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Litter decomposition: a Russian matriochka doll

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Abstract. Litter is decomposed in a sequential process. In a concerted action animals and microorganisms break down complex organic matter to mineral products. Higher animals fragment and partially solubilize plant material. Subsequently, microorganisms (protozoa, fungi and bacteria) further degrade the organic matter to end products that cannot be metabolized further under the prevailing environmental conditions. During the process of decomposition some parts of the organic substrate and the excess energy are used to form new biomass. Some free organic intermediates may interact chemically to form relatively recalcitrant organic matter, such as humic substances. The degree of mineralization depends strongly on the type of organic matter in the litter and the physical and chemical conditions of the environment.

1. Introduction

At a distance litter decomposition seems to be one process. However, closer examination reveals a variety of different processes nested in each other, like nesting Russian dolls. If the basic principles of this sequence are understood we may be able to predict the fate of a given compound in a specific environment. An understanding of the kinetics of decomposition processes is critical for the management and control of the organic matter content in various soils under different climatic conditions.

Below, we will briefly define the types of organic matter in litter, before discussing the various distinct processes that are involved in the mineralization of litter. Then, the principles of humic matter formation will be summarized very briefly. We propose to discuss the environmental influences on litter decomposition in general terms only, since other chapters will deal with it in more detail. All this information will be combined to describe quantitatively the fate of litter in soil and sediments. Finally, we will try to show the implications of present knowledge of litter decomposition for future soil management.

2. Types of organic matter in litter

Soil scientists have paid much attention to the composition of sections of soil, especially the organic horizons (Verhoef & Brussaard, this issue) and have spent

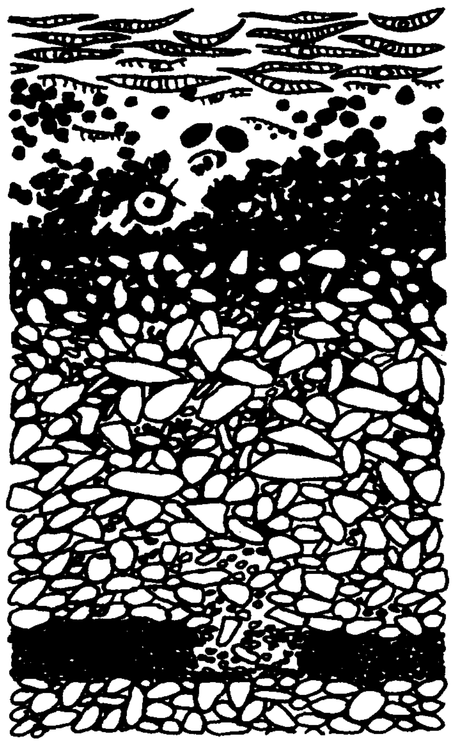

Fig. 1. Example of a forest soil profile (partly after Bal 1973) with Litter (L), Fermentation (F), Humus (H), and mineral soil layers in which organic matter has intruded (Ah_0, $Ah_{1/2}$).

much effort on classifying humus. Bal (1982) describes humus classification extensively. Figure 1 gives a generalized picture of a forest soil profile in which the different layers or horizons are defined by Trowbridge (1980) as:

L(itter): a terrestrial master organic horizon consisting of relatively fresh organic residues in which virtually entire original structures are discernible. Although there may be some discoloration and signs of biotic activity, the residues are not substantially comminuted and show macroscopically no obvious sign of decomposition.

F(ermented/decayed material): a terrestrial master organic horizon characterized by more or less disintegrated plant residues in which partial (rather than entire) macroscopically discernible vegetative structures are dominant.

H(umus): a terrestrial master organic horizon dominated by fine substances in which the original structures are macroscopically indiscernible. Fine substances are microscopically not definitively discernible and comprise cell wall fragments, plant cell tissue, fragments of fungal hyphae, etc. with a maximum size of approx. 100 μm. Colloidal substances with a maximum size of 1 μm form part of humus material.

The humus part may be split up in different sublayers such as Ah_0, Ah_1, Ah_2, but this is not relevant to our discussion. Comparing different types of soil profile it is clear that there are large differences in the components of the soil profile, which reflect the differences in the decomposition of the organic matter. Looking more closely it becomes clear that it is not just the difference in organic matter, but the total composition of abiotic (inorganic + organic) and biotic components. The division into Mull and Mor profiles was developed in accordance with this (Fig. 8). This classification gives as the first Russian doll some idea about differences in litter breakdown, but in order to understand the key processes one has to study the changes occurring during decomposition in more detail.

Although the organic matter contains various kinds of dead organic material such as plant tissues, microbial tissues, faunal tissues, dung, etc. the major part is leafy and woody plant material. Therefore, to understand the fate of litter it is necessary to investigate the decomposition of the basic plant cell components, in particular lipids, hydrocarbons, polysaccharides, hemicellulose, cellulose, protein, and lignin.

There is a considerable difference between monocotyledonous and dicotyledonous (deciduous and coniferous) leaf and stem material in terms of the fractions of organic components they contain (Table 1). There are also major differences in their inorganic components such as N, P, K, Ca, and Mg. According to Swift et al. (1979) herbaceous, graminaceous and deciduous leaf litter have the highest concentrations of these ions, woody tissues have the lowest concentrations and coniferous litter is intermediate. However, there is considerable variability among different plant tissues both between and within species.

Stout et al. (1976) showed that the composition of leaf material of snow tussock differed according to whether it was living, dead, newly shed, or had undergone a period of decomposition (Table 2). Even before senescence, the amount of water-soluble components in the leaves (mainly sugars and minerals) decreased, either by internal translocation to the roots or by leaching. These nutrient-rich leachates improve microbial activity in the litter layer (De Boois & Jansen 1976).

When the effect of leaching is reduced experimentally these sugars also show the highest rate of weight loss through decomposition. This suggests that the losses of soluble components are responsible for most of the weight loss occurring during decomposition. However, in absolute terms, the polysaccharides also show a considerable decrease, despite their lower rate of weight loss, because of their large absolute share in the composition of plant material. Besides these easily degradable constituents, lignin makes up a significant part of the litter material. This compound, however, hampers decomposition, at least in the first few years, as illustrated by Cromack (1973) who compared lignin content and exponential weight loss of a number of different litter types and found a distinct inverse relationship. After 3–5 years lignin and cellulose show similar decay rates (Melillo et al. 1989).

Table 1. Fractions of major organic components (carbon and energy substrates available to be decomposed).

	Deciduous leaf -young *Quercus* sp.	Deciduous leaf -old *Quercus* sp.	Conifer needle -old *Pinus* sp.	Grass leaf *Deschampsia flexuosa*	Grass stem *Zea mais*	Deciduous wood Range	Conifer wood Range
Lipid, ether soluble	8	4	24	2	2	2–6	3–10
Storage/metabolic carbohydrate, water soluble (cold and hot)	22	15	7	13	15	1–2	2–8
Cell wall polysaccharide, hemicellulose (alkali soluble)	13	16	19	24	18	19–24	13–17
Cellulose (strong acid)	16	18	16	33	30	45–48	48–55
Lignin, residue	21	30	23	14	11	17–26	23–30
Protein, N × 6.25	9	3	2	2	1	–	–
Ash, incineration	6	5	2	–	8	0.3–1.1	0.2–0.5

(Adapted from Swift et al. 1979)

Table 2. Chemical composition of snow tussock (*Chionochloa rigida*) leaves, standing dead material and surface litter (expressed as weight percentages).

	Green leaves	Standing dead material	Surface litter	Litter remaining (% after 1 yr ± s.e.)
Hot water soluble	17.7	5.2	7.9	52 ± 13
Protein/hemicellulose	49.7	52.8	53.0	84 ± 4
Cellulose	27.5	34.4	25.7	86 ± 2
Lignin	4.5	6.6	8.2	88 ± 7
Ash	0.6	1.1	5.2	

(From Stout et al. 1976)

3. Litter fragmentation and fauna/microflora interaction

After the first "attack" on leaf material by the phyllosphere-microflora which grow on the exuded sugars and simple organocarbons in the phyllosphere, the leaves are shed and fall to the ground. In general, the consumption of leaf material by phytophagous fauna is not included in the litter decomposition process in terrestrial ecosystems. In a beech forest the contribution of the phytophagous fauna to the total decomposition has been found to be small (see, e.g. van der Drift 1975). Amounts less than 1.5% of the total decomposition by fauna and microflora (expressed as kJ.) have been measured.

The role of the fauna in the total decomposition process has puzzled soil biologists for many years. According to several authors reviewed by Seastedt (1984), fauna should have a positive influence on decomposition, especially in forestry soils, because of their impact on more recalcitrant substrates (Seastedt & Crossley 1983). According to Crossley et al. (1989) this does not hold for agro-ecosystems. They ascribe this to the different composition of crop residues: a higher C:N ratio and lower content of recalcitrant components such as lignin, which make these residues more easily degraded by direct microbial action (see also Verhoef & Brussaard this issue).

Several authors (Swift et al. 1979; Cromack 1973) have meticulously described the changes occurring in litter composition during degradation. These descriptions do not explain, however, why these changes occur in the sequence they do. In order to understand these changes one has to study the acting organisms — soil fauna and soil microflora — in more detail. The fauna does not mineralize litter to a large extent, but it "pretreats" the litter to facilitate the further breakdown by the microflora (Reichle 1977).

This pretreatment comprises:
— mechanical comminution of leaf material, thereby increasing the total surface area available for further attack and from which nutrients may leach;
— intimate mixing of fragments with the microflora present in the gut of saprophagous soil animals;

— mixing of litter material through the soil (bioturbation);
— conversion of litter into the faunal body tissue, thereby changing the degradability of the starting material.

Schematically Decomposition (*Dec*) can be formulated as the integral of Catabolism (*C*), Diminution/comminution (*D*) and Leaching (*L*): $Dec = \Sigma(C + D + L)$. The total process of litter decomposition involves these processes being reiterated at different stages of the decomposition; the first stage being primary litter attack by macro-arthropods such as isopods, the secondary stage being the grazing and consumption of isopod faecal pellets consisting of fine particles of fragmented litter, etc. Again, it is a series of Russian dolls fitted one into another. Whereas the first stage explains the fragmentation there is a secondary process (pellet grazing) which further explains the decomposition process. In each stage the CDL sum plays a role, as shown schematically in Fig. 2. Within the soil these different stages occur at three different levels of the uppermost soil horizon: the Litter, Fermentation and Humus layers.

The first two aspects of the faunal contribution to litter decomposition — comminution of leaf material and mixing of leaf fragments with microorganisms — were described by Witkamp & van der Drift in 1958. Many scientists subsequently studied the food choice of *Collembola*, examining the gut contents or offering different fungal strains, but they did not combine this with a quantification of the contribution of the collembolan feeding activity to the total amount of litter decomposition. Van der Drift & Jansen (1977) observed that microbial respiration on fragmented leaf litter (isopod pellets) overgrown with fungal hyphae was stimulated by grazing by springtails (*Collembola*). Hanlon (1981a,b) found an increased bacterial activity with decreasing leaf litter particle size and attributed this to the enlarged inhabitable surface area of the particles. On the other hand Andrén & Schnürer (1984) did not measure any difference in respiration, mass loss or microbial biomass of straw samples with or without springtails. They did observe, however, a reduction in surface hyphae after springtails had been added. Fungal production accounted for less than 5% of the estimated microbial activity. Conflicting observations have also been reported with isopods and diplopods. Anderson & Bignell (1980) stated that they have a positive effect on microbial activity but van Wensem (pers. comm.) asserts that they have a neutral or even negative effect.

These apparently conflicting observations can be fitted into one conceptual framework by assuming that: 1. Fungivorous arthropods, through selective grazing on superficial hyphae, create fresh substrate for further microbial (= fungal) degradation and, hence, promote litter decomposition. 2. There is probably no direct relation between litter breakdown and microbial activity by bacteria. Bacterial numbers or activities change because of changes in substrate characteristics and substrate availability that may be only partly caused by the faunal activity. 3. Lysis of bacteria occurs within the gut, but a considerable portion of the microbial cell wall material is not digested (Gunnarsson & Tunlid 1986). As a result the faecal pellets contain enhanced levels of racalcitrant

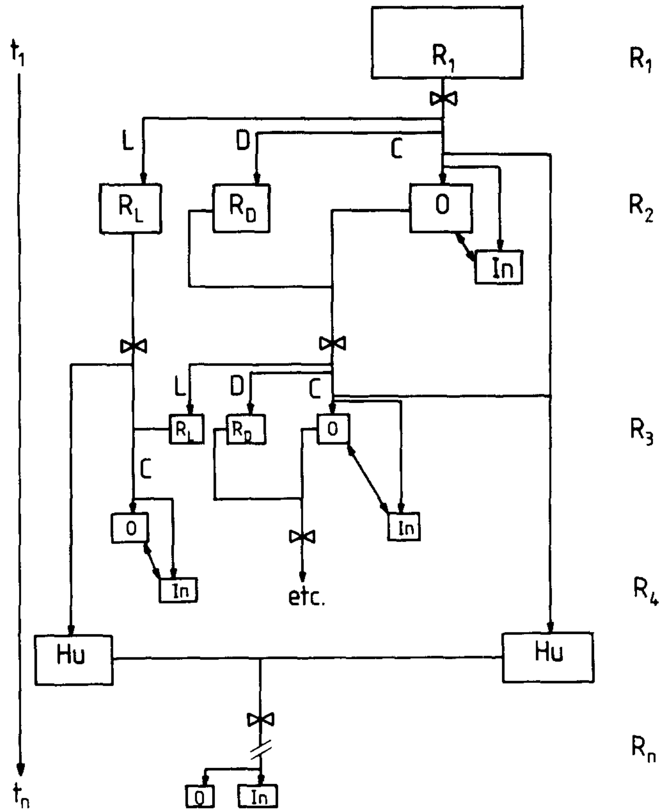

Fig. 2. General framework of organic matter decomposition by comminution, catabolism and leaching through consecutive soil horizons in conjunction with soil microorganisms. R_1, R_2, .. R_n = degradation stages coinciding with different soil horizons; $R_{C,D,L}$ = element pools of catabolized diminuted or leached material; C = Catabolism; D = Comminution; L = Leaching; In = Inorganic components; Hu = Humus; O = Organisms; X = rate variable influenced by physical environment, type/activity of organism, type of organic matter (From Verhoef pers. comm., after Swift et al. 1979).

components, and this restricts the further decomposition of the litter fragments within the pellets. 4. The main mechanisms underlying the stimulatory effect of comminution on microbial activity are increased area and increased release of soluble compounds (Nykvist 1963). In order to quantify the impact of this release Gunnarsson et al. (1987) measured the microbial growth on leachates of leaf litter particles of different sizes. They observed that bacterial respiration was highest on the leachate produced by leaching the largest particles for one day, and concluded that the inhabitable surface area is not the major factor regulating bacterial growth.

So there are indications that leaching of nutrients and phenolic compounds have important effects on degradation of leaf litter. Phenolic compounds can inhibit degradation in the first phase of leaching. The differences in the contents of various phenolic compounds in the litter types should therefore change the degradation rate. This is counteracted by the leaching of nutrients which promote microbial activity and, indirectly, will promote faunal feeding. The latter, plus the pure grazing of fungivorous springtails, will result in the fungi-overgrown leaf litter being fragmented in the way isopods prefer (Gunnarsson 1987).

When leaf particles are mixed with microorganisms in the gut of soil fauna the fungal thalli are easily degradable whereas bacteria are more resistant (Gunnarsson & Tunlid 1986) and even find a favourable environment for growth in the gut (Anderson & Bignell 1980). This boosts the numbers of bacteria in the faeces of saprophagous soil animals. During this period there is an intensified bacterial activity in the gut and also for a short period after defecation. The degradation rates of organic matter will be high. However, it is questionable whether this increased microbial activity will persist and permanently maintain increased microbial degradation activity. Several authors (Ineson & Anderson 1985; Reyes & Tiedje 1976) have listed the different fungal and yeast species in the guts of saprophagous arthropod species and found a specific indigenous gut microflora.

However, these studies did not prove that there is a functional relation between the activities of these microflora species in the gut *and* in the soil, and therefore it is not clear whether this mixing is relevant for the further degradation of organic matter/microorganism mixtures in the soil.

The impact of soil animals on bioturbation of organic material is well known, especially for earthworms (Lavelle 1988), but other soil fauna groups also show distinct bioturbation activities. See Spence (1986) for a recent review.

Bioturbation comprises the input of organic material (mostly litter) from the soil surface to lower soil horizons by earthworms (Stout 1983) and dung beetles (Brussaard 1985) and the mixing of organic material by consumption (by other earthworm species) of organic material within the litter and fermentation layer or of fine organic material which is taken up together with mineral material. Besides mixing organic and mineral particles, earthworms also add slime compounds to the defecated material, thereby enhancing the structural stability of the soil aggregates thus formed.

However, again, to understand litter decomposition better we have to study the further mineralization of the fragmented litter material. As indicated in section 2 this comprises more complex polymeric compounds as well as simple compounds such as sugars and protein.

4. Mineralization of litter

For a polymeric compound to be mineralized it has to be broken down by exo-enzymes to yield relatively small soluble molecules (monomers, dimers etc.

to oligomers) which can be taken up by the microbial cell. Once in the cell, mineralization to inorganic end products and conversion to new biomass proceeds along metabolic pathways.

The three major classes of compounds in litter are cellulose, hemicellulose, and lignin. They may make up more than 90% of the material by dry weight (Stout et al. 1976; Swift et al. 1979). Cellulose degradation is relatively well understood (Wagner & Sistig 1979; Eriksson 1981). The exo-enzyme endo-1, 4-β glucanase randomly cleaves at the 1,4-β linkages along the cellulose chain and produces new free ends in the chain.

The other exo-enzyme exo-1,4-β glucanase splits off cellobiose units from the non-reducing end of the cellulose chain. Cellobiose is hydrolysed by 1,4-β glucanase to glucose, which is broken down further by glucolytic reactions. As well as fungi, there are many actinomycetes, bacteria (aerobic and anaerobic), and protozoa (aerobic and anaerobic) that can hydrolyse and utilize cellulose as a source of carbon and energy (Haider 1986).

Hemicelluloses are composed of various hexoses, pentoses, uronic acids and other minor sugars. Hemicelluloses are functionally defined as short branched-chain heteropolysaccharides of mixed hexosans and pentosans that are easily hydrolysed. D-xylose and L-arabinose are the major constituents of pentosans, whereas D-glucose, D-mannose and D-galactose are the constituents of hexosans. Because hemicelluloses are heterogeneous, with different constituents linked by different types of bonds, their enzymatic hydrolysis requires several enzymes. Neither the total number of hemicelluloses nor the roles of individual enzymes are yet clear. Pure hemicellulose is, in general, readily degradable. However, in plant material the rates of degradation are slower. A possible reason is that these polysaccharides are closely associated with cellulose and lignin and that the latter hinders the attack of hemicelluloses (Gong et al. 1981). Lignin is a very branched, constitutionally undefined aromatic polymer. The phenylpropane units it is made of are randomly linked by different carbon–carbon and ether bonds, with the arylglycerol-β-aryl ether bond being most common. This variety of bonds combined with a highly complex structure, in which accessible ends of chains are often folded back within the rest of the molecule, will hamper degradation. Recently, research (Harvey et al. 1985) revealed that an extracellular enzyme ligninase is able to depolymerize and oxidize lignin and non-phenolic lignin model compounds. The peroxide character of the enzyme might explain lignin biodegradation (Schoemaker et al. 1985). Colberg (1988) demonstrated the influence of complexity on the biodegradation of small lignin molecules. With increasing mass weight and intermonomeric linkages both the rate and the extent of mineralization decrease.

As well as these basic microbial processes, chemical processes play a fundamental role in the final stages of decomposition: these final stages are still not fully understood and therefore their complexity has to be lumped together under the general, but rather vague term "humus formation".

5. Humus formation

Humus is the structureless component of the soil organic fraction. It is primarily derived from the higher plants and formed during the microbial decomposition of original plant constituents and of new substances synthesized by soil microorganisms. Therefore, humus formation is unique to biological systems (see also Moers et al. this issue). During the degradation of organic residues, not only do reactions catalysed by specific microbial enzymes occur, but reactive substances formed during the microbial metabolism, in particular phenols and their derivatives, may undergo chemical reactions. Aromatic plant constituents, especially lignins, are a very important source of phenolic units. The chemical reactions then lead to the synthesis of new, often very recalcitrant molecules, called humic substances (Fig. 3). Several researchers have simulated these chemical condensation reactions under laboratory conditions and succeeded in obtaining the abiotic formation of complex polymers that may act as building blocks for the synthesis of humus (for a review see Haider et al. 1975). The formation of litmus from orcinol, oxygen, and ammonia (Musso 1963) is an example of such an abiotic synthesis reaction (Fig. 4).

Humic substances are preferentially degraded by certain fungi; however, this process is very slow. Themean residence time for the "mobile" humus fraction (humic and fulvic acid) is between 250 and 800 years, whereas the humins are often older than 2000 years (Zehnder 1982).

6. Environmental influence

Besides the structure and the accessibility of a molecule, physical, physicochemical, chemical and biological factors will influence the degradability. The most important of these factors are temperature, pH, water availability, presence of oxygen, redox conditions, the presence of surfaces and their specific characteristics. In addition, the availability of nutrients and other substrates, as well as the presence or absence of the interacting organisms will have a marked influence on litter degradation (see also van Veen & Kuikman, this issue).

In soils, the aeration status is a continuum from virtually complete aerobic conditions in well-drained sands to permanently anaerobic conditions in marshes and swamps.

Within this range there are classes of soils with intermediate drainage and aeration characteristics, which result in temporary periods of anoxia or the presence of anaerobic microsites (mostly in aggregates) within a generally aerobic matrix. Because degradation of lignin structure requires oxygen (Schoemaker et al. 1985; Kirk 1981) litter mineralization is strongly affected by the availability of oxygen. Colberg (1988) studied the difference in decomposition of plant material under aerobic and anaerobic conditions in three different halophytes: salt marsh cord grass (*Spartina alterniflora*), needlerush (*Juncus roemerianus*) and freshwater sedge (*Cyperis walteriana*). She measured ^{14}C re-

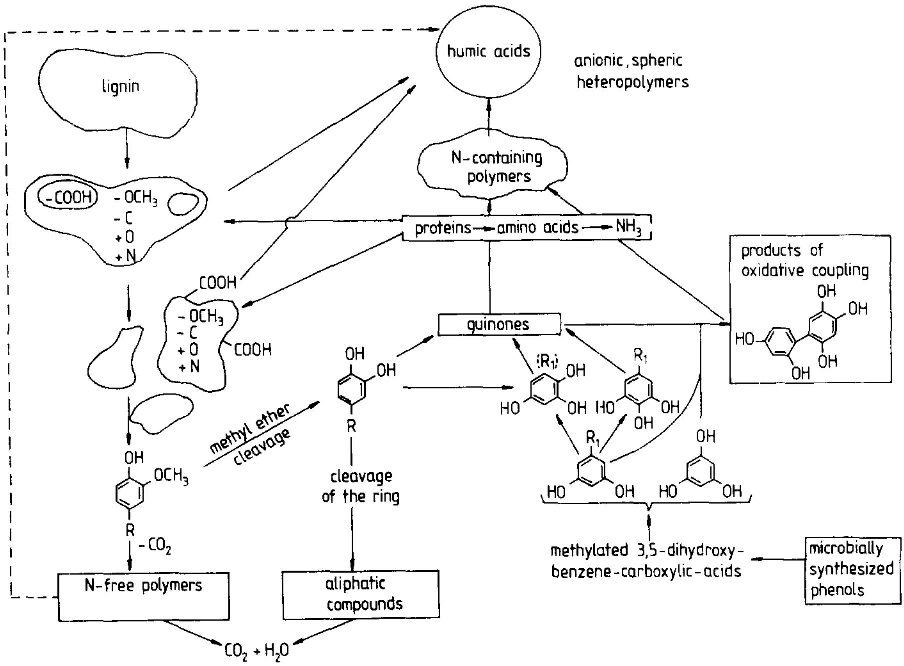

Fig. 3. Contribution of phenolic and nitrogenous structural units to the chemical composition of humic substances (From Flaig 1972).

lease of radio-labelled lignin and polysaccharide. The anaerobic degradation rates were about 4–8% of the rates under aerobic conditions for *S. alterniflora* and *J. roemerianus*, and 30–40% for *C. walteriana*. (Table 3). This clearly demonstrates that absence of oxygen significantly hampers the degradation of organic matter.

Table 3. Rates of anaerobic biodegradation of specifically radio-labelled lignocelluloses expressed as percentages of observed aerobic rates.

Substrate	Percentage of aerobic mineralization rates	
	^{14}C-lignin lignocellulose	^{14}C-polysaccharide lignocellulose
S. alterniflora	7.5	8.2
J. roemerianus	6.0	3.8
C. walteriana	33.0	40.2

(From Colberg 1988)

7. Fate of litter in soil

Because of the crucial role of fauna in pretreating the organic material for final microbial mineralization and the inefficient metabolic conversion rate of soil

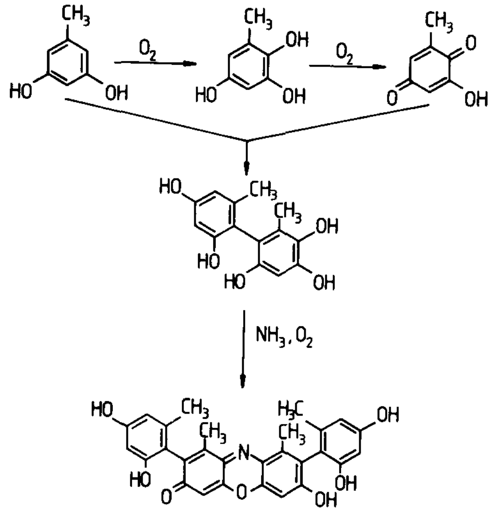

Fig. 4. Formation of litmus from orcinol by an oxidative reaction followed by a conjugation of two 2,3,5-trihydroxytoluene plus the chinon derivative by formation of an oxidative group with ammonia under alkaline conditions (adapted from Musso, 1963 and Haider et al. 1975).

animals, an impressive amount of organic material passes the faunal "tract" each year, as is evident in budgets of carbon fluxes through decomposer systems. These fluxes, combined with the different carbon pools have been summarized for a deciduous and coniferous forest in Fig. 5a, b.

Minderman (1968) calculated the breakdown rates of different groups of plant constituents (Fig. 6) assuming a logistic pattern in the breakdown of the main components of leaf litter. By integrating the specific degradation rates of the different compounds in relation to their contribution in a specific litter type, Minderman calculated the expected degradation rate. However, the calculated rates were much higher than measured rates. Janssen (1986) attributes this to the intertwining of substances such as cellulose and lignin (shielding the cellulose from microbial attack as also suggested by Gong et al. (1981), see section 4) and the simultaneous formation of recalcitrant humic material. Another explanation could be that a logistic breakdown rate overestimates the breakdown of complex litter constituents. Melillo et al. (1989) suggest a two-phase breakdown model with a first phase of rapid mass loss and a much slower second phase. Both models give a more realistic picture than the exponential model, as they encompass a levelling off resulting from the formation of humic compounds that are very resistant to decomposition. For a review on these models see Wieder & Lang (1982).

Minderman's approach was further elaborated by Kolenbrander (1969, 1974) for the decomposition of increasingly recalcitrant materials: green plant material, straw, manure, coniferous needles, sawdust and peat. The degradation rates of these materials fitted in a double log-relation with the general formula

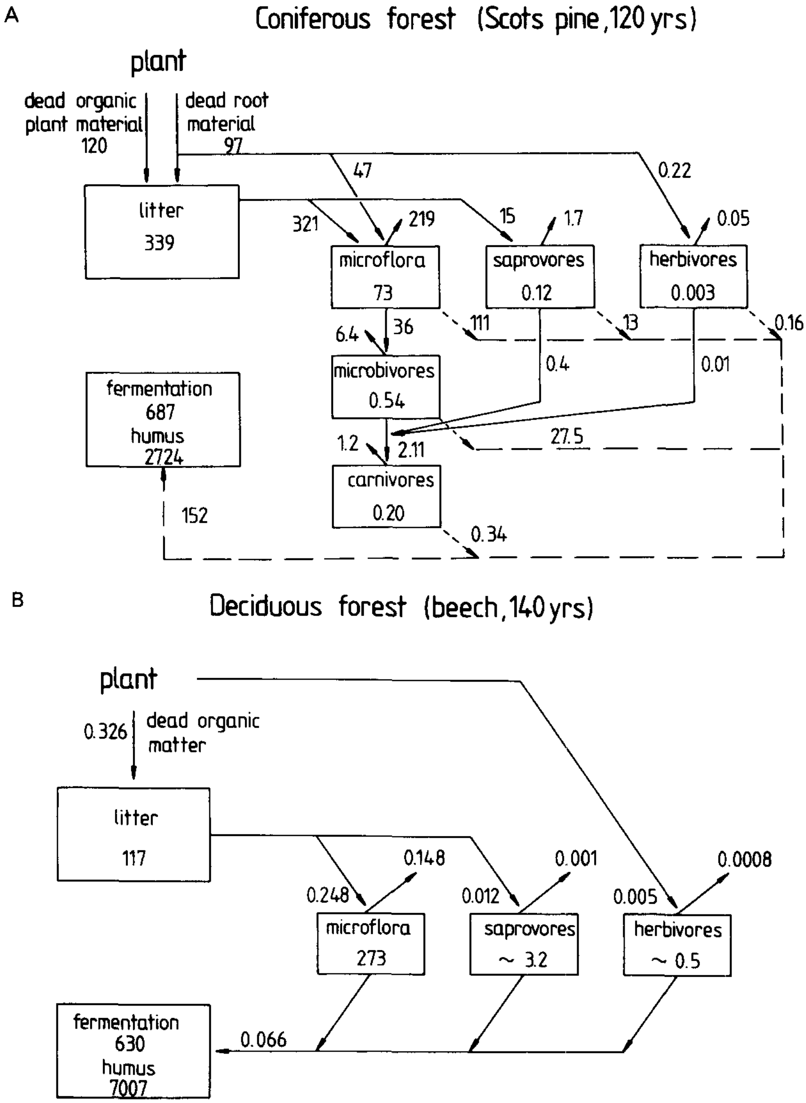

Fig. 5. Generalized carbon pools (g.m^{-2}) and fluxes (g.m^{-2}. yr^{-1} ↘ transfer ↗ respiration) in the forest floor of A. a coniferous (Scots pine) forest of 120 years old and B. a deciduous (beech) forest of 140 years old (adapted from van der Drift 1974, 1975, plus unpublished data and Persson et al. 1980). Dashed lines ending in an arrow denote transfer of dead (non-predated) organisms and faeces to d.o.m.

$k = k_i * t^{1,6}$ (Janssen 1984, 1986). To meet the log value at $t = 0$ an "apparent initial age" had to be introduced for each material. This initial age or initial breakdown phase may be compared with the first phase of Melillo's conceptual two-phase model which, moreover, quantifies both phases described by the formula $y_t = y_0 \exp. 4.7 \{(a + t)^{-0,6} - a^{-0,6}\}$. This has proved valuable for research in which the organic matter formation is calculated from different types of organic debris.

The considerably different degradation rates for litter result in very varying pools of fulvic acids and humic acid in soils. Moreover, accumulation rates vary, depending on the relation between litter production and decomposition. During vegetation succession this rate will theoretically give rise to a steady state with much or little accumulation (resulting in respectively a low or high organic matter content in the upper soil horizons) or a non-steady state with a continuing accumulation. Waksman (1952) gives a generalized approach. Humus-forming and humus-degrading processes are differently affected by temperature.

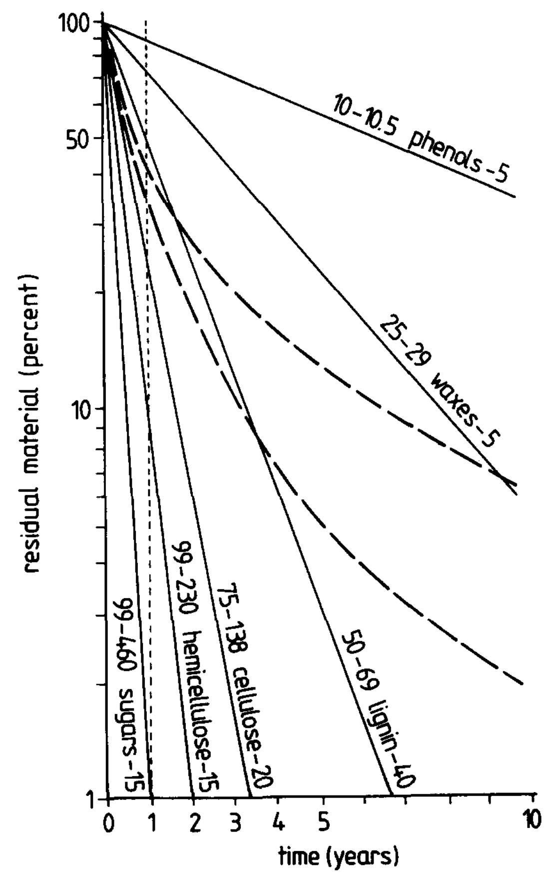

Fig. 6. Degradation rates of major leaf litter components. For each compound the percentage degradation one year after senescence, the specific accumulation factor and the share in weight in percentages are given. Lower dashed line gives the integrated breakdown rate of these compounds, upper dashed line the real breakdown rate (From Minderman 1968).

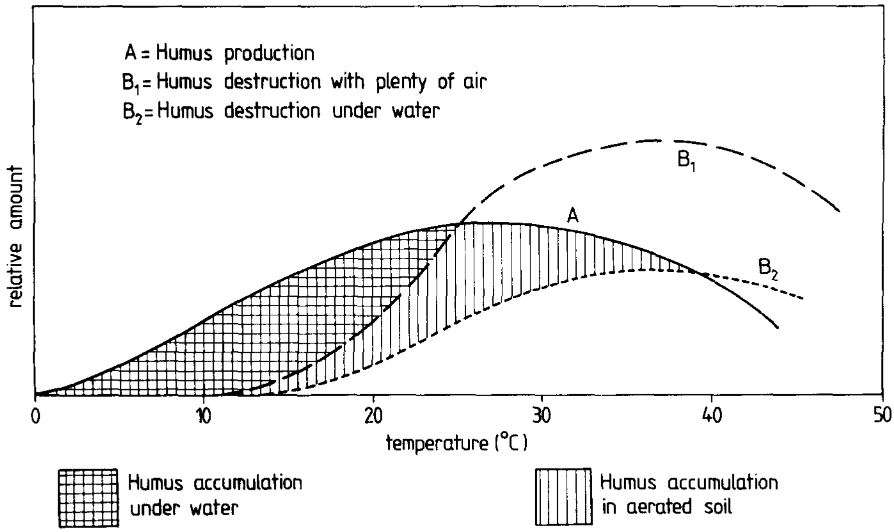

Fig. 7. Humus accumulation and decomposition under anaerobic and aerobic conditions for temperature ranges relevant for temperate to tropical soils (adapted from Waksman 1952).

Moreover, there is a distinct relation between the presence of oxygen and the degradation rate (Fig. 7).

In temperate zones these different patterns of humus-forming and humus-degrading processes have been described as Mull and Mor soils, which differ not only in organic matter content and composition but also in soil physical conditions and soil biota (Fig. 8). Nihlgård (1971) studied a soil profile of spruce forest planted in areas which formerly had beech forests and concluded that the litter quality had a major impact on profile development, resulting in Mor profiles on former Mull soils. In an oak forest on adjacent calcareous and acid loam soils Minderman (1960) found that the soil water regime as affected by soil texture and topography had the most important impact on soil profile formation. Both studies, however, were conducted on more or less mature profiles, whereas the most interesting phenomena occur at the primary stages of succession. A study on an afforested homogeneous blown sand in The Netherlands (van Berghem et al. 1986) planted with *Pinus sylvestris* 130, 90, 55 and 30 years ago revealed that different vegetations and organic soil profiles had developed in relation to the natural succession processes. Given a common soil type, litter apparently determines the abiotic conditions of the soil; consequently it influences the composition of the biotic communities, and hence the pattern of decomposition processes.

8. Aquatic systems and marshlands

Studies in aquatic environments have also recognized the different decomposition stages. Moreover, a horizontal layering can be discerned in the water body,

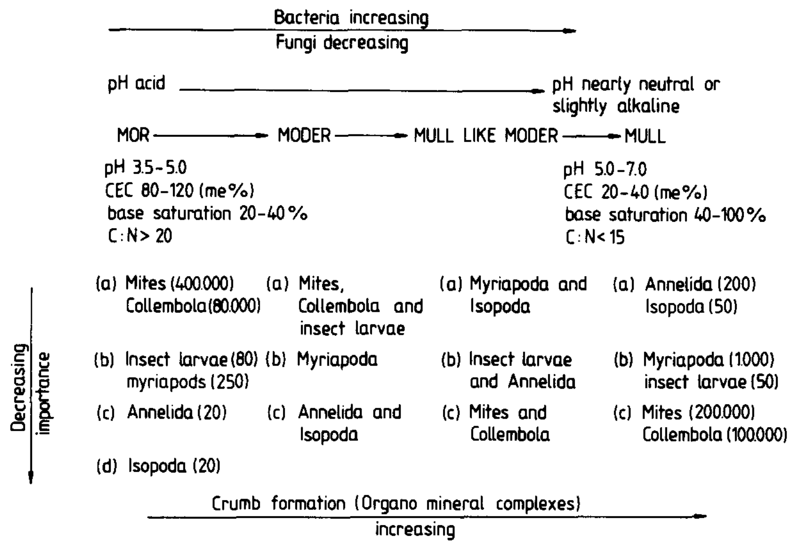

Fig. 8. Sequence of humus types and related characteristics. Figures in brackets indicate numbers of soil fauna per m^2. CEC = cation exchange capacity.

similar to that in the soil profile. The litter layer is comparable with the surface of the water, where floating leaves already show signs of comminution. The rest of the water body can be compared with the fermentation layer, as the plant residues are gradually diminished with increasing depth (Kok et al. this issue).

In aquatic systems the sediment is only generally defined without further elaboration of the spatial arrangement of the different sublayers. General conditions such as C content, redox conditions, clay content, Ca content, pH etc. are used to characterize sediments. It is reasonable to assume that different abiotic conditions of the water (pH, nutrient status) will result in a differently composed lotic and submersed plant community which in turn will harbour different faunal systems. This will result in more or less specific decomposition patterns and types of organic matter.

The spatial arrangement of these processes is somewhat different compared with that of soils. The first and major comminution occurs at the water surface and further degradation takes place when the litter particles slowly sink to the bottom. The organic matter is finally mineralized in the sediment. Nevertheless, the general scheme presented for terrestrial systems is also valid for aquatic systems.

Within aquatic ecosystems faunal consumption and the resulting sinking of leaf fragments and faunal excrement is a major factor in the total decomposition process. Kok et al. (this issue) describe this process and related phenomena in greater detail. Processes described for terrestrial systems where different substituents of litter promote and counteract decomposition may be active in aquatic systems, but quantitative information is scarce.

Bioturbation is very important within aquatic sediment systems, and several studies have measured the mass turnover of sediment. Bioturbation in relation to organic matter degradation, especially as a process that enhances biodegradation, has received much attention - especially with respect to marine sediments (Aller 1980). We will not go into further detail here.

Sediments are mainly anaerobic. Given that oxygen is essential for degradation (see also Fig. 7) it is clear that degradation will take place at a lower rate than in soils. This lower degradation rate, combined with a very high bioturbation and fragmentation activity of the benthic fauna will result in a finely fragmented loose organic matter package and an accumulation of humic substances.

Erosion, which is a far more important process in sediments than in soils, will limit the rate of accumulation. There are ample examples in which the combination of both processes results in a net accumulation; for example, the salt marshes along the North Sea coast).

Salt marshes represent a transition between terrestrial and aquatic systems. They allow high primary production by plants and their soils are almost always anaerobic. Salt marshes are shallow water production zones in which the rate of primary production exceeds the rate of community respiration. Salt marshes export energy and nutrients to deeper water of the estuary and adjacent coastal shelf (Odum 1971; Valiela et al. 1978). This export can be steady (as dissolved and particulate matter) or abrupt, as during storms. In fact, storms can transport large amounts of salt marsh vegetation and detritus either on to the higher land or into the coastal waters. Some detritus degradation takes place in the salt marsh itself by a complex detrital foodweb of a diversity of microorganisms, microflora and fauna, meiofauna, and animals at a higher level. Lee (1980) has presented a conceptual model of marine detrital decomposition and the organisms associated with this process.

In salt marshes most of the organic material of the detritus reaching the ground is degraded anaerobically. The anoxic mineralization can attain almost 100% and is dominated by sulphate reduction. Reduced sulphur compounds that reach the soil surface can be reoxidized. This sulphur oxidation contributes to autotrophic organic matter production (Howarth, 1984). The highest microbial activity is found in the first 20 cm.

Below that, the organic content decreases to an asymptotic concentration of ~ 100 mg/g, which presumably represents the buried "refractory" carbon, such as cellulose and lignin derivatives (Scudlark & Church 1989).

9. Implications for management

In management of soil systems whether in natural, agricultural or silvicultural areas, as well as in management of sediment systems, knowledge of organic matter decomposition is of great importance. This knowledge can be used to

Table 4. Input, standing crop, degradation rate and residence time of litter in different grassland and forest ecosystems.

	Boreal forest	Temperate deciduous forest	Tropical forest	Temperate grassland	Savannah
Litter input (= NPP in ton.ha^{-1}. year^{-1})	2.8 1.5–7.5	4.3 2.6–9.4	11.3 3.8–13.2	2.8 0.7–5.7	3.6 0.75–7.5
Litter standing crop (ton C.ha^{-1}. year^{-1})	13.2	5.7	1.9	1.9	1.1
k_L. Year^{-1} (input ÷ standing crop)	0.21	0.75	5.9	1.5	3.3
$5/k_L$ (= time taken for 99% of standing crop to decompose)	23.8	6.7	0.85	3.33	1.5

(Adapted from Swift et al. 1979)

regulate the organic matter supply as such and the nutrients and compounds (such as heavy metals) that have accumulated in the organic matter.

As organic matter decomposition depends on environmental conditions and litter quality, which in turn depend on vegetation cover, these variables are crucial for proper management.

The composition of the plant communities comprising the ecosystem in question will influence the composition of the litter layer and hence the decomposition processes (Table 4). The different pools of undecomposed litter, fulvic acids, and humic acids, each with their very varying decomposition rates, together contribute to what Reichle (1977) called the ecological buffering capacity of the soil. This buffering capacity mitigates the year-to-year fluctuations in litter input and degradation rates and so secures a stabilized release of substances such as plant nutrients. A limited buffering capacity, such as occurs in some tropical forests, increases the risk of irreversible changes in the forest floor resulting from changes in environmental conditions. It is not clear to what extent the buffering capacity of the organic matter itself also holds for sediment systems.

The organic matter supply also acts as a buffer for macro- and micronutrients and noxious compounds such as heavy metals. Enhanced degradation rates can result in increased fluxes of N, P, and also of Al and Cu. This may promote or depress plant growth. The buffering function of the sediment with respect to the accumulation and release of nitrogen and phosphate from the sediment and the water column is well understood. In various countries it is recognized as a key parameter in the management of nutrient-rich water bodies. Water quality has become largely dependent on the quality of the sediment. Management measures can directly affect decomposition processes by changing the litter compostion (compare the work of Kolenbrander described in section 7) or by changing the status of oxygen and moisture through soil cultivation or the lowering of the water table. Indirectly, shifts in the vegetation cover, as in clear-felled or replanted areas, will change environmental conditions in the upper soil layers and thus affect the decomposition processes. From the generalized picture of Waksman (Fig. 7) it is clear that the greater increase in decomposition rate under aerobic conditions with increasing temperatures will lead to a reduced rate of humus accumulation. Not everybody seems to have recognized this relation when managing soil and sediment systems, as can be seen from the many examples of mismanagement such as the reduction of organic matter content of virgin prairie by ploughing, of peaty soils by draining, or of virgin forest soils by cultivation. For example, the organic matter content of 28 soils in Georgia decreased by more than half (from 3.29 to 1.43%) after 25 or more years of cropping and the organic matter content of a virgin forest soil fell from 2.30% to 1.59% after three years of cultivation (Zehnder 1982). In The Netherlands the mineralization of peat deposits that results when water tables fall and the deterioration of deep ploughed "plaggen" soils (dalgrond) are clear examples of the relation between organic matter decomposition and management practices.

Management schemes aimed at restoring the environmental conditions necessary for a more balanced organic matter cycling are now being introduced (Elliott & Coleman 1988).

Management has indirect effects on heavy metals such as copper which are closely bound to the soil organic matter. An increased degradation rate of the organic matter may result in the bound copper being released. As high concentrations of heavy metals can hamper degradation processes the resulting accumulation of organic matter (Bengtsson et al. 1988) will lead to more copper being bound, and the effect will be reversed. This has been observed around heavy metal smelters in Canada, Sweden and The Netherlands. The mobility kinetics of other heavy metals are also closely related with the accumulation, mineralization and composition of organic matter. In this way major sinks have been formed (Stigliani 1988) and the management of the loading and controlled release of these, what may be called "chemical timebombs", is a matter of growing concern. In general we must realize that we have a responsibility to manage the limited amount of fertile soil on our planet appropriately. A thorough understanding of all the important processes involved in litter decomposition, including their limitations, will enable management to be optimal. This understanding can be obtained only by coordinated multidisciplinary soil research.

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