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Strategies used by soil biota to overcome soil organic matter stability — why is dead organic matter left over in the soil?

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Abstract

Aiming at an improved understanding of the conditional nature of soil organic matter stability, we present an overview of (1) biotic strategies and (2) ecological processes by which decomposer organisms gain access to, or are prevented from metabolising soil organic resources. The biotic strategies discussed comprise well-known activities, such as the release of exo-enzymes, the mechanical crushing of organic residues, the bioturbation of soil mass, and the fixation of carbon in the living biomass. The ecological processes described have received less attention regarding their importance in prolonging the persistence of soil organic matter. Model calculations illustrate that cell energy demand forces micro-organisms to operate at low decomposition rates, and that diffusion losses inhibit microbial growth and impede the formation of new microbial colonies. The specialisation of decomposer organisms towards particular microhabitats and substrates gives rise to refuges where organic resources are temporarily not accessed. We derive four stability criteria, by which we classify organic matter pools: passive versus active stabilisation, and partial versus absolute refuge. Two case studies confirm that in temperate soils a dominant quantity of organic material resides in the passive stabilisation/partial refuge status and persists in spite of being accessible and decomposable. We conclude that soil organic matter is stabilised by a complex of mechanisms that constrain decomposition rates, several of which are not based on substrate quality or soil conditions, but on the biology of the decomposing soil organisms.

Keywords: Soil organic matter; Decomposition; Cell energy budget; Enzyme kinetics; Diffusion; Non-equilibrium theory

1. Introduction

Soil organic matter is recognised as being crucial to soil quality and to the regulation of many soil functions (Piccolo, 1996). Moreover, soil carbon has received particular attention as a relevant source and sink for atmospheric CO2 in the context of global climate change (King et al., 1997; Smith et al., 1997). The

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mechanisms that regulate soil organic matter concentration are however not well understood (McDowell, 2003). Generally, three classes of mechanisms are considered that stabilise organic matter in soils (Christensen, 1996; Sollins et al., 1996): (1) inherent recalcitrance of specific organic molecules against degradation by micro-organisms and enzymes; (2) chemical stabilization due to various interactions of organic molecules, surface condensation, or sorption, leading to a decreased availability of the organic substrate; and (3) physical protection of organic substrates against access by decomposers, caused by occlusion of substrate within aggregates.

In this paper, we focus on the biological side of the substrate–decomposer interaction. We explore a fourth class of mechanisms that contributes to prolonging the persistence of soil organic matter and that are not based on substrate quality or on soil conditions, but are inherent to the decomposer organisms themselves. We start by discussing how decomposer organisms access their resources. Then, we explore biological mechanisms that restrict the activity of decomposer organisms. To assess the relative importance of these mechanisms, we finally present two case studies where we quantify the soil organic matter pools that are subjected to the biological restrictions of decomposition.

2. Active versus passive stabilisation of organic matter, and access by soil organisms

Throughout this paper, we use the term "organic matter" in the broad sense that includes both, the living biomass and the dead organic material present in the soil. We understand the living biomass to be an integral part of the organic matter transformation process, where the living biomass is itself subject to transformation. Due to the various adverse interactions of soil organisms among each other and with the environment, the living biomass is under permanent threat of being destroyed. As a consequence, all organisms have evolved strong mechanisms by which they defend their physical integrity. Here, we discern two classes of such mechanisms according to the energy demand involved: passive and active stabilisation. We understand passive stabilisation as the incorporation of stabilising, repellent, or antibiotic substances into living structures, such as lignin, cutin, and tannins deposited in plant tissue (Table 1). We define active stabilisation as the continuous rebuilding and repair of living tissue at the cost of energy, e.g., brought about by membrane cycling, tissue turnover, and moulting, as well as the various kinds of defensive behaviour. While active stabilisation is a constitutive property of the living biomass, much of the passive stabilisation remains effective in dead tissue. Thus, the observed stability of dead organic matter is in part a reverberation of the passive defence strategies of the formerly living organisms.

Table 1
Major classes of recalcitrant substances, their origin, and their decomposers compiled from various sources

Substance	Origin	Degrading enzymes	Decomposer organisms
Cellulose	Plants	Cellulase complex	Mainly fungi, many eubacteria, protozoa, some nematodes, some arthropods
Hemicelluloses (xylans, mannans, galactans, pectin)	Plants	Xylanases, mannanase, galactanase, pectinases	Many bacteria and fungi
Lignin	Plants	Complete oxidation of lignin polymers requires about 15 separate exo-enzymes	White-rot fungi
Cutin, suberin, waxes	Plants	Cutinase	Plant pathogenic fungi
Polyphenols (e.g., tannins)	Plants	Polyphenol oxidases, tannin hydrolases	Fungi, bark-colonising yeasts, and bacteria
Chitin	Arthropods, fungi, protozoa cysts	Chitinases	Bacteria
Beta-glucan	Fungi	Beta-glucanases	Bacteria, fungi, insects
Melanin	Fungi, some bacteria	E.g., ligninases	White-rot fungi
Peptidoglycan (murein)	Bacteria	Peptidoglycan hydrolases	Bacteria
Keratin	Higher animals	Keratinases	Some bacteria and fungi, some insects

On the other hand, soil organisms have evolved techniques to overcome the defence of their feeding sources. As a result, none of the stabilising substances listed in Table 1 exists without a corresponding decomposing enzyme or enzyme complex produced by some organism. Generally, there seem to be few organic compounds that are totally resistant to enzymatic attack. Vlieg et al. (2000) discuss the ways in which micro-organisms deal even with highly toxic compounds. Although several animal groups including termites, cockroaches, and nematodes dispose of cellulases (Watanabe and Tokuda, 2001), the soil fauna in general relies to a large extent on micro-organisms to derive the assimilates they need from organic substrate (Lavelle, 1997). The microfauna, which comprises small animals, mainly protozoa and nematoda, directly feeds on micro-organisms. Litter transformers, represented by microarthropods, enchytraeids, and litter arthropods, exploit the biochemical decomposition capabilities of micro-organisms and participate in the external rumen type of digestion. Organic resources that have been fragmented and moistened during gut transit are actively digested by the microflora. After some days of incubation, arthropods often reingest their pellets and absorb the compounds that were released by the micro-organisms and occasionally part of the microbial biomass. Ecosystem engineers, mainly earthworms and termites, are large enough to develop symbiotic relationships with the microflora within their gut. With the physical capacities of soil fauna to mechanically crush tissue, to disintegrate soil aggregates, and to relocate soil mass, and the biochemical decomposition capacities of micro-organisms combined, the decomposer community in its entirety does not exhibit an obvious ability gap that would leave a specific organic substance in a particular tissue compartment or soil micro-site totally inaccessible for biological decomposition.

A brief look at the long-term mass balance of litter decomposition confirms that organic material must, in fact, be completely decomposable in the long run. Considering for example, that around 1000–5000 kg dm foliage is produced per hectare per year in temperate forests (Scarascia-Mugnozza et al., 2000) and that plant leaves contain 5–8% lignin (Kögel-Knabner, 2002), the annual production of lignin can be roughly estimated to be 30–250 kg lignin-C per ha from foliage alone in such forests. Similarly, 24 kg lignin-C per ha per year was estimated to be introduced by maize root growth into agricultural soil (Augustin et al., 2002). Given these production rates, lignin must be effectively degraded as it would otherwise accumulate over a few hundred thousand years to a much higher proportion of soil organic matter than the 0.2% to 10% lignin-C/organic-C observed in different soils (Martens et al., 2003). Under industrial conditions, biochemical degradation of stable organic substances is forceful enough to be applicable for product purification and waste reduction in the paper, xylose, and textile industries (e.g., Spiridon and Popa, 2000; Riisgaard, 2001). Therefore, the question arises as to why the decomposer community does not exploit its primary feeding source more efficiently and does not rapidly mineralise soil organic matter to a low concentration. To answer this question, we focus on bottlenecks in the activity of soil micro-organisms, since, as described above, the entire soil decomposer food-web ultimately relies on microbial decomposition as the primary source for energy and nutrients. In the following sections we describe four biological mechanisms that prevent soil micro-organisms from being more effective decomposers in the natural field situation.

3. Physiological and ecological restrictions of decomposition rates

3.1. Cell energy demand

In order to survive in an active stage, microbial decomposers need to cover their energy expenditure by uptake of the reaction products of enzymatic breakdown of organic substrate. Schimel and Weintraub (2003) argued convincingly that the widely applied concept of first order decomposition kinetics, $dS/dt = S \cdot Ks$, where the decomposition rate dS/dt of a substrate is only dependent on the concentration S and reactivity constant Ks of the substrate, but is independent of enzyme concentration, is unrealistic in view of the fact that micro-organisms need to adjust enzyme production to their energy budget. If second order kinetics are implemented in the form of a Michaelis–Menten reaction $dS/dt = E \cdot SKs/(Km+S)$, where E is the enzyme concentration and Km is the

half-saturation constant, simulation results are still highly unrealistic. The proportional increase of decomposition rate with enzyme concentration lets micro-organisms profit from an ever increasing enzyme production and the microbial biomass ultimately either grows out of control or crashes in such a model. Therefore, Schimel and Weintraub (2003) implemented an "inverse" Michaelis–Menten equation of the form $dS/dt = SKs \cdot E/(Kes+E)$, where *Kes* is functionally a reverse Michaelis–Menten *Km*-value representing a saturating level of enzymes on the substrate, rather than a saturating level of substrates on the enzyme. The consequence of this modification is that as the enzyme pool increases, the activity per unit enzyme decreases, causing the total decomposition activity to increase more slowly than do energy requirements for basic maintenance and enzyme production (Fig. 1). Above a specific enzyme production rate, energy costs are not paid back by decomposition products, which establishes a negative feedback loop on microbial activity. The system ultimately reaches a stable state, where the microbial biomass is constant, and the rate of carbon flow from the substrate to the microbes is constant.

Such a stable model dynamics appears more realistic. It is not specifically dependent on the inverse Michaelis–Menten equation, but seems to emerge generally from saturation of enzyme efficiency with increasing enzyme concentration. In the context of the present paper, two important insights can be gained from these models: (1) As long as enzyme concentration is a term in the reaction rate equation, recalcitrance of the substrate cannot by itself induce limitation of decomposition rate. (2) As a consequence of efficiency saturation of enzymes, microbial substrate decomposition can be strongly limited even though substrate is plentifully available.

Schimel and Weintraub (2003) briefly outline the mechanism that may be responsible for enzyme saturation. Enzymes may compete with each other for binding sites, and as an organism produces more enzymes that must bind to substrates, they must diffuse further out from the cells, and the reaction products must diffuse further back. In the next section we analyse the contribution of diffusion to limiting the efficiency of microbial substrate decomposition.

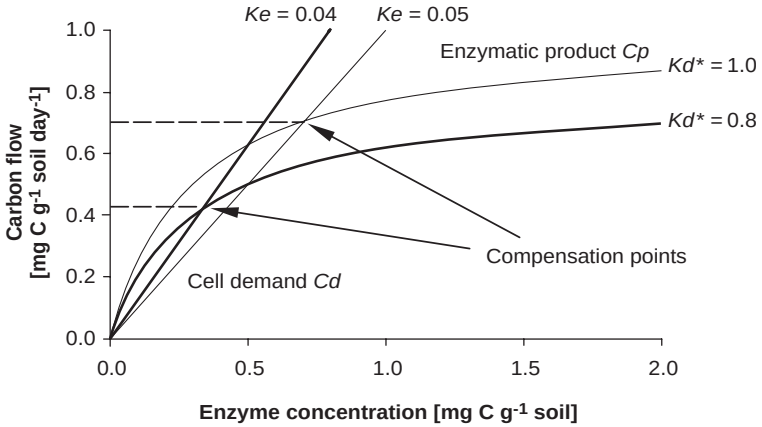

Fig. 1. Saturation of enzyme efficiency. Saturation of enzyme efficiency confines micro-organisms to operate at lower than maximum decomposition rates, because above a given enzyme concentration, enzymatic products from substrate decomposition do not meet the cell energy demand associated with enzyme synthesis. The compensation point is lowered further if conditions deteriorate, e.g. because the substrate is more recalcitrant (lower *Kd**) or because a smaller proportion *Ke* of the cell energy budget is available for enzyme production (thin lines). The figure was calculated from equations and parameter values given by Schimel and Weintraub (2003). Production *Cp* of assimilable carbon from organic matter breakdown follows an inverse Michaelis–Menten equation: $Cp = S \cdot Ks \cdot E/(Kes+E)$; where the term $S \cdot Ks$ is collapsed into a decomposition constant $Kd^* = 1.0\ day^{-1}$ (alternatively $0.8\ day^{-1}$), *E* is the enzyme concentration in mg C g^{-1} soil, and $Kes = 0.3$ mg C g^{-1} soil is the half saturation constant of enzymes on the substrate. Calculation of cell demand $Cd = 1/Ke \cdot E \cdot Kl$ is based on the assumption that microbial cells allocate on average a proportion *Ke* of 5% (alternatively 4%) of carbon uptake to exoenzyme synthesis and thereby must compensate a relative loss *Kl* of 5% enzyme concentration per day due to decay and sorption of enzymes.

3.2. Diffusion losses

Many bacteria have the ability to relocate themselves in a gradient (Parales and Harwood, 2002) and hyphal fungi can adjust mycelium growth to resource patterns (Ritz, 1995). However, the encounters of exo-enzymes with substrates, as well as the transport of decomposition products to the microbial cell are largely mediated by diffusion (Koch, 1990), which is a dispersive, not a directional process. Dispersiveness of transport implies that a considerable proportion of decomposition products may move away from the microbial cell rather than towards it. Fig. 2 depicts results of spatially explicit mathematical simulations of enzyme kinetics and diffusion in a soil cube. Without delving into the numerical details of the model, we use these figures to illustrate how microbial activity generally depends on the spatial configuration of pore space and microbial colonisation. In Fig. 2a, a single bacterial cell is floating in the soil solution at some distance from the pore wall. The cell releases exo-enzymes that catalyse the production of compounds of low molecular weight, which thereupon are taken up by the cell. Although the cell is modelled to consume catalytic products efficiently, a large proportion of the products diffuses away from the cell and dilutes in the soil solution, as is indicated by the whitish cloud forming around the bacterial cell in Fig. 2a. Removal of products from the cell happens inevitably, because diffusion drives products down the concentration gradient into the product-free volume of the soil solution. As a result, the bacterium receives relatively little payback on its investment into enzyme production and will eventually starve. The situation is greatly mitigated in Fig. 2b, where a large number of bacteria colonise the pore surface. Because diffusion is prevented to one side by the surface, and because individual cells profit from the diffusion clouds of their neighbours, product concentrations are markedly higher around individual cells and return on energy investment is substantially improved. Nevertheless, the configuration is not ideal as there are diffusion losses of soluble exo-enzymes (not visualised in the figure), and because enzymes and catalytic products can be swept away by convection. Fig. 2c depicts the sheltered situation in a narrow interstice. Here, diffusion losses of enzymes and catalytic products are largely minimised thereby enabling the bacteria to gain enzymatic products at a comparably low enzyme production. After some time however, the decomposition process will slow down because delivery of fresh substrate into the interstice is also limited.

Obviously, favourable conditions for microbial activity in the soil depend on a balanced combination of substrate availability, the presence of diffusion barriers, and vicinity to other microbes. The functional importance of the diffusion environment is emphasized by Redfield (2002), who interprets the releasing and sensing of autoinducer molecules, observed in many bacterial groups and known as *quorum sensing*, as a mechanism by which bacteria determine whether secreted molecules rapidly move away from the cell. Typically, cells produce a small

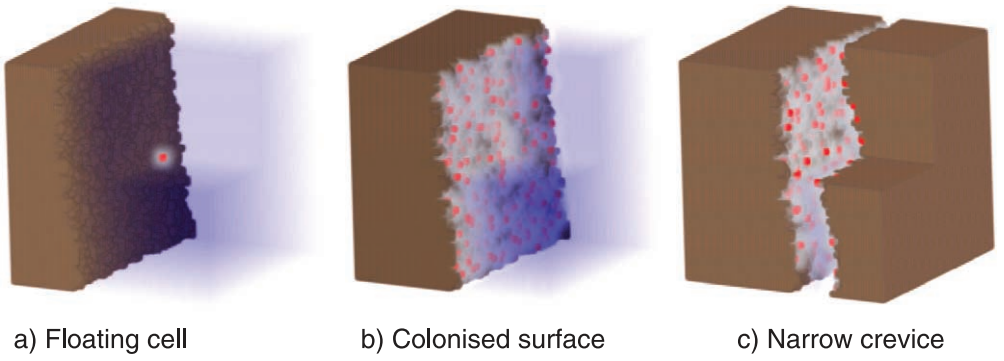

Fig. 2. Diffusion losses in different pore space constellations. The figure depicts results from a spatially explicit mathematical simulation of microbial activity in a water-filled pore space. The simulated soil cube is 50 μm wide and the upper front part is removed to enable a better view onto the pore wall. The whitish clouds represent enzymatic products that form around bacterial cells due to enzymatic cleavage of dissolved organic matter. Product concentration accessible to individual cells varies considerably with pore space geometry and bacterial density.

extracellular autoinducer molecule and simultaneously sense the concentration of the autoinducer at the cell surface. If the concentration exceeds a threshold, gene expression is induced, usually leading to the production of other extracellular products. The autoinducer accumulates when diffusion and convection are limited and when other cells release autoinducers in the vicinity. As a consequence, secretion of exo-enzymes is only induced when they can be productive. The autoinducer is rapidly diluted when diffusion or convection is high and populations are sparse, which prevents wasteful secretion of degradative enzymes and other effectors. It therefore appears likely that many bacteria remain inactive in an unfavourable diffusion environment, even if substrate is available.

The mutual benefit of neighbouring cells in reducing diffusion losses means that once a dense microbial population has built up, activity can be maintained under degrading conditions. Regularly, micro-organisms form multispecies biofilms with a complex three-dimensional architecture ranging from thick confluent layers to dispersed micro-colonies or stacks of cells protruding from a thin basal layer (Heydorn et al., 2000; Webb et al., 2003). Cells in these biofilms are embedded in a matrix of exopolysaccharides that ensure attachment and mechanical stability of the biofilm (Stickler, 1999; Tsuneda et al., 2003), and that can act as biosurfactants to increase the solubility of hydrophobic substrates and make them available for decomposition (Ron and Rosenberg, 2001; Johnsen and Karlson, 2004). Conversely, the high diffusion losses experienced by a single remote cell mean that new microbial colonies do not readily form on uncolonised surfaces, unless accessibility for micro-organisms is high and local conditions are favourable. As a result, microbial activity is confined to a few microhabitats that have the right set of conditions, and less than 5% of the overall available space in soil is occupied by living micro-organisms (Nannipieri et al., 2003). Specifically, microbial biomass tends to concentrate along preferential water flow paths in the soil, where transport of nutrients and of microbial propagules is high (Vinther et al., 1999; Bundt et al., 2001). Thus, the spatial pattern of microbial activity does not proportionally follow substrate quality across the soil. Instead, microbial activity tends to exaggerate differences in habitat quality and substrate supply, and the recent activity pattern is coined by stochastic events of past colonisation.

3.3. Selective habitat exploitation and preferential substrate utilisation

Spatial aggregation is by no means specific to micro-organisms. All soil fauna is known to be unevenly dispersed in space (Ekschmitt et al., 1997). The scales of habitat utilisation depend mainly on the size of the organism: a few μm for bacteria, less than 100 μm for fungi, between 100 μm and 2 mm for microarthropods, between 2 and 20 mm for macroarthropods (Coleman and Crossley, 1996). Correspondingly, microflora, microfauna, litter transformers, and ecosystem engineers operate at increasing scales of time and space (Lavelle, 1997). Across a hierarchy of scales, discernible spheres of influence are formed, classified as detritusphere, aggregatusphere, rhizosphere, drilosphere, and porosphere by Beare et al. (1995). More generally and based on the assumption that organisms evolve towards an optimal exploitation of their habitat, Ideal Free Distribution theory (Fretwell and Lucas, 1970; Fretwell, 1972) predicts that favourable microhabitats are preferentially colonised, and less favourable microhabitats are successively exploited only if the organisms' density rises high enough to reduce resource availability within the colonised areas below that of the uncolonised areas. Since population densities are almost always limited either by environmental conditions, such as drought, heat, and frost, or by adverse interactions with other organisms, such as competitors, parasites, and predators, organisms will on average leave a considerable part of the total habitat untouched in a natural and heterogeneous field situation.

In addition to being selective in the choice of habitat, organisms can be specialised towards using particular resources. A major characteristic of soil microbial populations is their enzymatic specificity for substrate degradation. Here, we use a broadly generalised classification of micro-organisms into r-strategists and K-strategists to illustrate the consequences of selective substrate use (Fontaine et al., 2003). Following fresh organic matter input to soils, many specialised micro-organisms grow quickly and only

decompose the easily assimilable parts of the substrate. These micro-organisms, commonly classified as r-strategists, are adapted to rapid growth, depending on availability of their substrate. After substrate exhaustion, r-strategists die or become dormant because they are unable to use the remaining recalcitrant substrate components. The late stages of decomposition are marked by the colonisation of plant residues by particular populations classified as K-strategists that slowly degrade the most recalcitrant substrate. These micro-organisms grow slowly and dominate only in the last stages of decomposition. Even if large amounts of easily degradable substrate are supplied, K-strategists may not have enough time to assimilate these because they respond too slowly compared to r-strategists. As a consequence, the decomposition of high quality and low quality substrate is largely decoupled. Many studies have shown that the supply of nutrients and quickly assimilable carbon such as soluble sugars, amino acids, root mucilage, or rhizosphere extract did not consistently increase the decomposition rates of recalcitrant substrates (Hamer and Marschner, 2002; Fontaine et al., 2003).

The combined effect of selective habitat exploitation and preferential substrate utilisation will inevitably be that at each given point in time, some proportion of accessible substrate is actually not accessed by the decomposer community. Particularly, those decomposition pathways that require a cascade of consequent degradation steps performed by different micro-organisms can be delayed by the accidental and temporary lack of one member of the succession chain (Moller et al., 1998). In the terminology of Non-Equilibrium Theory (DeAngelis and Waterhouse, 1987), the substrate which is temporarily not accessed by decomposers is protected in a partial refuge. The term "partial refuge", denotes a habitat that may rapidly lose its protective status when it is accidentally colonised by new organisms. The term "absolute refuge", in contrast, denotes a habitat that is inaccessible for those organisms and can therefore not be colonised. We consider sorption to mineral surfaces as the main mechanism that possibly can create an absolute refuge for organic matter, particularly so if organic matter is associated to micropores small enough to prevent access from biological attack (Kaiser and Guggenberger, 2003). Other mechanisms, such as occlusion of substrate within soil aggregates give rise to only partial protection, which ends when the aggregates are, e.g., crushed by earthworm activity. In the next section, we present quantitative examples of the relative proportions of soil organic matter protected in a relative, and an absolute refuge, respectively.

4. Sizes of stabilised and protected carbon pools

Fig. 3 depicts two examples of soil carbon pools, from a barley field at Kjettslinge, Sweden (Andrén

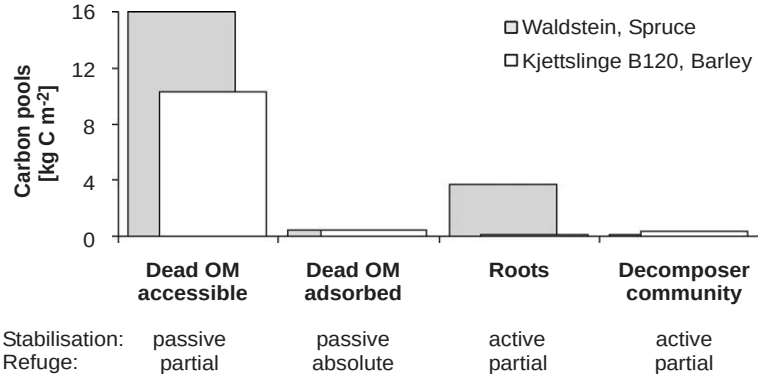

Fig. 3. Classification of soil organic matter pools. Two examples of carbon stocks in an agricultural soil (Kjettslinge, Sweden) and a forest soil (Waldstein, Germany) classified according to (1) passive or active stabilisation against degradation, and (2) partial or absolute refuge from decomposers. In both soils, a major proportion of organic carbon resides in the passive stabilisation/partial refuge status and is potentially accessible for decomposition. Data from Andrén et al. (1990) and Schulze (2000). The size of the absolute refuge was assessed by assuming that a maximum of 411 g C m^{-2} is adsorbed to mineral surfaces (Guggenberger and Kaiser, 2003) and is therefore inaccessible.

et al., 1990) and a spruce forest at Waldstein, Germany (Schulze, 2000). Carbon pools were separated according to passive or active stabilisation, and partial or absolute refuge. In both soils, a small proportion (0.4–3.4%) of organic carbon was allocated in the living biomass of the decomposer community. This pool is considered biologically active, stabilising itself against degradation at an energy cost of around 0.8–2.1 times the pool size respired as CO_2 per year. In the forest soil, a considerable amount (18.3%) of organic carbon was allocated to roots. This pool is actively maintained by plant photosynthetic production. The remaining parts of organic soil carbon belonged to the dead organic matter, which is only passively stabilised. In an analysis of seven forest soils, Guggenberger and Kaiser (2003) found that the capacity of mineral soils for sorption of organic matter was limited to a maximum of 411 g C m^{-2}. Taking these data as a reference, we estimated the sorbed carbon pools potentially representing a pool in an absolute refuge to amount to (less than) 3.7 and 2.0% of organic matter in the barley soil, and the spruce soil, respectively. Under these presumptions, the largest part of soil organic matter (92 and 79%) appears to reside in the least secured status. This pool is only passively stabilised, and it is located in only partial refuges, if any, and it is therefore potentially accessible to the soil community for decomposition.

5. Conclusions

In our review, we started from the notion that there is an apparent discrepancy between a high organic content persisting in soil, and the rather omnipotent decomposing abilities of the soil microflora and fauna. In the preceding section we confirmed that the largest proportion of soil organic content is potentially accessible to biological decomposition. We explained several reasons why decomposer organisms should be unable to exploit accessible organic resources more rapidly. Cell energy demand forces micro-organisms to operate at decomposition rates lower than the compensation point. Diffusion losses inhibit microbial growth and impede the foundation of new microbial colonies on uncolonised substrates. Specialisation of organisms towards particular microhabitats and substrates gives rise to partial refuges where organic resources are temporarily not accessed. In combination, these mechanisms act to reduce the rates of organic matter decomposition far below those of an optimally designed industrial process. The common background behind those mechanisms is certainly that evolution selects organisms towards persistence of populations and not towards maximum decomposition rates. It is a well-known problem of engineered microbial cultures that strains go through many generations and this generally favours selection for improved growth rates at the expense of reduced enzyme production rates, under conditions of high nutrient availability in the cultures (Zelder and Hauer, 2000). Specifically, in the case of K-strategists specialised towards degradation of recalcitrant substrates with low decomposition constants, the compensation point of decomposition rate will be low and micro-organisms will adapt to slow enzyme production and to the associated moderate gain of assimilable cleavage products and moderate growth. Thus, although perfectly able to degrade any substrate, the decomposer community will not evolve towards decomposing all substrates at a fast rate. We therefore conclude that the ecological limitations inherent to soil life play a substantial role within the complex of physical, chemical, and biological mechanisms that contribute to keeping decomposition rates low and to maintaining carbon stocks high in temperate soils.

Acknowledgements

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