

Chapter 1

Soil Microbiology, Ecology, and Biochemistry: An Exciting Present and Great Future Built on Basic Knowledge and Unifying Concepts

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I SCOPE AND CHALLENGES

The study of soil biota, their interactions, and biochemistry, the subject matter of this book, must strive for excellence in both its research and impacts as it gains ever-increasing importance in science, education, and applications. Text-books have a fundamental role to play in synthesizing information in a readable manner and making it available to a global audience. Knowledge in this field is expanding at an exponential rate at a time when global society faces a multitude of challenges to help maintain environmental sustainability. Many great opportunities exist. Advances in molecular techniques and analytical instrumentation are revolutionizing our knowledge about microbial community structure and are facilitating the integration of this knowledge with concepts concerning the composition and formation of soil organic matter (SOM), its interactions with the soil matrix, and its role in ecosystem functioning. Responses to climate

change and the possibility of increased natural disasters are at the forefront of our need to supply information on possible impacts. Questions about the role of soil biota and their processes, relative to food security for an increasing global population that needs to improve its diet at a time of economic globalization, will also need to be answered with sound science. Invasive species, water and air pollution, and plant diseases will probably be exacerbated by climate change and by intensification of management for food production and biofuels at the same time that we strive to protect our natural environments. Soil microbiology, ecology, and biochemistry will increasingly be called on to help provide the basic information required for biologically sustainable ecosystem services at a reasonable cost (Cheeke et al., 2013).

The history of our science is important to interpret today's knowledge and challenges. Perusing a few of the volumes of older literature can provide scientific insights and demonstrate approaches to problem solving that are very applicable today. The *Textbook of Agricultural Bacteriology* by Löhnis and Fred (1923) is an English translation and revision of the early 1913 German text. This book highlights the 1890 to 1910 "Golden Age of Microbiology" when representative microorganisms responsible for the major biogeochemical cycles were discovered. Although entitled "Agricultural Bacteriology," fungi and fauna are also discussed. Waksman and Starkey (1931) recognized the role of decomposition in the carbon (C) cycle. They calculated that the atmosphere over each acre of land at 0.03% CO₂ represented 5.84 tons of C when at that time a good yield of sugar cane consumed 20 tons of C. They also estimated that atmospheric CO₂ had a global turnover time of 35 years. The general content and format of that text were followed in subsequent volumes, including the current one.

Principles of Soil Microbiology (Waksman, 1932), a more extensive volume, recognized the rapid growth in the knowledge of mycorrhizal fungi, the solid foundation developed in the study of decomposition, the relationships between plant growth and microbial activity, and the interdependence between the activities of microorganisms and chemical transformations in soil. The availability of direct, microscopic counts showed that only 1-5% of the microscopic microbial count could be cultured and that the bacteria and fungi occupied only a tiny fraction of the soil volume. Waksman's, (1952) volume contains a good history of the field with pictures of our founding parents and grandparents. It did something I hope this volume also does by pointing out some of the more promising lines of advancement in our field and in suggesting some likely paths for future study.

Alexander (1961) recognized the interplay of microbiology, soil science, and biochemistry, and his book contains an initial section on microbial ecology and ecological interactions that summarizes community composition as understood before the molecular age. His chapters on the microbiology of plant component and pesticide decomposition, written before the major impact of isotope tracer research, are still well worth a trip to the library. Swift et al. (1979), in their volume, *Decomposition in Terrestrial Ecosystems*, highlighted the

importance of faunal-microbial interactions, as did *Fundamentals of Soil Ecology* (Coleman et al., 2004). Binkley's (2006) chapter, "Soils in Ecology and Ecology in Soils," highlights the integration of soils, plants, and animals and discusses interactions of soil science and ecology in the twenty-first century. Berthelin et al. (2006) wrote an interesting history of soil biology, and the writings of Feller et al. (2003) and Feller (1997) review the role of humus in soils. Earlier editions of this text have also provided a history of this field. The individual chapters of this volume provide further background information that highlights the rapid advances that will allow soil microbiology, ecology, and biochemistry to successfully advance into the future based on a solid past and exciting present. They also strive to follow the example of Waksman (1952) in suggesting some likely paths for the future.

II THE CONTROLS AND UNIFYING PRINCIPLES IN OUR FIELD

No field of knowledge stands alone, and modern science must provide impacts and applications for society, as well as for teaching and research. It is important that readers gain an integrated knowledge of studies on (1) all soil biota, which for historical purposes we still often lump under the term "microbiology"; (2) the relationship between organisms and their physical surroundings, which is referred to as their "ecology"; and (3) the physiology of organisms, enzymes and their relationships to SOM, nutrient cycling, and biogeochemistry, which we call "biochemistry." It is most important to have an understanding of how the different subjects are integrated. A number of unifying concepts can assist in such integration. Figure 1.1 shows some of the areas that define our field and also the multiple biotic and abiotic controls. The interactions would have to be shown in a third dimension and are best discussed with the use of models that adequately incorporate these concepts (Chapter 17). The discussion of biochemistry and physiology (Chapter 9) and that on the application of concepts in ecology (Chapter 10) help provide readers from a variety of backgrounds with some of the required information we need in integrating our diverse field of studies.

This volume will be used for teaching and research in biogeochemistry, microbiology, soil science, ecology, and biology classes. Applications in food, biofuel, and fiber production include forestry, agriculture, and range sciences (Chapter 18). Engineers and industry consultants are applying soil biological information to many studies, including pollution control. Today's societal questions include soil biotic responses to global change. We must be able to supply information on how to mitigate some of the negative effects of CO₂, CH₄, and N₂O as greenhouse gases. The role of tundra soils and peats in the global-C cycle must also be considered as the earth warms and changes in its precipitation patterns. The finding that frozen soils contain an amount of C equivalent to the rest of the terrestrial soil C supply is mind-boggling. However, much of this occurs in deep deposits, cryoperturbed sites, and peat deposits, often found in

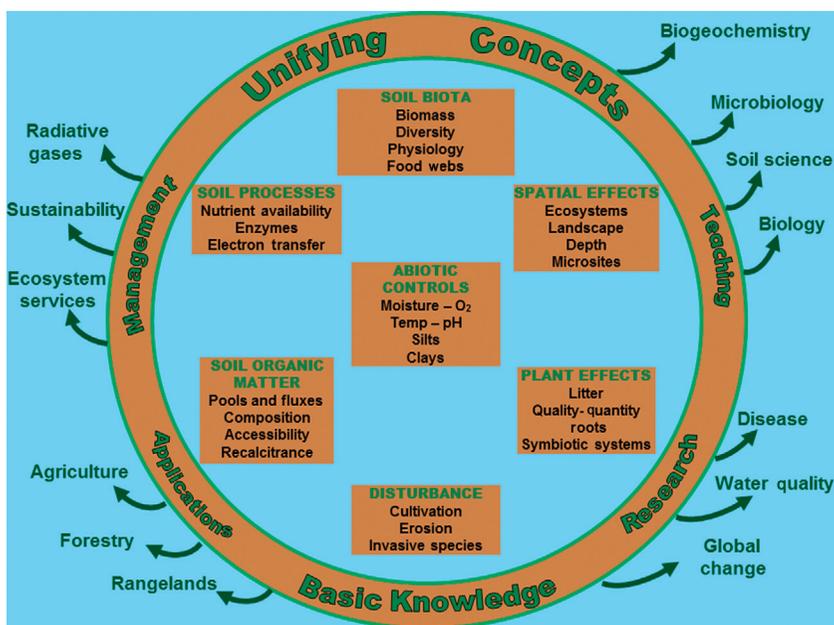


FIG 1.1 Controls and unifying concepts in soil microbiology, ecology, and biochemistry.

estuaries, where the water content may control its decomposition more than global warming. Increased human populations, along with a common desire across the globe for better living standards, will place demands on food and fiber production. Soils are the major resource for these efforts. Efficient utilization of nutrients involves not only C and N, but also P, S, Fe, and the minor elements (Chapter 16). Soil organisms will be called on to help maintain soil tilth, water penetration, resistance to erosion, and other ecosystem services, including water quality, invasive species, and disease prevention. The following section will highlight spatial distribution and community composition of organisms and their substrate, SOM composition, matrix interactions, microbial products, and spatial scaling. More detailed information and references are found in the succeeding individual chapters.

III THE SPECIAL ROLE OF ACCESSIBILITY AND SPATIAL SCALING OF BIOTA AND SOIL ORGANIC MATTER

The size, accessibility, and spatial distribution of the soil biota, enzymes, microbial products, and organic matter are recognized as being of prime importance in the reactions and processes discussed in this volume. Löhnis and Fred (1923) recognized that the very small size of microorganisms resulted in large surface areas and allowed very large numbers to persist in soil, water, air, and food. Waksman and Starkey (1931) showed pictures that related microorganisms

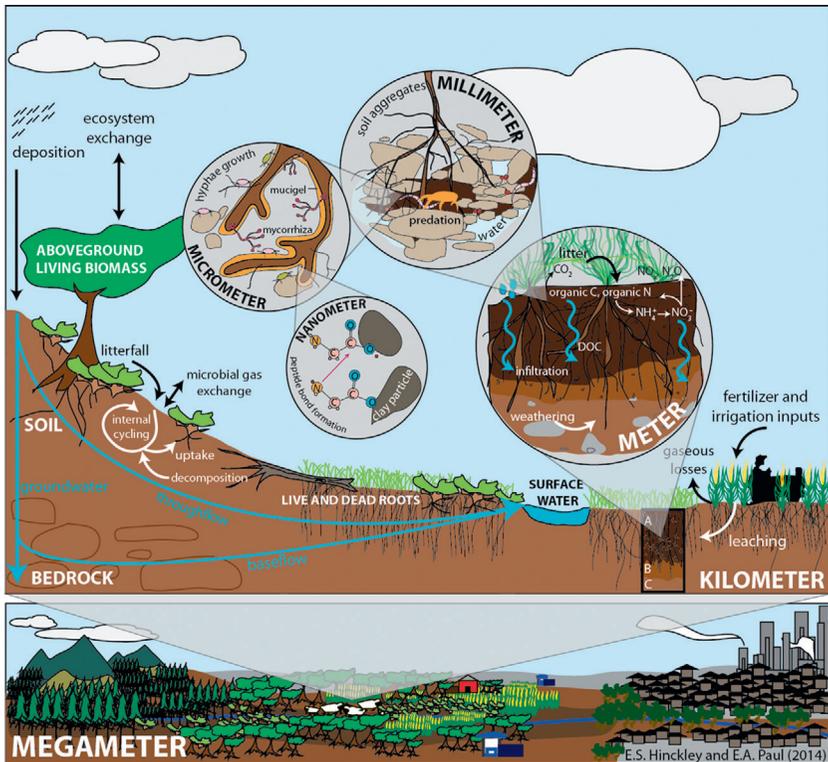


FIG 1.2 Spatial relationships from the nanometer to the kilometer and megameter must be understood to interpret soil microbiology, ecology, and biochemistry. *Drawn and copyrighted by E. Hinckley and E. Paul.*

to the soil's physical structure, recognized the colloidal nature of SOM, and calculated that 100 million bacteria in a gram of soil would occupy only 1/10,000th of the total soil volume.

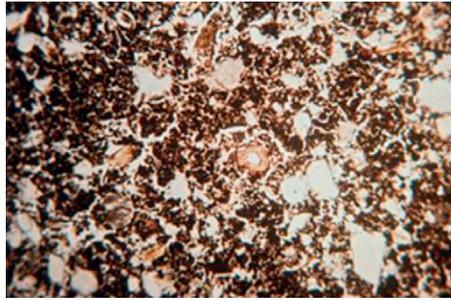
There is a widespread recognition of the need to interpret processes at multiple scales, including molecular (nm), microorganism (μm), soil fauna, aggregates and roots (mm), whole plant and soil pedon (m), field and landscape (km), and especially now to global levels (megameter), as shown in Fig. 1.2. The biochemical processes occur at the nm scale with individual bonds and atoms occurring at the even smaller Angstrom scale (not shown). Typically, enzymes are 3-4 nm in size, as are the micropores of minerals, such as allophane. Clay particles with lengths of 2 μm , but with an edge of 1 nm, have a surface area approaching 1000 m^2g^{-1} . We often assume that the soil organisms are associated with the clay fractions by attachment to the particles, but particles can often be attached to the microbiota, especially where sesquioxides are involved. Soil colloids, which are operationally defined, usually have a size of 1-1000 nm. Nanoparticles are defined as being 1-100 nm. The microorganisms in an

average soil with 2% SOM will often comprise an average biomass of $300 \mu\text{g C g}^{-1}$ soil. This is equivalent to $600 \mu\text{g g}^{-1}$ soil biotic biomass and represents 0.06% of the total soil volume, a value not that dissimilar from [Waksman's \(1932\)](#) estimate. Roots have been shown to occupy 1% of the soil volume of surface soils, with early microphotographs showing that the associated biota covered a small portion of that surface. Enzyme production has been said to be equivalent to 1-4% of microbial production with more being produced through biomass lysis ([Sinsabaugh and Shah, 2012](#)). Thus, enzymes occupy approximately 0.0025% of the soil volume demonstrating that the substrate and the enzymes mediating its turnover can easily be spatially separated. The soil matrix, especially clay particles, can protect both the enzyme and the substrate from attack, but may also concentrate the amounts and interactions for faster reactions.

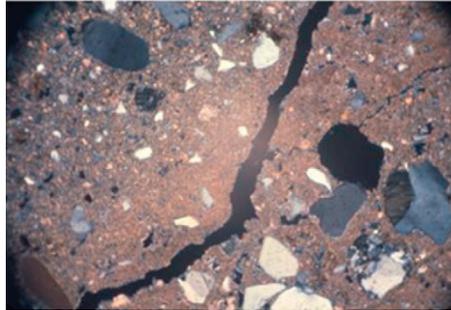
It is imperative that we interpret our studies at the appropriate scales relative to the interactions between processes and scales. An appropriate example of spatial scale challenges can be found for nitrogen (N) reactions in the biosphere. Where earlier editions stressed the need for increased N for agricultural production, present overuse of Angstrom-based, industrial N for fertilization at the plant (m) scale has resulted in two microbial reactions at the μm scale (i.e., nitrification and denitrification). The oxidation of ammonium to gain energy at the μm scale results in both NO_3 and N_2O . Nitrification could be called one of the worst diseases attributable to disturbance and agriculture. Soil microorganisms in the absence of oxygen at the μm scale use denitrification to oxidize other substrates producing some N_2O . Although these processes help close the N cycle, they also are one of the great ecological challenges at the megameter scale.

Visualization of the soil can now be achieved at the molecular (nm) level ([Chapter 7](#)). The μm to mm scale, found in thin sections, can also be useful. [Figure 1.3](#) shows the great differences in habitat and spatial accessibility between the parent material (C horizon) devoid of SOM and the surface horizon of a grassland Mollisol. It shows a cross section of a root as well as plant-residue particles that tend to concentrate substrates and organisms. The SOM, although accounting for only 3% of the volume of this soil, appears to be uniformly distributed due to its nm size and high surface area. This is very important in exchange reactions, aeration, and water-holding capacity due to its colloidal characteristics. The fungi and fauna will be concentrated on the plant particles and the outsides of aggregates ([Chapter 8](#)), whereas the aggregate interiors have more bacteria. From this figure, it also is easy to see why later chapters will show that much of the biological activity occurs in the upper soil surfaces.

The illustration "Mechanisms of soil organic matter stabilization: evolution in understanding" by J. D. Jastrow ([Fig. 1.4](#)), adapted from [Jastrow and Miller \(1998\)](#), shows (in green) three major categories of mechanisms responsible for stabilizing soil organic matter—biochemical recalcitrance, chemical stabilization, and physical protection ([Christensen, 1996](#); [Sollins et al., 1996](#)) and updates these to reflect evolving insights into the factors controlling



Surface soil



Subsurface soil

FIG 1.3 Thin section of subsurface and surface soil showing the general distribution of soil organic matter, aggregates, and plant particle concentration in the surface relative to the unaggregated, low SOM subsurface.

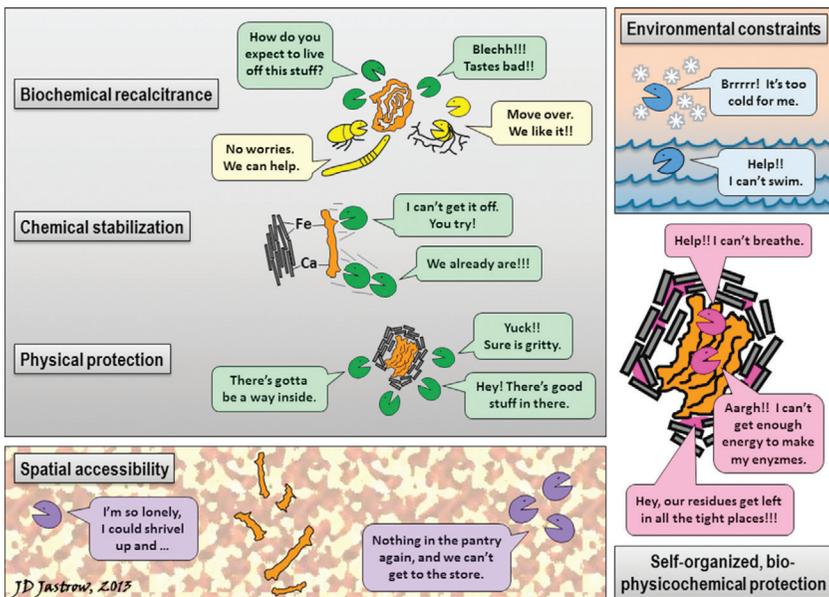


FIG. 1.4 Mechanisms of soil organic matter stabilization: evolution in understanding. *Courtesy of J. D. Jastrow, 2013.*

stabilization. Although biochemical recalcitrance may affect the rate of decomposition or transformation, recent research indicates that all types of organic materials are decomposable under the right conditions (illustrated in yellow). Thus, the intrinsic chemical characteristics of SOM are no longer believed to be a key determinant of its long-term persistence in most soils. The important role of environmental constraints (particularly at high latitudes and for wetlands) is highlighted in blue. In addition to the physical protection afforded by occlusion of organic matter in aggregates, decomposition can be limited due to spatial accessibility (shown in purple), that is, sometimes decomposer populations are simply not co-located with their substrates or are prevented from reaching them due to physical constraints, such as the distributions of water and air within the pore network. New understanding of the feedbacks between soil biota and soil structure suggests several integrated biophysicochemical stabilization mechanisms (shown in magenta) can occur via the dynamics of this self-organized system.

IV SOIL ORGANIC MATTER AS A CONTROL AND INFORMATIONAL STOREHOUSE OF BIOTIC FUNCTIONS

Löhnis and Fred (1923), who produced the first “cycle of matter” diagram, stated that all organic residues must be mineralized; otherwise the earth would long since have been littered with corpses. That proportion of primary production and animal products, stabilized against immediate mineralization, forms the life blood of our natural resources as SOM (Chapter 12). The study of this component and its interactions is receiving increasing attention because of its importance in global change and to breakthroughs in the methods of study (Chapter 13). The study of SOM, often referred to as humus or humic substances, has long been recognized as being of significance for soil quality and plant growth (Chapters 2 and 18). Soil organic matter has also long been recognized as significant to religious and mythological beliefs in ancient cultures (Feller, 1997). Wallerius, in his 1761 book on scientific agriculture, related humus to plant decomposition and water-holding capacity, although the belief that humus was a direct plant food source was later proven to be incorrect. In 1766, Archard first fractionated humus (peat) with alkaline solutions, and in 1804, de Saussure confirmed it was primarily composed of C, H, O, and N and could produce CO₂ (Kononova, 1961). In 1806, Berzelius described the interaction of dark black, brown, and yellow humic compounds with metals, a subject that today still requires further work in describing SOM stabilization. Waksman’s (1952) chapter on humus summarized his earlier review (Waksman, 1938) by stating, “Humus represents a natural organic system in a state of more or less equilibrium.” He predicted today’s discussion on the components of this important substrate by saying, “Frequently, the narrow definition does not differentiate between humus and humic acid, another ill-defined term occasionally used for the alkali soluble or alcohol soluble humus

constituents” (p. 125). The Russian author [Kononova \(1961\)](#) reviewed the extensive humic studies and argued that Waksman’s comments were inaccurate. However, today there are new questions regarding humic substance synthesis by polycondensation reactions of microbially transformed plant products. Many now believe that humus is a complex mixture of microbial and plant polymers and that their degradation products are associated in super structures, stabilized by hydrogen and hydrophobic bonds.

Earlier versions of this text stated that the materials stabilized by clays are the older, complex, humified components. Our present research is questioning this concept. It indicates that microbial products are associated with the clays and thus protected. It also shows that all soil fractions contain some proportion of young and old materials and that they all participate, to varying degrees, in the stabilization of SOM. The particulate fraction ($>53\ \mu\text{m}$), although primarily consisting of plant residues and associated microbial products, can also have older charcoal and organic-micelle protected residues. The older, mineral-associated fractions have a large concentration of materials that can be thousands of years old, but because clays also react with the recently produced microbial products, they also contain some young components. The wish to isolate defined fractions with very specific mean residence times will never be completely possible. All fractions constitute a part of a dynamic soil system and will have varying degrees of both old and young materials depending on the fraction isolated. Modern methodology now allows us to use a number of approaches that can give a great deal of information regardless of whether the SOM is defined on a biochemical, functional, or physical kinetic basis or as humic compounds (Supplemental Fig. 1.1; see online supplemental material at <http://booksite.elsevier.com/9780124159556>).

An SOM-spatial distribution complex in soils that deserves more attention involves extracellular polysaccharides. Extracellular polymeric slime has long been recognized in soils, especially in aggregation. It is also known to be involved in biofilms and on root surfaces ([Fig. 1.2](#)). The assemblage of microcolonies within a biofilm can involve protozoa, nematodes, fungi, and a broad range of prokaryotes. Biota embedded in biofilms often have altered phenotypic expressions and complementary functions ([Dick, 2013](#)). They are also considered to have cell-to-cell signaling and nutrient and energy transfer functions. There is a need to understand their role in interpreting community diversity and in soil enzyme functioning. Other complex interactions will no doubt be found as we delve deeper into the interesting field we call soil microbiology, ecology, and biochemistry.

V BIOTIC DIVERSITY AND MICROBIAL PRODUCTS

The significant breakthroughs in molecular biology that have occurred in the last 30 years, in conjunction with the recent advances in automated-gene sequencing ([Chapter 6](#)), will allow us to characterize a greater proportion of the soil biota as

well as determine their functional genes. There have been recent advances in both the organisms and processes in the N cycle (Chapters 14 and 15). Advances in automated analysis of physiological reactions, enzyme assays, and soil respiration (Chapter 7) are giving us the opportunity to relate information on community diversity to microbial ecology (Chapter 10), physiology and biochemistry (Chapter 9), and global distribution (Chapter 8). These techniques have identified the archaea and recognized many nonculturable soil inhabitants. It is important that we ask how this new information can be related to the controls shown in Fig. 1.1. We must ensure that the best available modern methodology is used to ask questions about the processes involved. Biodiversity by itself is an important question, with soil being the greatest repository of genes in nature (Chapters 3, 4, 5). As we ask questions about community composition, the role of genetic redundancy becomes important. The various chapters in this volume will show that the generalized processes such as decomposition, which can be carried out by numerous organisms, have significant genetic redundancy. Food web interactions (Chapter 5) can be complex and may require more information on specific organisms and genes as well as on interactions (Moore and de Ruiter, 2012). Specialized biogeochemical processes, such as those in nitrification (Chapter 14) and N fixation (Chapter 15), are carried out by restricted populations that can become limiting (Bardgett, 2005). Arbuscular and ectomycorrhizal fungi (Chapter 11) are associated with many plants, but not all associations will provide benefits and can even be parasitic in nature. Some of these fungi still cannot be grown in pure culture. Genomic analysis is vital for understanding the complex biotic interactions involved (Chapters 3, 4, and 5). The same is true for physiological processes such as symbiotic relationships (Chapters 11 and 15) and nutrient transformations (Chapters 16 and 18), in which the most competitive colonizers may not be the most efficient ones.

VI UNIFYING CONCEPTS

There is now significant research showing that unifying concepts can be developed for the controls in soil microbiology, ecology, and biochemistry (Fierer et al., 2009). Individual controls (Fig. 1.1) may dominate at a specific microsite; however, at the plant-pedon level and above (Fig. 1.2), many soils have a large number of similarities. Figure 1.5 summarizes some of the major biotic-abiotic components and controls that occur in soils. The plants affect the biotic community structure and, eventually, the amount of SOM, due to both the quality and quantity of their above- and belowground inputs and whether or not they produce a litter layer. The two bacteria, pictured in Fig. 1.5, were originally shown as colored inserts in Löhnis and Fred (1923). Decomposition involves many organisms providing genetic redundancy, but the enzymes involved in lignin degradation are somewhat specialized and have a slight home field advantage, where the organism in the litter below a certain type of plant will decompose that litter at a slightly faster rate. The lignin to N ratio is a good

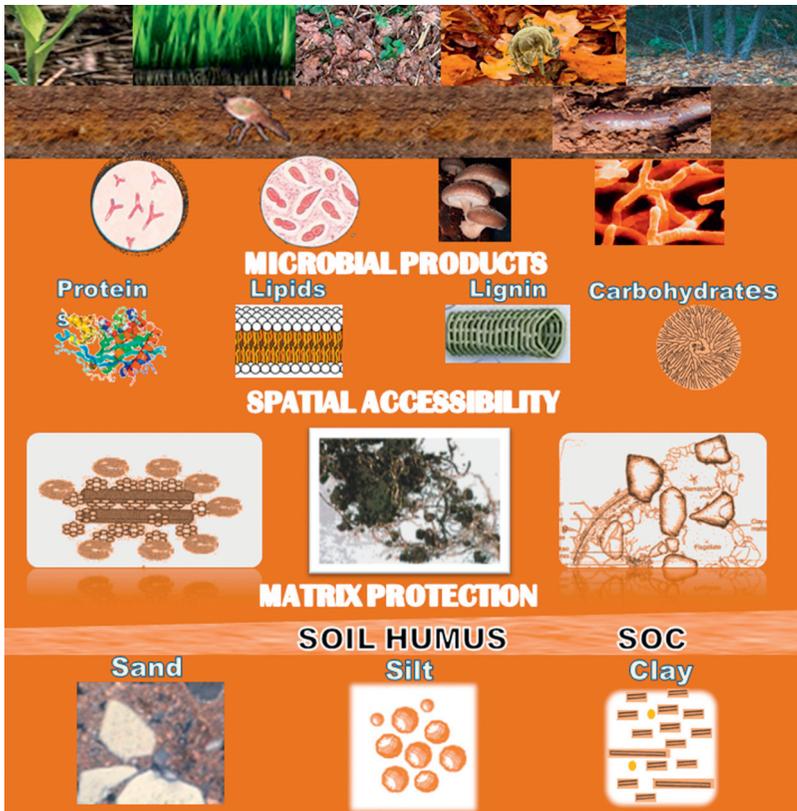


FIG. 1.5 Representation of the effects of plant litter quality and quantity on litter accumulation, microbial community structure, spatial complexity, humus composition, and soil matrix interactions involved in the control of the interactions in soil microbiology, ecology, and biochemistry.

general indicator of litter decomposition, but not of humus formation. In addition, lignin does not appear to persist in soils. [Cotrufo et al. \(2013\)](#) proposed the Microbial Efficiency-Matrix Stabilization (MEMS) framework ([Fig. 1.6](#)) to study and integrate litter decomposition and SOM formation. This was based on the current understanding of the importance of microbial C use efficiency (CUE) and C and N allocation in controlling the proportion of plant-derived C and N that is incorporated into SOM. The MEMS diagram also stresses the importance of soil-matrix interactions in controlling SOM stabilization. The factors directly controlling the proportion of plant-derived C and N retained in SOM pools versus mineralized, in the short-term, include microbial allocation of C and N to growth, enzyme production, and microbial products that interact with the soil matrix.

Results from NMR, pyrolysis molecular-beam mass spectrometry, XANES, and mid-infrared analyses show that humus from many different soils has a

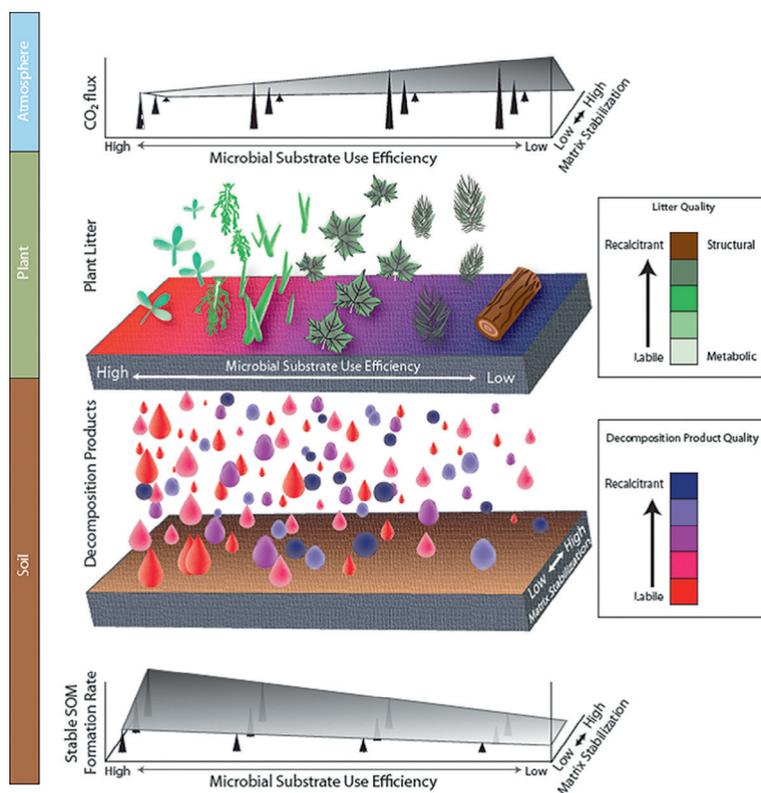


FIG. 1.6 Representation of the effects of plant litter quality on CO₂ efflux and soil organic matter (SOM) stabilization in the microbial efficiency-matrix stabilization (MEMS) framework. Above- and belowground plant litters undergo microbial processing, which determines the quantity and chemical nature of decomposition products. More dissolved organic matter, carbohydrates, and peptides are formed from high-quality (e.g., fine roots and herbaceous) litter than from low-quality (e.g., needle and wood) litter, which loses most of the C as CO₂. The fate of the decomposition products depends on their interactions with the soil matrix. More stable SOM accumulates in soils with a high soil matrix stabilization, including expandable and nonexpandable phyllosilicates: Fe-, Al-, Mn-oxides, polyvalent cation, or high allophane content. *Cotrufo et al. (2013)*.

somewhat similar basic complex of functional groups related to plant and microbial products. These darkly colored materials can be protected by self-aggregation, especially for micelles where hydrophobic lipids of both plant and microbial origin provide water repellency. The stabilization of substrate by clays, sesquioxides, and microaggregate formation results in the 1000-year-old SOM products so often found in soils. The protection of SOM by silts and clays results in SOM levels from the 0.6-8% soil organic carbon (SOC) usually found in mineral soils (Fig. 1.5). Protection by calcium and sesquioxide has long been known to exist, but has not been studied enough to allow quantification for model parameterization.

The advances in biotic, community structure analysis by techniques, such as pyrosequencing, should also provide enough information on biotic community composition to allow its incorporation into further understanding and model development. The interactive controls and the importance of enzymes and matrix stabilization of amino compounds tend to produce humus components low in C:N ratio and are somewhat similar in all soils allowing us to further seek unifying concepts. An example of the development of understanding through multiple approaches and modeling that will be covered in this volume is given in Supplemental Fig. 1.2 (see online supplemental at <http://booksite.elsevier.com/9780124159556>). The SOM at a long-term experimental site in Michigan was shown to have a kinetically determined, active fraction representing 5% of its C with a rapid turnover rate largely dependent on recent inputs. The slow pool, determined with tracers and long-term incubation due to its significant size and moderate turnover, is the most important pool in nutrient cycling and biogeochemistry. The large, resistant pool supplies long-term stability, but is still sensitive to recent management.

Symbiotic systems are an important part of nearly all plant soil relationships. Aboveground, beneath-ground photosynthate distribution, and root production are major factors in controlling many of the biota and organisms discussed in this volume. The high energy-requiring, symbiotic-N fixers require more photosynthate than the mycorrhizal fungi, but the mycorrhizal fungi contribute significantly to SOM formation. Due to an increased understanding of the size, activity, and community composition of soil biota, we can now assign some numbers to their roles in C cycling at this site. The bacteria are responsible for more of the C respired from the maize soybean rotation. However, the fungi dominate respiration in the poplar plantation illustrating that although similar controls exist, specific populations and abiotic controls affect individual ecosystem processes. The fauna play their major role as ecosystem engineers. The nanometer, micrometer, and kilometer effects and interactions shown in Fig. 1.2 all relate to the understanding and modeling (Chapter 17) of the global (megameter) aspects of the C cycle reflected in the rapidly rising atmospheric CO₂ contents. The controls and interactions must be considered as we ensure that the exciting present information on soil microbiology, ecology, and biochemistry outlined in this volume builds toward a great future created from a basic knowledge and unifying concepts.

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