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MACROCLIMATE AND LIGNIN CONTROL OF LITTER DECOMPOSITION RATES[1]

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Abstract. In order to develop a general model of litter decomposition rates suitable for the prediction of regional variations in decay rates, and to determine the relative control by macroclimate and litter quality on decomposition rates, data were selected from 5 locations ranging in climate from subpolar to warm temperate. Actual evapotranspiration (AET) was selected as an index of the climatic (energy and moisture) forcing function of the specialized decomposers which is superior to temperature and precipitation. Lignin concentration was selected as an index of litter quality and may be treated as a mediator of climatically (AET) regulated decay rates. In a stepwise, multiple linear correlation–regression, using AET, lignin concentration (%) and AET/lignin concentration (interaction), AET alone accounted for 51% of the variance in observed decay rates, AET/lignin concentration (interaction) added 19% and lignin concentration added 2% of the total (72%) variance accounted. Simple correlation of the five locations between lignin concentration and decomposition rate ranged from $r = .32$ to $r = .95$, however, the regression lines for each of the 5 locations indicated that these slopes progressively declined with AET. Moreover, the slope decline was not parallel, indicating a climatically variable control by lignin concentration on decay rates. In low-AET (not arid) climates, litter with high and low lignin, will decay at more nearly similar rates, but as the AET environment increases, the difference in decay rates becomes progressively greater than the increase in AET alone would seem to warrant. A general model of the interaction control by AET and lignin concentration on decomposition rates was formulated which overcomes the restraints of the multiple regression model. At the scale of subpolar to warm-temperate climates, the climate as indicated by AET is several orders of magnitude more important as a predictor of decay rate than is litter quality. This importance is evident in spite of the fact that the data on lignin concentration used in this analysis had a 12-fold range while the AET values had a 2.3-fold range.

Key words: actual evapotranspiration; climatic control; curve-fitting; decomposition rates; geography of decomposition; lignin; litter; macroclimate; North Carolina; Norway; Oregon; regional analysis, substrate quality; Tennessee; United Kingdom.

INTRODUCTION

Decomposition of litter is regulated by a host of variables including the litter's physical properties, climate and macro- and microfaunal responses. In spite of the complexity of the decay process, the 2 most important controls of litter decomposition rates are probably the prevailing climatic environment and susceptibility of the substrate to attack by the specialized decomposers, i.e., substrate quality. Waksman (1929) proposed general relationships of litter substrate quality to litter decomposition. Cromack (1973), Cromack and Monk (1975), and Fogel and Cromack (1977) have shown that lignin concentration of the substrate is an excellent index to use for prediction of the rate of disappearance and weight loss by forest litter samples. Lignin concentration gave the best correlation with decomposition when data of Lockett (1937) were analyzed statistically (K. Cromack, Jr., *personal communication*). Similarly, litter which decomposers break down slowly may have large C:N ratios (Hill 1926, Jensen 1929, Witkamp 1966). Van Cleve (1974), in a review of decomposition studies from circumpolar tundra and taiga sites, reports that P + Ca concentration, lignin + tannin, and carbohydrates including cellulose all have significant correlations with decomposition rates. He suggests that the dominant influence which lignin apparently exerts over decomposition rates may result from its ability to serve as a surrogate for the many physical and chemical properties which regulate litter decomposition rate. Minderman (1968) states that slowly decomposing litter components, such as lignin, tend to dominate the shape of the long-term decomposition curve once the more labile components have been removed.

Results of studies of the mobility and cycling of individual nutrients are numerous and the results reveal a great deal of variability among the rates for nutrients as well as variability from region to region. However, as a single, general predictor of the loss in litter dry weight with time, lignin concentration is indeed useful. D. M. Sharpe (*personal communication*) has used the lignin percentages of leaf litters to assist in the prediction of litter dynamics including standing litter biomass in Southern Applachian forests where macroclimate is fairly uniform.

Investigations of the role of the abiotic environment in decomposition rates are, however, few in number and quantitative studies of regional, continental or global variation in the abiotic control of decay rates are even fewer in number. Witkamp (1966) determined the seasonal change in CO_2 evolution from the forest floor at a site near Oak Ridge, Tennessee. Reiners (1968) monitored seasonal change in CO_2 evolution

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from 3 forested communities in Minnesota. Edwards (1975) presented a temperature model for litter CO_2 evolution utilizing an entire year's data from a hardwood forest. Bunnell et al. (1977*a*, 1977*b*) presented combined models for effects of temperature, moisture and substrate quality upon litter decomposition from arctic ecosystems. Van der Drift (1963) attempted to monitor the yearly variation in litter decomposition rates for a forest near Zutphen, the Netherlands and to relate these differences to the weather. Differences in decomposition rates between temperate and tropical sites were studied by Jenny et al. (1949). Meentemeyer (1977), working at a continental and global scale, found that litter decay rates in a vegetated system are predicted fairly well by a single meteorological variable—the actual evapotranspiration (AET). He demonstrated that AET has a correlation of r = .98 with average annual decomposition rate. Data from sites around the globe were used in this correlation-regression analysis, although data from arid and semiarid sites were unavailable. It is likely then that AET is also an index variable but representative of microenvironmental variables responsible for control of the decomposers. Because AET is a measure of the concurrent availability of energy and moisture to an ecosystem, it is not surprising that AET correlates well with decay rates. Furthermore, AET responds to the availability of moisture from soil and litter storage, a provision not possible using precipitation alone as a predictor. Actual evapotranspiration may be viewed as the climatic forcing function and lignin concentration as the substrate modifier of the efficiency of decomposition.

Both AET and lignin concentration have been independently shown to be good index predictor variables of decomposition rate. It is the purpose of this study to develop general statements of the dual control of climate and substrate quality on litter decomposition rates. Specific objectives include: (a) an assessment of the relative contribution of AET and lignin as predictors of decay rate; and (b) the variable control by lignin of decay rates in different climatic environments.

Data

In spite of the new wealth of information on decay rates from terrestrial ecosystems around the world, few of these data were found to be suitable for this study, the primary restriction being the lack of measured lignin concentration for the litter under investigation. Secondly, it is often impossible to reconstruct the AET or other specific measures of climate which occurred during the time that a litter-decay study was conducted either because the study site is so remote or its exact location and elevation so poorly described that even average annual values of AET cannot be calculated for the study site. Sometimes the site itself was found to be unrepresentative of the region, or the duration of the study too short to determine the true effects of AET and lignin on decay rates. It is recognized that litterbags were utilized at all sites used in this study and that their use may have excluded some of the large macrofauna or caused some alteration of forest floor microclimate. However, it is assumed that these effects will not be such as to mask major climatic differences between geographic regions. At all sites examined, litter substrates were treated in a similar manner. At both the North Carolina and Oregon locations, considerable numbers of microarthropods such as mites and springtails entered the litterbags.

No doubt the limited availability of lignin data is in large part due to the relatively uncommon analyses of forest litter substrates for lignin content. However, the work of Van Cleve (1974) and Fogel and Cromack (1977) makes the point that such data are needed if we are to compare substrate quality effects upon decomposition in a wide variety of ecosystems. The restricted availability of lignin measures can be overcome to a degree because lignin concentration of leaf litter for a particular species is fairly consistent from region to region (Ausmus 1973). This means that when a species' senescent leaf litter has had its lignin concentration measured, this measured value can usually be used as representative for studies in which the species are the same but the sites are different. K. Cromack, Jr. (*personal communication*) has examined this problem. He states that initial comparisons between the same species in different locations indicate that they are similar in lignin concentration, but individual species' lignin concentrations may vary to some degree from year to year, depending on climatic effects upon timing of leaf senescence and degree of translocation of soluble compounds prior to leaf abscission. Concentration of lignin in fast- and slow-decomposing litter species within systems tends to remain the same. The salient point of this work is that substrate quality information must be available if climatic effects are to be differentiated from differences due to substrate quality.

Five locations could be selected as having data of the correct specifications. These sites are: (1) Hardangervidda, Norway; (2) Moorhouse, U.K.; (3) H. J. Andrews Forest, Oregon; (4) Coweeta, North Carolina; and (5) Oak Ridge, Tennessee. The number of cases at the 5 sites totals 49. Data from (1) and (2) are reported and described by Van Cleve (1974), (3) by Cromack (1973) and (4) by K. Cromack, Jr. (*personal communication*). Site number 5 is a composite of the work reported by several authors (Shanks and Olson 1961; Witkamp and Olson 1963; Crossley and Witkamp 1964; Witkamp 1966; Thomas 1968, 1969, 1970; Witkamp and Frank 1969), all working in the Oak Ridge area.

To further simplify this analysis and to make the data as comparable as possible prior to analysis, the arctic and subarctic data presented by Van Cleve

TABLE 1. Pearson's product-moment correlation coefficients (r) between initial lignin concentration in percent and 3 measures of decomposition rate

Locality	Annual decay per-centage	Log_{10} of annual decay per-centage	k	N
Coweeta, North Carolina	−.971	−.966	−.947	6
H. J. Andrews Forest, Oregon	−.887	−.962	−.853	13
Moorhouse, United Kingdom	−.771	−.598	−.770	13
Hardangervidda, Norway	−.334*	−.320*	−.333*	7
Oak Ridge, Tennessee	−.801	−.763	−.815	10
				49

* Not significant at .05 level.

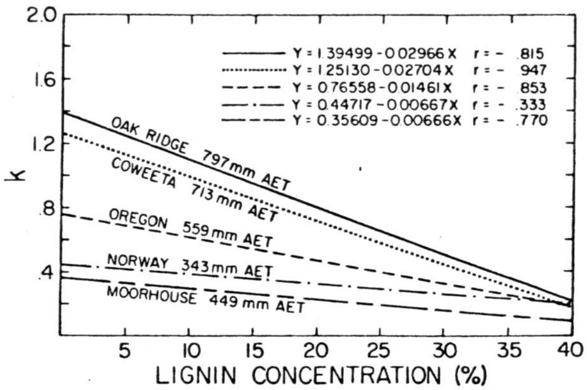

FIG. 1. Simple correlation-regression between initial lignin concentration (%) and annual decomposition rate (k) for 5 locations ranging in climate from subpolar to warm temperate. AET = actual evapotranspiration.

(1974) had to be adjusted. Studies from these sites reported the weight loss occurring over 2 yr. Olson (1963) recognized that there is a tendency for litter to decrease with time the rapidity with which it decays. He devised an exponential decay function (k) to define this change in rate which may be written as:

$$d\,X/X = -k dt,$$
$$\ln (X_t) = \ln (X_o) - kt,$$

where X_t is the amount of litter remaining after time t, X_o is the initial quantity of litter, and t is time. To adjust the 2-yr data to equivalent 1-yr data, the k function above was graphed for the subpolar data. This graph indicated that the 1-yr rates were approximately equal to 60% of the 2-yr rates reported and could be so adjusted.

RESULTS

As a first step, the correlations between initial lignin concentration and measured decay rates were calculated for the 5 locations used in this study. Table 1 presents these correlation coefficients, which were calculated or recalculated from the original data. Because of small errors in rounding, and in some cases interpretation from graphs, the r values may differ slightly from any previously reported. Correlations with 3 alternative and widely used expressions for decomposition rate are presented here: (1) the exponential decay rate, k; (2) the annual decay percentage; and (3) the $\log_{10}$ transformation of annual decay percentage. All decomposition rates presented in Table 1 are highly significant statistically except for the Norway values. The Norway decay rates were derived from sites of differing elevation, exposure and moisture characteristics. One measured decay rate appeared highly spurious but was included in the analysis. Had this variance not been introduced, the r values would have been near .79, which is barely insignificant at .05.

Of the 3 expressions of annual decay rate presented in Table 1, no single measure consistently had the highest r value for every location. The Coweeta and Oregon locations probably had the highest r values because uniform site and experimental methods were used, thereby reducing variance. The r value for Oak Ridge is remarkably high even though the data were derived from several independent studies which have been conducted at different sites during years of slightly differing AET at Oak Ridge. Furthermore, the lignin values for individual species of leaf litter in the Oak Ridge computation are the same as lignin values measured by Cromack (1973) for the same species.

Figure 1 presents the simple linear regression equation for the relationship between decay rate (k) and lignin (%) for each of the 5 locations. The Oregon, Hardangervidda, and Moorhouse curves are based on data which includes decay rates and lignin percentages for fine, nonfoliage litter. It is clear that the intercepts and slopes vary with climate. Each line in Fig. 1 presents the AET estimated for each location (797 millimetres at Oak Ridge, 713 millimetres at Coweeta, etc.). The k value was chosen here because of its wide acceptance and use in the decomposition literature. There is a progressive decrease in the slopes of the lignin relationship with a decrease in AET except for the Moorhouse and Norway curves which are inverted, with Norway (343 millimetres AET) being above the Moorhouse (449 millimetres AET) line.

In all cases, the AET value has been estimated using the method of Thornthwaite and Mather (1955). Since it is an estimate, some error variance must be contributed. The AET values for Moorhouse and Norway are average annual values based upon interpolations from surrounding stations and data taken from a high-quality climatic atlas (WMO and UNESCO 1970). The Oregon value is the average AET for 5 yr, 1970 to 1974, using weather data from McKenzie Bridge, Oregon. The Coweeta value is the average for the period

TABLE 2. Averages for decomposition rates (k), lignin concentration, and estimated actual evapotranspiration for 5 locations

Locality	Annual decay percentage		Log_{10} of annual decay percentage		k		Lignin (%)		AET (mm)
	A	B	A	B	A	B	A	B	
Coweeta, North Carolina	51.0	51.0	1.708	1.708	−.75	−.75	18.6	18.6	713
H. J. Andrews Forest, Oregon	31.2	41.7	1.494	1.620	−.41	−.53	24.1	13.6	559
*Moorhouse, United Kingdom	17.4	23.3	1.241	1.367	−.19	−.26	25.2	17.4	449
*Hardangervidda, Norway	21.4	21.4	1.330	1.330	−.25	−.25	29.1	29.1	343
Oak Ridge, Tennessee	52.6	52.6	1.721	1.721	−.81	−.81	19.7	19.7	797

A = Averages of all litter reported.
B = Average of foliage litter only.
* = 2-yr decay rates adjusted to equivalent annual rates by assuming 60% of the 2-yr rates.

1969, 1970, and 1971. The original experiment by Cromack (1973) was conducted from November 1969 to November 1971. Thus, the Coweeta example has the most exact reconstruction of the AET climate which occurred during the time litter samples were exposed. The Oak Ridge example uses the long-term, average annual value for AET because the litter decay data were taken over a period of years. In all cases, AET was estimated using the same water budgeting method and using an assumed moisture storage capacity of 300 millimetres for the rootzone soil including the substrate. Litter moisture is often different from that of mineral soil but has little actual bearing on total AET. Meentemeyer (1974*a*) has devised a special water budget for substrates which perhaps warrants experimentation in decomposition studies although this budget could not be applied in this study.

Table 2 presents the average measured decomposition rates for the 5 locations used in this study. Also included are the averages of all the measured litter decay rates, including in some cases bark, roots and twigs, and the measured rates for only the foliage litter. It is recognized that the ease of entry of moisture into and out of these litter parts must have a bearing on their decomposition rate, however, no provision for this effect was devised for this study. The average lignin concentrations for all litter and for foliage litter presented ranges from a low of 13.6% for Oregon to 29.1% in Norway. The last column presents the estimated AET in millimetres.

TABLE 3. Correlation matrix and summary table of step-wise multiple correlation. AET = actual evapotranspiration

Variable	1 Annual weight loss (%)	2 Lignin (%)	3 AET (mm)	4 AET/ Lignin
1	1.000	−.535	.715	.703
2		1.000	−.205	−.701
3			1.000	.440
4				1.000
Step number	**Variable entered**	**R**	**R^2**	**Increase in R^2**
1	3	.715	.511	.511
2	4	.836	.698	.187
3	2	.846	.716	.018

As a first step to formulating a general model of climate and lignin control on decomposition rates a stepwise, multiple linear regression was calculated. Predictor variables selected were lignin (percentage), AET (millimetres), and because of expected interaction between lignin and AET the third variable was stated as a ratio, AET:lignin percentage. The dependent variable is, in this case, the measured annual decomposition percentage (based on weight lost) for foliage litter. Table 3 presents the resulting correlation matrix and the multiple R values. With the use of AET alone, 51% of the variance ($R = .715$) in measured decay rates is accounted for. By adding AET/lignin, the multiple R is raised to .836 ($R^2 = .70$) and the standard error of estimate is 10.41. Thus, the actual decomposition percentage should be within 10.41 percentage points of the predicted value two thirds of the time. The addition of a third variable, lignin percentage, adds little to the explained variance because the effects of lignin are present in the AET/lignin ratio. The multiple linear equation predicting annual decomposition percentage is stated below:

$$Y_1 = -1.31369 + 0.05350\,X_1 + 0.18472X_2;$$

where Y_1 = annual weight loss (%),
X_1 = annual AET (millimetres),
X_2 = AET millimetres/Lignin (%).

In this equation the failure of lignin concentration as a significant contributor to the explained variance should not be interpreted to mean that lignin is not an important regulator. At any location and given AET, the litter apparently may have an ≈12-fold range in values and thereby lead to good correlations of lignin concentration with decomposition rates at that location. However, even small changes in climate, as indicated by AET, can produce large changes in decomposition rates. The data inputs of AET for this study had a 2.3-fold range in the span from subpolar to warm temperate climates. Had global data inputs been available, the contribution by AET to explained variance would have been markedly higher. In fact, Meentemeyer (1978) found that the AET to decay rate relationship at the global scale, using only leaf litters, is exponential. This, in part, explains the high r value of nearly +.98 calculated in that study.

A further complication in the prediction of decomposition rates using AET and lignin concentration is the fact that in every different climatic regime, the lignin concentration has a different control on decay rate. From Fig. 1, we see that the slopes of the linear curves are not parallel but become steeper with increasing AET. The slopes converge at a lignin concentration slightly in excess of 43% where (at least according to linear curves) the climate has little actual control on decay rates. For the Coweeta and Oak Ridge curves, no data for high-lignin, nonfoliage litter were available, so these extrapolations must be used with caution. Had more data on high-lignin litters been available, the variance accounted for by lignin concentration would have been somewhat higher.

Generally, litters with low lignin concentration should display the greatest variability in decay rate from region to region, as influenced by climate. Thus, dogwood litter with a lignin concentration of 3.9% (Cromack 1973) should have a k of ≈ 1.28 at Oak Ridge, 1.15 at Coweeta, 0.71 at the Oregon site, 0.33 at Moorhouse and 0.42 at the Norway site.

The greatest discrepancy between predicted and actual values in this study occurs for the subpolar sites because of the high variability and the conversion from 2-yr data to an annual rate of weight loss. Clearly, the regional analysis of decomposition using AET as a measure of macroclimate ignores microsite variations. In view of the suggested pervasive effects of climate on decay, these seemingly insignificant microclimatic variations may rival substrate quality as a control mechanism at the local scale.

It might be possible to use the multiple linear equation as a predictor of weight loss or the individual curves for the 5 locations used here. However, an ultimate objective is to produce a general model of decomposition rate, so an added advantage for visual evaluation would be the graphing of the relative contribution of AET and initial lignin percentage. The intercepts and slopes of the decomposition to lignin relationships are climatically determined. Therefore, in order to achieve further smoothing, a simple linear regression was performed using: (1) the k slopes; and (2) the k intercepts, presented in Fig. 1 as dependent variables and AET as the independent variable, with $N = 5$, the number of locations in this study. In all cases, the correlations between AET and slope and intercept were high (AET on intercept, $r^2 = .922$ and AET on slope $r^2 = .948$), suggesting that it would be reasonable to depict the AET-regulated decay with lignin relationship as a smooth progression of slopes. Figure 2 is a graphical representation of this additional smoothing. This figure also permits the 3 primary variables in this study to be plotted in 2 dimensions. One

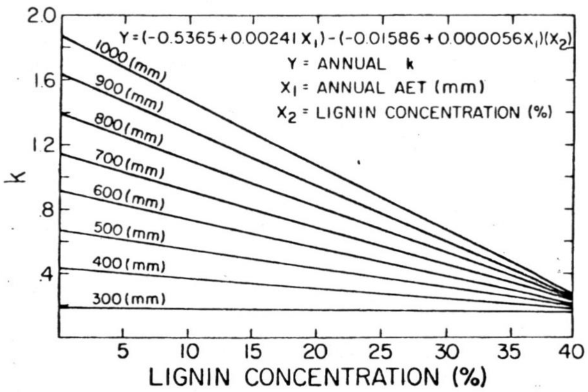

FIG. 2. Generalized model of the changes in the slope and intercept of the relationship between initial lignin concentration (%) and annual decomposition rate ($-k$) with changes in climatic actual evapotranspiration (AET in millimetres).

might then view AET as the predictor of the slope and intercept and lignin as the regulator of the point on each individual climate's slope.

Figure 2 presents the composite equation which can be formulated after the second stage of curve fitting. The first term in parenthesis permits AET to select the intercept, the second term permits AET to select the slope, and the third term, lignin concentration, selects the point on the slope of each AET. Representative slopes are presented in Fig. 2 for AET at 100-mm intervals. It might be cautioned, however, that this formulation should be used only for climates and lignin concentrations within the ranges of those used as data inputs. It seems unreasonable for the woody litter with high lignin concentrations shown on the right of Fig. 2 to be entirely unregulated by climate. This suggests that, when more data become available, additional, nonlinear curves may be desirable.

Figure 3 is similar to Fig. 2 but uses annual decay percentage, rather than k. The total variance accounted for using the composite equation presented in Fig. 3 is somewhat less than the formula using k. This further suggests the need for new curves among decay rate, climate and lignin concentration. For example, using the equation in Fig. 3, the convergence of the slopes occurs at a higher lignin value than do the slopes in the k formula used in Fig. 2.

We can determine some of the effects of the second stage smoothing by comparing the predicted k for dogwood litter using the first stage lines (Fig. 1) with the second stage lines (Fig. 2). At Oak Ridge, the predicted k becomes 1.37 vs. 1.28; 0.96 vs. 1.15 at Coweeta; 0.72 vs. 0.71 at Oregon; 0.51 vs. 0.33 at Moorhouse; and 0.28 vs. 0.42 in Norway. Again, most of the discrepancy is found at the subpolar locations where data inputs, though probably representative of the subpolar region, are quite variable.

The results in all figures suggest that the relative control by lignin concentration is not the same in dif-

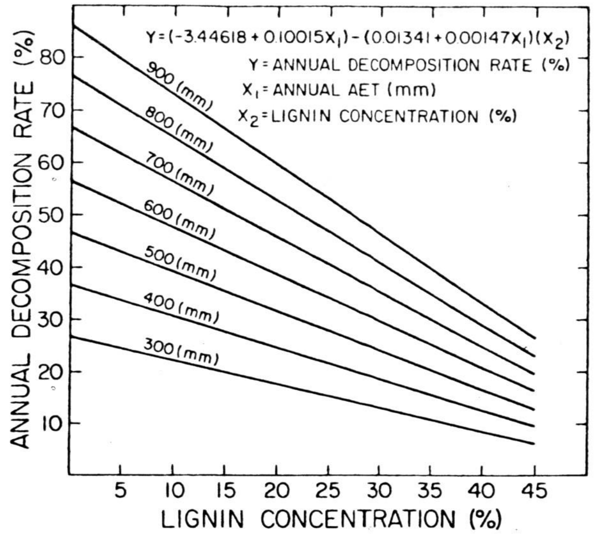

FIG. 3. Generalized model of the changes in the slope and intercept of the relationship between initial lignin concentration (%) and annual weight loss (%) with climatic actual evapotranspiration (AET in millimetres).

ferent climates. Thus, at low AET, litter with low and high lignin concentration will decay at more nearly similar rates. At high-AET locations, the differences in observed rates among litter types should be large. For example, at 400-millimetre AET, the expected difference in k between the intercept point (0%) and 30% lignin is only 0.196 but at 900-millimetre AET, the difference is 1.036. When using annual decay percentage as in Fig. 3, the effect is not apparently as large, probably because k is an exponential derivation, a transformation which permits better linear curve fitting.

As more information on the relationships between substrate quality and decomposition rates becomes available, there will, no doubt, be attempts to employ these models on a regional basis. For example, one might wish to predict the litter nutrient pool, or energy content or standing litter biomass. The results presented here suggest that these relationships vary with climate. Thus, it may be unwise to trust these relationships outside the regions of development or even in the same region in years of exceptional weather.

Discussion

For terrestrial ecosystems, the basic regulator of the pace of decomposition rates is the combined climatic energy and capillary soil and litter moisture availability, for which AET is an excellent index. Indeed, AET, which has been estimated in this study using water budgeting methods, has a higher correlation with measured decay rates than does lignin concentration, when, as in this study, climate ranged from subpolar to warm temperate. The consistent pattern leads one to expect that, on a global scale, the relative control by climate would be even more dominant than lignin content. However, in any particular region possessing reasonably uniform terrain and macroclimate, lignin concentration is an excellent predictor of decay rates of different litters as Cromack (1973) and Fogel and Cromack (1977) have verified.

The relative control by lignin over decomposition rate is not uniform over different climatic regions. Generally, the greater the abundance of energy and moisture, as indicated by AET, the faster the decay rate for a given lignin content but the higher the lignin content, the more energy and moisture are required to cause breakdown to be accomplished in a unit time, say a year. If this trend also applies at the global scale, then litter quality and physical properties must have their most pervasive control in tropical environments, least in polar environments. Unfortunately, the relative contribution by climate and litter properties for arid environments could not be determined in this study. There is some fragmentary evidence, however, that a different relationship of AET and lignin with decomposition rates may exist for the dry environments. Mack (1971) reports a litter decay rate of almost 50% per year in an area with <250 millimetre AET per year. C. L. Strojan (*personal communication*), who is conducting leaf litter decomposition studies in southern Nevada, reports that *Lycium andersonii* litter lost 40.9% of its dry weight in only 18 wk in this arid environment. A speculative explanation of the climatically varying role of lignin in decomposition can be based upon the work of Edwards and Heath (1963) concerning the role of fragmentation by invertebrate animals on decomposition rates. Apparently, when litter and soil animals are excluded from a decomposing litter, there is insufficient fragmentation leading to much-reduced consumption by microorganisms. Kevan (1962) suggests that the increase in surface area by fragmentation caused by microarthropods will lead to increased decomposition rates. However, Howard and Howard (1974) state that the overall effect on decomposition by small animals needs clarification and I would add that the effect of climate on soil animals, and their subsequent effect on decomposition also needs clarification. Perhaps the reduced control by lignin in cool climates is the result of reduced fragmentation ability by litter animals.

Seasonal decay rates have been predicted by Meentemeyer (1974*b*) using AET alone but the relative role of AET and lignin in various seasons can now be inferred from Figs. 2 and 3. If the generalizations developed in this study are correct, then one might find litters of greatly varying lignin concentrations decaying at nearly similar rates in the winter but diverging greatly in the early summer or high AET season.

Decomposition is a tremendously complex process and AET and lignin are surrogates for only some of the actual regulators of decay rate. In this study, AET has been estimated using water-budgeting techniques. While AET has been estimated in the same manner for each location used in this study, it is really derived from a measure of macroclimate. Specific sites varying because of aspect, soil or successional stage will have AET values differing from the macroclimatic terms presented here. Clearly, the curves presented in Figs. 2 and 3 must also include a great deal of error variance because of differences in the methodology of decomposition studies, variations in litter quality, and the fact that AET estimates have built-in assumptions, all introducing variance into the equations. In spite of the unknowns of decomposition not accounted for here, the formulations using AET and lignin may improve estimates of standing litter accumulations. Perhaps the decay rate of organic material of man-made origin may also be predicted by extending the observations on lignin to a variety of materials. The need was never more evident than now for the organization of systematic observational networks with standardized procedures and common test materials to verify the geography of decay rates.

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