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MEASURING LITTER DECOMPOSITION IN A TROPICAL FOREST ECOSYSTEM : COMPARISON OF SOME METHODS

F. BERNHARD-REVERSAT

Laboratory of Plant Ecology, O.R.S.T.O.M., B.P. 1386, Dakar, Senegal

ABSTRACT

The decomposition of litter has been measured in a tropical forest ecosystem using three methods: (1) direct measure of weight loss, (2) estimating a decay coefficient, and (3) integrating the seasonal weight loss curves and the monthly soil litter variations to obtain a curve of decay along the year.

The aim and precision of these methods are discussed in relation to the study of organic matter cycling in the forest; and other methods used in tropical forests are reviewed.

INTRODUCTION

Decomposition of forest litter has been extensively studied in temperate forests, in relation to various factors such as fauna (Bocock 1964, Witkamp and Crossley 1966, Weary and Merriam 1978), species (Heath *et al.* 1966) and other environmental factors (Bocock and Gilbert 1957, Witkamp and Van Der Drift 1961) or with the purpose of estimating nutrient release (Gosz *et al.* 1973, Lemee and Bichaut 1973).

Among the first authors who studied the decomposition of the litter in tropical forests, Jenny *et al.* (1949) indicated the rapid disappearance of tropical forest litter. This was emphasized by Bartholomew *et al.* (1953) and Laudelout and Meyer (1954). Several works on this subject have been carried out particularly in recent years, and many attempts have been made to compare the different results obtained (Hopkins 1978). In most cases the studies are concerned with the annual rate of decay and little attention has been paid to the seasonal variation of the decay rate. In this paper a method to calculate the amount of litter disappearing in the course of a year is given, and the different methods for studying the decomposition rate are compared.

LITTER DISAPPEARANCE IN THE BANCO FOREST (IVORY COAST)

Leaf litter disappearance was studied in a rain forest (Banco forest) of south Ivory Coast in two sites previously described (Bernhard 1970). The mean annual rainfall is 2100 mm. The atmospheric humidity is always high and ranges between 80 to 86%. Litter fall occurs mainly in the dry season (Bernhard 1970).

The weight-loss curves of the leaf litter are established approximately every two months (Bernhard-Reversat 1972). Known amounts of freshly fallen leaves were placed on the soil on a 2 mm mesh plastic netting, and covered with the same netting, the sam-

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ples were collected at various time, and dried and weighed. The leaf fall was collected weekly for more than two years, and its weight calculated for every two weeks.

The principle of calculation is to apply the weight-loss curves to the two weeks litter fall collection. Then for every two weeks intervals, the weight loss of the previous two weeks are cumulated to give the total amount of litter disappearing for this interval.

For the plateau site it is assumed that the weight loss curve is the same whatever the season (Figure 1). For the talweg site, where the disappearance rate is different according to the season, six different curves are applied to the leaf fall for two or three months each year.

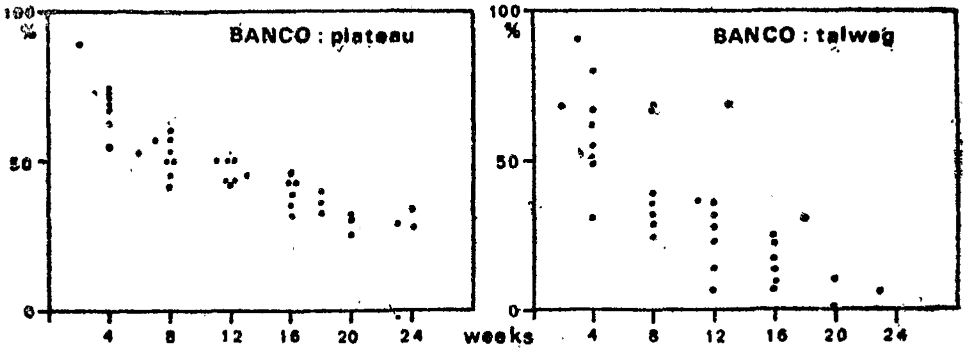

FIG. 1. Weight loss of the leaf litter : weight of litter (left) as per cent of the initial amount. Several experiments started at different period of the year are represented.

The mathematical model established follows the hypothesis of linearity; the disappearance rate is assumed to be the same whatever the amount of litter present at the time 0.

Let $c(t)$ be the litter fall curve, and $\rho(t)$ the weight loss curve. At time t_2 the amount of litter $q(t_2)$ remaining from an amount $q(t_1)$ present at the time t_1 is :

$$q(t_2)=\rho(t_2, t_1)\ q(t_1) \qquad (1)$$

At any particular moment t, the amount of litter falling on the soil is $c(\tau)\ d\tau$ and what remains at the time t is :

$$\rho(t\tau)\ c(\tau)\ d\tau$$

If $l(t)$ is the sum of all the fractions which remain from the litter fallen during all the previous moments τ, we have :

$$l(t)=\int_{-\infty}^{t} \rho\ (t, \tau)\ c\ (\tau)\ d\ (\tau)$$

the derived function of which is:

$$\frac{dl}{dt} = c(t) + \int_{-\infty}^{t} \left(\frac{d\ \tau\ (t, \tau)}{dt}\right) c\ (\tau)\ dt \qquad (2)$$

The disappearance of the litter is given by the equation:

$$D(t) = c(t) - \frac{dl}{dt}$$

which using the equation (2) becomes:

$$D(t) = \int_{-\infty}^{t} \left(-\frac{d\rho\ (t, \tau)}{dt}\right) c(\tau)\ dt$$

The latest equation is made to computerise the litter disappearance. In order to avoid the occurence of $-\infty$ the calculation is started at a date which is separated from the beginning of the measurements by a period longer than the total disappearance time.

The results obtained are shown on Figure 2. The aim of the method is to give the amount of organic matter that disappears and subsequently the amount of non-volatile nutrients which is incorporated into the soil for a given period. Our results emphasize the different behaviour of the litter in the two sites. In the plateau site, a great part of the litter is decomposed during the dry season and the nutrients which are returned to the soil at this time are not submitted to weathering by the heavy rainfall of the wet season. It represents a nutrient saving strategy compared to the talweg site where most of the litter is decomposed during the wet season and are likely to be weathered. In the plateau site, soil and vegetation are poorer in nutrients (specially P, K, and Ca) than in the talweg site.

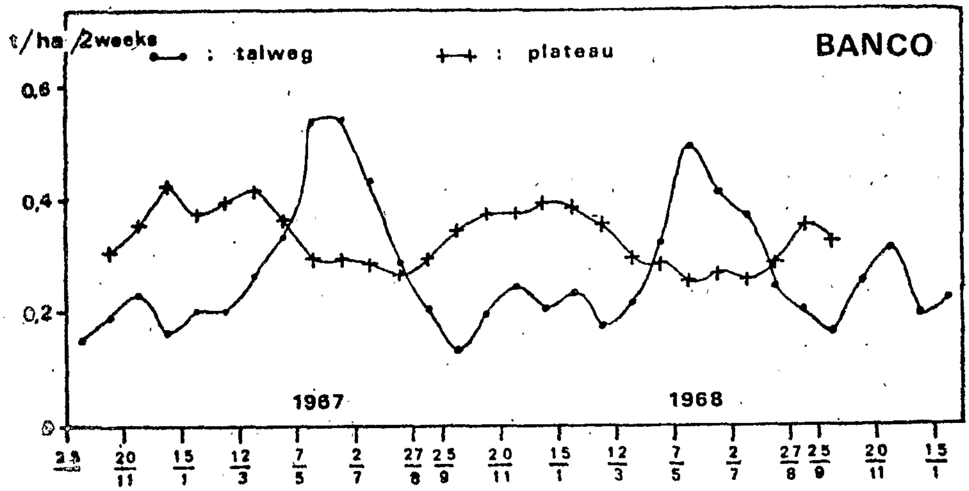

Fig. 2. Seasonal variations of the amount of litter disappearing during 2-weeks intervals.

The same model allows the calculation of the litter accumulation in the soil. The calculated amount is smaller than the result of direct measurements. It is possible that the experimental method by weight loss measurements overstimates the decay rate. In addition to the experimental study the decay rate has been estimated by calculating the decomposition coefficient (Olson 1963) from measurements of litter fall and litter accumulation in the soil (Bernhard 1970). The comparison of these two methods is shown in Table 1.

Table 1. *Disappearance time of the litter (in months) estimated by two methods*

Methods	Decay coefficient		Weight loss measurements	
Site	50%	95%	50%	total
Plateau	2.5	11	1.5—3.0	9
Talweg	2.0	8.5	0.7—4.0	5

Weight loss measurements give higher decay rates than the decay coefficient calculation (Table 1). Overestimate of the decomposition rate by the experimental method may be due to the compaction of the leaves resulting in a better conservation of water during the dry periods, hence better conditions for the microflora. The initial leaves sampling method may also be involved; the sampling is made by picking all the green or yellow leaves on the floor to represent freshly fallen leaves, and this method may cause a systematic error by discarding that which are brown when fallen. The calculation of decay coefficient also introduces errors because it assumes an exponential weight loss, which is not confirmed by the experimental curves (Edwards 1977).

DECAY COEFFICIENT *K*

Two methods of calculating k have been used. The models have been extensively studied by Olson (1963) who showed that the formula $k = \frac{L}{X+L}$ (where L is the annual litter fall and X the amount of litter on the ground) applied to forests having a discrete litter fall in a short period of time, while $k = \frac{L}{X}$ applied to forests having a continuous litter fall.

To calculate the disappearance time it is necessary to return to the equation $X/X_0 = e^{-kt}$ (Olson 1963) where X is the amount of litter remaining at the time t from an initial amount X_0. Since the weight loss curve is exponential it is not possible to calculate the total disappearance time, so the 95% disappearance time is often calculated. However some authors approximate the total disappearance time by assuming that X/L (or 1/k) is the number of years for total decomposition. Since D, the decomposition is equal to L in a steady state ecosystem, X/L=X/D gives the number of years for the disappearance of a quantity L of accumulated litter. But this amount is not entirely fresh litter since a part of it has already been decomposing. The term X/L is thus not the disappearance time for a given amount of fresh litter.

In Table 2 some of the results obtained for various tropical forests are given. No details are given of the type of forest because such table has been given (Hopkins 1978) showing the absence of reliability between the k coefficient and forest type or pluviometric factors. Meentemeyer (1978) shows the existence of a high correlation between k and the actual evapo-transpiration when both temperate and tropical forests are considered, but no relation was shown for tropical forests alone. Table 2 shows that the k coefficient separates the montane and premontane forests (k being about 1), and the lowland forests (k generally greater than 2). It would probably separate woodlands from humid forests, since a decay coefficient ranging from 1.1 to 1.3 have been calculated (Malaisse 1978); but only few data are available.

Although the exponential curve of decomposition does not fit the measured weight loss curves, the calculation of k is thought to give the most comparable values of decomposition rate between forests because of the apparent simplicity of the measurements.

However the difficulty of measuring the amount of litter on the soil is often underestimated. Most tropical forests have seasonal variation in litter fall and in decomposition resulting in large variation in the amount of litter on the soil : in the sempervirent Banco forest (Ivory Coast) the amount of litter ranges from 0.7 t ha^{-1} during the wet

TABLE 2. *Estimations of litter decomposition in different tropical forests (The bold figures are given by the authors ; the time unit has eventually been changed)*

Source and location (1)		Expression used by the authors and material concerned		$k=\frac{L}{X}$	95% disappearance time in month (3)	4
Wiegert (1970) Puerto Rico	M	leaf litter		0.94	38	2
Edwards (1977) New Guinea	M	k=L/X non-woody litter	Ridge	**1.07**	34	3
			Valley	**1.48**	24	
			Slope	**1.18**	30	
Herrera de Fournier *et al.* (1977) Costa Rica	M	decomposition rate[2] L-X **710** *g m*$^{-2}$ *month*$^{-1}$		1.2	30	6
Jenny *et al.* (1949) Colombia	P	$k=\frac{L}{X+L}$ **0.628**		1.6	23	
Madge (1965) Nigeria	P	k=L/X fine litter		**2.2**	17	24
Hopkins (1966) Nigeria	P	disappearance time=1/k=**2.4-6** semideciduous (2 years)		4.5—1.9	8-19	
		leaf litter **4.8** months evergreen		2.4	15	12
John (1973) Ghana	P	disappearance time k=1/k=**4.8** *months* leaf litter		2.5	14	S
Devineau (1976) Ivory Coast	P	k=L/X leaf litter		**0.1 to 3.0**	**12 to 36**	1
Whitmore (1978) Malaysia	P	disappearance time =1/k=4 *months*		2.8	13	
Laudelout and Meyer (1954) Zaire	P	$k=\frac{L}{L+X}$ =**0.76** fine litter		3.1	12	
Bernhard (1970) Ivory Coast	P	k=L/X leaf litter	plateau	3.3	11	12
			talweg	4.2	8.5	
Nye (1961) Ghana	P	k=L/X fine litter		4.65	7.7	1

(1) M=montane or premontane forest. P=Lowland forest

(2) L=litter fall. X litter on the ground

(3) from the equation : $X/Xo=e^{-kt}$

(4) number of sampling periods for X measurements. (S=several).

season to 3.5 t ha^{-1} during the dry season in the same site. Hence correct estimation of the mean annual amount needs several evenly-spaced sampling periods. The spatial variability is also high : in the Banco Forest the confidence limits interval (for $P=95\%$) reaches $\pm 35\%$ in the wet season and ± 15-20% in the dry season for 10 replicates of one square meter.

The interannual variability may be important in relatively dry climates. The results of Hopkins (1966) shows that the amount of leaves on the soil in a year with 1100 mm of rainfall is more than twice the amount in a year with 1500 mm. The variations are probably not so great in wet forests.

Besides the possibilities of imprecisions in measurements, Meentemeyer (1978) emphasizes the possible influence of the physical nature of the litter, such as lignin content. It has been shown from multiple linear regression equation of climate and lignin content that in tropical climates a small change in climate or in lignin content results in dramatic changes in decay rate (Meentemeyer 1978). This is confirmed by differences among species in tropical forests (Madge 1969, Bernhard-Reversat 1972, Ewel 1976, Edwards 1977). However this effect is weakened by the high number of species in tropical forests.

WEIGHT LOSS MEASUREMENTS

An evaluation of experimental methods of litter decomposition studies is useful for comparison. Allt he *in situ* methods used are alternatives to the litter bag method, where known amounts of fresh litter are placed on the soil.

The measured decay rate is affected by experimental condition such as the amount of litter in the bag, the type of bag, the mesh of the net, the way of placing the bag, the use of entire leaves or fragments. These sources of variations have to be considered when comparing the results.

The results usually shown by graphs, are difficult to enumerate. The instantaneous rate of disappearance in mg g^{-1} day^{-1} is often given. Although the time taken for its calculation theoretically does not interfere if the curve is exponential, it does introduce a very inaccurate term if the slowest phase of decomposition is included.

The time needed for 50% disappearance would be a better way to compare different results because it corresponds to the rapid phase of decomposition and give more precise figures.

Table 3 shows the difficulty of using different experimental results for comparing forests. The main conclusion of this analysis is that to compare different sites the same procedure has to be used.

CONCLUSIONS

The calculation of decay coefficient gives the rate of litter disappearance, if this rate is assumed to be an exponential function of time. This method allows the characterization of a biotope by an estimation of the turnover rate of organic matter, which expresses the biological activity of the forest floor. So emphasized are the differences of metabolism between forests of various climatic zones, e.g. temperate versus tropical, or montane versus lowland. More precise comparison, particularly among tropical forests, are difficult and would need more accurate measurements of the accumulated litter, than those currently in use.

TABLE 3. *Experimental measurements of litter decomposition in different tropical forests (The bold figures are given by the authors)*

Source and location (1)		Expression used by the authors, and material concerned	disappearance rate mg g^{-1} day^{-1}	50% disappearance time, weeks (2)
Wiegert (1970) Puerto Rico	M	Instantaneous disappearance time	**1.43**	
Edwards (1977) New Guinea		per cent disappearance in 325 days : **43 %** mean of 7 species	1.7	
Cruz (1964) Puerto Rico	M	per cent disappearance in 35 days : **50%**	16.9	**5**
Ewel (1976) Guatemala	P	per cent disappearance in 28 weeks : **43%** mean of 6 species	2.9	**10**
Bartholomew *et al.* (1954)—Zaire	P	per cent disappearance in 8 months **57%**	3.3	7
Bernhard-Reversat (1972) Ivory Coast	P	total disappearance time **9** *months* plateau; **5** *months* talweg	7.1; 13,1	7; 5
Madge (1969) Nigeria	P	total disappearance time 2 *to* 7 *months* leaf discs, mean of 3 species	10. 5 to 32. 8	6 to 19

(1) M=montane or premontane forest. P=Lowland forest
(2) estimated from the weight loss curves.

The experimental method of studying litter decomposition by weight loss measurements give more precise data, provided that the time intervals between collections are small. This method gives a more realistic relation between decay and time and the measurements of mineral nutrient release from litter. Moreover its accuracy allows the comparison between stations or treatments, and it can be used to study the influence of various factors, such as animals, soil, species dominance, topography, etc.... which may contribute to the understanding of decay processes. However the results obtained are largely dependent on the experimental conditions and it is generally not possible to compare results from different authors and countries.

When monitoring nutrient cycles, it is useful to know the amount of organic material disappearance and the amont of non-volatile matter that enters the soil in a given time according to the season, because nutrients behavicur with respect to rainfall depends on the seasonal pattern of nutrient release. For this purpose, the use of the litterfall curves and the weight loss curves, based on relatively accurate measurements, give more reliable results than calculations derived from decay coefficient estimation. In the model described in this paper, the weight of organic matter may be replaced by the weight of any mineral nutrient obtained from litter analysis.

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