

# Effects of nutrient enrichment and leaf quality on the breakdown of leaves in a hardwater stream

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## SUMMARY

1. The breakdown of leaf litter in streams is influenced strongly by leaf quality and the concentration of dissolved nutrients, primarily inorganic nitrogen (N) and phosphorus (P) in the water. We examined the effect of nutrient enrichment on the breakdown of three species of leaves in a hardwater, nutrient-rich stream. The rate of microbial respiration was also measured on the decomposing leaves.

2. The breakdown rates of dogwood (*Cornus stolonifera*), aspen (*Populus tremuloides*) and birch (*Betula occidentalis*),  $k$ -values of 0.0461, 0.0307 and 0.0186 day<sup>-1</sup>, respectively, were unaffected by nutrient enrichment and generally faster than reported previously. Microbial respiration on the leaves was greater than reported previously for leaves of congeneric species. It appears that leaf breakdown in the study stream was not nutrient limited.

3. Nitrogen-based measures of leaf quality, such as percentage N and carbon (C)/nitrogen ratio, did not correspond to measured breakdown rates among the three leaf types. The best predictors of relative breakdown rates were percentage lignin and the percentage of the total carbon that occurred as lignin. We suggest that, when leaf breakdown is not nutrient limited, measures of carbon quality (i.e. lignin-based measures) are a better assessment of overall leaf quality than are N-based measures.

4. Previous studies have indicated that the enzymes produced by aquatic hyphomycetes (microfungi) operate most efficiently at a basic pH and in the presence of calcium ions. The hardwater conditions (pH = 8.6, total hardness > 300 mg CaCO<sub>3</sub> L<sup>-1</sup>) and abundance of dissolved NO<sub>3</sub> and soluble reactive phosphorous (SRP) (approximately 50 µg L<sup>-1</sup>, each) in the study stream appear to have provided conditions that resulted in a high respiration rate and rapid breakdown of leaf litter.

*Keywords:* C/N ratios, dissolved nutrients, leaf breakdown, lignin, nitrogen

## Introduction

Many streams are dependent on inputs of organic carbon (C) from the terrestrial environment, particularly in the form of deciduous leaf litter (Cummins, 1974; Wallace *et al.*, 1997). Numerous investigations have suggested that leaf breakdown in streams is controlled by environmental factors, such as water

temperature, the activity of macroinvertebrates and the concentration of dissolved nutrients in the stream water (Webster & Benfield, 1986; Boulton & Boon, 1991). In general, high concentrations of dissolved nutrients, primarily nitrogen (N) and phosphorus (P), accelerate the processing of leaves (Kaushik & Hynes, 1971; Howarth & Fisher, 1976; Elwood *et al.*, 1981; Meyer & Johnson, 1983). Breakdown also appears to occur more rapidly in hardwater streams than in softwater streams (Suberkropp & Chauvet, 1995) and this is probably attributable to greater dissolved macro and micronutrients in hardwater systems.

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In addition to environmental factors, differences in breakdown rates among species have been attributed to intrinsic factors of the leaves (Webster & Benfield, 1986; Boulton & Boon, 1991). The absolute concentration of N and the amount of N relative to the amount of C (C/N ratio) have generally been considered of primary importance. Other work has indicated lignin concentration, rather than nutrients, as the factor limiting the breakdown rate of deciduous leaves (Melillo *et al.*, 1984; Gessner & Chauvet, 1994). Lignin is a structural component of plant material and is highly resistant to enzymatic degradation. It is possible that microorganisms growing on lignin-containing substrates experience C limitation because of the masking of the more labile cellulose by lignin (Gessner & Chauvet, 1994). Similarly, our previous research in a warm, nutrient-rich river suggested that litter breakdown might be limited by C availability rather than dissolved nutrients (Royer & Minshall, 1997).

To date, the roles of dissolved nutrients and leaf quality generally have been studied independently. Our goal was to examine how these two factors might interact. We examined the breakdown of three species of deciduous leaves under ambient and nutrient-enriched conditions in a hardwater, mountain stream that contains relatively high background concentrations of dissolved N and P. In this stream, we expected that breakdown would not be nutrient limited and, if so, that lignin-based measures of leaf quality would be superior to N-based measures in predicting the relative rate of breakdown among species.

## Methods

### Site description

This research was conducted in a reach (42° 42' N, 112° 25' W; altitude = 1647 m) of the South Fork of Mink Creek (hereafter Mink Creek) in the Caribou National Forest in south-east Idaho. The riparian community is predominantly willow (*Salix* spp.), dogwood (*Cornus stolonifera* Michx.), birch (*Betula occidentalis* Hook) and aspen (*Populus tremuloides* Michx.). The stream bed consisted of cobble mixed with gravel. Livestock graze in the Caribou National Forest but were not present during the experiments and the riparian community at the study site was not

noticeably damaged by grazing. Other anthropogenic impacts on the stream are minor.

Water chemistry at the site was measured approximately weekly during the autumn of 1997 and 1998. Portable meters (Orion, Inc., Beverly, MA, U.S.A.) were used to measure pH and conductivity. Total alkalinity and hardness were determined using standard titration methods (APHA, 1995). The concentration of NO<sub>3</sub>-N was analysed on an ion chromatograph (Dionex, Inc., Sunnyvale, CA, U.S.A.). Ammonium and soluble reactive phosphorus (SRP) were determined with a Technicon AutoAnalyzer (Technicon). General chemical and physical characteristics of the site are presented in Table 1.

### Leaf breakdown experiments

We used the litter-bag technique in which leaves are placed into mesh litter bags and anchored to the streambed (Boulton & Boon, 1991). The use of litter bags has been criticised as unrepresentative of natural conditions (Cummins *et al.*, 1980) and this may be the case if the mesh inhibits water flow through the bag or prevents organisms reaching the leaves. Our litter bags were constructed of rigid nylon with a mesh size of 5 mm and allowed water flow through the bags and the access of macroinvertebrates. The trade-off for a relatively large mesh size is the potential for the leaves to be fragmented and lost from the litter bags as large particles. In this stream, decomposers skeletonized the leaves and these were easily discernible from physically fragmented leaves. Visual examination of leaves after removal from the stream indicated that the loss of mass in Mink Creek was

**Table 1** Means and standard deviations (SD) for physical and chemical characteristics of the study site on Mink Creek, Idaho. Chemical data were collected approximately weekly during autumn 1997 and 1998

	Mean	SD
Width (cm)	280	13
Depth (cm)	11	1
Baseflow discharge (L s <sup>-1</sup> )	97	–
pH	8.6	0.1
Conductivity (µS cm <sup>-1</sup> at 25 °C)	532	11
Total alkalinity (mg CaCO <sub>3</sub> L <sup>-1</sup> )	199	17
Hardness (mg CaCO <sub>3</sub> L <sup>-1</sup> )	332	38
NO <sub>3</sub> -N (µg L <sup>-1</sup> )	54	13
NH <sub>4</sub> -N (µg L <sup>-1</sup> )	17	2
SRP (µg L <sup>-1</sup> )	54	3

as a result of biological action rather than physical breakage.

The leaves of three tree species were used: dogwood, aspen and birch. Senescent leaves were collected from several trees of each species at the study site during the time of natural abscission and stored at room temperature for up to 5 days. A known amount (between 2.0 and 2.5 g dry mass) of leaves was placed in each of the litter bags, which in turn were anchored to bricks and placed in riffles. Forty litter bags were constructed for each species, 20 of which received nutrient enrichment (see below) and 20 of which did not. Three additional litter bags of each species were used to correct for handling losses. Birch and dogwood leaves were placed in the stream on 5 October 1997 and aspen leaves on 20 October 1997. These dates coincided with natural abscission for each species. Five bags of each species and treatment were removed after 1, 3, 11 and 29 days in the stream (1, 6, 15 and 30 days for aspen). After removal from the stream, all litter bags were placed into individual plastic bags and returned to the laboratory on ice. In the laboratory, the material in each litter bag was rinsed of sediment, invertebrates and extraneous detritus and the final ash-free dry mass (AFDM) determined by combustion at 550 °C for 2 h. Initial AFDM in each litter bag was determined from a linear regression of AFDM against dry mass ( $R^2 > 0.92$  in all cases). Breakdown was calculated as the percentage loss of initial AFDM.

Nutrient enrichment was accomplished with a slow-release fertilizer developed specifically for streams (Mouldy Ewing & Ashley, 1998) and used successfully in studies of leaf breakdown (Robinson & Gessner, 2000). Pellets of the fertilizer are approximately 8 g in mass and cylindrical in shape with dimensions of approximately  $7 \times 1.5$  cm. The pellets dissolve at a constant rate of  $0.5\% \text{ day}^{-1}$  and contain 7% N and 18% P in the form of  $\text{NH}_4$  and  $\text{PO}_4$ , respectively (Mouldy Ewing, 1998); this equates to a release from each pellet of  $2.8 \text{ mg NH}_4\text{-N day}^{-1}$  and  $7.2 \text{ mg PO}_4\text{-P day}^{-1}$ . Pellets were placed in the litter bags assigned to the nutrient enriched treatment; one pellet per bag for birch and dogwood, two pellets per bag for aspen. All litter bags that received fertilizer pellets were placed in a reach 5 m downstream of litter bags in the ambient treatment. The effect of nutrient enrichment on leaf breakdown was tested individually on each leaf type with ANCOVA.

Five additional litter bags, each containing approximately 1 g dry mass, were constructed for each leaf species and used for measurement of microbial respiration on the decaying leaves. This was the maximum size that would fit inside the metabolism chambers (see below). These bags were placed in the stream on the same dates as described above. Microbial respiration was measured after 15–17 days in the stream by placing individual litter bags in recirculating metabolism chambers and recording the change in the concentration of dissolved oxygen over time. The chambers are plexiglass cylinder equipped with a recirculating pump and an in-line port for a dissolved oxygen electrode. The internal design of the chambers creates a uni-directional flow of water across the leaf packs. Each chamber holds approximately 2 L of stream water. A detailed description of the chambers was given by Bott *et al.* (1997). The dissolved oxygen inside each chamber was measured with portable meters and electrodes (Orion Inc., model 840).

Chamber incubations ranged in duration from 50 to 60 min and were conducted in the stream immediately downstream of the study site, using ambient stream water. At the outset of the study, empty litter bags were placed together with the bags containing leaves and were used to correct the respiration of biofilms on the litter bags themselves rather than on the decomposing leaves. Four chambers were used during an incubation: three with leaves and one with an empty litter bag. One incubation was conducted for each leaf species. During the incubations, the chambers were covered with opaque plastic to prevent photosynthesis. Following incubation, the material in the litter bags was returned to the laboratory and the AFDM determined as described above. Mean respiration rate ( $n = 3$ ) was then expressed as  $\text{mg O}_2 \text{ g AFDM}^{-1} \text{ h}^{-1}$ .

#### *Initial leaf quality*

Initial leaf quality was assessed for each species using leaves collected at the same time as those used in the litter bags. The N and C concentrations were determined with a Fisons Instruments (model NA 1500 NC; Fisons, Beverly, MA, U.S.A.) elemental analyser; C/N ratio was calculated as percentage C divided by percentage N. Lignin concentration was determined following the method of Goering & Van Soest (1970). Leaves were ground to a fine powder and then

refluxed in acid-detergent solution. Following refluxing, the material was rinsed several times with decahydronaphthalene and acetone and then soaked in chilled 1 N sulphuric acid. Finally, the remaining leaf material was filtered onto a 0.45 m glass fibre filter and the AFDM determined as described above. Differences among leaf types in N concentration, C/N ratio and lignin concentration were tested with one-way analysis of variance (ANOVA) ( $n = 5$ ) and a Bonferroni *posthoc* test. Data were  $\ln(x + 1)$  or  $\arcsin(x^{0.5})$  transformed prior to statistical tests (Zar, 1984).

## Results

### Leaf breakdown

The analysis of covariance (ANCOVA) indicated there was no effect of nutrient enrichment on the breakdown of any of the three leaf types examined (Fig. 1; birch:  $F = 1.046$ ,  $P = 0.35$ ; dogwood:  $F = 2.381$ ,  $P = 0.18$ ; aspen:  $F = 0.014$ ,  $P = 0.91$ ). Under ambient conditions, birch leaves lost approximately 50% of initial AFDM during the 1-month incubation in Mink Creek. Dogwood and aspen leaves were processed more rapidly, losing about 80 and 60%, respectively, of initial AFDM. Each leaf type displayed a substantial loss of AFDM during the first 24 h in the stream. Exponential decay rates, or  $k$ -values (Webster & Benfield, 1986), were  $0.0461 \text{ day}^{-1}$  for dogwood,  $0.0311 \text{ day}^{-1}$  for aspen and  $0.0186 \text{ day}^{-1}$  for birch, averaged across ambient and enriched treatments.

Microbial respiration rates corresponded to the overall loss of mass among the leaf types. The mean respiration rate was greater on dogwood leaves than on birch or aspen (Fig. 2), although the differences among leaf types were not statistically significant (ANOVA:  $F = 4.546$ ,  $P = 0.06$ ). After 15–17 days in Mink Creek, the mean rate on dogwood leaves was  $1.5 \text{ mg O}_2 \text{ g AFDM}^{-1} \text{ h}^{-1}$  and  $0.75 \text{ mg O}_2 \text{ g AFDM}^{-1} \text{ h}^{-1}$  on birch and aspen leaves.

### Initial leaf quality

Birch leaves were 0.92% N, which was significantly greater ( $P < 0.001$ ) than either dogwood or aspen leaves, both of which contained approximately 0.65% N (Fig. 3). The C/N ratios were significantly different among leaf types ( $P < 0.001$ ). The lowest

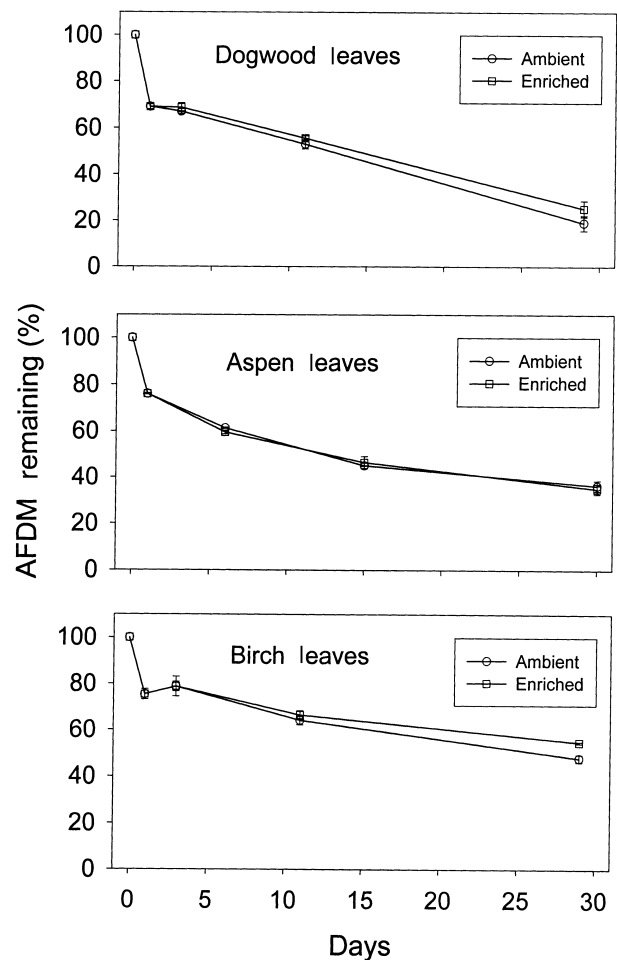


Fig. 1 Mean ( $\pm 1$  SE;  $n = 5$ ) % AFDM remaining for dogwood, aspen and birch leaves over time during autumn 1997 in Mink Creek, Idaho, under ambient and nutrient enriched conditions.

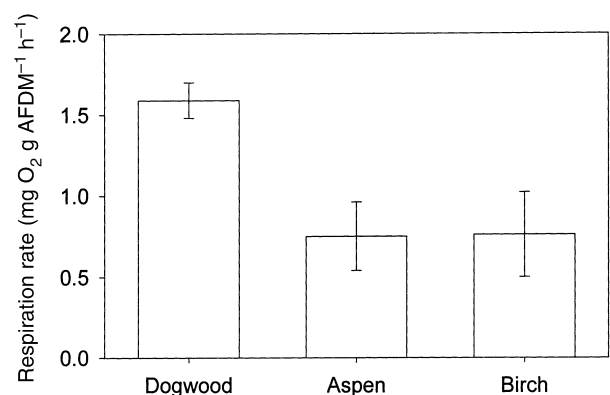


Fig. 2 Mean ( $\pm 1$  SE) respiration rates on dogwood, aspen and birch leaves after 15–17 days of in-stream processing in Mink Creek, Idaho, during autumn 1997.

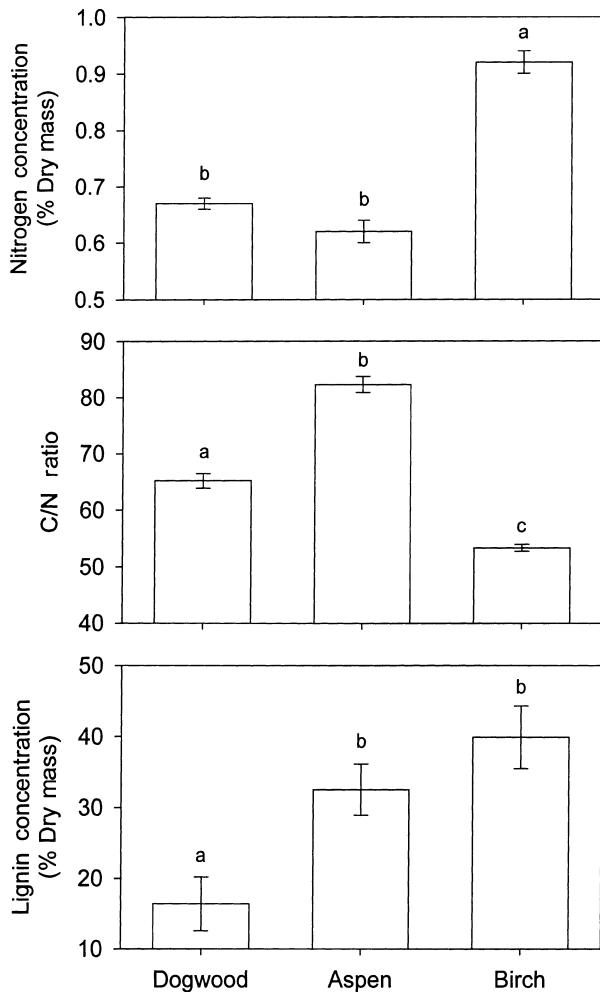


Fig. 3 Mean ( $\pm 1$  SE;  $n = 5$ ) N concentration, C/N ratio and lignin concentration in senescent dogwood, aspen and birch leaves prior to placement in Mink Creek, Idaho. Bars with the same letter are not statistically different.

C/N ratio (53) was for birch leaves, the greatest (80) for aspen, while dogwood was intermediate at 65. Dogwood leaves contained significantly less lignin than either birch ( $P = 0.02$ ) or aspen ( $P = 0.02$ ). Approximately 35–40% of the dry mass of birch and aspen leaves was lignin whereas dogwood leaves were about 15% lignin (Fig. 3). Using mean values of N, C and lignin concentrations, we calculated for each leaf species the lignin/N ratio and estimated the percentage of the total C that occurred as lignin. The lignin/N ratios were 24, 43 and 53 for dogwood, birch and aspen, respectively. About 22% of the total C in dogwood leaves occurred as lignin, compared with about 40 and 50% in aspen and birch respectively.

Based on respiration rates and mass loss, the relative order of breakdown among the three leaf types was dogwood > aspen > birch. The traditional measures of leaf quality, such as percentage N and C/N ratio, did not correspond to the measured order of breakdown. Lignin concentration and the percentage of the total C as lignin were the best indicators of relative breakdown rates among dogwood, aspen and birch leaves in Mink Creek.

## Discussion

### Leaf breakdown

Previous comparative studies have reported faster mass loss (Elwood *et al.*, 1981; Meyer & Johnson, 1983) and greater fungal growth and sporulation rates (Suberkropp, 1995; Suberkropp & Chauvet, 1995; Weyers & Suberkropp, 1996) in streams or stream reaches with higher nutrient concentrations. Similarly, manipulations in microcosms generally have found faster processing with increased nutrient concentrations (Kaushik & Hynes, 1971; Howarth & Fisher, 1976) but this result is not universal (Triska & Sedell, 1976). We found no effect of nutrient enrichment on the processing of leaves in Mink Creek. This apparent anomaly has two possible explanations: (1) the nutrient-diffusing pellets used in the experiments did not function as a true nutrient enrichment treatment, or (2) the processing of leaf litter in Mink Creek is not nutrient-limited. The first explanation is unlikely because the efficacy of the fertilizer pellets has been extensively studied (Mouldy Ewing & Ashley, 1998) and shown to accelerate leaf breakdown in a stream of low nutrient concentration (Robinson & Gessner, 2000).

We suggest that leaf breakdown was not enhanced by the addition of dissolved inorganic nitrogen (DIN) and SRP because leaf breakdown was not nutrient limited in Mink Creek. The ambient concentrations of DIN and SRP in Mink Creek each averaged  $> 50 \mu\text{g L}^{-1}$  (Table 1). Studies reporting a significant stimulation from nutrient enrichment typically examined streams containing much lower concentrations of DIN and/or SRP than Mink Creek. For example,  $\text{PO}_4$  enrichment accelerated processing of deciduous leaves in Walker Branch, Tennessee, where the ambient concentration, typically  $< 10 \mu\text{g L}^{-1}$ , was increased to an average of  $60 \mu\text{g L}^{-1}$  (Elwood *et al.*, 1981),

a concentration similar to the  $54 \mu\text{g L}^{-1}$  SRP found in Mink Creek (Table 1). Increasing  $\text{PO}_4$  concentration to an average of  $450 \mu\text{g L}^{-1}$  did not further enhance leaf breakdown in Walker Branch (Elwood *et al.*, 1981) nor did the P provided by the fertilizer pellets accelerate breakdown in Mink Creek.

Nitrogen was the expected limiting nutrient in Mink Creek based on molar N/P ratios and the abundance of a nitrogen-fixing cyanobacterium (*Nostoc*). The nutrient enrichment used in the present study did not accelerate leaf processing in Mink Creek, despite providing  $2.8 \text{ mg NH}_4\text{-N day}^{-1}$  from each fertilizer pellet. Newbold *et al.* (1983) increased  $\text{NH}_4$  concentration in Walker Branch from  $10 \mu\text{g L}^{-1}$  or less to over  $60 \mu\text{g L}^{-1}$  but found no effect on leaf breakdown. Under ambient conditions, total dissolved inorganic N in Walker Branch averaged about  $31 \mu\text{g L}^{-1}$  compared with  $70 \mu\text{g L}^{-1}$  in Mink Creek. We conclude that ambient concentrations of dissolved inorganic N and SRP were sufficient in Mink Creek to preclude nutrient limitation of leaf breakdown.

#### Leaf quality and breakdown rates

Perhaps the most extensively studied aspect of leaf breakdown in stream ecosystems is the variability among different species of leaves (e.g. Webster & Benfield, 1986). Early studies attributed these differences to the amount of N in the leaves and their palatability to shredding insects (e.g. Kaushik & Hynes, 1971; Petersen & Cummins, 1974). Traditionally, two characteristics have been considered of primary importance: % N and C/N ratio. However, in Mink Creek neither of these variables correctly predicted the measured order of breakdown. The rationale for expecting C/N and lignin/N ratios to correspond to breakdown rates is based on the assumption that fungi on a decaying leaf obtain N from the leaf itself. Recent studies indicate that fungi growing on leaves may obtain N and P from the water column, rather than the leaf substrate (Suberkropp, 1995; Suberkropp & Chauvet, 1995). In Mink Creek, where leaf breakdown is not limited by dissolved N and P, it is likely that carbon quality of the leaves is more important to fungal activity and leaf breakdown than is the amount of N in the leaves.

Gessner & Chauvet (1994) found that percentage lignin was the most important leaf characteristic controlling the decay of seven types of leaves in a

French stream. Lignin is a refractory, structural component of leaves that must be degraded concurrently with cellulose because the two compounds often are intertwined. Even in streams with relatively low concentrations of dissolved nutrients fungi on leaf litter can experience C limitation (Gessner & Chauvet, 1994). This suggests that the form of the C is at least as important as nutrient concentration in the leaf litter and the stream water. We found lignin-based measures of leaf quality to be more accurate predictors of relative decay rates than percentage N or C/N ratio. In particular, the percentage of the total C that occurred as lignin was the best indicator of relative breakdown rates among aspen, dogwood and birch leaves in Mink Creek. For streams where leaf breakdown is not limited by dissolved nutrients and hence fungi are not dependent on leaf-N or leaf-P as a nutrient subsidy, measures of carbon availability (i.e. lignin-based measures) will probably provide the best indication of relative breakdown rates among species.

#### Microbial respiration and rapid breakdown in Mink Creek

Tank, Webster & Benfield (1993) reported microbial respiration on sweet birch (*Betula lenta* L.) leaves in North Carolina of  $0.12$  and  $0.09 \text{ mg O}_2 \text{ g AFDM}^{-1} \text{ h}^{-1}$ , respectively. In Mink Creek, birch leaves (*Betula occidentalis*) supported rates of  $0.75 \text{ mg O}_2 \text{ g AFDM}^{-1} \text{ h}^{-1}$ . Schade & Fisher (1997) reported a peak respiration rate on cottonwood leaves (*Populus fremontii* Wats.) in Sycamore Creek, Arizona, of  $0.52 \text{ mg O}_2 \text{ g AFDM}^{-1} \text{ h}^{-1}$ , slightly less than the  $0.75 \text{ mg O}_2 \text{ g AFDM}^{-1} \text{ h}^{-1}$  measured on aspen (*Populus tremuloides*) leaves in Mink Creek. Dogwood leaves in Mink Creek supported microbial respiration rates of up to 10 times greater than the species examined by Tank *et al.* (1993) or Schade & Fisher (1997). Regardless of the study, the leaves that displayed the greatest respiration rates also decayed most rapidly, emphasizing the importance of microbial processing in the breakdown of leaf litter in streams (e.g. Petersen, Cummins & Ward, 1989).

The processing of leaf litter in Mink Creek was rapid compared with other North American streams. Reported  $k$ -values for species of Cornaceae are  $< 0.03 \text{ day}^{-1}$  (Webster, Wallace & Benfield, 1995; Webster & Benfield, 1986) whereas *Cornus stolonifera* in this study had a  $k$ -value of  $0.0461 \text{ day}^{-1}$ . For

streams in eastern North America, the upper ranges of reported  $k$ -values are approximately 0.010 and 0.017 day<sup>-1</sup> for Salicaceae and Betulaceae, respectively (Webster *et al.*, 1995). The  $k$ -value for aspen in Mink Creek was 0.0307 day<sup>-1</sup>, or nearly twice as fast as observed for species of Salicaceae in other streams. The difference was less striking for birch, although the  $k$ -value in Mink Creek of 0.0186 day<sup>-1</sup> is at the upper end of the range given for Betulaceae (Webster *et al.*, 1995; Webster & Benfield, 1986). Biological half-lives, i.e. the time needed for 50% of the initial material to be lost, provide an alternative to  $k$ -values when comparing breakdown rates from various studies. Petersen & Cummins (1974) presented half-life values of < 46, 46–138 and > 138 days for 'fast', 'medium' and 'slow' species, respectively. In Mink Creek, the half-life for both dogwood and aspen leaves was 13 days and 27 days for birch leaves. Thus, all three species we examined in Mink Creek would qualify as 'fast' species, although aspen leaves were the most slowly decaying species studied by Petersen & Cummins (1974) with a half-life of > 138 days.

We suggest two reasons for the rapid processing of leaves in Mink Creek. First, the ambient nutrient concentrations were such that fungi on the leaves did not have to obtain N and P from the leaves, both were readily available in dissolved inorganic form in the water. Suberkropp & Jones (1991) found that the fungi *Tetracladium marchalianum* de Wild., *Lemonniera aquatica* de Wild., *Alatospora acuminata* Ingold, *Flagellospora curvula* Ingold and *Heliscus lugdunensis* Sacc. & Therry, each of which occurs in Mink Creek (Royer, 1999), can produce acid phosphatase and alkaline phosphatase. Although these taxa are capable of liberating P from leaves, in Mink Creek they probably did not require these enzyme systems and may have diverted energy from the production of phosphatase to the production of enzymes capable of degrading the cell walls of plants (Chamier, 1985).

Second, the enzymes used by aquatic hyphomycetes to degrade pectin, lignin and cellulose appear, on the basis of limited research, to have pH optima of about 8.0 and to operate most efficiently under alkaline conditions (Suberkropp & Klug, 1980; Chamier, 1992). The water chemistry of Mink Creek, with an average pH of 8.5–8.6 and total alkalinity > 180 mg CaCO<sub>3</sub> L<sup>-1</sup>, provided nearly optimal conditions for the enzymatic breakdown of deciduous leaves by aquatic fungi. Together, the hardwater and

nutrient-rich conditions created an environment for aquatic fungi that resulted in high respiration rates and rapid breakdown of leaf litter.

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