

## Substrate control of litter decomposition in four Rocky Mountain coniferous forests

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The influence of chemical and physical quality of litter on its rate of decomposition was examined by measuring mass loss from 19 diverse litter types, including leaves, needles, forbs, wood, and roots in the Kananaskis Valley of Alberta, Canada. Litter samples drawn from three adjacent forests of lodgepole pine, white spruce, and Engelmann spruce – subalpine fir, and from a small clearcut area, were allowed to decompose for 3 years at their sites of origin. The best predictors of mass loss were the initial concentrations of lignin and labile material in the litter. Adding N or P contents as a second term, rather than as a lignin to nutrient ratio, significantly improved mass loss predictions. There were abrupt limits for the influence of lignin (above 28%) and N (below C:N of 30:1); similar limits were observed for all predictors except labile content. None of these chemical parameters, nor a physical measure, particle diameter, were useful in predicting rates of decomposition of high-lignin, woody substrates. The relative importance of the various litter quality parameters in determining rates of mass loss in the clear-cut area was very similar to that in the forests, despite considerably more rapid decomposition in the clearcut.

*Key words:* decomposition, lignin, litter, nutrients, Rocky Mountains, wood.

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L'influence de la nature chimique et physique de la litière sur son taux de décomposition fut étudiée en mesurant la perte de masse de 19 différents types de litière, incluant des feuilles, des aiguilles, des herbes, des branches et des racines, dans la Vallée Kananaskis en Alberta, Canada. Des échantillons de litières furent recueillis dans trois forêts adjacentes de pin lodgepole, d'épinette blanche, et d'épinette d'Engelmann – sapin de l'Ouest ainsi que sur un petit parterre de coupe. Ces échantillons ont été remis sur les sites d'origine et laissés pour se décomposer pendant 3 ans. Les pertes de masse sont mieux prédites par les concentrations originales de lignine dans la litière. L'addition d'azote ou de phosphore comme deuxième terme dans les régressions (plutôt que le rapport lignine à élément nutritif) a amélioré significativement les prédictions de perte de masse. Il y avait des limites abruptes sur l'influence de la lignine (au dessus de 28%) et de l'azote (en dessous du rapport C:N de 30:1); de la même façon, il y avait des limites abruptes pour toutes les autres régressions, sauf celle concernant la matière labile. Aucune de ces mesures chimiques, ni une mesure physique (le diamètre) ne furent utiles pour prédire les taux de décomposition des échantillons de bois, qui avaient tous des teneurs élevées en lignine. L'influence relative de chaque mesure de qualité de la litière est demeuré la même sur le parterre de coupe que dans les forêts, malgré que les taux de décomposition était plus rapide sur le parterre de coupe.

*Mots clés :* décomposition, lignine, éléments nutritifs, montagnes Rocheuses, bois.

### Introduction

The rate of decomposition of plant litter is pivotal to many ecosystem functions such as soil formation and nutrient cycling. When climate and site factors such as soil type are constant, decomposition rates are regulated primarily by the chemical composition and physical structure of the litter, features often jointly termed substrate quality (Swift *et al.* 1979). Because many litter types accumulate exogenous nitrogen during early decay, the initial N content or the ratio of C to N are often considered to be critical to decomposition (Melin 1930; Bockock 1964; Anderson 1973; Edmonds 1980; Hunt *et al.* 1988; and others). In other situations, phosphorus, or the C:P ratio have been found to limit decay rates (Heal and French 1974; Schlesinger and Hasey 1981; Stååf and Berg 1982; Berg *et al.* 1987), and frequently both N and P are retained and

either could potentially be limiting (Berg and Stååf 1980; Woods and Raison 1983).

Berg and co-workers (Berg and Stååf 1980; Berg 1984) have advanced the view that nutrients control litter decay rates only until about 20–35% of the mass is lost; thereafter rates are determined by cell wall components, particularly lignin. Melillo *et al.* (1982) suggested combining the two parameters to form the lignin to nitrogen ratio and demonstrated that this ratio was negatively correlated with decay rates of northern hardwood leaves. Other studies have confirmed the importance of lignin in determining long-term decay rates of hardwood leaves and conifer needles (Meentemeyer 1978; Edmonds 1984; Stohlgren 1988; White *et al.* 1988; Upadhyay and Singh 1989).

Most successful tests of lignin content as a decay-rate predictor have been done on small groups of similar litter types, such as hardwood leaves or conifer needles (Harmon *et al.* 1990). In contrast, several studies involving a wider variety of litter types have found that initial lignin content or the lignin to N ratio were poor predictors of mass loss rates (Schlesinger and Hasey 1981; Moore 1984; McClaugherty *et al.* 1984, 1985; Taylor *et al.* 1989; see also Scheffer *et al.* 1985).

A further element of substrate quality, physical structure, has not received much consideration. Physical structure is

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TABLE 1. Characteristics of the four sites

	Pine	Spruce	Fir	Clearcut
Elevation (m)	1530	1500	1830	1410
Age	90	120	350	13
Overstorey composition	Lodgepole pine	White spruce Lodgepole pine	Subalpine fir Engelmann spruce	
Understorey composition	White spruce	White spruce Douglas-fir	Subalpine fir Engelmann spruce	White spruce Lodgepole pine
Tree density (stems/ha)	1716	750	1177	
Stand basal area (m <sup>2</sup> /ha)	30.5	39.1	40.0	
Mean DBH (cm)	12.2	16.4	11.6	
Forest floor depth (cm)	6.4	11.9	12.0	3.9
Forest floor mass (kg/m <sup>2</sup> )	4.7	7.4	9.0	4.4
pH of organic layer	5.2	5.5	4.8	5.9
pH of mineral soil	5.8	6.1	5.9	6.0
Soil type	Eutric brunisol	Dystric brunisol	Eutric brunisol	Eutric brunisol

likely to be important for litter such as needles because of their complex internal structure (Edmonds 1984; Fyles and McGill 1987), as well as for larger detritus such as roots, boles, and branches (Graham and Cromack 1982; MacMillan 1988).

Long-term, broadly based studies involving a wide range of litter types are necessary to discover general patterns of litter decay rates and the features of substrate quality that control them. The present study examined rates of decay of a wide variety of substrates, including grasses, forbs, leaves, needles, roots, and wood in three coniferous forests in the Rocky Mountains of southwestern Alberta. Rates of mass loss from each litter type were related to their initial concentrations of lignin, labile material, N, and P to determine the relative influence of each of these factors on rates of decomposition. Repetition of the experiment in a clear-cut area allowed the generality of conclusions to be tested in the face of microclimatic variation.

## Methods

### Study sites

The forests used in this study are in the Kananaskis Valley, in the Front Range of the Rocky Mountains of Southwestern Alberta, Canada (51°2'N, 115°3'W). The region has a dry continental climate with warm, dry summers and long, cold winters modified by intermittent warm chinook winds. Mean monthly temperatures at the Kananaskis Centre for Environmental Research, less than 5 km from any of the sites, range from -10°C in January to 14°C in July. Mean annual precipitation is 660 mm, of which 290 mm occurs as snow. Snow cover is discontinuous because of frequent chinook winds throughout winter. There is considerable variation in climate, depending upon aspect and elevation, with south- and west-facing slopes being warmer and drier, and higher elevations experiencing cooler temperatures and greater winter precipitation.

Four stands of distinctly different overstorey composition were selected, all lying within 5 km of one another in the basin of Lusk Creek (Table 1). The pine site was a dense stand of lodgepole pine (*Pinus contorta*), 70–90 years old at 1530 m elevation. The spruce site was located at 1500 m in a 130-year-old stand of white spruce and lodgepole pine. The fir site was situated at 1830 m in a stand of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), the latter up to 350 years old. The clearcut site was situated at 1410 m elevation, in a 1500-m<sup>2</sup> area cut from lodgepole pine forest of similar composition to the pine site. Woody vegetation there was composed of pine (<15 years old) spruce, willow, aspen, buffaloberry, and alder. Further details of vegetation at the sites, including biomass, productivity and nutrient status, are given in Prescott *et al.* (1989).

### Decomposition rates

Samples of each of the predominant litter types in each forest (Prescott *et al.* 1989) were collected in September 1984 (1985 at the clearcut site). Most litter types were oven-dried at 35°C; grasses and forbs were dried at 25°C to reduce breakage, and moss was dried at 80°C to ensure death of tissues. Samples of known dry mass of large litter (20 cm long portions of branches, twigs, and stems, as well as female cones) were tagged and pinned directly to the ground. Cut ends of branches (1.5–3.0 cm diameter) and twigs (0.5 cm diameter) were painted with yellow plastic to reduce artificial exposure of interiors and to make them easier to find.

Known masses of smaller litter types (grass, moss, leaves, needles) were enclosed in 8 × 10 cm fibreglass bags of 1-mm mesh size, tagged, and pinned to the forest floor. Bags containing moss were inserted into the lower moss layer. Coarse roots (>1 mm diameter) were tagged only; fine roots (<1 mm diameter) were put in bags prior to insertion under the organic layer. All substrates were returned to the site from which they were collected in October 1984 (1985 at the clearcut site). Lodgepole pine needles collected from one fallen tree at the pine site were used as a standard substrate and allowed to decompose at all four sites. Ten samples of each litter type were retrieved from each site in May and October of the following 3 years. Each sample was redried at the original temperature and weighed to determine mass remaining.

### Litter quality

Concentrations of lignin, labile material, C, N, and P were determined from three replicate samples of original material of each litter type. Material was first oven-dried at 80°C and ground through a 40-mesh sieve in a Wiley mill. Labile material was separated from the lignocellulose fraction by successive hot water and ethanol–benzene extractions (Crawford and Crawford 1978); the lignocellulose was separated into cellulose and Klason lignin (acid-insoluble residue) by digestion in hot sulphuric acid by the method of Effland (1977). Total C content was determined by combustion in a Leco furnace. Total N and P contents were determined colorimetrically on a Technicon II autoanalyzer (Technicon Instruments 1976, 1977) following digestion with sulphuric acid and hydrogen peroxide (Lowther 1980).

Complementing these chemical determinations, particle diameter, or thickness, was also measured as an index of physical litter quality. Diameter was measured to the nearest 0.1 mm (nearest 1 mm for branches, twigs, and coarse roots) across the shortest axis of 10 replicates of each litter type. The mean diameter was applied to all litter of that type from all sites. For forb stems, which are hollow, diameter was measured as the distance from the outside wall to the inside, not the diameter of the whole stem. For female pine cones, diameter was that of whole cones (20 mm); for all other cones, diameter of the individual scales was used (0.2–0.8 mm).

TABLE 2. Initial chemical quality of the litter types

Substrate	% C	% N	% P	% lignin	% labile
Forb leaves	42.9–46.4	0.6–0.95	0.07–0.17	6.8–13.8	48.5–62.8
Buffalo-berry leaves	48.3	1.79	0.04	9.2	55.6
Alder leaves	48.5	1.89	0.10	16.2	53.7
Grass	40.7–43.7	0.77–1.16	0.10–0.20	11.0–12.9	28.3–31.6
Forb stems	42.7–44.9	0.23–0.38	0.04–0.12	10.0–13.8	26.5–35.2
Spruce needles	47.4	0.57	0.12	14.6	48.9
Forb roots	40.4–44.0	0.79–1.51	0.14–0.26	13.6–19.0	36.5–48.8
Pine needles	51.2	1.04	0.09	24.5	32.5
Bearberry leaves	51.1	0.75	0.13	16.6	58.1
Conifer coarse roots	48.2–51.0	0.34–0.50	0.03–0.17	20.5–23.9	21.7–38.8
Bearberry stems	46.7	0.51	0.06	20.7	24.5
Fir needles	52.3	0.49	0.04	14.6	54.4
Moss	44.9–46.5	0.89–1.05	0.12–0.15	25.3–25.9	16.4–17.2
Twigs	49.2–50.3	0.25–0.39	0.01–0.02	24.6–33.1	12.2–15.6
Grass roots	31.1–41.5	0.49–0.99	0.08–0.11	21.3–26.7	21.7–22.7
Female cones	47.5–49.8	0.19–0.79	0.03–0.07	22.0–39.2	9.8–13.0
Male cones	50.7	0.86	0.06	35.3	29.4
Branches	46.7–50.8	0.10–0.21	0.01	25.7–28.6	9.9–14.3
Conifer fine roots	49.7	0.72–0.97	0.06–0.32	35.2–36.9	17.2–29.4

NOTE: For litter types at more than one site, the range of each parameter is given.

TABLE 3. Spearman rank correlations among litter quality parameters at the three forested sites

Correlates	Pine	Spruce	Fir	All sites
Lignin and labile	-0.555*	-0.681	-0.845	-0.655
Lignin and N				
Lignin and P	-0.341			
Lignin and C	0.736	0.516		0.484
Lignin and N	0.755	0.593		0.450
Labile and P	0.709			0.467
Labile and C				
N and P	0.855	0.610	0.909	0.782
N and C				
P and C	-0.718		-0.664	
n	11	13	11	35

NOTE: Only significant correlations ( $p < 0.05$ ) are shown. \*, significant at  $p < 0.10$ .

## Results

### Litter quality

Except for understorey plants, the litter types used in this experiment were high in lignin. Still, the range of initial lignin contents at any of the forested sites was roughly 10–40% (Table 2), sufficiently wide that any controlling influence of lignin should be readily apparent. The range of initial nutrient contents was also very wide (Table 2). For example, at the pine site, N content of litter ranged from 1  $\text{mg}\cdot\text{g}^{-1}$  in branches, to  $> 10 \text{ mg}\cdot\text{g}^{-1}$  in pine needles. Litter P contents ranged from 0.07  $\text{mg}\cdot\text{g}^{-1}$  in branches to 2.6  $\text{mg}\cdot\text{g}^{-1}$  in forb roots.

Most of the litter quality parameters considered were to some degree intercorrelated (Table 3). Initial lignin and labile contents bore a strong negative correlation at all sites, as did labile and N contents. However, this latter correlation, although significant at the pine and spruce sites (Table 3), was nowhere near significant at the fir site ( $r_s = 0.06$ ), perhaps indicating differing mineral nutrition at this site. On the other hand, the strong correlation of N and P contents was consistent across all sites. This correlation has been noted before (Stååf and Berg 1980; Taylor *et al.* 1989; Upadhyay and Singh 1989) and appears to be general for litter within a given stand. There was a surprising lack of correlation between initial lignin content

and proportions of N and P at any site; percent P and percent lignin were weakly negatively correlated if data from all three forested sites were pooled (Table 3). Most other correlations were weaker or site-specific and are probably not biologically important.

### Decomposition rates

Decomposition of most substrates followed the usual negative exponential pattern of mass loss (Fig. 1). After 3 years in the field, mass loss ranged from  $> 70\%$  for forb (*Epilobium angustifolium*) leaves, to as little as 6% for some branches (Fig. 1). Values of  $k$  ranged from 0.03 to  $> 0.35$ , a full order of magnitude (Table 4).

Although there were significant and consistent differences in absolute decomposition rates among the four sites (analysis to be presented elsewhere), relative decay rates of similar substrates were similar among sites. This is illustrated in Table 4, which presents 3-year  $k$ -values, ranked by mean decay rate, at all sites. For the present work, this pattern means that decay rate predictors based on substrate quality should be equally applicable at least to all three forested sites, if not also to the clearcut site. Therefore, we undertook to establish regressions of mass loss on substrate quality parameters using data from the forested sites and to test the regression equations by extending them to the clearcut site.

### Simple regressions

Plots of mass remaining after 3 years against initial lignin content, lignin to N, or lignin to P, revealed an abrupt lower plateau, or floor, corresponding to about 28% lignin content and 15% mass loss (Fig. 2). Above the floor, the lignin – decay rate relationship was quite strong and clearly linear; once the floor was reached, there was no apparent relationship between decomposition rate and lignin content. The C:P and C:N ratios showed the same effect, again with the floor at about 15% mass loss. Here, however, the data were widely scattered, and a strong linear trend above the floor was not evident. These data rather defined a low C:N (or C:P) and a high C:N region. Only labile content showed a recognizable linear trend across the whole range of data; possible weak lin-

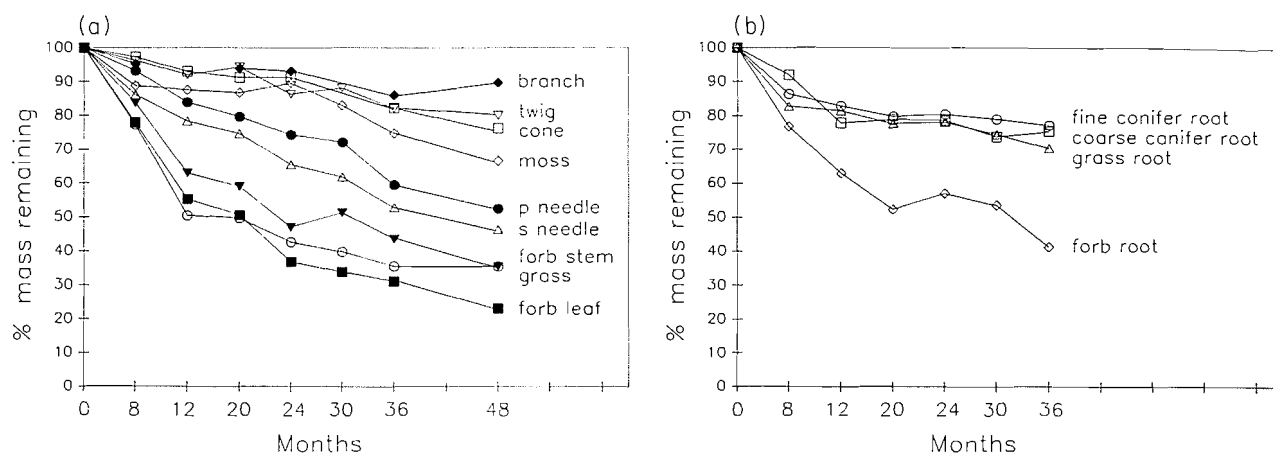


FIG. 1. Decomposition rates over 4 years of (a) aboveground litter and (b) belowground litter at the spruce site. Very similar patterns were observed at all other sites. Each point is the mean of 10 replicates.

TABLE 4. Decomposition rate constants ( $k$ ) in the negative exponential model for the various litter types after three years decay in three forests and a clearcut in the Rocky Mountains

Litter types	Pine	Spruce	Fir	Clearcut
Forb leaves	0.2375	0.3330	0.3534	0.2549
Buffalo-berry leaves				0.2363
Alder leaves				0.2179
Grass	0.2372	0.2012	0.2022	0.3168
Forb stems	0.1803	0.2280	0.1776	0.2388
Spruce needles		0.1828		
Forb roots	0.1743	0.2517	0.0202	0.2700
Pine needles*	0.1151	0.1735	0.1063	0.1845
Bearberry leaves				0.1298
Conifer coarse roots	0.1902†	0.0766	0.0290	
Bearberry stems				0.0941
Fir needles			0.0933	
Moss		0.0874	0.0444	
Twigs	0.0549	0.0549	0.0620	0.0810
Grass roots	0.0473	0.0613	0.0484	0.0892
Female cones	0.0307	0.0691	0.0437	
Male cones	0.0440			
Branches	0.0521	0.0265	0.0353	
Conifer fine roots	0.0267	0.0393	0.0314	

NOTE: Data are ranked from highest to lowest mean decomposition rate at the forested sites.

\*Identical samples at all four sites.

†Rate probably exaggerated by breakage.

ear trends of mass loss with N or P contents were obscured by the variability of the results (Fig. 2).

Similar relationships, between decay rate of leaf litter and its lignin to N ratio (Melillo *et al.* 1982; Harmon *et al.* 1990), have been described with a power function, of the form

$$[1] \quad -k = a(\text{lignin}/N)^{-b}$$

where  $k$  is the exponential decay rate and  $a$  and  $b$  are constants.

To describe the two-part behaviour of the more general responses observed here, and in particular to determine if the relationships had true lower limits, we used a piece-wise regression equation of the form

$$[2] \quad \text{Year 3} = b_0 + b_1 X_1 - b_2 (X_1 - b_3) (X_1 > b_3)$$

where Year 3 is mass remaining after 3 years,  $b_0$  is the intercept,  $X_1$  is the mass loss predictor,  $b_1$  is the first slope component,  $b_2$  is the second slope component,  $b_3$  is the hinge point, and the phrase  $(X_1 > b_3)$  has a conditional value of 1 or 0.

For values of the litter parameter below the hinge point on the  $x$ -axis, the equation defines a simple linear function with slope  $b$ . Beyond the hinge point, the equation simplifies to a second line with slope  $(b_1 - b_2)$  (Neter *et al.* 1983). Equations were fitted by repeated least squares regression, with different values of  $b$  supplied for each iteration.

Piece-wise regression is advantageous because an apparently complex curve can be closely approximated without recourse to nonlinear methods or data transformations, so that hypotheses about the regression parameters may be tested using ordinary least squares regression techniques. Hence, the slope of the relationship beyond the hinge point could be estimated and tested for significance in a piece-wise regression, which would not be possible with the power function model. The piece-wise regression also seemed more appropriate here because the relationships between litter quality and mass loss often appeared to reach a well-defined limit, rather than gradually approach an asymptote. Simple linear regressions were used for percent labile, percent N, and percent P.

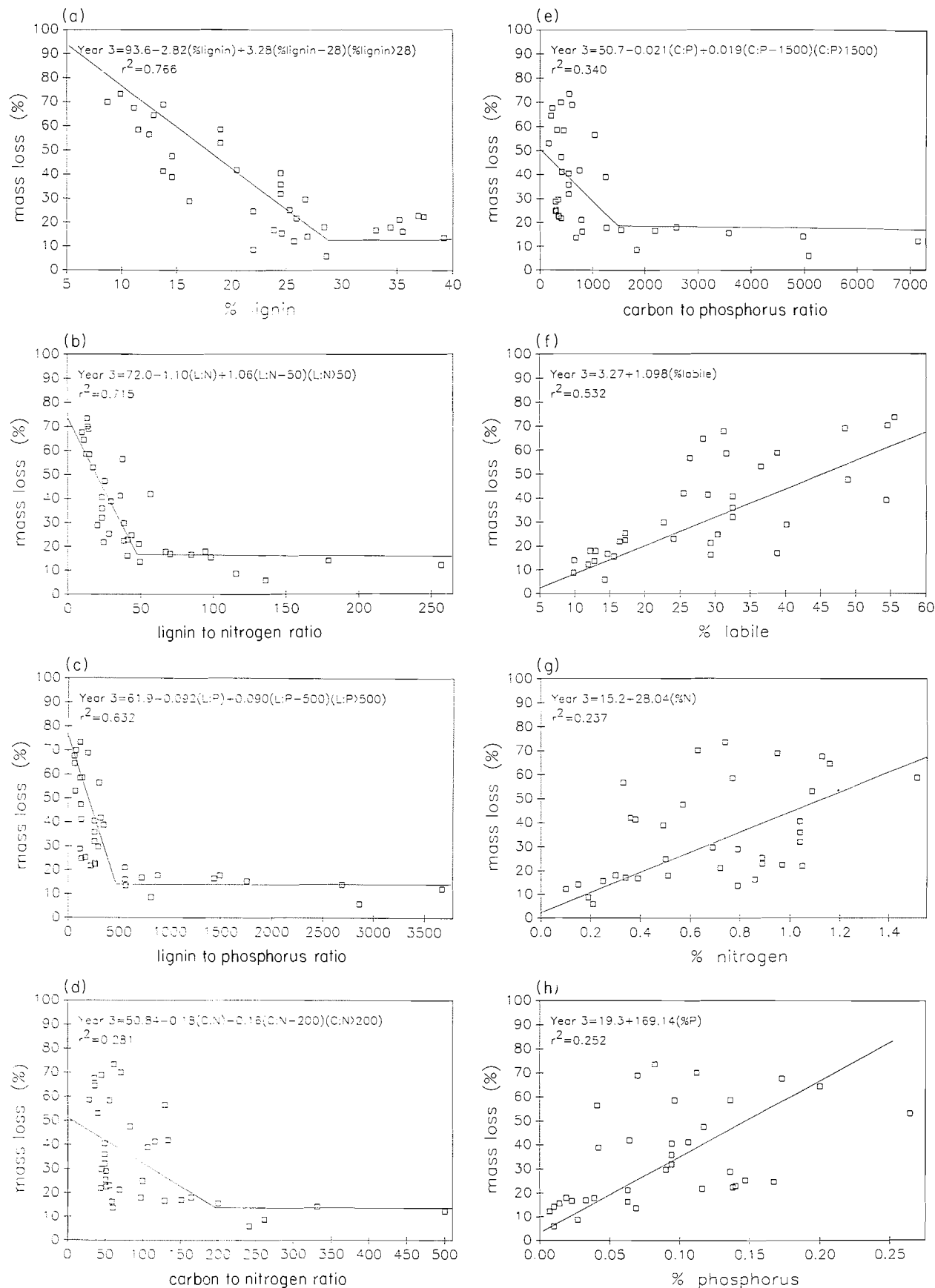


FIG. 2. Mass loss after 3 years' decomposition of various litter types at the three forested sites as a function of initial litter quality. Solid line is the best-fit linear regression. Each point is the mean of 10 replicates. Litter quality parameters are (a) percent lignin, (b) lignin to nitrogen ratio, (c) lignin to phosphorus ratio, (d) C:N ratio, (e) C:P ratio, (f) percent labile, (g) percent N, and (h) percent P.

TABLE 5. Multiple regressions of 3-year mass loss on litter quality parameters, extending piece-wise lignin regressions by the addition of a second variable

With percent nitrogen			
Year 3 =	73.50	- 2.49 (% lignin)	+ 2.37 (floor) + 20.50 (% N)
	(5.83)	(0.23)	(0.60) (3.69)
$R^2 =$	0.883, $F = 77.9^{**}$		
With percent phosphorous			
Year 3 =	81.09	- 2.53 (% lignin)	+ 2.76 (floor) + 74.53 (% P)
	(7.57)	(0.31)	(0.77) (28.59)
$R^2 =$	0.808, $F = 43.5^{**}$		
With percent labile			
Year 3 =	74.73	- 2.34 (% lignin)	+ 2.70 (floor) + 0.310 (% labile)
	(12.56)	(0.41)	(0.85) (0.180)
$R^2 =$	0.787, $F = 38.08^{**}$		

NOTE: All forested sites are combined;  $n = 35$ . Figures in brackets are standard errors of the estimates. See [2] for explanation of piece-wise regression. Note that floor = (% lignin - 28) (% lignin > 28). \*\*, significant at  $p < 0.01$ .

For all predictors tested with piece-wise regression, the difference between the first and second slope components (and hence the slope of the line beyond the hinge point) was not significantly different from zero, indicating that the relationships have a true limit, rather than simply a reduced slope beyond the hinge point. Lignin produced the strongest regression, accounting for >76% of the total variance (Fig. 2). The relationship with the lignin to N ratio was only slightly weaker ( $r^2 = 0.715$ ), but this is still surprising given that the ratio incorporates lignin with a second correlate of decay rate, which should have strengthened the regression. Reasonably good fits were also obtained with the lignin to P ratio and labile content, but N and P concentrations, alone or as C ratios, were markedly poorer predictors, accounting for a third or less of the total variance (Fig. 2). In all these regressions, using 1st-year or 2nd-year mass-remaining data resulted in nearly identical regressions, except that  $r^2$  values were lower. Also, exclusion of root litter had no large effect on regressions. The litter types that were beyond the limit of the regressions for each litter quality parameter were all woody materials such as twigs and cones or tree roots.

#### Multiple regressions

Since even the best simple and piece-wise regressions left a portion of the variance in mass loss rates unexplained, a better model might be produced by incorporating two or more parameters. We tested this by adding percent N, percent P, or percent labile as a second term to the piece-wise regression of mass loss on percent lignin. Addition of percent N resulted in a sharp improvement in the fit of the regression, which then accounted for nearly 90% of the variance (Table 5). Adding percent P also increased the  $R^2$  by a small but significant amount. In contrast,  $R^2$  was augmented only 2% by inclusion of a percent labile term (Table 5), and the partial  $F$  for the second slope coefficient was barely significant. Finally, the regression was not improved by adding litter diameter as a second variable ( $p < 0.10$ ), or by adding a dummy variable to account for edaphic and microclimatic differences among the three forested sites. No other model could be constructed that was even nearly as strong (in terms of  $R^2$  value) as that with lignin and N. Results were very similar if only data below the floor (lignin < 28%) were included, except that of course a piece-wise regression was no longer necessary.

#### Decay of high-lignin substrates

We searched for a predictor for woody litter using forward step-wise regression with percent N, percent P, percent labile, diameter, and forest site (a dummy variable). Surprisingly, none of the measured chemical or physical parameters entered the regression; a simple regression on forest site was the only statistically significant model for these data ( $r^2 = 0.344$ ,  $n = 9$ ). Hence, none of the chemical variables measured nor physical size of the litter had any significant influence on prediction of decomposition rate of high-lignin litter types. The effect of site of decay, which accounted for about 34% of the variance in these samples, is not strictly a litter-quality effect and cannot be used predictively.

#### Extrapolation of regressions

We tested the best regressions from the forested sites (based on  $R^2$  values) by comparing observed mass losses at the clearcut site with those predicted by the equations. That comparison is complicated by the substantially faster decomposition rate observed for all substrates at the clearcut site. Comparing decay of pine needle litter from a single source placed at all four sites, it appears that 2 years' decay at the clearcut site (mass loss = 39.4%) was equivalent to 3 years' decay at the forested sites (mass loss = 31.3–40.5%), so 2-year data from the clearcut site were used for the comparison.

The five best regressions, those of mass loss with percent lignin, lignin to N, and lignin to P (piece-wise regressions), with percent labile (simple regression), and with percent lignin plus percent N (multiple regression) all performed similarly, on balance, when applied to the data from the clearcut site. Accuracy of predictions varied widely from one litter type to the next, with errors of < 1% to > 20% common to any one equation.

To assess the relative accuracy of the five regressions, we computed the sum of the squares of the errors (where error = observed - predicted) as a measure of quantitative accuracy, as well as Spearman correlations of predicted with observed mass losses, as a measure of the degree to which rank order of decay rate was correctly predicted. By both criteria the regression on percent lignin was best and that on percent labile was worst (Table 6). Both the lignin to N and lignin to P regressions produced rank correlations > 0.7, although their error sums of squares were substantially greater than that for

TABLE 6. Sums of squared errors and Spearman correlations ( $r_s$ ) between 2-year mass losses from litter decomposing at the clearcut site and mass losses predicted from litter quality regressions derived from the forested sites ( $n = 10$  for each predictor)

	Lignin	Lignin to N	Lignin to P	Labile	Lignin + N
Sum of squared errors	691	1248	967	2480	1712
Sum of squared errors without N-fixers*	654	991	571	2248	446
$r_s$	0.879	0.709	0.745	0.552	0.818
$r_s$ without N-fixers*	0.857	0.810	0.929	0.667	0.952

\*N-fixing shrubs, alder, and buffalo-berry.

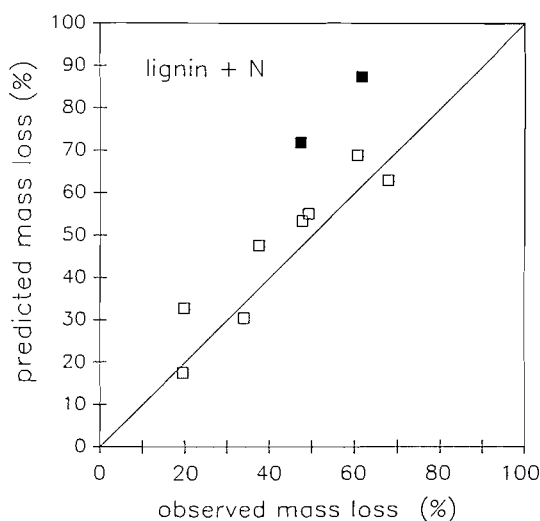


FIG. 3. Two-year mass losses from litter decomposing at the clearcut site compared with losses predicted from the regression on percent lignin plus percent N derived from the forested sites. Solid line is the 1:1 line. Solid symbols represent leaves of the nitrogen-fixing shrubs *Shepherdia canadensis* (buffalo-berry) and *Alnus crispa* (alder).

percent lignin (Table 6); the ratio with P produced somewhat more accurate predictions than that with N. The lignin-plus-N regression was disappointing, producing no more accurate ranking than percent lignin alone, and that with a much greater sum of squares. However, much of the total error arose from predictions for alder and buffalo-berry leaves, both of which lost 25% less mass than predicted (Fig. 3). Both these species are nitrogen-fixers, and their litter N concentrations were consequently high (1.8–2.0%). Without these two species, the lignin-plus-N regression had the lowest sum of squares and the best rank correlation of observed and predicted mass losses (Table 6).

### Discussion

Two principal conclusions may be drawn from this study. First, at least for this range of litter types, lignin is the most reliable indicator of decomposition rate, and nutrient content is an important secondary influence. Second, lignin content, and most of the usually proposed decomposition rate predictors, do not apply to all litter types. In woody litter (branches, twigs, cones, and tree roots) with a lignin content > 28%, further increases in initial lignin content had no effect on decay rate. A similar limit was evident for all of the parameters tested except labile content and N or P content.

Our results confirm the conclusions of Melillo *et al.* (1982) and Harmon *et al.* (1990) who have found a strong curvilinear

response of leaf litter decay rate with lignin to N ratio. Our results show that this curve may be described as a two-phase linear response: a rapid decrease in decomposition rate with increasing lignin to N below a critical ratio, and a negligible change above that critical ratio. While the work of Melillo *et al.* (1982) and Harmon *et al.* (1990) was restricted to leaf litter, it appears that the same principles apply to plant litter of other kinds as well.

Our results differ from those of others, however, with respect to two important details. First, both Harmon *et al.* (1990) and Melillo *et al.* (1982) found a conspicuously curved pattern of decay rate versus lignin to N, rather than the abrupt transition observed here (Fig. 2b). Second, the inflection point occurred near a lignin to N ratio of 30:1 in the above-cited work, compared with 50:1 here. However, this latter discrepancy may only reflect the different regression models used, or different methods of measuring lignin.

In the present study, lignin to N ratio was not the strongest predictor of mass loss, as would be expected based on previous work, but this appears to be largely a statistical problem, arising from the peculiar frequency distributions of ratios. When that problem is corrected by adding percent N as a second term in a piece-wise regression with percent lignin, the strength of the relationship improves in accord with expectations. Lignin to N correlations were unexpectedly weaker than for lignin alone in other studies (e.g., Upadhyay and Singh 1989), suggesting that this may be a common problem, and the two-term regression is therefore recommended.

Taylor *et al.* (1989) studied eight litter types from an aspen forest adjacent to the sites used here. They also found a strong linear correlation of mass loss with lignin content, but in their data, N content and C:N ratio were substantially stronger predictors. This discrepancy probably reflects the choice of substrates used. Taylor *et al.* (1989) used a wide variety of leaf litter types, but excluded wood, and deliberately biased the data toward low-lignin substrates (mean lignin content of 13%). The present study included wood and other high-lignin substrates and is therefore biased in the opposite direction (mean lignin content, Pine site of 22%). A stronger correlation of mass loss and percent lignin with increasing initial lignin content of the litter was predicted by Taylor *et al.* (1989), but the much poorer performance of N content, and especially C:N ratio, in the present study was not anticipated.

The uneven performance of the C:N ratio as a predictor of mass loss is probably a result of two factors. First, in high-lignin substrates the form of C (i.e., lignin or nonlignin) would be more important than the gross C content (e.g., Aber *et al.* 1990). Second, the importance of N or any other nutrient appears to depend on both the nutritional richness of the litter and the forest floor in which it is decomposing (Melillo *et al.* 1982). For example, mass loss and initial N content of litter

were reasonably well correlated at the pine site (0.66) and spruce site (0.67) but not at the fir site, which is richer in available soil N (C. Prescott, unpublished data). Similarly, there was a strong correlation of mass loss and initial phosphorus content only at the pine site. Decay-rate predictors based on nutrient content combine an internal factor (litter nutrient content) and an external factor (forest floor nutrient content) and so vary in predictive strength from site to site. The generalizations based on pooled data from all three forested sites would be weakened by the variation in nutrient availability between the individual sites. In the microcosm experiments of Taylor *et al.* (1989) all of the litter decomposed on soil from the same forest, so correlations with decay rate were not weakened by site-to-site variation.

Lignin and labile contents, conversely, are strictly internal factors, depending only on the chemical quality of the litter itself. Hence, these factors were equally strong predictors of decay rate at any site or at all three sites combined. It would be expected that the same difficulty of site variation would arise in any more general application of decay rate prediction based on N or P contents, or C:N or C:P ratios.

The success of initial labile content as a predictor of decomposition rate was surprising, since in most leaf litter labile contents are leached or metabolized within a year, and strong relationships with long-term decay rates have seldom appeared in other studies (McClaugherty *et al.* 1985; Taylor *et al.* 1989). Even the decay of woody litter, with a labile content of 15% or less, could be predicted, albeit with limited precision, by labile content, apparently because of the overwhelming importance of mass loss in the 1st year, when labile content was important.

It was significant that the three parameters that showed no regression limit (N, P, and labile content) were all those for which the correlation with mass loss rate was positive rather than negative. This suggests that these relationships might have a limit at the other end, i.e., a ceiling rather than a floor, where they would become great enough that they no longer limited microbial growth. Data from the clearcut site do suggest such a limit for nitrogen. Predictions of mass loss from alder were very good if based on lignin content (error = -0.6%), but very bad if based on lignin plus N (error = -25%), even though the latter formed the superior regression for data from the forested sites. Alder leaves had an N content of 1.9%, and the same result emerged for buffalo-berry leaves, with an N content of 1.8%. These very high N contents are far outside the range of the regression data base, and the failure of the extrapolation suggests that there is an upper limit to this regression. Such a limit would be expected to occur around a C:N ratio of 30:1, at which point microbial decay, broadly speaking, is no longer N-limited. The C:N ratio of alder is 26:1, and buffalo-berry is 27:1. Harmon *et al.* (1990) found a similar deviation for red alder (*Alnus rubra*) with an N content of 1.7–2.2%. Since the lignin content of buffalo-berry leaves is < 10% (Table 2), it is the high N content alone, and not the combination of high lignin and high N contents in alder leaves, that leads to slower than predicted decay rates.

Rates of mass loss from woody litter types bore no apparent relation to any of the quality parameters measured, not even to diameter, which for larger, three-dimensional litter like branches should correlate well with accessibility of the inner tissues to decomposers. After 3 years in the field, woody litter had lost only 15% mass, and it may be that decay was not advanced enough for rate differences to become apparent. But

the significant correlation of wood decay rate with forest site alone strongly suggests that decomposition of these litter types was controlled by factors external to the litter itself, probably the site moisture regime. Perhaps moisture was so overwhelmingly limiting in these dry forests that differences in diameter or content of nutrients or lignin had no effect on decomposition rates. Climatic differences among these three contiguous forests would be small compared with regional differences or even compared with the Clearcut site. This illustrates the sensitivity of woody litter decay to microclimate, a sensitivity apparently not shared with other, more rapidly decomposing substrates.

Other workers have also noted the inutility of chemical quality as a predictor of decomposition rate of woody litter. Edmonds *et al.* (1986) found only a very weak relationship between percent lignin and mass loss for alder and Douglas-fir wood (lignin contents 23–34%) even though their sample size was large ( $n = 72$ ). Working with branches, twigs, and cones of conifers, Edmonds (1987) found no correlation between decay rate and lignin content of all litter types (16–41% lignin), but did find a correlation for branches alone (16–33% lignin). Thus it appears that there are two distinct classes of plant litter, and that different factors control decomposition rates of low-lignin and high-lignin litter.

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