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Soil structural aspects of decomposition of organic matter by micro-organisms

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Abstract. Soil architecture is the dominant control over microbially mediated decomposition processes in terrestrial ecosystems. Organic matter is physically protected in soil so that large amounts of well-decomposable compounds can be found in the vicinity of largely starving microbial populations. Among the mechanisms proposed to explain the phenomena of physical protection in soil are adsorption of organics on inorganic clay surfaces and entrapment of materials in aggregates or in places inaccessible to microbes. Indirect evidence for the existence of physical protection in soil is provided by the occurrence of a burst of microbial activity and related increased decomposition rates following disruption of soil structures, either by natural processes such as the remoistening of a dried soil or by human activities such as ploughing. In contrast, soil compaction has only little effect on the transformation of ^{14}C-glucose.

Another mechanism of control by soil structure and texture on decomposition in terrestrial ecosystems is through their impact on microbial turnover processes. The microbial population is not only the main biological agent of decomposition in soil, it is also an important, albeit small, pool through which most of the organic matter in soil passes.

Estimates on the relative importance of different mechanisms controlling decomposition in soil could be derived from results of combined tracer and modelling studies. However, suitable methodology to quantify the relation between soil structure and biological processes as a function of different types and conditions of soils is still lacking.

Introduction

Decomposition of organic matter is essential to the functioning of terrestrial ecosystems. Through the process of decomposition of organic matter, energy is provided to organisms and nutrients are released for uptake by both micro-organisms and plants. The techniques for the analysis of decomposition of organic compounds in soil are limited. In case of specific, simple compounds chemical analyses of the product and the transformation products might be possible, but for the bulk of organic material present in soil or entering the soil as plant debris, decomposition may only be assessed through the determination of end-products such as CO_2 and NH_4^+. These products are the result of a series of sequential biological processes whereby organic compounds are transformed from one form into the other at different rates. Tracers, such as ^{14}C and ^{15}N allow for the determination of the dynamics of C and N in different forms or pools of organics such as the microbial biomass or separate organic matter fractions and, eventually, CO_2 or other inorganic end-products (Paul & Van Veen 1978), thus enabling the assessment of turnover times of carbon and

nitrogen through these pools. The rate of decomposition of an, originally labelled product to inorganic compounds can be determined as the summation of the turnover times of the tracers through the intermediate pools.

Bacteria and fungi are the numerically most abundant organisms in terrestrial ecosystems and are the primary decomposers of organic matter in soil. Their relative abundance and decomposing activities have been a matter of dispute for years. It was suggested that on average, fungal biomass outweighs bacterial biomass by a factor of approximately 3 in arable soils (Anderson & Domsch 1978; Jenkinson & Ladd 1981). This ratio of 3:1 was used as the basis for the assessment of the proportionality factor (k_c) used in the determination of microbial biomass with the chloroform fumigation-incubation method (Jenkinson & Ladd 1981). However, Hunt et al. (1987), Holland & Coleman (1987) and Hassink et al. (unpublished results) showed that bacterial biomass could considerably exceed fungal biomass in grassland and arable soils. Nonetheless a k_c-value of 0.45 or 0.41 (Jenkinson & Ladd 1981), independent of the actual ratio for given (soil) conditions, is commonly used for the assessment of microbial biomass using the chloroform fumigation incubation method.

Recently, reports have suggested that differences in the roles of fungi and bacteria in decomposition processes depend on soil management practices (Holland & Coleman 1987). Hendrix et al. (1986) put forward the hypothesis that in cultivated ploughed soils, in which crop residues were incorporated in the top layer, the soil food web was bacteria-dominated. However, in no-tilled soils, with surface-placed crop residues, food web interactions were fungi-dominated. The rationale was on the one hand the relative immobility of bacteria in soil, which allows these organisms to use only nearby placed substrates and on the other hand the capacity of fungal hyphae to explore relatively distant substrates as well.

Soil is structurally very complex and characterized by a considerable heterogeneity in its physical, chemical and biological composition and properties. This heterogeneous structure is not fixed, but changes continuously; yet, at the level of micro-organisms, mixing might be limited, as compared, for instance, to aquatic systems. Moreover, in spite of the apparent abundance of 10^9 or more bacteria and hundreds of meters of fungal hyphae per gram of soil, the surface area in soils covered by micro-organisms is less than 1% of the total surface area (Adu & Oades 1978; Jenkinson & Ladd 1981). These factors, plus the relative immobility of bacteria and to a lesser extent of fungi, causes the soil architecture, i.e. structure and texture, to be the dominant control over the accessibility of substrates and thus, over decomposition processes in terrestrial ecosystems. While much attention has been given to the effect of abiotic variables such as temperature and moisture on decomposition, soil structure and texture has only recently received similar attention (Oades 1988; Van Veen & Van Elsas 1986).

Here we will illustrate the impact of soil matrix on decomposition processes in terrestrial ecosystems by reviewing some of the work of the senior author on

the decomposition of ^{14}C-labelled organic compounds under different soil conditions (Paul & Van Veen 1978; Van Veen & Paul 1981; Van Veen et al. 1984, 1985 and 1987; Van der Linden et al. 1989).

Effect of spatial arrangement in soil on the availability of substrates to microorganisms

The retention of organic matter in soil is controlled mainly by environmental variables such as moisture regime and temperature, the chemical constitution of the organic matter, and by the spatial distribution of and physico-chemical interactions with other soil constituents (Oades 1988). Large differences between the turnover rate of particular compounds in liquid microbial cultures and in soil indicate that soil provides a measurable degree of protection against microbial decomposition. For example, amino acids added to liquid culture or soil had turnover rates of less than 1 day whereas soil amino acids produced during microbial growth *in situ* at the expense of ^{14}C-acetate and incorporated into soil organic matter had turnover rates as high as 2200 days (Sørensen & Paul 1971).

To estimate the magnitude of certain aspects of the protective process, i.e. the proportion of the organic compounds that is protected and how protection affects the decomposition rate, the data of Sørensen & Paul (1971) were analyzed with a computer simulation model shown in Fig. 1 (Van Veen & Paul 1981). The decomposition rate constants of the non-protected amino acids and the acetate (initial concentration 2000 $\mu g\,C\,g^{-1}$ soil) were set at 0.3 day^{-1}. This estimate was based on literature data (see Van Veen & Paul 1981). The best fit (Fig. 2) was obtained by assuming that 50–60% of the amino acids were protected, with the decomposition rate constant being 0.01–0.005 times the rate constant of the non-protected metabolites. Alteration of the decomposition rate constant for the amino acids had little effect during the simulation period being examined. This means that the level of stabilization and not the initial decomposition rate controlled the amount of amino acid present. The degree of protection of 50–60% of the amino acids proposed was in agreement with other estimates of the fraction of physically protected organic matter in soil by Legg et al. (1971) and Anderson (1979).

Several mechanisms have been proposed to explain the physical protection of organic matter in soil against decomposition. One of the mechanisms mentioned is the adsorption of organics onto surfaces such as clays or organic complexes (Oades 1989). Proteinaceous and other complex materials have been shown to be resistant to microbial attack through adsorption to inorganic colloids or organic matter (Pinck et al. 1954; Simonart & Mayaudon 1961; Sørensen 1967). Aringhieri & Sequi (1978) showed that the organic matter of aggregates, stable to wet sieving, was more tightly bound to the inorganic colloids and was less oxidizable by H_2O_2 than the organic matter of the more unstable aggregates. However, the biological meaning of sensitivity to oxidation by peroxides is unknown.

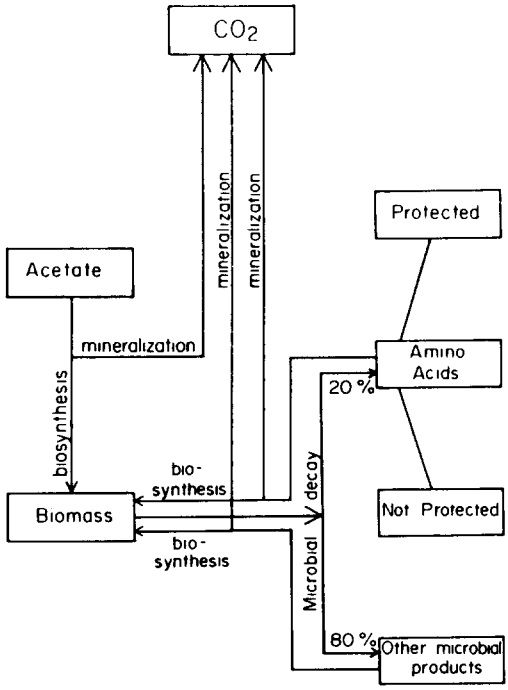

Fig. 1. Model used to quantify the effect of physical protection on microbial product stabilization in soil (after Van Veen & Paul 1981).

In comparing retention of labelled organic matter in soils with clay contents ranging from 5 to 42% and no major differences in climatic conditions, Ladd et al. (1985) showed that the retention of organic C was nearly proportional to the clay content of the soils. Oades (1988) provided additional data on the negative correlation of clay content with decomposition of crop residues. Similar observations were made by Sørensen (1975, 1981). Organic matter levels in

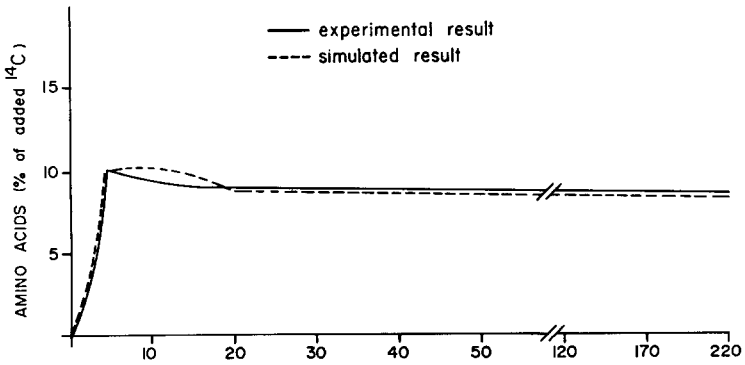

Fig. 2. Experimentally determined and simulated stabilization of amino acids in Bradwell soil after addition of acetate-^{14}C (after Van Veen & Paul 1981).

soils have been shown to correlate with clay content of soils (Schimel et al. 1985a and 1985b). Oades (1988) confirmed the latter but stated, that it is difficult to find unequivocal evidence to support this relationship. Clay content is also associated with other factors such as plant growth and moisture regime, which are related to organic matter levels. Also large differences in the characteristics of different clay minerals undoubtedly have a considerable impact on their surroundings and behaviour. Sørensen (1975, 1981) showed that during incubation of ^{14}C-labelled substrates in soils with different clay contents, differences among soils in the amount of ^{14}C-cellulose retained were established after 10 days and remained roughly unchanged during a subsequent 1600 day period. These results suggested that the effect of clays on the retention of substrates coincides with the maximum microbial activity that follows upon the addition of energy-rich substrate. Another explanation of these phenomena could be that certain clays increase the biosynthetic efficiency of microbes. Sørensen (1983) calculated that after 10 days in soils with clay contents of 4, 11, 18 and 34%, the efficiency of utilization of ^{14}C-cellulose for synthesis of new cellular material was respectively 27, 39, 50 and 55%. He also found that the microbial biomass comprised a higher percentage of native-C in clay-rich soils than in sandy soils.

However, the biosynthetic efficiency of the utilization of ^{14}C-glucose, added to a clayey and a sandy soil and incubated for three days, was not significantly different for both soils (Van Veen et al. 1985). On the contrary, fits between model output and experimental results of ^{14}C-glucose dynamics in two soils with different clay contents were improved when assuming a larger utilization efficiency of glucose and microbial metabolites in the clay-rich than in the sandier soil (Van Veen et al. 1985). In his review, however, Filip (1979) referred to more contrasting data on the effects of clay on the efficiency of substrate utilization. This makes the explanation by a different utilization efficiency of substrate for the larger retention of C in clayey vs sandy soils rather disputable. An extensive review on organic matter associations with soil minerals is presented by Oades (1989).

Another explanation for the physical protection of organic matter in soil is the entrapment of organics in aggregates, which renders them inaccessible to the decomposing microbial community. Bacteria within soil aggregates are mentioned to exist in pores at least three times their diameter (Kilbertus 1980). Thus, although soil bacteria are generally less than 1 μm in diameter, this means that 95% of the pore space in soil is not accessible for bacteria. Much of the organic matter in soils is particulate, and not evenly distributed. Thus, organisms and substrates are generally separated by physical barriers. Using synthetic aggregates in soil, Bartlett & Jones (1988) showed that surface applied amino acids decomposed more rapidly than amino acids uniformly mixed in soil aggregates. Adu & Oades (1978) provided evidence that ^{14}C-labelled starch was protected from microbial attack by entrapment in aggregates formed when slurries of a fine sandy loam soil were dried. The transmission electron micrographs made by Foster and co-workers (Foster et al. 1983, 1988) nicely illustrate the physical separation in the soil matrix between microbes and organic matter particles.

Microbial biomass turnover in the soil matrix

Decomposition of organic matter in soil to CO_2 is the resultant of turnover processes through a series of pools of which the microbial biomass is a key intermediate station. Soil microbial biomass has been called 'the eye of the needle through which all the natural organic material that enters the soil must pass' (Jenkinson 1978). Thus, the microbial biomass, viewed as an entity, may be regarded as a transformation station: materials are taken up, converted into new products, and subsequently released actively or passively. The transformation processes occur simultaneously and are interdependent. Uptake and efficiency of use of substrates from solutions have been described rather extensively, although Bazin et al. (1976) correctly pointed out the limits of the application of models developed for steady state laboratory cultures to models of soil ecosystems, which are subject to environmental perturbations and consequently, are unlikely to reach true steady states.

Based on these observations and the aforementioned concepts it was postulated that soils have characteristic capacities to preserve both organic matter and micro-organisms (Van Veen et al. 1984, 1985).

Concepts of microbial processes other than those of growth, i.e. maintenance, have been developed for chemostat systems. The concept of cell maintenance has been defined for pure cell cultures, and cannot be readily applied to mixed cultures. Further, the concept of cell maintenance does not express the dynamics of microbial death, nor of cryptic growth or of turnover of nutrients through the microbial biomass. It seems therefore more appropriate to describe microbial biomass turnover of C and N in soils by using either first order rate kinetics (McGill et al. 1981; Van Veen & Frissel 1980) or exponential functions (Smith 1982) to calculate the formation and release of microbial metabolic products and their availability as substrates for successive populations.

The accuracy of these gross estimates of biomass turnover in soils is seriously hampered by a lack of knowledge of the mechanisms of microbial death and of other processes by which organic substrates become available for decomposition or are conserved by the microbial population.

Predation of microbes by protozoa and nematodes and interactions with organisms of higher trophic levels have been proposed as an important mechanism of nutrient turnover in soil (Verhoef & Brussaard this issue; Elliott et al. 1980; Hunt et al. 1987; Kuikman & Van Veen 1989). The soil pore volume accessible to protozoa and nematodes is limited. Less than 10% of the pore space in a loamy soil consists of pore with diameters of $> 1\ \mu m$, which is hardly wide enough to be accessible for the smallest amoebae (Oades 1988). Elliott et al. (1980) showed that trophic interactions in soil were largely determined by available soil pore space. Also, respiration rates were relatively higher when both nematodes and amoebae were grown with bacteria than when either grazer was grown singly with bacteria. Thus, it was hypothesized that amoebae made nutrients (i.e. derived from bacteria) more available to nematodes by entering soil pore spaces inaccessible to nematodes and that these trophic interactions

were more pronounced in fine-textured than in coarse-textured soils. They concluded that 'microbial trophic structure in relation to soil texture and habitable pore space is an important factor influencing energy flow in terrestrial ecosystems'. Additional evidence on the significance of soil architecture for the interaction between predators of micro-organisms and their prey is provided by recent studies on the dynamics of introduced bacteria in soil (Van Elsas et al. 1986; Postma et al. 1989; Heijnen et al. 1988). These studies showed that introduced bacteria are subjected to enhanced predation, and thus exhibit poor survival as compared to indigenous bacteria, mainly due to their different localisation in soil. When introduced bacteria were made to enter originally present or artificially created protective microniches, their survival increased substantially.

Ladd et al. (1985) observed differences between soils of different texture in the formation of microbial biomass ^{14}C and ^{15}N during the incubation of labelled substrates. Finer soils of higher clay content generally retained higher amounts of residual organic ^{14}C and ^{15}N in microbial biomass. Preservation of micro-organisms could be the result of protection against predation and/or amelioration of harsh environmental conditions. Microbial biomass that is formed in excess of a soil's preservation capacity, which is defined as the biomass content of the undisturbed soil, is assumed to have a relatively high turnover rate. Furthermore, micro-organisms and their immediate products of decay are considered to form a tightly closed system from which only small proportions of the products leak out to become temporarily available for utilization.

These concepts were mathematically formulated in a simulation model schematically presented in Fig. 3. This model was tested using data from experiments in which ^{14}C- and ^{15}N-labelled substrates and bacteria were added to two soils with different texture. Two soils, one a sandy loam from Roseworthy, South Australia and the other of relatively higher clay content from Northfield, South Australia, were incubated with ^{14}C-glucose and ^{15}N-$(NH_4)_2SO_4$ for 101 days.

First the model was tuned to the continuously moist incubation of Northfield clay soil. Then, the values of only three key parameters were altered to simulate other cases, e.g. the Roseworthy sandy soils and to test the aforementioned concepts which are reflected through these parameters. These parameters were

— the capacity of a soil to preserve micro-organisms,
— the fraction of microbial products remaining in the vicinity of survivors and
— the efficiency of utilization of glucose for biosynthesis (Table 1).

The values for the capacity of the soils to protect or stabilize biomass (MAXPB) were derived directly from assays of biomass C in the two soils sampled under young pastures, i.e. in soils not recently tilled or freshly amended with large inputs of plant materials. The Northfield clay soil, assayed at various times during the incubation, averaged 75 mg biomass C $100\,g^{-1}$ soil; the Roseworthy sandy loam averaged 28 mg biomass C $100\,g^{-1}$. The same batches of soil, stored moist at 4 °C for 12 months, contained 62 and 23 mg biomass C $100\,g^{-1}$ soil, respectively. Two fresh batches of soil from the same sites but sampled 12

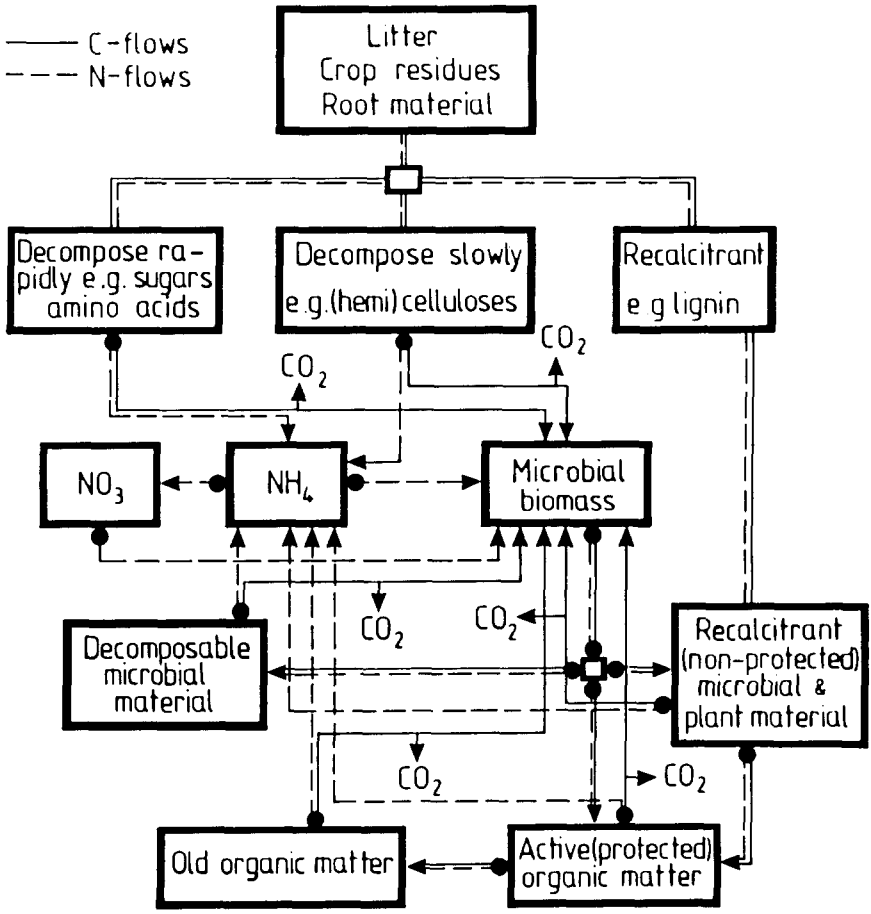

Fig. 3. Scheme of the detailed carbon turnover model (after Van Veen et al. 1985).

Table 1. Parameter value sets for case studies at different moisture regimes (c.m. = continuously moist; d.w. = dry/wet) in Northfield clay and Roseworthy sandy loam (after Van Veen et al. 1985).

Symbolic name	Definition	Set values			
		Northfield		Roseworthy	
		c.m.	d.w.	c.m.	d.w.
MAXPB	Capacity of a soil to protect micro-organisms (mg C 100 g^{-1} dry soil)	75	50	28	20
FOPV	Fraction of microbial products remaining in vicinity of survivors	0.7	0.5	0.5	0.4
EFFC	Efficiency of utilization of glucose (%)	60	60	40	40

Table 2. Decomposition rates (k^*) or organic ^{14}C in a clay soil and a sandy loam amended with [^{14}C]glucose (after Van Veen et al. 1985).

Soil	$k \times 10^{-3}$ (day^{-1}) after sampling at days							
	3	10	24	38	59	73	87	101
Sandy loam	157	21	10	6	4	4	3	2
Clay	117	12	5	3	2	2	1	1

* $k = -\ln[C_t/(C_t - t)]t$. In the period (t) prior to sampling at time t.

and 21 months after the initial assays contained 73 and 23 mg biomass C 100 g^{-1} soil, respectively.

Materials released from cells following death in clay soils were considered to be mainly retained in the vicinity of surviving organisms. For Northfield clay soil this fraction was arbitrarily set to 0.7 of the total amount of microbial products. A smaller proportion of microbial products was considered likely to be retained near surviving micro-organisms in the coarser-textured, sandy loam. Thus, for Roseworthy sandy loam soil a value of 0.5 was used. Differences in utilization efficiency were assumed on the basis of the differences in the content of clays.

Soils differed significantly in their rates of ^{14}C–CO_2 evolution after amendment and incubation with ^{14}C-glucose. Rates (k) of decline of residual organic ^{14}C are given by the following Eq. 1.

$$k = -\ln \frac{(^{14}C_{resid})t_2}{(^{14}C_{resid})t_1} (t_2 - t_1) \quad (1)$$

where $(^{14}C_{resid})t_1$ and $(^{14}C_{resid})t_2$ are the residual ^{14}C contents at the time t_1 and t_2, respectively. From day 10 until the end of the experiment, net decomposition rates in the Roseworthy sandy loam were twice as fast as in the Northfield clay soil (Table 2).

The good fit between model output and experimental observations (Figs. 4, 5) showed that the differences between the clayey soil and the coarser sandy soil may be explained largely if the clayey soil

— has a greater capacity to preserve or protect biomass;
— provides an environment for closer interaction between micro-organisms and products of decay; and
— promotes a higher efficiency of utilization of glucose and metabolic products by the soil biota.

Similarly, the hypotheses were tested with data from experiments in which a mixture of triple-labelled (^{14}C, ^{15}N and ^{32}P) bacterial cells was added to the two soils, which were then incubated for up to 100 days (Van Veen et al. 1987). In general, the relative behaviour of the isotopes in the two soils was similar to that found for soils in which ^{14}C and ^{15}N were added as soluble substrates and in which biomass and metabolites were formed *in situ* (Fig. 6). Also, satisfactory model predictions were obtained, when assuming similar differences between the

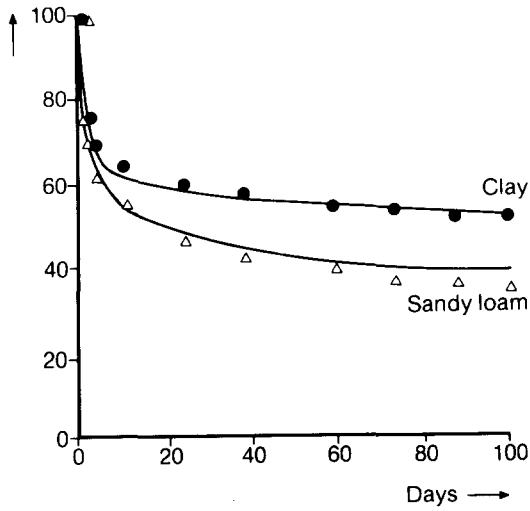

Fig. 4. Residual organic ^{14}C calculated from $^{14}CO_2$-evolution from Northfield clay and Roseworthy sandy loam soil after incubation with ^{14}C-glucose. Observed data: ● Northfield clay, △ Roseworthy sandy loam. Model output: solid lines (after Van Veen et al. 1985).

values of the three parameters which described preservation of microbial cells and microbial metabolites and the efficiency of organic matter utilization. The simulation assumed that the added bacteria were not protected. This assumption was based on work on the survival of added bacteria, which often decrease to undetectable levels after introduction (e.g. Van Veen & Van Elsas 1986).

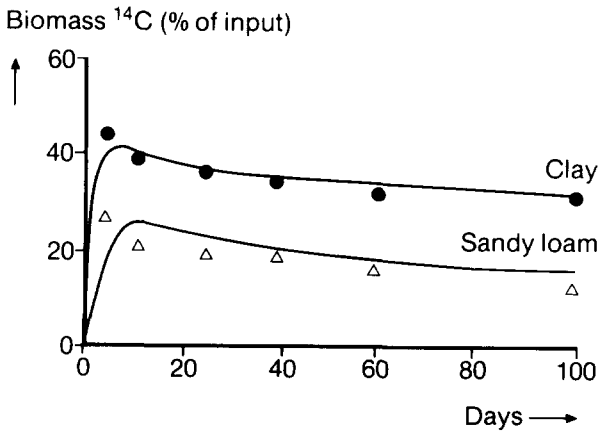

Fig. 5. Biomass ^{14}C in Northfield clay and Roseworthy sandy loam soils after incubation with [^{14}C] glucose. Observed data: ● Northfield clay; △ Roseworthy sandy loam. Model output: solid lines (after Van Veen et al. 1985).

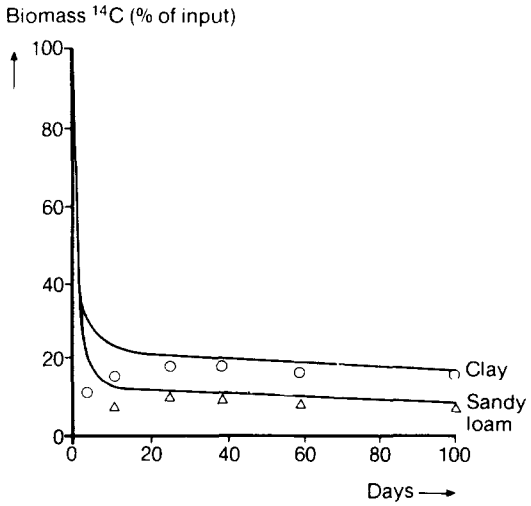

Fig. 6. Biomass ^{14}C in Northfield clay and Roseworthy sandy loam after amendment of ^{14}C-labelled bacterial cells: Observed data: o Northfield clay, ΔRoseworthy sandy loam. Model output: solid lines (after Van Veen et al. 1987).

Effect of changes in soil structure on decomposition and microbial turnover processes

Both climatic changes and human and faunal activities influence soil structure and thereby affect microbial activity. Here we will show three examples of the impact of changes in soil structure on microbially mediated transformations of soil organic matter. We will discuss

— the dramatic decreases in soil organic matter levels after cultivation of virgin prairie grassland and we will show with the use of simulation models that this decrease can largely be explained by the assumption of enhanced accessibility of organic matter for microbial utilization and transformation;
— recent experimental results of the effect of soil compaction on ^{14}C-glucose decomposition and microbial biomass formation; and
— the phenomena, that have often been observed after the remoistening of dried soils.

Cultivation

Native prairie soils in North America have accumulated large amounts of organic matter. Dryland cropping, consisting primarily of cereals and fallow in rotation, has resulted in a substantial decrease in soil organic C and N (Lipman & Blair 1921; Voroney 1979; Voroney et al. 1981; Schimel et al. 1985a). Greenland (1962) reported that organic N in the surface of some Australian soils had decreased by up to 50% after cultivation. Similar losses of organic matter were recorded by Saunder & Grant (1962) for cultivated Rhodesian soils when compared to indigenous grass cover. In Western Canada, after 60–80 yr of

cultivation, the concentration of organic C decreased by 50–60% and organic N decreased by 40–50% in the Ap horizon of Chernozemic soils (Campbell et al. 1976). The depletion of organic C and N with cultivation can be attributed to changes in the magnitude of a number of biological and physical processes in soil such as changes in climatic conditions, temperature and soil moisture, in input rates of organic matter and in erosion pattern.

In order to test the hypothesis that disruption of soil structure renders organic matter more accessible for biological decomposition, Van Veen & Paul (1981) developed a model to describe soil organic matter dynamics in virgin and cultivated grassland soils and compared it with data on soil organic matter levels in a Chernozemic soil. The model embraces the concept that organic matter will be more exposed to biological degradation following the disruption of the soil structure by tillage operations than in non-cultivated soils. The change in physical protection and its impact on soil organic matter levels is the key issue of the model. Native organic matter was divided into three major fractions in the model:

1. microbial biomass;
2. decomposable organic matter comprising microbial products and lignin fractions of litter and roots; and
3. old, recalcitrant organic matter fraction.

The latter two fractions are assumed to be affected by physical protection processes that were previously discussed. This fractionation is basically similar to the one used to simulate the turnover of ^{14}C-glucose, which has been discussed before (Fig. 3). For long-term simulations the pools of decomposable microbial materials and non-protected recalcitrant materials (Fig. 3) were assumed to form the non-protected part of fraction (2). The, so-called, old organic matter fraction of Fig. 3 was split into a protected and non-protected part, together with fraction (3). The percentage of both fractions that is protected was indicated by a protection coefficient. Protection leads to a decrease in the decomposition rate constant of the decomposable soil organic C fractions.

For the simulation of the effect of cultivation on soil organic matter, it was assumed that, besides differences in input rates, only the degree of physical protection, controlled by changing the value of the protection coefficient FOPV, was diminished.

Under grassland conditions, 50% of the organic matter was considered to be protected. Under cultivation, this value was reduced to 20% for the 0- to 15-cm layer and 40% for the lower layers. The model was very sensitive to the estimate used for physical protection (Fig. 7). Cultivation, at least initially, was assumed not to change the extent of adsorption of organic C by clays.

The model accurately predicted the organic C level in the soil pedon after 70 yr of cultivation (Table 3). The main difference between the experimentally determined and the predicted level was that the model over-estimated the loss of organic C in the second and third layers. One explanation might be that the assumed decrease in the proportion of microbial products entering the protected subfraction, i.e. from 0.5 in the native prairie to 0.4 in the cultivated soil for the 15- to 40-cm layer, was not appropriate for a Black soil.

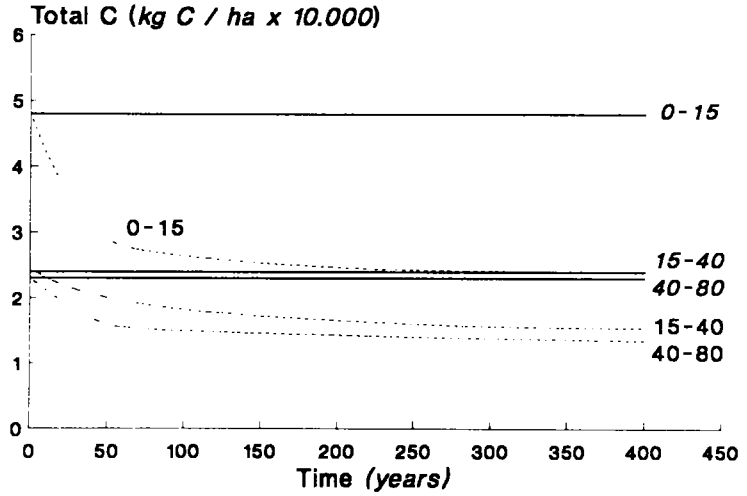

Fig. 7. Effect of changes in physical protection on the total C content of a grassland soil (Sceptre). Physical protection coefficient, FOPV, of virgin sites: 50%; of cultivated sites: 20% in the surface layer and 40% in subsurface (after Van Veen & Paul 1981).

The model also predicted that the soil organic matter should approach a steady state at approximately 60% of its original level after about 100 yr of cultivation. The different cereal rotations considered did not significantly alter the steady-state organic C level if organic matter turnover alone was considered.

Similar concepts were included in the soil organic matter model of Jenkinson & Rayner (1977) and later models of Van der Linden et al. (1987) and the CENTURY model of Parton et al. (1988).

Compaction

The compaction of soil in intensive agriculture due to heavy traffic loads of modern farm machinery is apparently opposite to the effect of ploughing. One passage of a tractor wheel may result in local bulk densities up to 1700 kg m^{-3} (Soane et al. 1982). The increased bulk density might negatively affect the accessibility of soil for mesofauna and macrofauna such as springtails, mites, earthworms (Soane et al. 1982). Soil compaction may negatively affect the

Table 3. Comparison of experimental data with predicted levels of organic C after simulation of 70 yr of cultivation of an Oxbow soil (after Voroney et al. 1981).

Depth (cm)	Decrease in organic C as:			
	kg ha^{-1}		%	
	Experimental	Model	Experimental	Model
0–15	54,000	51,000	57	55
15–40	8,200	11,000	22	29
40–80	4,000	4,900	20	22

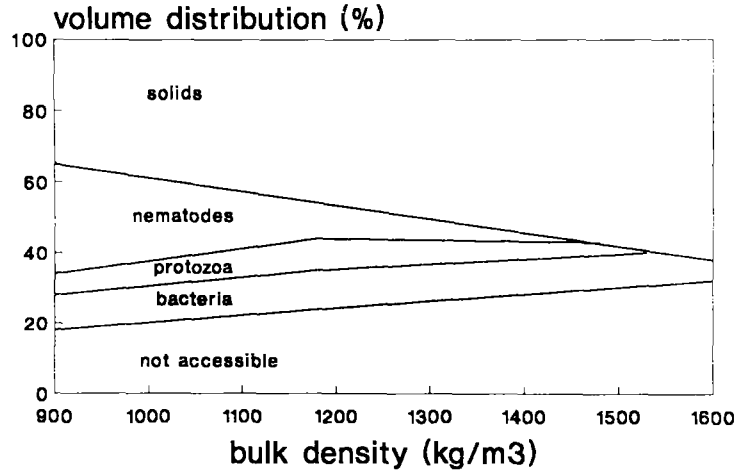

Fig. 8. Pore size distribution in a silt loam soil at different bulk densities and the assumed accessibility of pore fractions for siol biota: Accessible pores with neck diameter p: nematodes: $p > 30\,\mu m$; protozoa: $p > 5\,\mu m$; bacteria: $p > 0.2\,\mu m$; not accessible: $p < 0.2\,\mu m$ (after Van der Linden et al. 1989).

predatory activity of protozoa and nematodes through the decrease in available pore space and so, through the decrease in accessibility of the prey, bacteria and fungi. The activity of microfauna and -flora might also be affected directly because of changes in aeration and nutrient availability (Frey et al. 1985).

In order to investigate the effects of compaction on microbially mediated decomposition processes, ^{14}C-glucose decomposition and related biomass-^{14}C formation were studied in soils compacted to three different bulk densities (Van der Linden et al. 1989). Here, only data will be presented from one of the soils used, a silt loam.

On the basis of the water retention curves, a rough estimation of the pore size distribution of the soils was calculated (Fig. 8). The volume taken by solids increased from about 40% at a bulk density of $1000\,kg\,m^{-3}$ to about 63% at a bulk density of $1600\,kg\,m^{-3}$, so the void volume decreased from 60% to 37%. The pore space taken by pores having an equivalent diameter of $0.2\,\mu m$ or less increased from 20% of the total soil volume to 32% (33% respectively 85% of the pore space). The volume taken by pores having an equivalent diameter between 5 and $30\,\mu m$ at first increases upon soil compaction but gradually declined to zero at bulk densities of up to $1500\,kg/m^{-3}$. Larger pores ($> 30\,\mu m$) disappeared at a bulk density of $1460\,kg/m^{-3}$.

a rough approximation. It is based on the concept of equivalent pore diameter and disregards the normally observed hysteresis in the water retention curve. The advantage of the estimation according to the water retention curve is that the necks of pores are responsible for retention or loss of water in specific pores and at the same time they form the entrance to the pores. Therefore, they determine largely the accessibility of a pore for organisms.

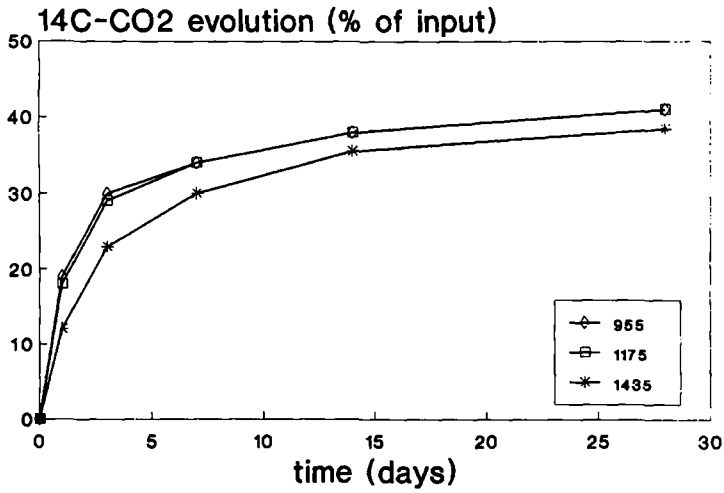

Fig. 9. ^{14}C–CO_2 evolution from a silt loam soil, incubated with ^{14}C-glucose, at different bulk densities (after Van der Linden et al. 1989).

The decomposition of ^{14}C-glucose was retarded at higher bulk densities (Fig. 9). ^{14}C–CO_2 evolution in the soil with a bulk density of 1435 kg m^{-3} decreased within the first 5 days after glucose addition after which ^{14}C–CO_2 evolution seemed to be similar for all treatments. This retardation in ^{14}C-glucose decomposition suggests a slower turnover rate through the microbial biomass. However, this was not reflected in a larger incorporation of ^{14}C in the microbial biomass (Fig. 10).

It was hypothesized that more compressed soils contained more protective

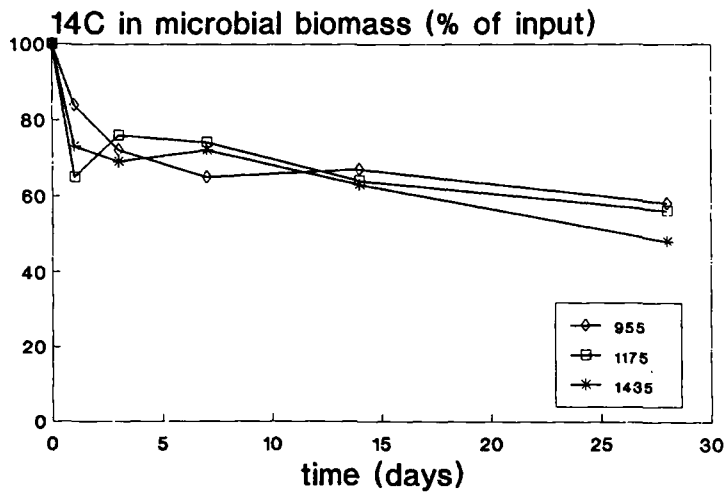

Fig. 10. Biomass ^{14}C formation (as % of input ^{14}C) in a silt loam soil incubated with ^{14}C-glucose at different bulk densities (after Van der Linden et al. 1989).

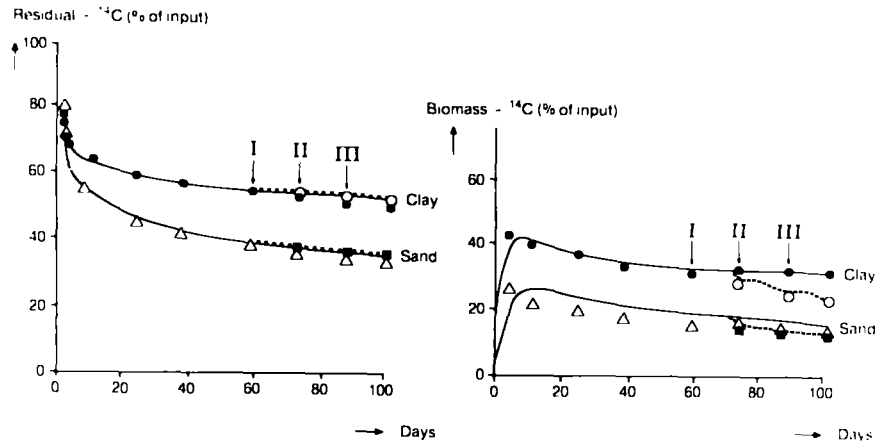

Fig. 11. Observed and simulated ^{14}C glucose decomposition and related biomass ^{14}C-formation in a clayey and a sandy Australian soil at different moisture regimes: Observations: ● continuously moist, ○ dry/moist, clay; △ continuously moist, ■ dry/moist, sand. The lines represent the output of the model and the points arrowed, I, II and III refer to the commencement of dry/moist cycles (after Van Veen et al. 1985).

sites for microbes against predators and thus turnover of C was slower and more materials remained conserved in the microbial biomass. In the soils with a bulk density of 1435 kg m^{-3}, pores accessible for the main predators of bacteria and fungi had nearly disappeared. A minimum neck-diameter of 4 μm for protozoa and of 30 μm for nematodes has been suggested (Jones & Thomason 1976; Elliott et al. 1980). Nevertheless both biomass ^{14}C formation and ^{14}C–CO_2 evolution are lower at higher bulk densities. This seemingly conflicting observation might be the result of an initial, rapid, uptake of ^{14}C-glucose in the microbial cells, followed by release of ^{14}C from the microbial biomass as ^{14}C-organic matter which is less accessible for cryptic growth and further transformation by successive microbial populations at a higher bulk density. It is evident that more data are necessary in order to adequately explain these phenomena. Yet, it appears that considerable increases of soil bulk densities may lead to relatively moderate effects on microbial turnover processes.

Soil moisture

Another form of alteration of soil structure which has often been reported to affect organic matter transformation is that which occurs following rewetting of a dried soil (e.g. Stevenson 1956; Birch 1958). Compared to soils kept moist continuously, air drying of soils followed by rewetting and incubation results in a flush of evolved CO_2 from the soils (e.g. Birch 1958; Jager & Bruins 1975).

Explanations of this observed flush of CO_2 include death of organisms and subsequent release of amino acids upon drying (Harada & Hayashi 1968; Marumoto et al. 1982) and an increased availability of organic matter to

decomposing organisms due to disruption of soil structure by rewetting the soil (Sørensen 1974).

The effects of intermittent drying in remoistening of soils on ^{14}C and ^{15}N turnover processes were investigated in the same studies (Van Veen et al. 1985, 1987) on the turnover of ^{14}C and ^{15}N through the microbial biomass after addition of labelled glucose, $(NH_4)_2SO_4$ and bacteria. The results were analysed with the model in Fig. 3. Both a flush of CO_2 evolution and N mineralization for 4 days after remoistening the dried soils was observed after addition of glucose + NH_4 and bacterial cells. However, the overall C and N-mineralization rates were slightly less after repeated drying and remoistening of soils than when these soils were incubated continuously moist.

The effects of drying and remoistening of soils were simulated and assumed to be due to a temporary decrease in the capacity of soils to protect or stabilize biomass for 3 days following water addition to dry soils (from 75 to 50 mg biomass C $100\,g^{-1}$ Northfield soil, and from 28 to 20 mg biomass C $100\,g^{-1}$ Roseworthy soil), and a larger release of microbial products from the microbial communities to become temporarily unavailable for utilization. The alteration of key parameters for the different moisture conditions is given in Table 1.

Comparison of model outputs and experimental data showed that the effect on both biomass ^{14}C and $^{14}CO_2$ release can be simulated by assuming a temporary decrease in the capacity of the soil to preserve biomass (Fig. 11) tening of the dried soil.

This was further illustrated by Kuikman et al. (1989) who studied the impact of protozoan grazing on the mineralization of microbial ^{15}N-nitrogen in soils planted with wheat and incubated under three soil moisture regimes. The stimulating effect of protozoan grazing on the uptake of bacterial ^{15}N-nitrogen was more pronounced under a soil moisture regime characterized by periods of drought than under regimes with rather stable soil moisture regimes. Thus, it was concluded that bacterial biomass was made available for predation to a larger extent by drying and rewetting a soil than under constant moist conditions (see also Verhoef & Brussaard, this issue).

Conclusions and perspectives

Soil structure and texture are dominant controls over decomposition of organic matter by microbes. This is reflected in the differences in decomposition rates between different types of soil. Finer, clayey soils show, on average, slower decomposition rates and higher retention of organic matter than coarse, sandy soils.

Two mechanisms are proposed to describe the role of soil architecture on biological transformations of organic matter. The accessibility of organic matter in soil for utilization as substrate by micro-organisms is limited. Mixing of substrates and microbes as found in laboratory systems or in aquatic ecosystems is very much restricted in soil due to limitation of both water flow and microbial

movement. Thus, substrates even at distances of micrometers or less might not be readily available for micro-organisms. Moreover, organic material might not be available for decomposition due to adsorption on clay minerals or other surfaces or by entrapment in pores or aggregates which cannot be entered by micro-organisms. These pores comprise more than 90% of the surface area in certain soils, which leads to the conclusion that soil is a sterile system for most of its surface. The other mechanism proposed is through the effects of soil architecture on microbial turnover processes. Turnover of organic material through the microbial pool is the key process in decomposition in terrestrial ecosystems. Microbial turnover comprises the processes of uptake, intracellular transformation and release of organic materials. The first two processes might be influenced by soil architecture. Experiments have shown that the utilization efficiency of organic substrates might be increased in clay-rich soils, thus enhancing the retention of organic matter in soil. However, contradictory results have also been published. Release of organic matter from the microbial biomass and subsequent further transformation might also be affected by soil structure. Food-web relations, which largely control microbial turnover, are influenced by soil architecture.

Traditionally, soil physical conditions have been studied in terms of macroscopically measurable properties, which were considered to be characteristic of substantial volumes of soil (Smiles 1988). Similarly, the biology of a soil has usually been described as being homogeneously distributed over large volumes of soil. We need descriptions on the level of soil pores or aggregates to understand the behaviour of micro-organisms in the physical environment of the soil. One of the most promising methodologies in this respect is the fractionation of organic matter in decomposable and recalcitrant fractions on the basis of the distribution of aggregates of different sizes as proposed by Elliott (1986) and based on Tisdall & Oades (1982). He showed, that organic matter associated with micro-aggregates (roughly < 0.3 mm) was more recalcitrant than organic matter associated with macro-aggregates. The latter consists of micro-aggregates bound together by organic matter, which is the primary source of nutrients released when organic matter is lost under cultivation.

Simulation models that include both the accessibility of organic matter to microbes and the effects of soil architecture on microbial turnover adequately simulated C and N transformations in different soil types or in soils at different conditions of management and moisture regime. However, these descriptions include rather undefined concepts such as the physical protection and protective capacities of soils for microbial biomass. These concepts have helped to focus the attention on the prime importance of soil architecture in terrestrial decomposition processes and enabled an adequate fit between model output and a particular set of experimental results. In order to be able to quantitatively determine the impact of soil architecture on decomposition processes, and to be able to compare soils of different types and under different management regimes, we need to find quantitative relationships between soil physical and biological properties.

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