocity are typically correlated, and it is expected that differences in breakdown rates

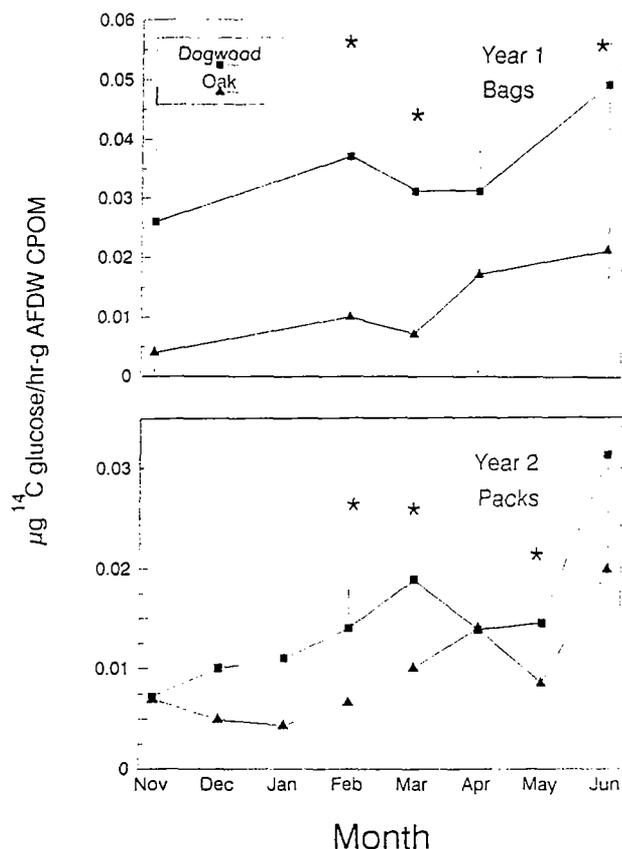


Fig. 6. Microbial respiration (μg glucose respired g^{-1} AFDW) of dogwood and oak leaves during year 1 (1987-88) and year 2 (1988-89). Asterisk denotes significance at $p < 0.05$ (t -test).

obtained from these studies may be due to differences in velocity. Breakdown rates obtained in this study were much slower than rates obtained in natural streams in the absence of shredders (Wallace *et al.*, 1982) (Table 1). Comparing rates obtained in this study with those of Wallace *et al.* (1982) revealed that dogwood leaves broke down 4.2 times faster in the natural streams than in the artificial streams while oak leaves only broke down 2.8 times faster, indicating that the higher velocity in the natural streams affected dogwood leaves to a greater extent than oak leaves.

Comparing rates obtained by Wallace *et al.* (1982) in 1st order streams and rates obtained by Webster & Waide (1982) in a 2nd order stream with higher discharge also suggest that dogwood leaves may be affected more by physical factors

than oak leaves (Table 1). Shredding of leaves by invertebrates also appeared to affect dogwood and oak leaves to different extents. Comparing Wallace *et al.* (1982) data from a 1st order streams with and without shredders revealed that in the presence of shredders, dogwood leaves decomposed 1.6 times faster than without shredders while rates for oak leaves were 2.7 times faster with shredders than without. Comparisons suggest that discharge may be a more important determinant of breakdown rates for dogwood leaves, while shredders may be more important to the structurally tough oak leaves.

This study supports previous conclusions that chemical composition of leaves, velocity, and shredders influence leaf breakdown. But perhaps a more important conclusion to be drawn from this study is that species with different amounts of structural components are differentially affected by constraint techniques and that velocity and/or shredders may be more important to some leaf species than others.

Acknowledgements

We would like to thank Ben Stout, Steve Golladay, and Sherri Gernhoffer for assistance building the artificial streams and John Hutchens and Nick Zemo for help processing the samples. Special thanks also goes to all those at the Coweeta Hydrologic laboratory for their generous help.

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