



Relationship between Chemical Characteristics of Autumn-Shed Leaves and Aquatic Processing Rates

Author(s): M. L. Ostrofsky

Source: *Journal of the North American Benthological Society*, Vol. 16, No. 4, (Dec., 1997), pp. 750-759

Published by: The North American Benthological Society

Stable URL: <http://www.jstor.org/stable/1468168>

Accessed: 12/06/2008 15:11

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=nabs>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We enable the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

## Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates

M. L. OSTROFSKY

*Biology Department, Allegheny College, Meadville, Pennsylvania 16335 USA*

*Abstract.* Processing rates of autumn-shed leaves in aquatic habitats are highly variable. It has been hypothesized that these processing rates may, in part, be regulated by the concentrations of residual tannins in the leaves. Tests of this hypothesis have been inconclusive, and experimental designs may have been compromised by the use of both processing rates and tannin concentrations taken from a variety of sources using highly variable methods, sites, and experimental conditions. Here, processing rates of 48 species of deciduous leaves are measured using uniform conditions, and related to concentrations of leaf tannins, N, P, C:N, lignin, and toughness. The results indicate that condensed tannin, N, C:N, and lignin are significantly correlated with processing rates, although the predictive power of these simple relationships is weak. A multiple regression model using tannins, measured as total phenolics, N, and lignin explained almost 50% of the variation in processing rates, suggesting that the inhibition of processing by tannins is modified by other measures of leaf quality.

*Key words:* leaf processing, leaf litter, tannin, lignin, nutrients, toughness.

Food webs in temperate woodland stream and pond communities are supported to a large, and perhaps overwhelming, extent by organic matter imported from the forest canopy in the form of autumn-shed leaves (e.g., Fisher and Likens 1973). The temporal stability of these food webs is most likely the result of the broad refractory range of much of this organic matter (Wetzel 1995). Labile materials are quickly metabolized, skewing the organic pool to increasingly recalcitrant materials. These materials are only very slowly metabolized, yet because of the large pool, may be as important in supporting food webs as the more labile materials.

Ecologists use mass loss as an analog measure of metabolic processing of autumn-shed leaves, although it should be acknowledged that much of the mass loss can be a result of non-metabolic processes such as leaching and abrasion (Ostrofsky 1993). Processing rates, defined as  $\ln(W_d/W_o)/d$  (Peterson and Cummins 1974), vary over orders of magnitude as a function of species, temperature, water chemistry, habitat (stream, marsh, lake, etc.), and experimental protocol (leaf pack vs mesh bags). A compilation of processing rates from the published literature reveals a range among plant families examined of 2 orders of magnitude (Webster and Benfield 1986), and a range among species of 3 orders of magnitude. Much of this variation is undoubtedly the result of different methods and sites, but species differences are real as evidenced by the results of multispecific compari-

sons using a common method at a single site (e.g., Peterson and Cummins 1974). There has been much recent interest in explaining these species differences.

Stout (1989) made a compelling argument for the influence of residual defensive compounds, notably tannins, and supported this argument with literature data on processing rates and condensed tannin concentrations. The results showed a semiquantitative relationship between processing rates ( $k$ ) and ordinal measures of condensed tannins in 39 mid-latitude and 16 tropical tree species. Although Stout found significant differences among the 3 categories of tannin (absent to low, intermediate, high) for mid-latitude species, there were no differences between the processing rates in the intermediate and high tannin categories. Small sample size precluded analysis of the tropical species. To better evaluate the relationship between tannins and leaf processing and conditioning rates, Ostrofsky (1993) measured tannins quantitatively in leaves of 48 species of temperate trees and sought correlations with published processing rates (from Webster and Benfield 1986) and measured conditioning (microbial colonization) rates. Here again, no significant relationships were found.

There are at least 3 possible reasons for the failure to demonstrate a convincing relationship between tannins and leaf-processing rates. The 1st is that rates are not dependent on tannin concentrations. The 2nd is that by using the pro-

cessing rates of Webster and Benfield (1986), a great deal of noise is introduced into the analysis. Their compilation included studies using a variety of methods, temperatures, water chemistries, habitats, etc., so the variability of processing rates even within a single species is high. For example, Webster and Benfield (1986) presented 33 different processing rates for *Acer rubrum* taken from 10 different published sources representing experiments conducted in lake, swamp, and stream habitats. As a consequence of variations in experimental conditions and sites, these rates ranged from 0.0007 to 0.0354/d. Third, it is possible that the effects of tannins are masked by other leaf characteristics such as fiber content or foliar nutrient concentrations. As Campbell and Fuchshuber (1995) warned, "the influence of tannin level on processing may only be apparent when the "noise" caused by variation in other aspects of leaf chemistry . . . is reduced".

Here I present further analysis of the potential relationship between leaf characteristics and leaf processing rates. I have attempted to reduce the variation in the data set by calculating processing rates on a collection of 48 species using uniform methods and conditions. I have analyzed a suite of leaf chemical characteristics and combined these data with the previously reported data on tannins (Ostrofsky 1993).

### Methods

Collection, drying, and preliminary treatment of leaves is described by Ostrofsky (1993), and the results of the analyses for condensed tannins, total phenolics, and protein-precipitating capacity from that report are used in the analyses reported here. Additional analyses performed on the same sample material (collected in 1991) include P and N content, C:N ratio, and lignin. Additional leaf material was collected in 1994 to determine processing rates and leaf toughness. This new material was collected in the same manner, and from the same individual trees as the material collected for the 1991 chemical analyses.

#### *Processing rates*

A known mass (~2 g) of leaves of each species, air-dried in the laboratory, was placed in 15×15-cm mesh bags made of fiberglass win-

dow screening (mesh size ~1.5 mm). One bag of each of the 48 leaf species was fastened to a line, and the entire line was anchored to the bottom of a permanent woodland pond at Allegheny College's Bousson Environmental Research Reserve. A single line of bags was retrieved at 1, 2, 3, 4, 6, 9, 13, 18, and 24 wk. Leaf material was gently washed while still in the bags to remove silt, epiphytes, and invertebrates, and was then hung in the laboratory to air-dry for at least 1 wk. Remaining leaf material was weighed, and the % initial mass remaining was calculated. The natural log of % mass remaining was regressed against time, and the slope of the regression was taken to be the processing rate,  $k$  (units/d). It was assumed that leaf processing followed the general form  $\ln(W_t/W_{t_0}) = \text{intercept} - kt$ , where  $W_t$  and  $W_{t_0}$  were final and initial leaf masses, respectively, and  $t$  was time in d (Peterson and Cummins 1974). Because mass loss is a function of both leaching and processing and some researchers (e.g., Wieder and Lang 1982) have argued for the use of biphasic kinetics models to describe mass loss, I did not include 100% mass at time 0 in the regressions. As a consequence,  $k$  values reported here describe rates of mass loss only after the 1st week. There was little evidence in the resulting graphs that biphasic models would better describe mass loss, although the need for such models is evident if  $W_{t_0} = 100\%$  at  $t = 0$  is included as a data point.

#### *Leaf characteristics*

In general, a single leaf did not contain sufficient material for all chemical analyses, so anywhere from 6 to ~50 leaves of each species, depending on leaf size, were ground together for analysis. This approach precluded the examination of between-leaf variability within species.

*P content.*—Leaves were ground with a mill to a fine powder, as described by Ostrofsky (1993). A known mass of oven-dried leaf powder was placed in acid-washed, 50-mL flasks and digested with  $\text{HNO}_3$  and  $\text{HClO}_4$ . After digestion, volume was made up to 50.0 mL with distilled water and aliquots were analyzed for P using the spectrophotometric heteropoly blue technique (Strickland and Parsons 1968). Results are expressed as %P of leaf mass, and are the means of triplicate analyses.

*N content, C:N ratio.*—Oven-dried leaf powder

was analyzed for N and C with a LECO model 600 elemental analyzer. All analyses were done in triplicate, and mean %N of leaf mass is reported here. Mean N and mean C were used to calculate C:N ratio.

**Lignin.**—Lignin content was estimated using the gravimetric technique of Ryan et al. (1990). Data reported are means of triplicate analysis.

**Toughness.**—To estimate leaf toughness, I constructed a penetrometer similar to that described by Feeny (1970). Air-dried leaves were rehydrated by a 24-h submersion in distilled water at 10°C. The punch (0.64-mm diam.) was placed in the center of an area bounded by the midvein, leaf margin, leaf base, and the midline between base and tip. Steel shot was loaded on a piston until the punch broke through the leaf. The mass (g) of shot necessary to break through the leaf was taken to be a measure of toughness. Data reported are the means of 10 replicate trials per species.

#### Statistical Analysis

Analysis of the data followed standard simple and step-down multiple regression techniques (Zar 1974).

### Results

The results of all analyses are shown in Table 1. Calculated ks ranged from 0.0006 to 0.0054/d (mean = 0.0022/d). All of the regressions of  $\ln(W_t/W_0)$  vs time were significant, indicating a constant rate of mass loss with time. None of the regressions, however, had a 0 intercept (fitted intercept significantly <100%), indicating that the rate of mass loss was significantly greater during the 1st week than in subsequent weeks (Fig. 1). This result is consistent with a brief period of rapid mass loss—probably leaching—that is independent of microbial activity. The consistent linearity of the data beyond the 1st week, and the paucity of data points prior to the 1st week, preclude the fitting of double exponential decay equations to the mass-loss data (Riggs 1963). However, if it can be assumed that mass loss during the 1st week is largely abiotic leaching, and mass loss thereafter is largely biotic processing, then the mass lost to abiotic leaching may be estimated as the difference between the  $W_{t_0}$  and  $W_{t_1}$ . Results here range from a low of 6% in *Quercus palustris*, *Q.*

*rubra*, and *Carya laciniosa*, to 39% in *Cornus stolonifera*. Further, the mass lost in the 1st week was significantly correlated with processing rate ( $r = 0.343$ ,  $n = 48$ ,  $p < 0.02$ ), suggesting that those leaves with the most rapidly soluble components are also those that are processed fastest following the loss of those components.

The P content of the leaf material examined ranged from 0.065% in *Betula populifolia* to 0.615% in *Gleditsia triacanthos*, and the N content ranged from 0.38% in *Liquidambar styraciflua* to 2.89% in *Robina pseudoacacia* (Table 1). Carbon:nitrogen ratios ranged from 16.8 in *Robina pseudoacacia* to 120.8 in *Liquidambar styraciflua*. Lignin content ranged from 13% in *Cornus florida* to 39% in *Aesculus hippocastaneum*. Toughness ranged from 153 g for *Betula lutea* to 621 g for *Fraxinus americana*.

Leaf processing was significantly correlated with condensed tannin ( $r = -0.34$ , Fig. 2), %N ( $r = 0.50$ , Fig. 3), and C:N ratio ( $r = -0.50$ , Fig. 4), but not to total phenolics, protein-precipitating capacity, %P, %lignin, or toughness. Regression equations for significant correlations are as follows:

$$k = 2.70 \times 10^{-3} - 6.43 \times 10^{-3} (\text{cond. tannin})$$

$$n = 48, \quad r^2 = 0.12 \quad p < 0.02$$
[1]

$$k = 9.60 \times 10^{-4} + 9.99 \times 10^{-4} (\%N)$$

$$n = 48, \quad r^2 = 0.25 \quad p < 0.001$$
[2]

$$k = 3.53 \times 10^{-3} - 2.87 \times 10^{-5} (\text{C:N})$$

$$n = 48, \quad r^2 = 0.25 \quad p < 0.001$$
[3].

Although these correlations are statistically significant, the regressions have poor predictive power. Percent lignin was not correlated with k, but %lignin combined with %N was correlated with k (Fig. 5):

$$k = 3.32 \times 10^{-3} - 3.95 \times 10^{-5} (\% \text{lignin} : \%N)$$

$$n = 48, \quad r^2 = 0.26 \quad p < 0.001$$
[4].

The predictive power of %lignin:%N is only slightly improved (to  $r^2 = 0.32$ ) by natural log transformation of the ratio. Finally, a stepwise regression indicated that better predictive pow-

er can be attained using several independent variables:

$$k = 5.15 \times 10^{-3} - 1.48 \times 10^{-3} (\text{tot. phenol.}) \\ + 8.29 \times 10^{-4} (\%N) - 1.04 \times 10^{-4} (\%lignin) \\ n = 48, \quad r^2 = 0.47 \quad p < 0.001$$

[5].

This result supports the hypothesis that processing rates are positively affected by leaf nutritional quality (%N) and negatively affected by both refractoriness (%lignin) and deterrence (total phenolics).

### Discussion

The results presented above indicate that total phenolics, protein-precipitating capacity, %P, %lignin, and toughness are not related individually to processing rates. The best individual predictors of leaf processing rates are %N, C:N ratio, condensed tannins, and %lignin:%N ratio, although these variables have low predictive power. Processing rates are best explained by a combination of factors related to nutritional quality, refractoriness, and residual deterrents, as indicated by a multiple regression using %N, %lignin, and total phenolics as independent variables. However, even this combination of factors is only capable of explaining ~50% of the variation in processing rates, and there remains a group of unmeasured factors that is equally important.

The processing rates reported here are within the ranges reported in other studies (e.g., Peterson and Cummins 1974, Webster and Benfield 1986). However, a matched-pairs *t*-test between the rates calculated here and the mean of the rates compiled by Webster and Benfield (1986) for 26 species in common indicates that the means obtained by Webster and Benfield (1986) are significantly higher. It should be kept in mind, however, that the results reported by Webster and Benfield (1986) include data from studies using leaf packs and coarse-mesh leaf bags; both methods allow for a more rapid loss of small leaf bits, resulting in high apparent processing rates. This result underscores the caution necessary in attempting to compare processing rates derived using different methods.

Leaf P values obtained in this study compare well with those reported by other published

studies. For comparisons, I ran matched-sample *t*-tests with 13 common species analyzed by Day and Monk (1977) from North Carolina, 20 common species analyzed by Ricklefs and Matthew (1982) from southern Ontario, and 11 common species compiled by Chapin and Kedrowski (1983) from the subtropics to the taiga. There were no significant differences. All 3 of these data sets were based on leaves collected in late summer (August) or from mature foliage.

Nitrogen, on the other hand, was significantly different from other published data. My N data were significantly lower (by ~50%) in pairwise comparisons with data from the above 3 studies. One possible explanation is that the 3 comparison studies were based on leaf material collected during the growing season, whereas my data were based on autumn-shed leaves. Potter et al. (1987) presented data showing that *Acer rubrum*, *Quercus prinus*, and *Cornus florida* resorb ~50% of foliar N and ~60% of foliar P during October leaf senescence. It is not clear, however, why the P data were not also lower.

The lignin values are significantly higher than those reported by Ricklefs and Matthew (1982), although different analytical methods were used, and my technique may be more inclusive. There may also be a seasonal effect as noted for the N data. There was a highly significant correlation between the lignin concentrations reported in both data sets when the 20 common species were examined ( $r = 0.63$ ,  $p < 0.01$ ).

I expected little absolute agreement with the toughness values reported by Ricklefs and Matthew (1982) because toughness values are relative measures only in that constructed penetrometers are unique to each laboratory. There was, however, a highly significant correlation between the 2 data sets ( $r = 0.66$ ,  $p < 0.01$ ), indicating good relative agreement.

Although processing rates are significantly correlated (often very highly so) with several of the leaf characteristics, none of the simple regressions have much predictive power, suggesting that processing rates are regulated by a variety of factors simultaneously. The observation that total phenolics, N content and lignin combined explain almost 50% of the observed variation in processing rates supports this contention.

Leaf litter processing is also of considerable interest to terrestrial ecologists. Melillo et al. (1982) showed that for 6 species of hardwood litter common in Hubbard Brook Experimental

TABLE 1. Processing characteristics for 48 species of deciduous leaves. Nomenclature follows Gleason and Cronquist (1963).

Family and species	k (d <sup>-1</sup> )	% N	% P	C:N	% Lignin	Toughness (g)
<b>Aceraceae</b>						
<i>Acer negundo</i>	0.0054	1.71	0.112	24.1	25.42	209
<i>Acer saccharum</i>	0.0033	0.73	0.411	60.9	21.49	341
<i>Acer rubrum</i>	0.0020	0.92	0.162	52.5	19.86	297
<i>Acer saccharinum</i>	0.0041	1.55	0.226	30.4	15.52	264
<i>Acer platanoides</i>	0.0019	1.14	0.366	35.8	20.39	314
<b>Anacardiaceae</b>						
<i>Rhus typhina</i>	0.0026	1.17	0.117	41.1	14.31	238
<b>Betulaceae</b>						
<i>Betula lutea</i>	0.0019	1.55	0.381	28.5	32.76	153
<i>Betula populifolia</i>	0.0024	0.70	0.065	67.9	25.71	212
<i>Carpinus caroliniana</i>	0.0020	1.17	0.067	39.2	22.50	338
<i>Alnus rugosa</i>	0.0026	2.30	0.140	20.7	26.97	230
<b>Bignoniaceae</b>						
<i>Catalpa speciosa</i>	0.0054	2.00	0.410	21.6	28.10	267
<b>Caesalpiniaceae</b>						
<i>Cercis canadensis</i>	0.0036	2.29	0.303	19.1	29.45	420
<i>Gleditsia triacanthos</i>	0.0014	0.96	0.615	47.9	34.99	244
<b>Cornaceae</b>						
<i>Cornus florida</i>	0.0019	0.48	0.101	97.0	13.28	343
<i>Cornus stolonifera</i>	0.0010	1.98	0.175	25.5	23.65	183
<i>Nyssa sylvatica</i>	0.0017	0.79	0.433	58.3	17.17	496
<b>Fabaceae</b>						
<i>Robinia pseudoacacia</i>	0.0024	2.89	0.134	16.8	29.89	404
<b>Fagaceae</b>						
<i>Fagus grandifolia</i>	0.0010	1.28	0.101	37.2	33.23	242
<i>Quercus palustris</i>	0.0006	0.75	0.291	64.7	30.10	337
<i>Quercus coccinea</i>	0.0011	0.74	0.140	65.5	26.20	367
<i>Quercus muehlenbergii</i>	0.0011	1.03	0.080	46.3	28.28	379
<i>Quercus alba</i>	0.0006	0.67	0.212	67.3	36.67	419
<i>Quercus prinus</i>	0.0006	0.70	0.153	69.3	30.57	345
<i>Quercus rubra</i>	0.0011	0.53	0.086	93.6	35.96	551
<b>Hamamelidaceae</b>						
<i>Hamamelis virginiana</i>	0.0024	1.06	0.113	40.4	34.00	275
<i>Liquidambar styraciflua</i>	0.0009	0.38	0.073	120.8	33.11	372
<b>Hippocastanaceae</b>						
<i>Aesculus hippocastaneum</i>	0.0034	2.06	0.191	22.8	39.03	260
<b>Juglandaceae</b>						
<i>Juglans nigra</i>	0.0044	2.52	0.293	18.0	25.24	215
<i>Juglans cinerea</i>	0.0023	1.57	0.121	30.3	35.73	216
<i>Carya glabra</i>	0.0033	0.62	0.130	70.7	33.12	526
<i>Carya laciniosa</i>	0.0016	1.14	0.151	39.7	38.37	381
<i>Carya ovata</i>	0.0016	1.07	0.194	41.3	30.53	366
<b>Lauraceae</b>						
<i>Sassafras albidum</i>	0.0017	0.96	0.096	47.9	33.64	243

TABLE 1. Continued.

Family and species	k (d <sup>-1</sup> )	% N	% P	C:N	% Lignin	Toughness (g)
Magnoliaceae						
<i>Liriodendron tulipifera</i>	0.0034	0.92	0.106	49.4	27.82	466
<i>Magnolia acuminata</i>	0.0043	0.84	0.429	52.6	24.72	351
Oleaceae						
<i>Fraxinus americana</i>	0.0024	0.98	0.175	46.6	31.03	621
Platanaceae						
<i>Platanus occidentalis</i>	0.0007	0.95	0.089	50.5	38.92	489
Rosaceae						
<i>Crataegus</i> sp.	0.0027	1.15	0.077	38.7	26.13	324
<i>Pyrus malus</i>	0.0024	1.37	0.114	35.9	22.14	310
<i>Prunus serotina</i>	0.0023	1.67	0.165	29.8	22.43	438
Salicaceae						
<i>Salix discolor</i>	0.0011	0.83	0.281	56.5	26.54	324
<i>Salix nigra</i>	0.0024	2.24	0.121	21.0	37.15	344
<i>Populus deltoides</i>	0.0039	2.38	0.088	19.7	25.39	522
<i>Populus tremuloides</i>	0.0013	1.14	0.092	43.0	28.84	492
<i>Populus grandidentata</i>	0.0009	0.92	0.083	52.4	33.04	446
Tiliaceae						
<i>Tilia americana</i>	0.0020	1.83	0.189	25.2	28.60	330
Ulmaceae						
<i>Ulmus</i> sp.	0.0009	0.59	0.098	74.3	24.47	260
Ginkgoaceae (Gymnospermae)						
<i>Ginkgo biloba</i>	0.0019	0.68	0.518	68.9	30.15	565
Mean	0.0022	1.25	0.193	46.4	28.18	349
Standard deviation	0.0012	0.61	0.132	22.4	6.41	111
Coefficient of variation (%)	56	49	68	48	23	32

Forest, leaf mass remaining on the forest floor after 12 mo was highly correlated with %lignin, but not with %N, although %lignin:%N was a better predictor than %lignin alone. These results were supported by another data set from North Carolina (Cromack 1973). Cromack (1973) concluded that %lignin:%N was a good predictor of terrestrial litter decomposition, although where exogenous N is abundant, lignin alone might be a better predictor. The results reported above (equations 1-5) suggest that in aquatic systems, %lignin alone is a poor predictor and %lignin:%N is little better than %N alone. Perhaps the influx of autumn-shed leaves into aquatic systems introduces large quantities of carbonaceous litter, which induces more severe N limitation than in terrestrial systems. Further, perhaps the range of %lignin in au-

tumn-shed leaves is too small for the effects of lignin to be revealed through regression analysis. However, in microcosm experiments of litter decay using a much expanded range of leaf lignin concentrations, Taylor et al. (1989) were able to show that neither %lignin nor %lignin:%N were able to predict decomposition rates as well as C:N or %N alone.

The results of this study suggest that tannins play an ambiguous role in aquatic leaf-processing rates. In previous studies (Stout 1989, Ostrofsky 1993), in which processing rates were drawn from the compilation of Webster and Benfield (1986), the lack of a convincing relationship between tannins and leaf-processing rates could be attributed to the possibility that the variations in sites and methods represented in Webster and Benfield (1986) simply masked

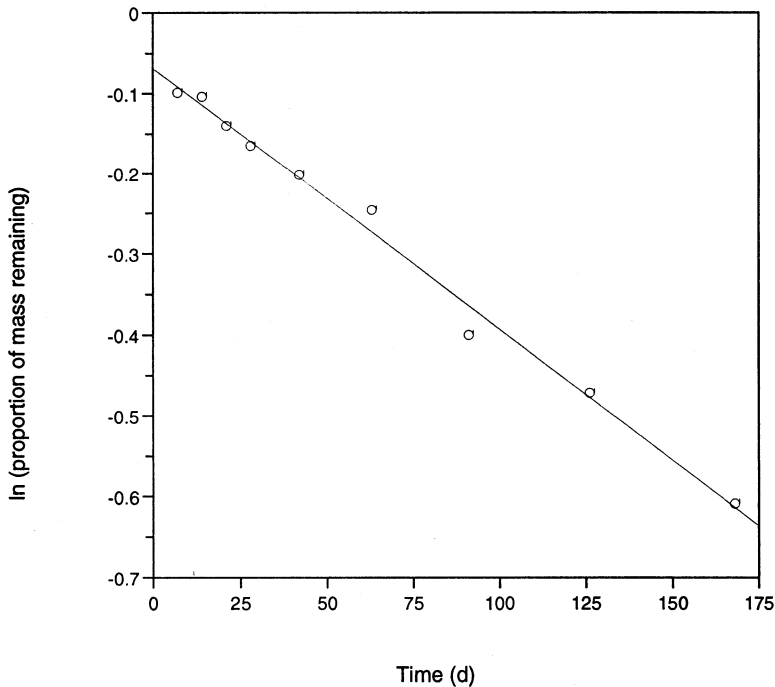


FIG. 1. Processing (mass loss) of pignut hickory (*Carya glabra*) vs time. After the 1st week, mass loss proceeds at a constant rate. The rate of mass loss in the 1st week, however, is significantly greater than in subsequent weeks, and may be attributed to abiotic leaching.

any such relationship. I hypothesized that a relationship would emerge if variations caused by other factors could be minimized. However, in simple regressions reported here, where processing rates were calculated based on mass loss under uniform conditions, there was no correlation between processing rates and total phenolics or protein-precipitating capacity, 2 measures of tannin content. There was only a weak correlation with condensed tannins, having poor predictive power. On the other hand, 1 measure of tannin (total phenolics) does emerge as a contributor to multiple regression model [5], and the elimination of total phenolics from this model greatly reduces its predictive power (to  $r^2 = 0.33$ ). The best single predictors of processing rates emerging from this study are the traditional measures of leaf quality, %N, C:N, and %lignin, which have been used with some success in predicting rates of litter decomposition on the forest floor (Melillo et al. 1982).

There is a rich literature demonstrating that processing rates are highly variable in cross-system comparisons. Many hypotheses have been proposed suggesting that leaf processing rates

are affected by a particular factor (e.g., water temperature, litter age, nutrients). For the most part, these hypotheses have either not been supported, or have received only ambiguous support from the field data. For example, neither Irons et al. (1994) nor Rowe et al. (1996) were able to demonstrate a clear effect of temperature on processing rates. Leff and McArthur (1990) could find no difference in the processing rates of fresh (green) or senescent litter. On the other hand, Meyer and Johnson (1983) did demonstrate a clear effect of stream nitrate concentration. Nevertheless, in this study, where all leaf species were contained in litter bags of uniform mesh size and were exposed to the same populations of decomposer organisms, temperatures, and water chemistry, almost 50% of the variation in processing rates was explained by litter quality—specifically, total phenolics, %N, and %lignin. The 50% of the variation yet to be explained may be a function of some yet unconsidered dimensions of litter quality, year-to-year variation in litter quality, or some behavioral response of aquatic shredding insects to variations in leaf palatability.

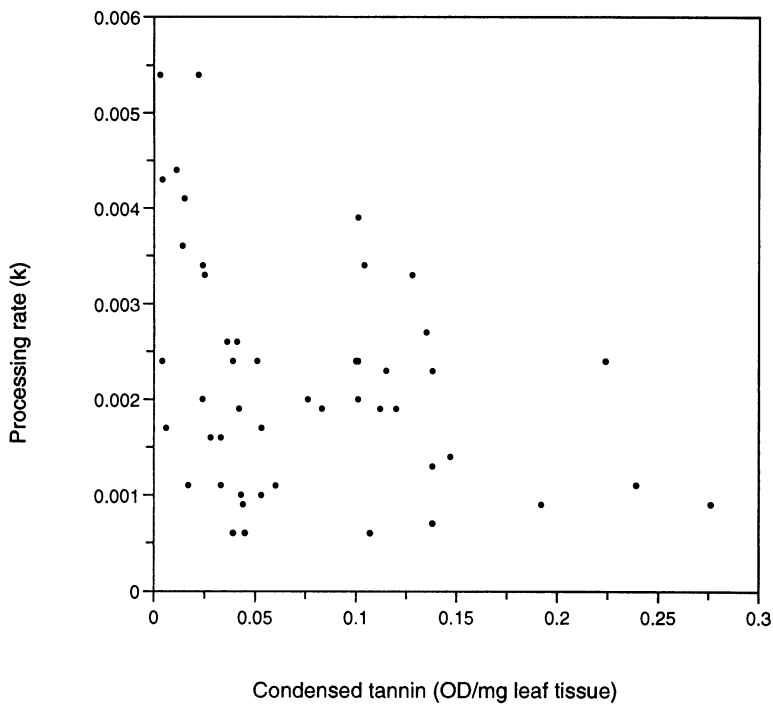


FIG. 2. Relationship between condensed tannin concentration and processing rate ( $k$ ) of 48 species of deciduous leaves. OD = optical density (see Swain and Hillis 1959 for details of the analytical technique).

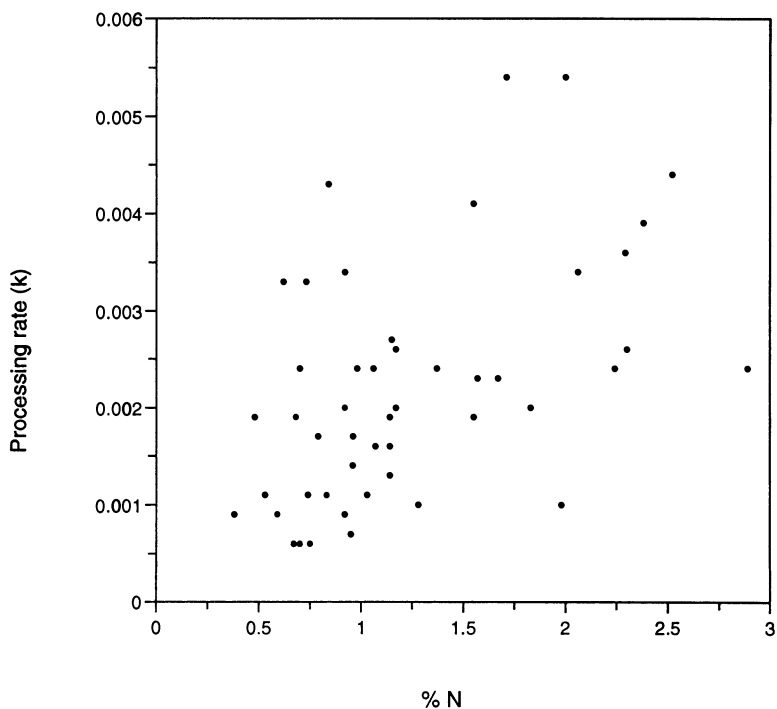


FIG. 3. Relationship between foliar N and processing rate ( $k$ ) for 48 species of deciduous leaves.

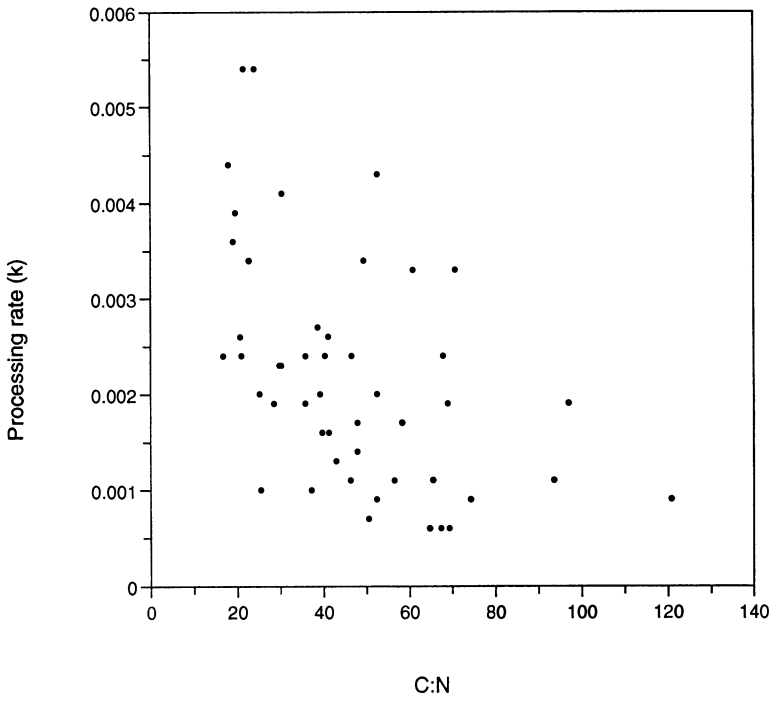


FIG. 4. Relationship between C:N and processing rate (k) of 48 species of deciduous leaves.

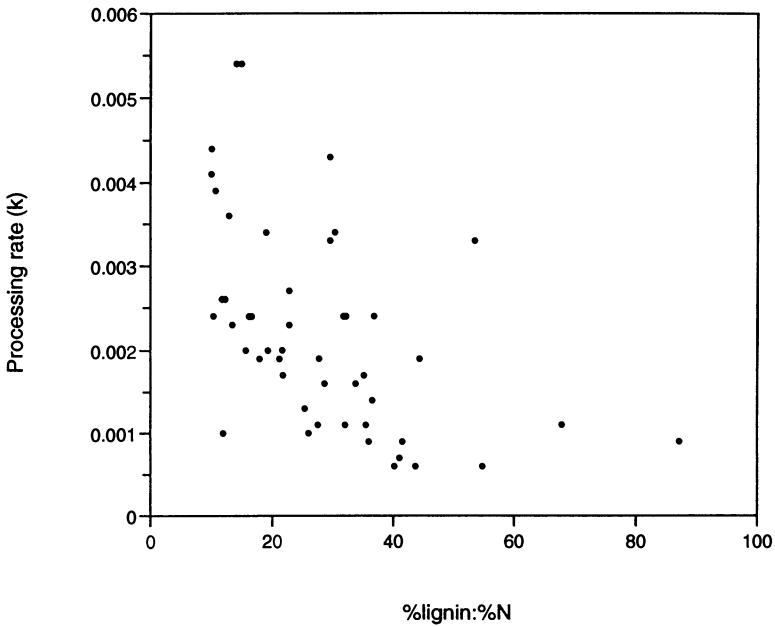


FIG. 5. Relationship between %lignin:%N and processing rate (k) of 48 species of deciduous leaves.

### Acknowledgements

I am grateful to L. L. Drew, M. E. Houle, J. L. Lamb, E. J. Ostrofsky, and T. R. Walmsley for field and laboratory assistance. R. M. Newman and 2 anonymous reviewers suggested improvements to an earlier version of the paper.

### Literature Cited

- CAMPBELL, I. C., AND L. FUCHSHUBER. 1995. Polyphenols, condensed tannins, and processing rates of tropical and temperate leaves in an Australian stream. *Journal of the North American Benthological Society* 14:174-182.
- CHAPIN, F. S., AND R. A. KEDROWSKI. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* 64:376-391.
- CROMACK, K. 1973. Litter production and litter decomposition in a mixed hardwood watershed and in a white pine watershed at Coweeta Hydrologic Station, North Carolina. PhD Dissertation. University of Georgia, Athens, Georgia.
- DAY, F. P., AND C. D. MONK. 1977. Seasonal nutrient dynamics in the vegetation on a southern Appalachian watershed. *American Journal of Botany* 64:1126-1139.
- FEENY, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51:565-581.
- FISHER, S. G., AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* 43:421-439.
- GLEASON, H. A., AND A. CRONQUIST. 1963. *Manual of vascular plants of northeastern United States and adjacent Canada*. Van Nostrand, New York.
- IRONS, J. G., M. W. OSWOOD, R. J. STOUT, AND C. M. PRINGLE. 1994. Latitudinal patterns in leaf litter breakdown: is temperature really important? *Freshwater Biology* 32:401-411.
- LEFF, L. G., AND J. V. MCARTHUR. 1990. Effect of nutrient content on leaf decomposition in a coastal plain stream: a comparison of green and senescent leaves. *Journal of Freshwater Ecology* 5:269-277.
- MELILLO, J. M., J. D. ABER, AND J. F. MURATORE. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621-626.
- MEYER, J. L., AND C. JOHNSON. 1983. The influence of elevated nitrate concentration on rate of leaf decomposition in a stream. *Freshwater Biology* 13:177-183.
- OSTROFSKY, M. L. 1993. Effect of tannins on leaf processing and conditioning rates in aquatic ecosystems: an empirical approach. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1176-1180.
- PETERSON, R. C., AND K. W. CUMMINS. 1974. Leaf processing in a woodland stream. *Freshwater Biology* 4:343-368.
- POTTER, C. S., H. L. RAGSDALE, AND C. W. BERISH. 1987. Resorption of foliar nutrients in a regenerating southern Appalachian forest. *Oecologia* 73:268-271.
- RICKLEFS, R. E., AND K. K. MATTHEW. 1982. Chemical characteristics of the foliage of some deciduous trees in southeastern Ontario. *Canadian Journal of Botany* 60:2037-2045.
- RIGGS, D. S. 1963. *The mathematical approach to physiological problems*. The M.I.T. Press, Cambridge, Massachusetts.
- ROWE, J. M., S. K. MEEGAN, E. S. ENGSTROM, S. A. PERRY, AND W. B. PERRY. 1996. Comparison of leaf processing rates under different temperature regimes in three headwater streams. *Freshwater Biology* 36:277-288.
- RYAN, M. G., J. M. MELILLO, AND A. RICCA. 1990. A comparison of methods for determining proximate carbon fractions of forest litter. *Canadian Journal of Forest Research* 20:166-171.
- STOUT, R. J. 1989. Effect of condensed tannins on leaf processing in mid-latitude and tropical streams: a theoretical approach. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1097-1106.
- STRICKLAND, J. D. H., AND T. R. PARSONS. 1968. *A practical handbook of seawater analysis*. Fisheries Research Board of Canada Bulletin 167. Fisheries Research Board of Canada, Ottawa.
- SWAIN, T., AND W. T. HILLIS. 1959. The phenolic constituents of *Prunus domestica*. I. The quantitative analysis of phenolic constituents. *Journal of Agricultural and Food Chemistry* 10:63-68.
- TAYLOR, B. R., D. PARKINSON, AND W. F. J. PARSONS. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70:97-104.
- WEBSTER, J. R., AND E. F. BENFIELD. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17:567-594.
- WETZEL, R. G. 1995. Death, detritus, and energy flow in aquatic ecosystems. *Freshwater Biology* 33:83-89.
- WIEDER, R. K., AND G. E. LANG. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology* 63:1636-1642.
- ZAR, J. H. 1974. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.

Received: 18 February 1997

Accepted: 1 August 1997