THE TIME FACTOR IN THE DECOMPOSITION OF CONIFEROUS LEAF LITTER[1]

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Abstract

A method is described for determining the duration of the various stages in the decomposition of coniferous leaf litter on mor sites. Knowledge of the time required for the decay process in different species would allow useful comparisons to be made of their inherent mor-forming tendencies.

One of the immediately apparent differences between a mor and a mull is the great accumulation of plant debris, chiefly leaf litter, often to be found on the former, and its relative absence from the latter. This accumulation of litter is eminently suitable for ecological studies of microbiological succession, owing to its development of characteristic strata which correspond to well-marked stages in a successional process of decay. Such organic horizons under conifers have the added advantage that the needles of which the upper layers are largely composed lend themselves admirably to the processes of sampling and experimentation without loss of identity or integrity. The present study was concerned with the organic horizon under a pure stand of Scots pine at Delamere Forest, Cheshire, England. The recognizable strata are described here in order to obviate any confusion which might otherwise arise from the unexplained use of their familiar, but often variously interpreted, designations. Litter or L layer: recently fallen, relatively undecomposed needles, often light brown to buff in color, with high tensile strength and relatively low moisture content, lying in a loose uncompacted layer at the surface. Fermentation or F layer, here divisible into F_1: needles grey to black, tissues softened, very low tensile strength and relatively high moisture content, lying in a more closely packed stratum immediately below the L layer, and characterized by intensive fungal activity; and F_2: needles grey, often fragmentary, flattened, lying in a tightly compressed mat below the F_1 layer and characterized by intensive meiofaunal activity. Humification or H layer: brown and more or less amorphous, consisting largely of animal faeces and fungal remains, as needles have now undergone complete physical reduction. Fine tree roots are common in this layer, which lies immediately above the uppermost layer of the mineral soil, the humus-stained A_1 horizon.

Despite the fact that this habitat proved so suitable for many quantitative studies of the decomposition processes, one of the most important of such quantitative aspects, the time factor, was not directly measurable. This

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paper discusses a method by which a time scale was derived for the decomposition of the pine leaf litter at Delamere Forest, and the wider implications of that method.

The first step was to measure the total annual leaf litter production per unit area of forest floor. The second was to remove the entire organic horizon from a carefully chosen sample plot, each of the component layers being carefully segregated and collected in a separate container. In the laboratory, numerically equal samples of needles from the L, F_1, and F_2 layers were selected, and their dry weight determined. In addition the total dry weight of each layer was found, needles being weighed separately from the twig, cone, and bark fragments. From the data obtained, the percentage loss in dry weight of needles from the lower layers compared with the recently fallen needles from the surface layer could be determined. The application of suitable conversion factors derived from this known loss in dry weight enabled the equivalent amounts of fresh litter represented by the L, F_1, and F_2 layers to be found. Comparison of these figures with the measured year's fresh litter production allowed the approximate average time spent by a needle in each layer to be determined.

Litter production was traced by installing a litter trap, 1 m square, in a suitable location, and collecting the litter falling therein at intervals throughout the year. Thus not only the total amount of litter produced but also the distribution of litter production around the year could be followed. The data obtained from the litter trap are given in Table I. The autumnal needle drop, accounting here for two fifths of the entire year's litter, is evident. Previous records of annual litter production by various species of pine, quoted by Handley (5), showed that the greatest range was found by Ebermayer (4), who reported amounts varying between 1700 and 5150 kg ovendry weight per hectare. The figures of other authors fell within this range, as did those

TABLE I

Determination of litter production by the needle trap

	Ovendry wt., g
Total litter production for 1957	476
Total leaf litter	408
Twig, cone, and bark fragments	68

Distribution of litter fall round the year

Month	% of total	Month	% of total
January	3	July	2
February	3	August	42
March	6	September	9
April	10	October	5
May	5	November	6
June	7	December	2

obtained in the present study. The amount of litter collected from the trap during 1957 was equivalent to 4760 kg per hectare ovendry weight. Of this, 4080 kg was accounted for by leaf litter, and the remaining 680 kg by twig, cone, and bark fragments.

Alway and Zon (2) found variations in dry weight of litter produced from year to year on a single plot, and from plot in 1 year, of up to 25%. These workers quoted the average annual litter production as equalling from one-fourteenth to one-sixth of the organic matter content of the underlying forest floor. At Delamere Forest the fraction appears to be approximately one-tenth. Here it must be mentioned that exceptional circumstances may bring about much larger irregularities in litter production than those observed by Alway and Zon. Dimock (3) reported that extremely low winter temperatures may lead to litter production at three times the normal rate in the following year. A needle rust on white spruce in Manitoba and Saskatchewan sometimes causes the loss of almost all needles formed in the previous year (Rowe, private communication). In the defoliation of balsam fir by spruce budworm, very few unattacked needles reach the ground (Redmond, private communication). Finally, cone production is much greater in some years than in others. This may have an effect on needle development and therefore on subsequent litter production. Thus it would appear to be most desirable to have some knowledge of the recent history of the stand being studied before attempting to work out a time scale for the decomposition of its leaf litter.

The total amounts of ovendry material in the different layers of the organic horizon at Delamere are shown in Table II. Previous figures obtained from the L layer under pine species ranged from 1150 kg per hectare for Scots pine (Ovington (9)) to over 6600 kg per hectare for Norway pine (Alway, Methley, and Younge (1)). For the F layer, Alway, Methley, and Younge found quantities of organic matter ranging from 12,600 kg per hectare under jack pine to 28,000 kg per hectare under white pine. The same workers reported amounts for the H layer varying from 19,000 kg per hectare for jack pine to 46,000 kg per hectare for white pine. On the experimental plot at Delamere, the L layer was equivalent to 2080 kg per hectare, the total F layer to 30,160 kg per hectare, and the H layer to 14,000 kg per hectare of ovendry matter.

One hundred needles from each of the three layers, L, F_1, and F_2, were oven-dried and weighed. This procedure showed that the F_1 layer needles had lost 24%, and the F_2 needles 47% dry weight, as compared with needles of layer L. Table II shows the total weights of actual leaf litter per hectare in the L and F_1 layers on the Delamere site to be 1720 kg per hectare and 6280 kg per hectare respectively. Using a multiplication factor of 4/3 to compensate for loss in dry weight of the F_1 needles, it is seen that the F_1 layer contains the equivalent of 8370 kg per hectare of freshly fallen leaf litter, or nearly five times the amount represented by the L layer. Relating these figures to the measured leaf litter production of just over 4000 kg per hectare for a complete year, it is found that the L layer, as constituted when sampled, represented less than half of the total year's litter production, while the F_1

TABLE II

Amounts of ovendry material in the different layers of the organic horizon

Layer	Description of litter	Equivalent in kilograms per hectare	Equivalent in kilograms of fresh litter
L	Needles	1,720	1,720
	Twig, cone, bark fragments	360	
	Total L	2,080	
F_1	Needles: grey	480	
	grey-black	3,440	
	black	2,360	
	Total	6,280	8,370
	Twig, cone, bark fragments	1,380	
	Total F_1	7,660	
F_2	Needles	15,750	29,720
	Twig, cone, bark fragments	6,750	
	Total F_2	22,500	
	Total F_1 and F_2	30,160	
H	Total H	14,000	
Total organic horizon		46,240	

layer contained the litter of more than two years at the same rate of production. These figures suggest that a needle may be incorporated into the F_1 layer rather less than a year after falling to the ground. That this is indeed the case has been demonstrated by marking needles of the L layer with paint immediately before the autumnal leaf fall. By late spring the following year, the needles were seen to have entered the F_1 layer, some being grey-black, others completely black and extensively colonized by the dominant fungi of the F_1 layer (Kendrick (6, 7, 8)).

The total dry weight of leaf litter in the F_2 layer was found to be equivalent to 15,750 kg per hectare. Applying a multiplication factor of just less than 2, to compensate for the known loss in dry weight of F_2 needles, the F_2 layer is seen to contain materials equivalent to approximately 30,000 kg per hectare of freshly fallen litter, or to about seven and a half years' needle fall at the measured rate. It may be noted that twig, cone, and bark fragments, while constituting only 14% of the measured year's litter fall, are found to make up 30% of the total dry matter of the F_2 layer. This apparent increase is due to the slower breakdown of the twig and cone fragments, the latter appearing particularly resistant.

The various figures quoted above show that needles falling to the ground may spend on average approximately six months in the L layer, approximately two years in the F_1 layer, and about seven years in the F_2 layer.

No claim of absolute accuracy can be made for these results, as a representative average figure for annual litter production, on which the exactness of the method depends, can be obtained only by maintaining litter collections for several years. However, excluding the influence of extreme climatic conditions, severe disease, or pest infestation (none of which, so far as the writer knows, have occurred at Delamere Forest in recent years), and allowing for the normal 25% variation from year to year found by Alway and Zon, the figure obtained is not likely to be more than 12% from a true mean, and the errors in the time scale will not exceed a few months in the case of L and F_1 layers, and a year in the case of the F_2 layer. This method of determining the time scale cannot be applied to the H layer, as the needles have lost their identity prior to incorporation with this layer.

The figure for the L layer may vary widely depending on whether the organic horizon samples are taken before or after the autumnal needle fall, and it would seem advisable to sample at the same season of year in any such investigation, so that results may remain strictly comparable. In the present study the sampling was carried out in June, and a consideration of the factors involved shows that it is probably preferable to sample before, rather than after, the seasonal precipitation of litter. Although this method is very useful for obtaining generalized information on the average time spent by needles in each layer, it must be borne in mind that individual needles, and even different segments of the same needle, may fluctuate from the mean in either direction, depending on the time of year at which they fall, the rate at which they are colonized by fungi and animals, and the identity of the microorganisms which bring about the various stages of colonization.

Provided that the recent history of the stand under consideration is known, this method should be applicable to any reasonably undisturbed organic horizon in which the individual microunits of litter retain their identity during the greater part of the time required for decomposition, so that their loss in dry weight at the various stages can be measured.

At Delamere Forest under Scots pine, the 10-year period required for the complete reduction of the leaf litter indicates very strong mor-forming tendencies. Mor formation is not, however, a function solely of the leaf litter, although this is at present thought to play a dominant role in dictating the course of the decomposition (Handley (5)). Factors of climate and soil also play some part in determining the course of the breakdown, and it is certain that not only different species but also the same species in different locations will show considerable variation in their time scales. The utility of this method lies in its ability to provide a basis for comparison between such species and locations and in its capacity to provide information on the fourth dimension of an important biological process. Although it seems unlikely that the method could be very widely applied, owing to certain limitations mentioned above, it would appear that time scales could be obtained for sites under intensive long-term investigation whose foliar health record is known, and whose litter production may already have been determined, or could readily be measured.

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