. Impact of Soil Fauna

Activities of mobile as well as sessile soil fauna can reduce soil heterogeneity. Mobile soil fauna in search for food move through the soil following existing void systems, enlarging pore necks where the passage is hampered and/or creating new channels. They exploit local zones where food is available and produce excrements on their way. In arable land, food sources are related to the root systems of the crops, incorporated organic matter and organic matter deposited at the surface. As soil organisms are generally strongly related to specific zones where the same moisture and temperature conditions prevail, the same architecture can develop in whole zones. A characteristic example is a moder humus zone in a spodosol (Figure 14a), in The Netherlands, which often occurs below a plaggen epipedon. The organic matter together with the fine-grained mineral material becomes conversed into shaped organo-mineral excrements produced by small soil fauna, chiefly microarthropods such as enchytraeids and collembola. The excrements occur in open or close packed, individual or slightly welded clusters between the larger mineral grains. Nearly all fine-grained mineral material is present in the organo-mineral excrements.

Sessile soil fauna create their own channel system which is in use for prolonged periods. They, however, also move around in search for food, but retreat into their own channels. These animals deposit their excreta at the surface or, less often, into old side-branches of their channel system. With time and presence of enough food homogeneous zones are formed. A characteristic example of this type is a mull humus in a mollic epipedon (Figure 14b). In a mull humus the organic material is intimately mixed with the mineral material forming a clay-humus complex. This type of humus form is produced by earthworms, who consume organic as well as mineral material. The excreta form clusters or small aggregates of strongly welded or shapeless material.

2. Impact of Diffusion

Diffusion is driven by, but also reduces concentration gradients. Diffusion is thus one of the major processes leading to homogeneity of the soil, although complete uniformity is approached at an infinitely slow rate, and new disruptions will have taken place before the soil is completely uniform. To get a feeling for the speed at which such homogenization occurs, Figure 15 shows the time course of the average concentration of a sphere of soil of 1 cm radius, inside a second sphere of 20 cm radius (see appendix for equations). At time zero, the concentration in the inner sphere is 1.0 and in the surrounding sphere 0. When we take typical values for the diffusion coefficient representing nitrate in a soil at field capacity, diffusion is so rapid, that the soil will be uniform for all

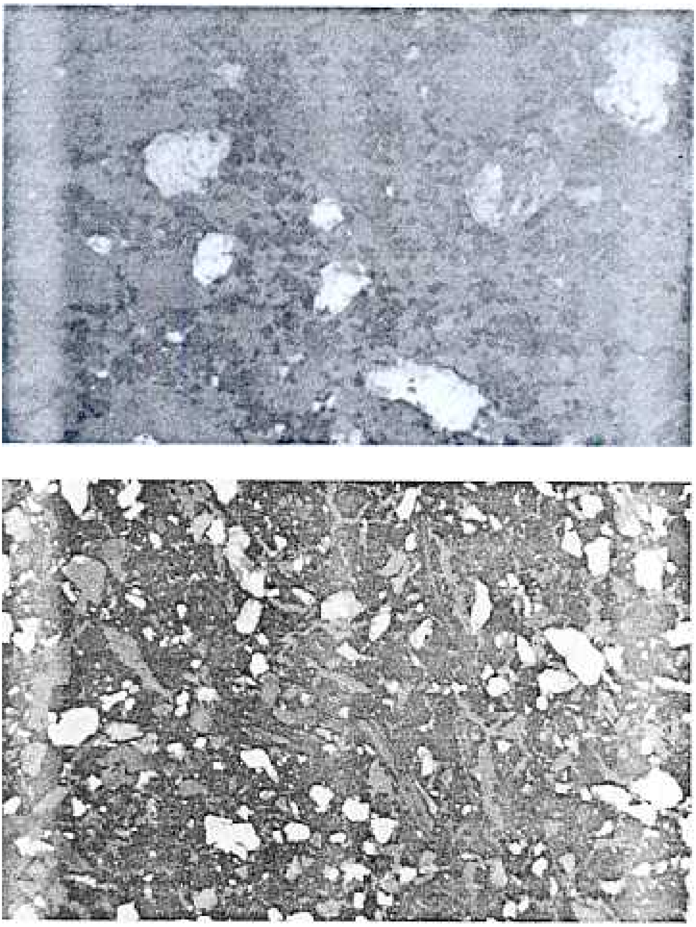

Figure 14. Humus forms produced by soil fauna. a. black moder humus; b. mull humus (magnification a: x 62; b: x 25).

practical purposes within a few days. For K it may be one or a few weeks, but for phosphate it will take weeks or months, depending on the P adsorption constant of the soil to reduce the concentration in the inner sphere to 50% of its original value. The time is scaled with the effective diffusion constant, and a tenfold reduction in mobility, leads to a tenfold increase in the time required for a set degree of homogenization. In drier soil conditions, the mobility of nutrients is reduced. So and Nye (1989) showed that for a tenfold decrease in D* from its value at field capacity (pF = 2.0) a sandy loam has to dry out until pF 3.3

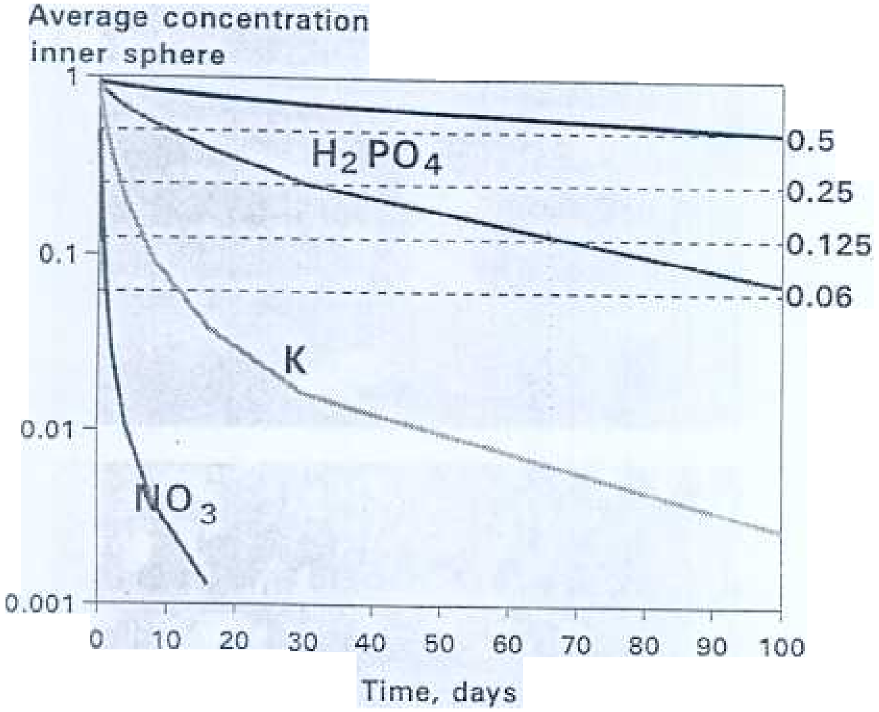

Figure 15. Concentration decrease by diffusion from a 'hot spot' (initial concentration 1), consisting of an inner sphere of radius 1 cm in a 'cold' sphere (initial concentration 0) of radius 20 cm, with values of the effective diffusion constant 1, 0.1 and 0.01-0.001 cm^2 day^{-1}, taken to be representative for nitrate, potassium and phosphate, respectively. Calculations based on equation (3) in the appendix.

and a silty clay until pF 4.5. Such a decrease in soil water content renders the diffusion of NO_3 in a dry soil similar to that of K at field capacity.

Homogenization of concentration by diffusion also depends on the absolute size of the 'hot spot'; in the spherical model the time required for homogenization is (approximately) proportional to the second power of the radius. Hot spots of nitrate of 3.2 cm radius thus will follow the line indicated for K hot spots of 1 cm radius. Heterogeneities at short distances are thus of practical relevance for solutes with an effective mobility as low as, or lower than that of inorganic phosphate. The diffusivity of oxygen in water is 10^4 times slower than that in free air, but the diffusivity of oxygen in a water saturated soil is still similar to that of nitrate. Equilibration of oxygen concentration in a soil with aggregate sizes of 1 to 3 cm radius is thus a matter of hours to days (weeks), at least in the absence of oxygen consumption. With a continuing oxygen demand local differences in oxygen concentration and even local anaerobiosis can persist in (nearly) water saturated soil. The overriding importance of consumption on maintaining steep gradients was also shown for glucose diffusion into soil aggregates by Priesack and Kisser-Priesack (1993).

IV. Consequences of Heterogeneity for Processes and Resulting Patterns at Higher Levels of Complexity

This section is focused on the upper part of the chain as given in Figure 7. To what extent does soil structure and the distribution of soil carbon influence processes at a higher level of organization, such as water and nutrient use efficiency of agricultural systems? If a 'good' soil structure is to help in reducing negative environmental impact of agriculture, how does this work and how can it be used to the full extent?

Water and nutrient use efficiency of an agricultural system primarily depends on how well supply and demand are mutually adjusted. As long as demand exceeds supply, resource use efficiencies are generally high. It is difficult to achieve a high efficiency with a resource supply which does not limit productivity. Yet, highly productive but at the same time efficient agricultural production systems are needed for the next century. The 'efficiency gap' between well maintained experimental plots and current farmer's practice (Whitmore and Van Noordwijk, 1995) is at least partly due to difficulties in predicting rates of biologically mediated soil processes and to field scale spatial variability beyond the area exploited by an individual plant. Several of the components of the demand-supply balance are related to soil structure: root growth, mineralization, denitrification and leaching all are influenced by soil structure. To close the 'efficiency gap' a better quantitative understanding of the underlying patterns and processes is needed. In this context we may come back to the question of whether models can be based on the concept of a perfectly mixed homogeneous medium responding uniformly to outside influences or should be based on the recognition of soil as a highly structured, heterogeneous environment with large zones of little activity and scattered 'hot spots' full of activity. At first sight, the apparent success of many model descriptions of major soil processes, based on a homogeneous soil concept seems to indicate that the heterogeneity is more of academic than of practical interest.

The majority of transport models consider soil heterogeneity implicitly rather than explicitly. Relevant parameters are normally measured on the scale of an 'elementary soil volume' which can be thought to be representative. Thus, a soil may be described as if it were homogeneous, but with an average gas diffusivity assigned to it which is based on the macropores, a water diffusivity dominated by the mesopores, and a by-pass flow description, based on the continuous macro-voids. The way in which these overall parameters are influenced by soil structure, and by variations in soil structure due to management actions remains obscure in many instances.

Models of nutrient uptake are normally based on assumptions of a regular root distribution. The consequences for uptake processes of non-regular root distribution and incomplete root-soil contact imposed on the root architecture by a structured soil can now be quantified (Van Noordwijk et al., 1993a; Veen et al., 1992). To a considerable extent, such effects of soil structure can be expressed as a reduction factor on the measured total root length and can be overcome by the plant by making more roots. Such reduction factors can give an alternative explanation to the reduction factors employed to estimate the 'live' fraction of a root system, but the two aspects are as yet difficult to separate and quantify. In many cases, models are used to evaluate the consequences of root length densities actually found in the soil and do not attempt to predict how root development depends on soil conditions, as mediated by soil structure.

Mineralization patterns do depend on soil structure. The consequences for food web functioning of the restricted accessibility of bacteria in small sized pores for protozoan predators are a recent focus of attention (Hassink et al. 1993; Wright et al. 1993). Soil food web models (De Ruiter et al., 1994) so far are remarkably similar to those for aquatic systems, and do not explicitly consider spatial structure of a soil, and the 'hot spot' nature of organic substrates. With the existing food web models, the measured N mineralization patterns in field soils can be predicted within a factor-two error range and they thus form an alternative to the C pool based model approach. Again, their relative success does not implicate that soil heterogeneity is not important for the functioning of the soil food web, as the calculations are based on actually observed population densities and do not attempt to predict the population development as such. Some mineralization models based on C pool sizes do include the concepts of 'physical protection' of soil carbon against bacteria and of bacteria against grazers (Verberne et al., 1990) but the protection factors are not yet completely operationally defined. Present attempts to do so are largely confined to soil texture and do not yet attempt to include soil structure. In the next generation of models, the mobility of soil organisms and their relations with soil structure may be more fully described.

Leaching rates critically depend on 'by-pass flow' through macropores. Considerable progress in field measurement of these properties has been made (Edwards et al., 1993). Despite considerable progress at the single aggregate level (Leffelaar, 1993), our understanding of denitrification, and its relation with measurable aspects of soil architecture is still far from comprehensive. Development of anaerobic sites and denitrification depend on the presence of decomposable organic substrates under conditions of slow oxygen replenishment. Soil structure and soil water content determine the oxygen transport rates, but the spatial distribution of oxygen demanding bacteria is probably related to the hot spots of organic substrates.

Using larger amounts of organic inputs is not a simple recipe to obtain a better soil structure and a more efficient and yet productive type of agriculture. If they are integrated with other aspects of crop management, however, biological means of maintaining and improving soil structure can give a real contribution to overall resource use efficiency. Biological management of soil structure by earthworm and root channels remains an exciting option (Dexter, pers. comm.) for extensive land use systems; one should not expect miracles however and where the soil building has been severely mistreated, e.g. during deforestation in the tropics, the biological soil architects will take a very long time to reconstruct anything similar to the original structure.

V. Importance of Heterogeneity for Carbon Retention in Soil

The organic carbon present in the soil is derived from aboveground organic materials incorporated as part of tillage activities or below ground organic inputs from primary producers (see part I and Figure 2). The incorporated organic inputs have a heterogeneous distribution. The method of incorporation determines the spatial pattern: e.g. inverted soil surfaces deposited by plough shares (Figure 3), more finely mixed material with other tillage implements. The same is true for the below ground organic inputs from primary producers, viz. leaves pulled into wormholes or roots with a distinct distribution pattern in the soil, whether or not redistributed by tillage activities. This heterogeneous distribution by itself may not be very important for decomposition rates or its complement, carbon retention in soil. The same organic material can be decomposed via different pathways and in different time lapses. Thus it is not the location as such of organic carbon which matters, but its effects on accessibility of the organic input for decomposing bacteria and fungi, predators and water, gasses and solutes. If the accessibility is affected, e.g. because a crop residue is incorporated in groundmass, decomposition can be very slow, while residues a few cm away along a crack are quickly fragmented and partly consumed (Figure 16). The accessibility for incorporated organic matter differs strongly and cannot be predicted. Those of the original below ground organic materials, such as roots, exudates and mycorrhizal hyphae are in principle far more accessible, as their locations are determined by both the root distribution pattern itself and the root preference for existing void systems.

In more natural arable systems (e.g. in agroforestry), faunal activity is the major determinant of incorporation of above ground organic inputs. Considerable differences in litter layer exist between vegetation types, but also over small

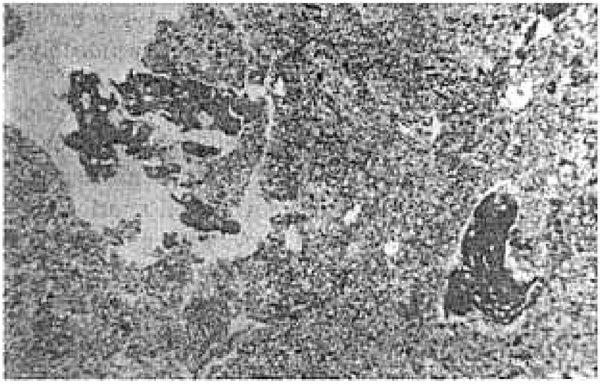

Figure 16. Difference in accessibility of crop residues in the plowlayer; the crop residue along the crack is partly consumed and fragmented by enchytraeids; the residue embedded in the groundmass remains intact (magnification x 2).

distances within a single forest type. Burghouts (1993) analyzed such patterns for a Bornean rainforest and concluded that differences in deposition rates rather than turnover rates were responsible for the apparent differences in carbon retention on the soil surface. Within a structured soil, however, possibilities for differences in turnover rates are substantially larger than on the soil surface.

Primary organic matter is decomposed faster than secondary organic matter present in excreta. The most decomposable excrements are those of the large macrofauna such as earthworm excreta. Mesofauna (enchytraeids, mites and collembola) consume coarser fragments of the incorporated organic material, sometimes leaving their excrements in the cavity they produced. Excrements can be conserved in the soils for centuries, in spite of tillage activities, without microscopic recognizable changes (e.g. Kooistra, 1978). Otherwise excrements disintegrate slowly forming shapeless organic coatings and bridges between mineral grains as in moder podsol soils.

VI. Summary and Conclusions

Soil structure has a biological component, the purposely made architectural part, which is highly variable in quality and quantity, occurs at different scales and varies throughout the year. The biological impact of belowground communities and plant roots depends on the different requirements and can be mutually exclusive, mutually complementary or dependent, completely independent or mixtures of these. The biological component of soil structure, therefore, is far less predictable than the physical part of soil structure dealing with swell/shrink and freeze/thaw cycles, and the human impact by tillage and management operations.

Nearly every observable/measurable biotically related soil phenomenon has a heterogeneous distribution in the soil. Increase and decrease of heterogeneity can be based on similar processes, but at different time scales, or on different processes. Recognition of and understanding of the dynamics of these heterogeneities appears to be essential for a 'real' understanding of what's going on in the soil. Yet, for many purposes models which treat soils as (a number of) black boxes, with average rates assigned to them have been highly successful. Such models are based on empirical 'fudge' factors, which are not always properly acknowledged in so-called 'process-based' models. Progress will be made when the empirically determined average parameter values for the black boxes can be explained on the basis of the underlying heterogeneity, the real actors and the variation in internal heterogeneity between sites. A number of new concepts and methods is now available for such an excercise.

The heterogeneous distribution by itself is not the main controlling factor in regard to decomposition rates or carbon retention in soils. Rather, it is the accessibility (not the location) of the organic input for decomposing bacteria and fungi, predators, water, gasses and solutes which is of primary importance. In studying these phenomena, new methods for analyzing and interpreting distribution patterns of single features across a range of scales are needed, especially methods to quantify the spatial correlations of patterns and their significance for turnover of organic inputs in the soil. As some of the products of turnover (e.g. anaerobically formed gasses such as CH_4 and N_2O, and solutes such as NO_3) are definitely undesirable when they reach other compartments of the environment (e.g. atmosphere, groundwater), research on soil structure may gain new relevance.

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Appendix

Diffusion out of a 'hot spot'

Consider a spherical 'hot spot' of radius R_0 and concentration C_0 inside a larger sphere of radius R_1 and uniform low concentration C_1. For the concentration $C_{r,t}$, a function of radial distance r and time t, the following equation can be derived from Carslaw and Jaeger (1959):

$$C_{r,t} = C_1 + (C_0 - C_1)\,[\frac{R_0^3}{R_1^3} + \frac{2}{rR_1} \sum_{n=1}^{\infty} \sin(r\,\alpha_n)\, e^{-D^*\alpha_n^2 t}\, F_{\alpha_n}] \qquad (1)$$

The function $F_{\alpha n}$ is equal to:

$$F_{\alpha n} = \frac{(1 + (\alpha_n R_1)^{-2})\ [\sin\,(\alpha_n R_0) - \alpha_n R_0\, \cos(\alpha_n R_0)]}{\alpha_n^2} \qquad (2)$$

where the α_n are the roots of the equation cot $(\alpha\ R_1) = 1/(\alpha\ R_1)$.
For large t the term with the exponential function in equation (1) is approaching 0 and the concentration everywhere in the sphere becomes equal to the weighted average of the two initial concentrations. By integration the average concentration in the inner sphere can be derived as:

$$\overline{C_{i,t}} = C_1 + (C_0 - C_1)\ [\frac{R_0^3}{R_1^3} + \frac{6}{R_1 R_0^3} \sum_{n=1}^{\infty} e^{-D^*\alpha_n^2 t}\, F_{\alpha_n}] \qquad (3)$$

Time t and the effective diffusion constant D^* only occur as a product, and thus the solution for solutes with different mobility can be considered as shifts in time, directly proportional to D^*.