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Leaf-Litter Decomposition in the *Picea/Tsuga* Forests of Olympic National Park, Washington, U.S.A.

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ABSTRACT

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The factors controlling litter decomposition of eleven species of leaf litter were examined in the Hoh Rain Forest, Olympic National Park, Washington, using the litter-bag method. Leaching of litter decreased the decay rate-constant as compared to unleached litter. This decrease was in proportion to the readily leachable fraction (RLF) in the litter. Decay of both leached and unleached litter was highly correlated ($P<0.001$) with lignin:nitrogen ratio, although the regressions differed significantly between leached and unleached litter. Of the unleached litters used, *Cornus nutallii* decayed fastest ($k=2.35$-2.46/year), and *Pinus monticola* decayed slowest ($k=0.38$/year). A double-exponential regression was used to fit decay time-series from four species. This analysis indicated that species differed markedly in the proportion of fast and slow components and that the fast component was correlated with RLF for three of four species tested. Fast components decayed an order of magnitude faster than slow components. The rate at which these components decayed varied between species, indicating that both the amount and decay rate-constant of fast and slow components must be estimated to use the double-exponential equation.

INTRODUCTION

The decomposition of leaf litter is an important part of nutrient cycling in forests; there are many factors that influence decomposition rates of this material, such as substrate quality, invertebrates, and climate (Swift et al., 1979). Because litter decomposition is also affected by deposition of heavy metals (Chaney et al., 1978; Strojan, 1978; Coughtrey et al., 1979), and possibly acid rain (Moloney et al., 1983; Sheehan et al., 1984), human industry may be indirectly influencing nutrient cycling and productivity in forests exposed to these pollutants. To critically assess whether airborne pollutants affect litter decay, it is first necessary to understand how natural factors control decay in relatively clean environments before meaningful comparisons with polluted sites can be made.

In this study, we tested three hypotheses concerning decay of leaf litter in a relatively unpolluted temperate rainforest. The first hypothesis was that decay rate-constant was an inverse function of the initial lignin : nitrogen ratio as proposed by Melillo et al. (1982). Our approach differed from that study in that we tested a wider range of lignin : nitrogen ratios in the field. The second hypothesis concerned the effect of readily leachable fraction (RLF) on decomposition. Because the exposure of litter to rainfall prior to collection for experiments varies, it is important to understand how leaching affects decay rate. We hypothesized that unleached litter would decay faster than leached litter and that the leachable fraction did not interact with the unleachable fraction during decomposition. Our third hypothesis concerned the fact that leaf litter does not decay at a constant rate as assumed by the single-exponential model, but can be divided into an early rapid phase and a later slower phase (Bunnell and Tait, 1974). A double-exponential model was used to test if differences between species were controlled by the proportion of fast and slow components, or if the components differed in decay rates among species. We hypothesized that the proportion of components differed between species, but that the decay rate of the components did not differ among species.

STUDY AREA

The experiments were conducted in the Twin Creeks Research Natural Area, Olympic National Park, Washington (47°50′N latitude and 123°53′W longitude). The climate is maritime and cool with abundant rainfall. Total precipitation averages 355 cm/year, 75% of which falls between November and April. The mean pH of rainfall between 1980 to 1984 was 5.42 (Baker et al., 1987). Temperatures fluctuate between 8 and 27°C in summer and between −2 and 4°C during winter. Mean annual temperature is 8.90°C and potential evapotranspiration is 525 mm (Smith and Henderson, 1986).

The study was conducted within a 1.0-ha plot on an old river terrace at 167 m elevation, in conjunction with studies on litter fall, moss and lichen production, and needle retention (Baker et al., 1987). The study area is within the *Picea sitchensis* zone (Franklin and Dyrness, 1973) and the forest is typical of those on alluvial terraces approaching the climax stage of succession (Fonda, 1974). The study plot was old-growth *Picea sitchensis* (Bong) Carr. (Sitka spruce), *Pseudotsuga menziesii* (Mirbel) Franco (Douglas fir), and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), with a basal area of 74.4 m^2/ha and a per-ha density of 221 trees >5-cm diameter at breast hight (D_{bh}). Woody understory plants were dominated by *Acer circinatum* Pursh (vine maple), *Vaccinium alaskaense* Howell, and *Vaccinium parvifolium* Smith. Common herbaceous plants include *Oxalis oreganum* Nutt. and *Tiarella trifoliata* L., which both overlie a moss cover. Soils are of the Queets series: Typic Dystrochrepts that are strongly acid (pH 4.0–4.4) silt-loams, moderately well-drained, with a winter watertable at a depth of 1–2 m (Fonda, 1974; McCreary, 1975).

METHODS

The leaf litter used in the experiments was collected just prior to leaf-drop from MacDonald Forest, Corvallis, Oregon, Cascade Head Experimental Forest, Otis, Oregon or H.J. Andrews Experimental Forest, Blue River, Oregon, depending upon availability. Species common within the study area were selected so that a wide range of nitrogen and lignin concentrations could be tested. Leaves were caught on plastic or burlap tarpaulins; branches were shaken. In 1985, green needles of Sitka spruce and western hemlock were taken from freshly cut branches because fresh litter was not available. After collection, the litter was placed in paper sacks and allowed to air-dry for a 2-week period at room temperature.

The standard litter bag was 20×20 cm and made of 0.8-mm polyester mesh. Approximately 10 g of air-dried litter was placed in the bags. Subsamples were taken to determine moisture, nitrogen, acid detergent fiber (ADF), lignin, cellulose, and readily leachable fraction (RLF) content of each species. The bags were placed in the field in late November or early December in a randomized, complete-block experimental design, with five blocks. Moss growing on the forest floor was removed so the litter bags were in contact with the litter layer. A methodological study conducted in 1983 and 1984, which compared litter bags of Douglas fir and *Thuja plicata* Donn. (red cedar) under moss with those on the litter surface did not indicate a significant placement effect on the decay of either species. After a 1-year incubation, the bags were removed from the field, litter was separated from extraneous matter (e.g., moss) and then oven-dried for 48 h at 55°C.

A number of experiments were performed which deviated from the procedures described above. The effect of leaching organic matter from litter on decay rate was tested in 1983 and 1984. Depending upon the RLF content of a species, the amount needed to yield 10 g dry-weight of litter after leaching was added to litter bags. The bags were then soaked in distilled water for 48 h to extract RLF and then placed in the field next to the unleached bags. The experimental design was a split-plot of complete, randomized blocks. There were five blocks, eight to ten species (depending upon the year), and two leaching treatments. The incubation period was one year.

Although most incubations were one year, a time-series of a subset of species was used to assess temporal trends in litter decay. In 1984, bigleaf maple and Douglas-fir leaves were set out so that monthly samples could be taken over a

2-year period. The experimental design was a split-plot with two blocks, two species and 24 incubation times. In 1985, vine maple, bigleaf maple, *Populus trichocarpa* T&G (cottonwood), and Douglas-fir were incubated for 0.5, 1, 2, 3, 4, 6, 8, 10 and 12 months. The experimental design was a split-plot of complete randomized blocks, four species and six incubation times.

Readily leachable fraction (RLF) was determined by soaking 5-g samples of air-dried litter in distilled water at room temperature for 48 h, and then drying for 48 h at 55°C. Air-dry moisture content was determined after drying for 48 h at 55°C and was used to adjust the initial air-dry weight to an oven-dry basis. Three subsamples of leached and unleached litter were analyzed for total Kjeldahl nitrogen (Isaac and Johnson, 1976), lignin, cellulose, acid detegent fiber (ADF) and ash content (Goering and van Soest, 1970) at the University of Alaska Soil Laboratory.

Analysis of variance and regression analysis were performed using the decay-rate-constant k as the dependent variable (PC-SAS procedure GLM; Anonymous, 1986). The decay rate-constant was calculated by dividing the natural logarithm of the fraction of litter remaining by the time (years) incubated. In the case of the k-lignin:N-ratio regression, a double logarithmic transformation was applied. Nonlinear regression methods (procedure NLIN, Anonymous, 1979) were used to calculate the parameters of the double-exponential model for the 1984 and 1985 time-series.

RESULTS

Litter leaching

The 48-h leaching treatment reduced the decay rate-constant for all species in the 1983 and 1984 incubations. For both years the effects of species, leaching, and the interaction between species and leaching was highly significant ($P<0.01$). The difference in the decay rate-constant between leached an unleached litter for a species increased with increasing RLF (Tables 1 and 2). The nitrogen content of litter was not significantly reduced by leaching. The leaching treatment therefore decreased substrate quality by removing soluble labile carbon and leaving nonsoluble lignin, cellulose, and other cell-wall constituents. The changes in lignin, cellulose, and ADF content caused by leaching can be calculated from RLF content with the following formula:

$$X_{\text{leached}} = X_{\text{unleached}}/100 - \text{RLF} \tag{1}$$

where X is the carbon component and RLF is the readily leachable fraction (%). The predictions from this equation correlated significantly ($P<0.01$, $N=12$) with the observed changes in substrate quality, and with the concentration of lignin ($r=0.92$), cellulose ($r=0.90$), and ADF ($r=0.96$) after leaching all increasing with RLF content.

TABLE 1

Readily leachable fraction (RLF), lignin, cellulose, acid detergent fiber (ADF), and nitrogen content of the litter[a] used in experiments

Species	RLF[b]	Lignin	Cellulose	ADF	Nitrogen[c]
1983					
Abies procera	6.1(0.4)	22.0(0.7)	22.5(0.4)	49.0(2.6)	0.83(0.04)
Acer circinatum	29.9(2.5)	13.6(0.4)	15.8(0.7)	31.5(0.4)	1.46(0.08)
Acer macrophyllum	14.7(0.4)	19.2(0.5)	20.1(0.5)	41.2(1.7)	1.08(0.07)
Alnus rubra	25.0(0.8)	9.8(0.5)	12.9(0.6)	22.8(0.9)	1.72(0.08)
Cornus nuttalii	29.0(1.1)	6.0(1.0)	17.1(1.3)	23.7(2.0)	1.12(0.02)
Picea sitchensis	5.5(0.7)	25.1(0.3)	27.8(0.2)	54.0(0.2)	0.79(0.02)
Populus trichocarpa	25.3(0.9)	12.4(0.7)	17.4(0.4)	31.7(1.2)	1.02(0.02)
Pseudotsuga menziesii	7.3(0.2)	15.5(0.5)	20.1(0.4)	37.9(0.2)	0.66(0.03)
Thuja plicata	5.5(0.8)	18.0(0.8)	26.9(0.4)	46.0(0.5)	0.49(0.01)
Tsuga heterophylla	8.5(0.2)	19.1(0.3)	26.4(0.7)	46.6(0.6)	0.75(0.03)
1984					
Acer circinatum	20.7(1.1)	15.2(0.7)	19.7(1.0)	35.9(0.9)	1.51(0.17)
Acer macrophyllum	14.1(0.3)	14.9(1.0)	22.7(1.1)	38.9(1.9)	0.87(0.01)
Alnus rubra	14.8(0.5)	13.0(0.9)	18.1(0.8)	31.2(0.2)	2.20(0.03)
Cornus nuttalii	23.8(3.4)	7.5(0.7)	18.5(0.2)	26.7(0.6)	1.18(0.03)
Pinus monticola	3.5(0.4)	22.7(2.9)	34.9(3.2)	58.1(0.8)	0.45(0.03)
Picea sitchensis	4.5(0.9)	13.7(0.2)	25.4(0.4)	39.4(0.2)	1.12(0.05)
Populus trichocarpa	25.0(1.0)	15.4(0.4)	17.0(0.2)	34.9(0.5)	0.90(0.09)
Pseudotsuga menziesii	7.7(0.6)	23.7(0.6)	19.5(0.5)	45.6(0.7)	0.77(0.02)
Thuja plicata	5.6(0.5)	27.9(0.8)	27.6(0.8)	56.2(0.1)	0.47(0.02)
1985					
Acer cricinatum	32.2(0.7)	6.3(0.3)	16.0(0.3)	24.8(0.5)	0.68(0.03)
Acer macrophyllum	16.9(0.4)	13.0(1.2)	24.8(0.3)	39.9(1.3)	1.00(0.21)
Alnus rubra	23.8(0.7)	6.4(0.7)	14.8(0.8)	22.2(0.2)	1.93(0.09)
Cornus nuttalii	38.0(1.1)	2.7(0.1)	14.1(0.2)	17.5(0.1)	0.79(0.03)
Piunus monticola	3.7(0.9)	19.5(0.5)	37.3(0.6)	57.7(0.1)	0.32(0.02)
Picea sitchensis	4.2(0.2)	21.6(1.4)	42.4(1.5)	64.7(0.7)	0.64(0.01)
Populus trichocarpa	20.3(1.3)	12.0(0.6)	18.5(1.9)	33.2(2.8)	0.87(0.07)
Pseudotsuga menziesii	6.7(1.1)	16.2(0.9)	23.7(0.3)	42.5(0.7)	0.45(0.01)
Thuja plicata	4.1(1.3)	23.4(1.2)	28.9(1.1)	53.8(0.1)	0.30(0.01)
Tsuga heterophylla	3.7(0.6)	23.8(1.7)	33.9(1.9)	58.3(0.4)	0.74(0.05)

[a]Percentage; ± 1 SE.
[b]Mean (standard error), $n = 3$.
[c]Standards with nitrogen content of 0.97 and 2.36% N were analysed as having 1.01 and 2.34% N, respectively.

The differences in k between leached and unleached litter increased with RLF in a predictable manner. Assuming RLF would be lost the first year by either leaching or biological decomposition, the decay rate of unleached litter could be predicted by adding RLF to the initial weight of the leached litter.

TABLE 2

Effect of leaching treatment on the decay rate-constant of leaf litter placed in the Hoh Rain Forest

Species	Decay rate-constant (*k*/year)	
	Unleached	Leached
1983		
Abies procera	0.382 (0.007)[a,b]	0.301 (0.011)[c]
Acer macrophyllum	0.698 (0.016)[b]	0.420 (0.048)[c]
Alnus rubra	0.930 (0.034)[b]	0.487 (0.045)[c]
Cornus nuttalii	2.465 (0.215)[b]	1.420 (0.060)[c]
Picea sitchensis	0.751 (0.042)[b]	0.507 (0.031)[c]
Populus trichocarpa	0.681 (0.013)[b]	0.263 (0.019)[c]
Pseudotsuga menziesii	0.475 (0.036)[b]	0.339 (0.001)[c]
Thuja plicata	0.386 (0.001)[b]	0.289 (0.017)[c]
1984		
Acer circinatum	0.874 (0.056)[b]	0.529 (0.072)[d]
Acer macrophyllum	0.665 (0.029)[b]	0.523 (0.063)[d]
Alnus rubra	0.472 (0.155)[b]	0.462 (0.039)[d]
Cornus nuttalii	2.349 (0.296)[b]	2.192 (0.364)[d]
Pinus monticola	0.383 (0.019)[b]	0.228 (0.027)[d]
Picea sitchensis	0.845 (0.036)[b]	0.825 (0.041)[d]
Populus trichocarpa	0.605 (0.032)[b]	0.358 (0.031)[d]
Pseudotsuga menziesii	0.390 (0.017)[b]	0.297 (0.019)[d]
Thuja plicata	0.291 (0.012)[b]	0.280 (0.033)[d]
Tsuga heterophylla	0.724 (0.036)[b]	0.626 (0.069)[d]

[a]Mean (standard error).
[b]$n = 10$.
[c]$n = 7$.
[d]$n = 5$.

Observed decay rate-constants and those calculated by this method were significantly correlated ($P<0.01$, $r=0.96$, $n=18$), indicating that RLF did not interact strongly with the other portion of litter to control annual k.

Substrate quality

Decay rate-constant decreased significantly ($P<0.001$) with increasing ADF, lignin, cellulose, and lignin:nitrogen ratio. In contrast, k significantly increased with nitrogen and RLF content. Of the three models used in regression analysis, the double-logarithmic had the highest coefficient of variation, although the semilogarithmic and untransformed models also resulted in highly significant ($P<0.01$) regressions.

Stepwise regression analysis indicated that double-logarithmic regression of k and initial lignin:nitrogen ratio proposed by Melillo et al. (1982) explained the most variation of all the regressions examined. Addition of other variables such as nitrogen or lignin did not significantly improve the regression. Decay rate-constant did not respond markedly to lignin : nitrogen when this ratio exceeded 30 (Fig. 1). Below this value, k increased dramatically with small decreases in lignin : nitrogen ratio. An exception to the overall pattern was *Alnus rubra* Bong. (red alder), which decayed much slower than expected for all three years.

Leached litter decayed slower than unleached litter even when the lignin : nitrogen ratio was similar. Analysis of covariance indicated the slope for leached litter was significantly ($0.01 < P < 0.05$) steeper than that of unleached

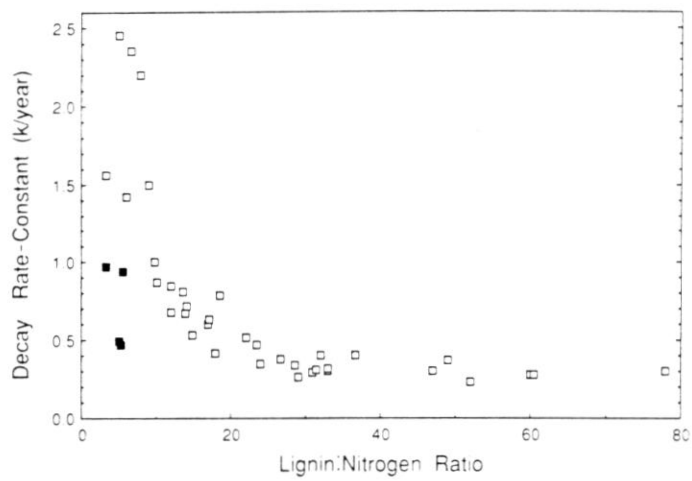

Fig. 1. Decrease in the decay rate-constant with increasing lignin : nitrogen ratio. Leached and unleached leaves are included. *Alnus rubra* is indicated by closed squares, while all other species are open squares.

TABLE 3

Coefficients for regression between decay rate-constant and initial lignin : nitrogen ratio for unleached litter at Hoh Rain Forest

Year	B_0[a]	B_1	r^2[b]	n[c]
1983	2.50	−1.01	0.91**	7
1984	2.02	−0.81	0.87**	7
1985	1.23	−0.60	0.96**	8
Pooled	1.73	−0.74	0.87**	22

[a]The regression was $\ln(k) = B_0 + B_1 \ln$ (lignin : nitrogen).
[b]$^{**}P < 0.01$.
[c]*Alnus rubra* and *Picea sitchensis* excluded.

litter. This indicates that changes in the lignin : nitrogen ratio caused by leaching were not sufficient to explain the effect of leaching on k.

The relationship between lignin:nitrogen ratio and k also varied significantly among three years it was examined (Table 3). Presumably, these differences were related to differences in weather; mean air temperature was similar all three years, precipitation varied between years, and the regression slope and y-intercept were greatest when precipitation was highest.

Time-series

All four species examined had an initial rapid phase of decomposition followed by a slower phase (Fig. 2). The simple exponential model was a poor predictor of the biomass remaining in the time-series examined. In contrast, the double-exponential model, which accounts for fast and slow-decomposing components separately, was a better predictor of the biomass remaining (Table 4).

Vine maple and bigleaf maple had the largest amount of 'fast' component (29–40%), whereas Douglas fir had the least (7–13%). In the case of Douglas fir, cottonwood, and vine maple, the proportion of litter in the fast component was significantly correlated to RLF ($r=0.97$, $P<0.01$, $N=4$). For bigleaf maple, however, RLF was smaller than the fast fraction by a factor of 2, indicating that nonsoluble substances were also included in the fast fraction.

The decay rate-constant of the fast component ranged from 5.54/year for vine maple to 15.45/year for Douglas fir, indicating an inverse relationship

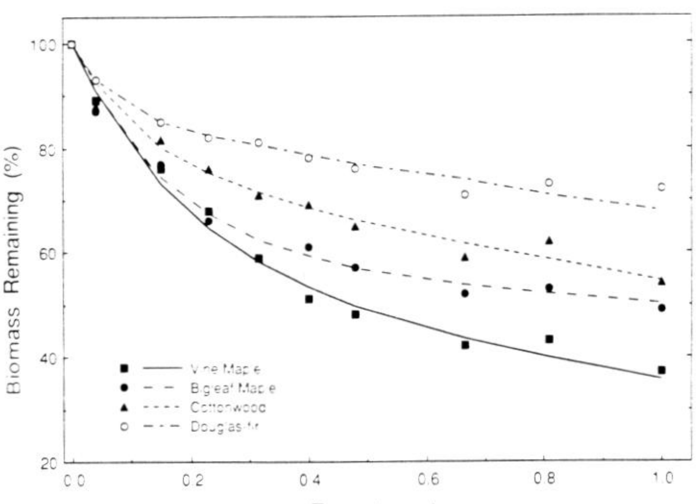

Fig. 2. Biomass of *Acer circinatum*, *Acer macrophyllum*, *Populus trichocarpa*, and *Pseudotsuga menziesii* remaining as a function of incubation time. Lines are from regressions from Table 4.

TABLE 4

Coefficients for the double-exponential regression used to fit time-series data from Hoh Rain Forest

Species[a]	Slow fraction (%)	k_{slow}	k_{fast}	r^2	n
Samples set out in 1984					
Acer macrophyllum	71	0.18	6.51	0.74	24
Pseudotsuga menziesii	93	0.26	12.17	0.89	23
Samples set out in 1985					
Acer circinatum	61	0.54	5.54	0.99	10
Acer macrophyllum	60	0.18	6.12	0.98	10
Populus trichocarpa	79	0.37	8.92	0.97	10
Pseudotsuga menziesii	87	0.25	15.45	0.97	10

[a]The model used was $Y = F_{slow} e^{-k_{slow}t} + (1 - F_{slow}) e^{-k_{fast}t}$ where t is time (years), F_{slow} is the fraction of litter that is slowly decaying, k_{slow} is the decay rate-constant of the slow fraction, and k_{fast} is the decay rate-constant of the fast fraction.

between the amount of fast fraction and its k. Of the 'slow' components, that of vine maple decayed most rapidly ($k = 0.54$/year), and that of bigleaf maple, least ($k = 0.18$/year). The decay rate-constant of the slow fraction exhibited a significant negative correlation with ADF and cellulose content. In contrast, lignin content and lignin : nitrogen ratio were not significantly correlated with the decay of the slow fraction. The decay rate-constant of the slow component was similar to that of leached litter for vine maple, cottonwood, and Douglas fir, which suggests that RLF was the fast component for these species. For bigleaf maple, leached litter decayed much more rapidly than the slow component, indicating that non-water soluble substances contributed to the fast component.

DISCUSSION

As suggested by Melillo et al. (1982), the initial lignin : nitrogen ratio of litter is closely correlated with annual k. Our field experiments confirmed that the power-curve relationship used by Melillo et al. (1982) to fit the laboratory data of Daubenmire and Prusso (1963) is valid for field incubations as well. This relationship, however, did not fit all the species we tested. Red alder, for example, decayed slower than predicted. As suggested by Herman et al. (1977), the combination of high lignin and high nitrogen content may retard decay. The lignin : nitrogen ratio of red alder was quite similar to that of dogwood, although the former contained greater concentrations of both substances.

A shortcoming of predicting k from lignin : nitrogen ratio is that the degree of leaching affects the relationship. While decay rates of leached and unleached litter were both highly correlated to lignin : nitrogen ratio, the regressions differed significantly. Removal of labile substrate by leaching reduces k more than predicted in changes in the lignin : nitrogen ratio. Despite its shortcomings, lignin : nitrogen ratio is a useful way to account for substrate quality differences and the effect of climate and other factors on k.

The effect of climatic variables such as mean annual temperature, precipitation, and potential evapotranspiration on the relationship between k and lignin : nitrogen ratio is not clear, based on the few studies that have examined this relationship for a wide range of species (Fig. 3). Of the species studied by Cromack and Monk (1975) in North Carolina, all except *Cornus florida* fall on our regression line despite the warmer (13°C) and drier (annual precipitation 180 cm) climate. *Cornus florida* decomposed at a slower rate than *C. nutallii* even through their lignin : nitrogen ratios were similar. All the species studied at Hubbard Brook by Melillo et al. (1982) had k-values below that predicted by our regression line. These differences may have been caused by cooler (5°C) and drier (annual precipitation 130 cm) climate at Hubbard Brook. Pandey and Singh (1982) examined litter with lignin : nitrogen ratios from 0.8 to 15 in a Himalayan oak/conifer forest. Their values also fall along our regression, despite the fact their site was warmer (16°C) and drier (annual precipitation 285 cm). Comparing sites based on potential evapotranspiration also does not explain differences in decay rates. For example, the curves for Pandey and Singh (1982), Cromack and Monk (1975) and our study are quite close despite the fact that potential evapotranspiration was 700, 702, and 525 mm, respectively. Comparison of these studies seems to indicate that the relationship between k and lignin : nitrogen ratio is not strongly influenced by climatic vari-

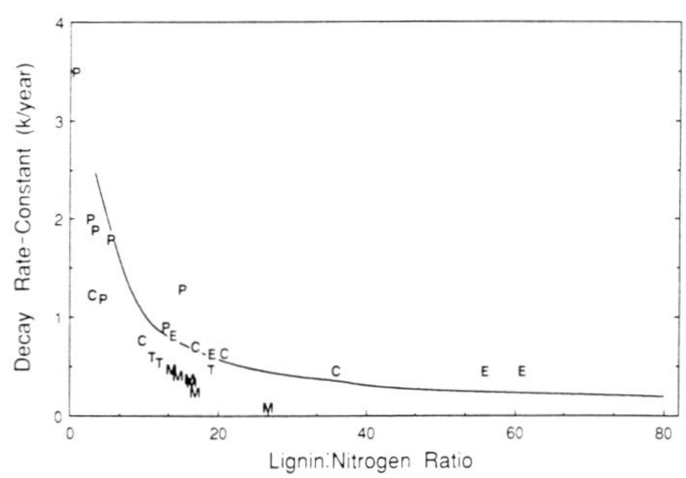

Fig. 3. Comparison of decay rate-constant and lignin : nitrogen ratio for various studies. Line, this study; C, Cromack and Monk, 1975; E, Edmonds, 1980; M, Melillo et al., 1982; P, Pandley and Singh, 1982; T, Topik, 1982.

ables. In order to confirm this conclusion, data from other sites for a wide range of lignin : nitrogen ratios is needed.

The single negative-exponential equation has been used widely to model decay of leaf litter (Wieder and Lang, 1982). While the decay-rate constant calculated from this model is a useful index of decay, it can be misleading if the incubation time varies. Because leaf decay is initially dominated by a period of rapid loss, a short incubation time increases the decay-rate constant. As incubation time increases, slower decomposing components influence the decay dynamics and the decay-rate constant decreases (Edmonds, 1980, 1984; Berg et al., 1982). The double-exponential model proposed by Bunnell and Tait (1974) circumvents these problems by modeling both phases of decay. The double-exponential model fits our time-series very closely. The proportion of components and the rates that these components decay varies with species. For most species, RFL content closely matched the amount of fast component estimated by regression (Table 4). The decay rate-constants of the slow fraction appear to be correlated with ADF content. The flexibility of the double-exponential model to fit the early as well as the later phases of litter decay warrant its wider use. Our study indicates that, for three of the four species studied, the proportion of litter in the two categories as well as the decay rate-constants may be predicted from an initial analysis of litter.

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