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Soil Microbiology, Ecology, and Biochemistry in Perspective

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GENERAL HISTORY AND SCOPE

The processes that occur within soil are closely related to those in sediments and aquatic environments. They are also associated with the beginning of life on this planet. Biochemical and biological changes were associated in the earth's early stages. Molecular biomarkers, isotope modification (such as differences in ^{34}S and ^{13}C), and identifiable fossils are important in the study of the earth's history. The primordial soup theory of Oparin and Haldane assumed that organic compounds in water underwent polymerization and condensation reactions similar to those that describe modern soil organic matter formation. The formation of macromolecules that catalyze their own replication is known to be assisted by clays, metals, imidazole derivatives, and selective adsorption onto mineral surfaces that promote concentration and polymerization (Bada and Lazcano, 2003). Carbon and associated N substrates may have arrived on meteorites in association with minerals.

The first written history of soil and soil biota originated in the East, where scholars were recognized in the early Chinese royal courts. Coleman *et al.* (2004)

stated that soils were classified during the Yao Chinese dynasty from 2357 to 2261 BCE. This dynasty should be recognized for both basic and applied studies of soils as they used a soil classification for taxation purposes. The ancient Chinese regarded earthworms "as angels of the earth." Romans, such as Aristotle, considered earthworms as "intestines of the earth" (Coleman *et al.*, 2004). Further evidence for the early recognition of soil is that the Hebrew word for soil is "adama," from which is derived Adam, the first man in Semitic religions (see Hillel, 1991). The ancient Vedic literature of India classified soils by color (and thus organic matter content) and recognized the importance of land forms, erosion, vegetation, land use, and human health implications.

Fungi were known for their fermentation reactions in wine, beer, and bread making and also as a food source that could at times be toxic. Inscriptions on Egyptian walls from 2400 BCE show the production of beer and bread involved the use of a starter and required an incubation time. Eastern, and later Roman, scholars recognized the soil-improving qualities of legumes and crop residue additions. Roman literature on agriculture and soil management was extensive. This was updated and condensed into a single volume by Petrus Crescentius in 1240 CE and for many years was copied, even into the time of the printing press (e.g., Ruralium Commodorium libri duodecin Augsburg, 1471).

Knowledge stagnated in Europe for the one and a half thousand years prior to the Renaissance at the end of the 15th century; not from a lack of intelligence, but from the firmly held belief that the world was governed from the outside and was not an object to be questioned (i.e., intelligent design). The end of the 15th century marked the end of the Western medieval world with the emergence of the perspective that laws that govern the world are subject to study. The concept of biological and abiotic controls that can be studied and influenced by humans marked the beginning of our present knowledge of the soil biota and their processes. The ability to transmit this knowledge by the printed word after the invention of the printing press also greatly aided scientific discovery and discussion.

We are getting further away from our historical roots, an understanding of which is so important to our thinking and ability to formulate scientific questions. The advent of the computer with its easy access to recent literature seems to delay visits to the library to look at not only the original thinking in our field during the early 20th century, but also important literature from 1950 to 1980. I have tried to summarize briefly some of the important early discoveries. In doing so, I have not referred to the original literature, but to reviews often found in textbooks that should be available in many libraries. The history of our science is not merely a listing of the important discoveries, but an important example of scientific thought processes and the relation between methodology, ideas, and concepts.

Our field is still methodology-driven as shown by the great increase in knowledge being derived from molecular techniques and tracers. Another methodology breakthrough was nearly driven to excess, as shown by the fact that the three most cited papers from the *Soil Biology and Biochemistry Journal* from 1975 to 2000 involved the application of the fumigation technique (earlier used by Schloesing and Müntz for nitrification studies) for the measurement of microbial biomass. Today we are benefiting greatly from the availability of automated techniques, the use of computers in data transformation, modeling and knowledge dissemination, and the presence of active scientists in many new parts of the globe.

A look at our history shows how ideas were generated. It also shows that we should look at some of the misconceptions of the past to help us clearly define our thoughts and concepts. I realize that my biases show and that I have concentrated on the positive. The literature is full of examples showing that many of our founders also developed some "doozies." It would also be rewarding to look at what did not pass the test of time so that our own ideas do not end up in the same dustbin. A brief survey of citations in some search engines, such as the U.S. National Agricultural Library, Commonwealth Agricultural Bureau, ISI Science Citations, and Biological Abstracts, shows that the words "soil ecology" elicit more responses than "soil microbiology," which is followed in interest by "soil biochemistry" and "microbial ecology." There are differences in relative rankings dependent on the search engines, but processes generally involve more citations than microorganisms. Soil N is most popular, followed by soil C, N_2 fixation, and the rhizosphere. The citation survey shows that new methods of analysis are being applied to continuing problems with pollutants and pesticides and their effects on the soil population. These topics are continuing to receive a great deal of attention, as is soil biodegradation. If you really want to gain a further appreciation of our field, try general search engines, such as Google, which lists 9,050,000 items for "soil microbiology," 25,100,000 for "soil ecology," and 7,800,000 for "soil biochemistry." An understanding of the interest in the word "humus" would require the perusal of 4,760,000 items. This, however, includes recipes for a common Mediterranean prepared food, hummus, so maybe a better search would be for "soil organic matter," with 14,600,000 items.

SOIL MICROBIOLOGY

Fungi in certain forms can be readily seen without a microscope; thus, they received early study. The first book solely about fungi ("Theatrum Fungorium") published in 1675 by J. F. van Starbeck drew heavily on the drawings of Charles de'Egeluse prepared as early as 1601 (see Atlas, 1984). In 1665, Hooke published a work on the fruiting bodies of fungi, and by 1724, spores were known as fungal reproductive agents. Fungus-root associations were noted by earlier authors, but in 1877, Pfeffer recognized their symbiotic nature, and in 1885, Franck coined the word "mycorrhiza." Franck later distinguished between ecto and endo associations; a classification that is still applicable in present, extensive literature on this subject. In 1886, Adametz isolated fungi from soil and gave them names. The first detailed classification of soil fungi was conducted by Oedemans and Koning in 1902 (see Waksman, 1932). In the 1920s, Charles Thom made a detailed study of soil fungi, especially *Penicillium* and *Aspergillus*, the dominant soil fungi on most agar plates. Waksman also published extensively on soil fungi and actinomycetes.

Leeuwenhoek (1632–1723) is recognized as being the first to see bacteria in his self-designed microscopes. He observed the small animalcules in natural water and in water amended with a substrate (pepper or meat broth). The comprehensive classification system produced by Linnaeus in 1743 perhaps foretold the modern difficulties in bacterial classification when he placed all the organisms seen by Leeuwenhoek in infusions of vegetable matter and meat broth into the genus *Chaos*. In 1776, Nagelli (see Atlas, 1984) suggested that bacteria be placed into their own class entitled Schizomycetes. The work of Warington, Lawes, and Gilbert established the biological nature of many of the processes involved in N transformations, especially those involved with the growth of leguminous crops. Pasteur (1830–1890), in discrediting the theory of spontaneous generation, laid the foundation for microbiology. Although trained as a chemist, he developed vaccines for rabies and investigated many food microbiology problems. Pasteur and Liebig had both postulated that the process of nitrification was bacterial in nature. While studying sewage purification by land filters, Schloesing and Müntz found that the ammonia content of sewage passed through a sand filter did not alter for 20 days. After this period, ammonia was changed to nitrate, but the process could be stopped by a small amount of chloroform. The process could be restarted by soil extract, thus proving that this process was due to microorganisms or, as they said, "organized ferments."

S. Winogradsky (1856–1953) is recognized as the founder of soil microbiology for his contributions to nitrification, anaerobic N_2 fixation, sulfur oxidation, and microbial autotrophy (Winogradsky, 1949). He succeeded in isolating two bacterial types involved in nitrification with the keen insight that they obtained their C from CO_2. He thus also established autotrophy in microorganisms. In the period 1872–1876, Cohn published the first comprehensive study of the bacterial content of soil. Hellriegel and Wilfarth, in 1888, grew peas in the absence of a fixed N supply, showing that legumes obtained their N from the atmosphere, whereas oats did not have this capability. They knew that the peas had nodules, but could not isolate the bacteria within. Beijerinck, in 1888, isolated the bacteria that he called "*Bacillus radicicola*" (now usually called "*Rhizobium*"). This showed the dependence of the N cycle on bacteria. The N cycle was completed when Goppelsröder observed that nitrates were reduced to nitrites in the presence of soil organic matter. In 1868, Schoenbein ascribed the reaction to bacteria and Gayon and Dupetit further developed the knowledge that led to denitrification studies.

The latter half of the 19th century saw more details on microbial processes including symbiotic and asymbiotic N_2 fixation, denitrification, and sulfate reduction and oxidation. The research on fermentation led to the delineation of anaerobic metabolism. Waksman, in his 1952 textbook "Soil Microbiology," gives a detailed account of the early contributions and also published photographs of many of our academic forefathers in soil microbiology. His 1932 book gives detailed historical references in each of the chapters, as well as a listing of the textbooks on the various topics to that date. He gives credit (together with Winogradsky) for the foundation of soil

microbiology as a discipline to Martinis Beijerinck (1851–1931), who not only extracted the first viruses from plants, but also isolated many N_2-fixing organisms and developed enrichment techniques. Basic and applied sciences were as intertwined in the beginning of our science as they are now. Winogradsky and Beijerinck are also recognized as founding members of microbial physiology and microbial ecology.

The first textbook to include soil microbiology was that of Löhnis, "Vorlesunen über Landwirtschaftliche Bäkteriologi," published in 1910 and 1913. English readers can gain an insight into its contents in the English version he published together with E. B. Fred in 1923, entitled "Textbook of Agricultural Bacteriology." That text contains very readable accounts of bacteria, fungi, and protozoa and a good discussion of relationships of microorganisms to their environment. J. G. Lipman (1874–1939), who established the Department of Soil Chemistry and Bacteriology at Rutgers University in 1901, was especially interested in the effects of soil organisms on soil fertility and plant growth. His 1911 book entitled "Bacteria in Relation to Country Life" was the first American treatise in this field. Waksman (1952) named the period from 1890 to 1910 as the Golden Age of soil microbiology when representatives of the soil biota carrying out the major soil and biogeochemical processes were identified. The identification of at least representative members of the microorganisms mediating soil fertility and nutrient transformations led to the belief that this knowledge could do for agriculture what the identification of major disease organisms did for medical treatment.

Successes in legume inoculation led to several premature attempts to alter soil C and N transformations by inoculation and to relate microbial numbers to soil fertility. This discussion continues to this day in the many questions concerning biodiversity and ecosystem functioning addressed later in this volume. The attempts to inoculate bacteria, other than symbionts, and control microbial pathogens of plants were seldom successful because of the lack of knowledge of microbial ecology and the other controls involved. These studies did, however, help transfer attention from pure cultures and laboratory investigations to field experiments and the need for replication to account for soil heterogeneity. This period also contained the interesting conclusion that if an organism did not grow on a gelatin or agar plate, it could not be important and thus was not worth studying.

The years from 1910 to the Second World War witnessed the employment of soil microbiologists in numerous new institutions in many parts of the world. This led to a better knowledge of the global distribution of, and management effects on, organisms capable of growth in the laboratory medium. The development and use of direct microscopy led to the realization that approximately only 1% of the soil population could be grown on laboratory media. The failure of inoculants, except in the case of symbiotic N_2 fixation, to create meaningful management effects was a worry at that time. It is only now that we realize the huge number of unidentified organisms and that the unknown interactions between them and their environment (ecology) explain the often observed lack of impact of introduced organisms.

It was at first assumed that bacteria were the major players in soil fertility and decomposition as typified by the books of Löhnis in 1910 and Löhnis and Fred in

1923. In 1886, Adametz showed that fungi are abundant in soil. Additionally, Hiltner and Störmer had studied actinomycetes, which at that time were thought to be different from the bacteria. Cutler had studied the protozoa, and Russell and Hutchinson developed the theory that by consuming bacteria, protozoa could control the soil population and, thus, soil fertility. The early textbooks took as much license with their titles as modern ones. The Löhnis and Fred publication on agricultural bacteriology included extensive sections on the protozoa and fungi discussed under sections such as "Bacteria and related microorganisms." Waksman's "Soil Microbiology" included sections we would today call biochemistry. The effects of environmental factors on the rate of soil organic matter decomposition were described by Waksman in his 1932 book entitled "Principles of Soil Microbiology" and the Waksman and Starkey 1931 book entitled "The Soil and the Microbe."

The period between the two world wars saw work on microbial interactions and nutrient transformations. Fred, Baldwin, and McCoy's 1932 comprehensive volume on "Root Nodule Bacteria and Leguminous Plants" set the stage for the continued success in symbiotic N_2 fixation. The C:N ratio required for plant-residue decomposition without N immobilization was determined as approximately 25:1, a number that is still appropriate unless large amounts of poorly degradable residues are involved, as in forest litter. Attempts to measure many of the microbial processes in soil were frustrated by the inaccuracy of the measurement techniques relative to the large stock of nutrients in soil. Waksman (1932) commented that it was difficult to measure N_2 fixation by free-living organisms at levels less than 40 lb per acre, which was (and still is) the inherent error in the Kjeldahl or other methods of measuring total N. The Finnish scientist A. I. Virtanen received the 1945 Nobel Prize in Chemistry for his major contributions to legume nutrition, especially the role of rhizobia in symbiotic N_2 fixation. Lie and Mulder (1971), in "Biological Nitrogen Fixation in Natural and Agricultural Habitats," provide a record of the many advances made in that field.

The Second World War led to a concentration on the war effort. This was, however, not without its success as witnessed by the use of the fungal antibiotic, penicillin, and the development of streptomycin, for which Waksman received the Nobel Prize in Medicine in 1952. The war also resulted in studies to overcome food spoilage and rotting of clothes, as well as the beginnings of biological warfare in both preventive and causative formats. Alexander's 1961 and 1977 "Introduction to Soil Microbiology" continued the general organization utilized by Waksman in his earlier volumes. He organized the section on the soil environment and bacteria, actinomycetes, fungi, algae, protozoa, and viruses into a section entitled "Microbial Ecology" and recognized the multitude of microbial and microbial–plant interactions. The 1960s saw an influx of new scientists that worked on symbiotic and asymbiotic N_2 fixation, S cycling, the rhizosphere, mycorrhizas, and the effects of herbicides, pesticides, and pollutants on the microbial population. The mycorrhizal history to 1969 can be found in Harley (1969). The use of ^{15}N and alternate substrates and inhibitors for specific enzyme interactions made possible for the first time the quantification of the processes in the N cycle at the levels that they occur in soil. However, method availability still hindered testing of concepts regarding

microbial populations and diversity, and it was not until the advent of nucleic acid methodology, automated biochemical measurements, such as phospholipid fatty analysis (PLFA), computers, and modeling that the great thrust of knowledge covered in the subsequent chapters of this volume could come to fruition.

Volumes on soil microbiology include Subba Rao (1999), "Soil Organisms and Plant Growth," 4th ed.; Killham (1994), "Soil Ecology;" Lynch (1983), "Soil Biotechnology;" Metting *et al.* (1992), "Soil Microbial Ecology;" Alef and Nannipieri (1995), "Methods in Applied Soil Microbiology and Biochemistry;" Van Elsas *et al.* (1997), "Modern Soil Microbiology;" and Sylvia *et al.* (2005), "Principles and Applications of Soil Microbiology." Other volumes include Tate in 1994, "Soil Microbiology;" Harley and Smith in 1983, "Mycorrhizal Symbiosis;" Read *et al.* in 1992, "Mycorrhizas in Ecosystems;" and Makerji, Chamola, and Singh in 2000, "Mycorrhizal Biology." A community and ecosystem approach to the biology of soil is presented by Bardgett (2005) and the role of microbial diversity as a supplier of ecosystem services is presented in two edited volumes (Bardgett *et al.*, 2005; Wall, 2004).

The advances in molecular techniques utilizing culture-independent direct retrieval of 16S rRNA genes have allowed an examination of the occurrence and biodiversity of microorganisms. A survey conducted by Morris *et al.* (2002) examined the primary scientific literature from 1975 to 1999 in 525 journals. Figure 1.1 shows data for six soil-associated habitats.

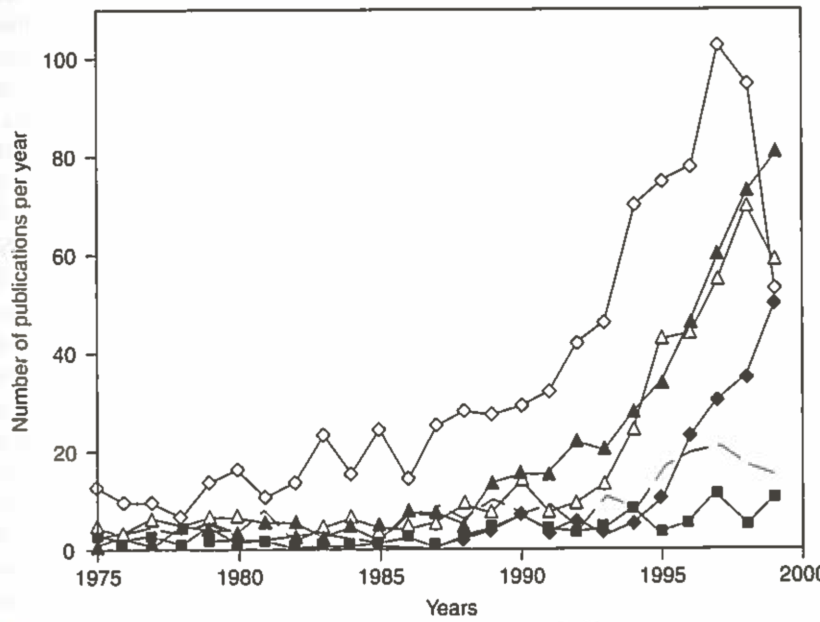

FIGURE 1.1 Publications per year from 1975 to 1999 in microbial diversity: (◇) fungal–plant pathosystems, (▲) rhizosphere and mycorrhiza, (△) microbial habitats in soil, (◆) aquatic systems, (—) bacterium plant systems, and (■) food microbiology (Morris *et al.*, 2002).

Fungus–plant pathosystems outnumbered the other five habitats and showed a 10-fold increase in papers; however, that number peaked in 1996. The rhizosphere, including mycorrhizas, was still rapidly increasing in popularity in 1999. Microbial habitats in soil showed a similar trend, as did aquatic systems. Molecular techniques hold great promise for increasing our understanding of the links between organisms, processes, and the environment; thus soil microbiology, biochemistry, and ecology are best treated in one volume. The recent finding of ammonia-oxidizer genes in previously immeasurable Archaea is one example of new functional groups and maybe even new functions and processes that will be discovered by the readers of this book.

SOIL ECOLOGY

Soil ecology is the second leg of the scientific tripod supporting this textbook. Ecology has numerous definitions. The one that applies to this text is the interaction of organisms and their environment. Smith and Smith (2001) stated that Haeckel developed the term "ecology" in 1869 from the Greek term "oikos," meaning home or place to live. The first ecological publications are credited to the Greek scholar Theophrastus (371–288 BCE), who wrote nine books on "The History of Plants" and six on "The Causes of Plants." Continued work by naturalists during the 15th century, especially in the Middle East, was followed by the plant geographers, such as Wildenow (1765–1812) and Von Humboldt (1769–1859). These described vegetation by physical type and environmental conditions and coined the word "association" (see Smith and Smith, 2001). More plant geography, such as that of Schouw, who studied the effects of temperature on plant distribution, and Paczoski, who studied microenvironments created by plants, led to the study of plant communities. Scientists such as Coulter, Bessey, and Clements developed concepts of succession and gave ecology its hierarchical framework (see Major, 1969).

Aquatic research contributed much to ecological theory. In 1887, Forbes, who interestingly had no college degree (see Hagen, 1992), wrote the classic "The Lake as a Microcosm," which was a predecessor to ecosystem ecology and introduced the concepts of interrelationships through food chains. In 1931, European biologists Thieneman and Forel used the concept of organic nutrient cycling and developed the terms "producers" and "consumers." In 1926, agronomist Transeau was interested in improving agricultural production through a better understanding of photosynthetic efficiency and initiated our understanding of primary production. The early ecologists tended to concentrate on native plant and animal associations, whereas at that time soil microbiologists were associated with either agronomy or microbiology departments. Agronomists were primarily concerned with cultivated fields and the processes therein. To the soil zoologists, these fields seemed depauperate of interesting organisms, while the ecologist's obsession with native sites, and to some extent the environmental movement, was thought by the agronomists to greatly limit their interpretive capability.

Ecosystem science, a term coined by Tansley in 1935 (see Hagen, 1992), led to a more experimental approach and interdisciplinary work. The textbook organized around the ecosystem concept, "Fundamentals of Ecology" by E. P. Odum (1971), went through three editions and was translated into more than 20 languages. The International Biological Programme of the 1960s and 1970s demonstrated the need to investigate all the interacting components of the ecosystem and to model them using mathematically defined transformation processes. This required the active interaction of soil microbiologists and biochemists with plant and animal ecologists and agronomists. During this program, G. M. Van Dyne, a strong advocate of the ecosystem concept, described the editor of this volume as standing on a four-stranded barbed wire fence between ecology and agronomy, with the warning that some day I would slip, with the obvious drastic consequences. The title and chapters in this book indicate to me that this fence has finally been ripped out. Future great advances lie in the study of our exciting field by scientists with a variety of backgrounds and employment in institutions often as heterogeneous as the soils and organisms they study. At the same time, the more classically trained ecologists recognize that the soil, with its multitude of interacting organisms and complexity of interactions, is the last great frontier of ecology.

Today's researchers are finding that replicated, managed fields are excellent for studying and developing ecological and biogeochemical concepts in that they often have greater, more easily measured, nutrient fluxes than those in perennial vegetation. Uncultivated systems, whether prairie or forest, are essential as reference points, often with greater diversity. Other work, such as that in the Amazon Basin, is recognizing that many of the forests that were once thought to be pristine have had major past human interventions.

Russell's 11th edition of "Soil Conditions and Plant Growth," edited by Wild (1988), noted that Gilbert White, in 1777, observed that earthworms were promoters of vegetation by perforating and loosening the soil and drawing leaves underground. Feller *et al.* (2003a) note that Darwin first reported on the effect of earthworms in 1837, followed 34 years later by the publication "The Formation of Vegetable Mould through the Action of Earthworms." At that time, the term "vegetable mould" was used to designate surface horizons in a manner not that different from the earlier use of the term humus. Darwin showed that earthworms were important in soil formation by affecting rock weathering, humus formation, and profile differentiation. This led Feller *et al.* (2003a) to credit Darwin for the first scientific publication in Europe on the biological functioning of soils. In 1839, Ehrenberg had shown the presence of soil protozoa (see Feller *et al.*, 2003a). Russell's work on partial sterilization and its benefits to fertility had involved the protozoa. Cutler and Crump, in 1920, observed the often reciprocal increase and decrease of amoebae and bacteria and attributed the concept of soil sickness resulting in lowered fertility to this phenomenon (see Waksman, 1932). This is in direct contrast to Russell's, and more recent, concepts in which faunal-derived microbial turnover is considered an advantage in nutrient release (Coleman *et al.*, 2004). Stout *et al.* (1982) gave a detailed resume of the soil protozoa that included the slime molds.

The "Manual of Agricultural Helminthology" (Filipjev and Shuurmans-Stekhoven, 1941, published in The Netherlands), summarized nematode anatomy, systematics, methodology, and plant–parasite interactions to that date. G. Steiner states in the edited volume on nematology (Sasser and Jenkins, 1960) that the Incas of Peru had a regulation by which the replanting of potatoes on the same land needed to be deferred by a few years to control what must have been golden nematode infestation. He also stated that the "bush culture" that involved burning of tropical forests followed by planting of crops was not done on adjacent plots to stop invasion of nematodes from the old agricultural plots to the new ones. Kevan's 1965 description and count of soil fauna per square meter of a European grassland were quoted in the first edition of this textbook. A good introduction to the various members of the soil fauna is given by Burges and Raw (1967) and is updated by Lavelle and Spain (2001) and Coleman *et al.* (2004).

Wilde (1946) stated that the principals of soil science and ecology were introduced to silviculture by the German forester Grebe in his doctor's thesis in 1840. Grebe forecast Dokuchaiev's studies by stating,

> "As silviculture horizons widen, the importance of environmental conditions becomes more sharply pronounced. It appears clearly to foresters that the form of forest management is determined by a number of physical influences related to topography, geology, type of soil, and climate."

In not mentioning organisms, maybe the quote does not belong in this book, but 80% correct isn't all bad.

Russian scientists have long credited Dokuchaiev and his associate Kostytchev with being the founders of soil science and for having a great influence on ecology. Wilde (1946) quotes Dokuchaiev as saying,

> "The eternal genetical relationships that exist between the forces of the environment and physical matter, living and nonliving domains, plants and animals and man, his habits, and even his psychology—these relationships comprise the very nucleus of natural science."

Dokuchaiev recognized the effects of animals in soil formation in using the word "crotovina" for the filled-in remnants of mammal burrows. Russian soil science, ecology, geography, and plant ecology have always been closely associated (Major, 1969). Their word "biogeocoenoses" emphasizes the biology–landscape interactions, as well as exchanges of matter and energy, discussed so often in this text. Hilgard translated Dokuchaiev's work to English and mapped American soils relative to landscape, climate, and vegetation. Wilde credits Hilgard's 1906 publication "The Relation of Soils to Climate" for perhaps unintentionally laying the foundation of soil ecology in America. The interactions of Dokuchaiev's five factors of soil formation, climate, parent material, organisms, topography, and time were reiterated and placed in an equation form by Jenny (1941). Liebig has been credited as one of the first physiological ecologists for his work on mineral nutrition of plants.

The influence of Müller's 1878 monograph in characterizing forest soils in relation to the type of organic matter (Mull, Moder, and Mor) has been extensive. Wilde lists an extensive number of European authors who emphasized the role of soils in forest management. Other reviews on forest–microbiology–nutrient cycling include Jordan (1985), Pregitzer (2003), and Morris and Paul (2003). Rangeland science is equally dependent on soil processes, some of which are detailed in "Grasslands, Systems Analysis and Man," edited by Breymeyer and Van Dyne (1980), and in "Grassland Ecophysiology and Grazing Ecology" (Lemaire *et al.*, 2000).

I did not know whether to place microbial ecology under soil microbiology or soil ecology. In concepts, methods, and application, microbial ecology has been closer to soil microbiology than to classical ecology. Numerous authors have bemoaned the fact that there is not an extensive idea and concept exchange between microbial ecology and ecology in general. However, this is rapidly changing with the recognition that the diverse and extensive soil and aquatic and sediment biota can now be studied with molecular methods. The great diversity and close interactions of organisms with mineral particles makes soil an ideal place to develop and test ecological concepts. According to Marshal (1993), microbial ecology has the goals of defining population dynamics in microbial communities and the physiochemical characteristics of microenvironments and understanding the metabolic processes carried out by microorganisms in nature. It recognizes as its founders the same scientists (Leeuwenhoek, Winogradsky, and Beijerinck) that developed soil microbiological thought. Microbial ecology has the ability to transcend different habitats, asking questions about soils, plants, animals, fresh waters, oceans, and sediments, as well as geological strata. It also has received great impetus from the recent advances in nucleic acid techniques and, thus, one of its more modern pioneering works has to be that of Watson and Crick, which eventually led to the nuclear-based techniques.

The first textbook published with the title "Microbial Ecology" was that of Brock (1966). Brock (1975), in "Milestones in Microbiology," published the key papers of Pasteur, Koch, and others in a translated, annotated format. The publication of the triennial meetings of the International Society of Microbial Ecology provides a useful chronology of advances in this field. Some include Ellwood *et al.* (1980), "Contemporary Microbial Ecology;" Klug and Reddy (1984), "Current Perspectives in Microbial Ecology;" and Guerrero and Pedros-Alio (1993), "Trends in Microbial Ecology." Other reviews include Lynch and Poole (1979) and the series "Advances in Microbial Ecology" published by Plenum Press. The training and background of microbial ecologists are often very different from those of classical ecologists, and until recently, there has not been enough cross-fertilization of ideas between the fields.

SOIL BIOCHEMISTRY

Soil biochemistry, as defined in this book, refers to the characteristics and dynamics of organic matter and the biochemical transformations brought about by enzymes and organisms in soil. Biochemical reactions appear to have proceeded without microorganisms. Later microorganisms were active without the presence of plants and animals for long periods of the earth's history. Biochemical reactions similar to those occurring in modern soils are thought to have occurred for an extended period before the occurrence of the first bacteria identified in rocks that have an age of approximately 3.8 billion years. Phototrophic bacteria and cyanobacteria have been identified in rocks that are 2.8 billion years old. Vascular plants and mammals are a product of only the past 500 million years.

Experiments with iron sulfides, at the elevated temperatures and pressures found in hydrothermal vents, have indicated the possibility of the formation of prebiotic, organic substrates. These are believed to involve organo-metal interactions often studied in today's soil biochemistry. Another theory involves an alkaline world in which the activity of negatively charged clay minerals, such as smectite, organized fatty acid micelles and lipids into vesicles that contained active clays. These are said to have concentrated and polymerized RNA and DNA. Once formed, vesicles such as these are postulated to have grown by extrusion through small pores. These reactions are all familiar to the soil biochemist, as are the concepts involving micropores, enzymatic activity, and habitat formation so important in early life studies (Bada and Laszano, 2003).

Waksman (1938), in his book entitled "Humus," states that from Theophrastus (373–328 BCE) to the time of Wallerius (1709–1778 CE), the concept of oleum untuosm, equating fertile soil with the fatness of the land, dominated the ideas of naturalists. The word "humus" was extensively used in Virgil's (79–19 BCE) poetry about farming, food production, and the joys of country life. His poetry is extensively quoted relative to soil fertility, decomposition, gardening, nature, the environment, and organic agriculture, with the 39 BCE quote from the second Georgics

> "pinquis humus dulcique uliine laeta; Quique frequens hebis et fertilis übre campus"

being the most familiar. The word humus, together with terra and solum, was used for earth. It is the root word for humans, homo, and even posthumous, after the earth or death. Virgil referred to dark soil as fertile, and the ancients knew that dark-colored soil was more productive, absorbed more water, and was easier to till than its lighter colored counterparts in the landscape. They had also observed that exposure to flames often lightened the soil. Feller (1997) quotes Pliny the Elder (23–79 CE) as saying

> "the lupin penetrates the humus and wheat needs two feet of humus."

The period of alchemy and the phlogistic theory continued to use the original Latin definition of humus as soils or earth, as did Linnaeus (1707–1778), the great Swedish botanist. He classified soils as *Humus daedalea* (garden soil), *Humus rualis* (field soil), and *Humus latum* (muck soil). The concept that the application

of dung to the soil replaced some substances that had been removed by plants was established in the 16th century. Van Helmont's (1577–1644) experiments that concluded that water was the source of plant nutrition were repeated by Robert Boyle with the same conclusion. However, Woodward in 1699 showed that impure water, such as that from the river Thames, increased the growth of mint. He also reported that dung that returns parts of either vegetables or animals was the best way of restoring soil. Böerhavein, in a 1727 textbook of chemistry, wrote that plants absorb the juices of the earth. Tull in 1730 stated that small, earth-like particles serve as nutrients for plants.

Wallerius in 1753 (see Feller, 1997) used the Latin word humus for loam or mold, which at that time referred to the organic surface horizon relative to decomposing organic matter, and is thus credited with the modern use of humus for organic matter. This was made easier by the fact that the later Roman and Latin texts then utilized the word terra rather than humus for earth. Wallerius went along with the thinking of that time in assuming humus was the essential nutritive element and that other soil constituents acted in mixing or dissolving it and, thus, assisted uptake by plants. Lime was considered to help dissolve the fat (humus) of the land and the function of clay was to fix or retain this fatness. The Russian scientist Komov, in his 1782 book on agriculture, associated the hydrophysical properties of soil and its richness in nutrients with the presence of humus and stated that the "nutritive juice" of soil was produced by rotting.

De Saussure, known for his chemical studies, also spent considerable time on humus. In 1804, he described humus as being of various complexes (oils and salts), capable of absorbing oxygen and producing CO_2. He showed that it contained more C and less O and H than the plant residues that went into its formation. He also established that plants synthesize their organic matter from CO_2 and give off O_2. Thaer in 1808 differentiated between peat formed in limited O_2 and mild humus formed under adequate O_2. He ascribed to the humus theory of plant nutrition, which stated that humus was the direct source of plant nutrients. Thaer also has been called the father of sustainable agriculture (see Feller *et al.*, 2003b). One of his books stated,

> "Latterly the practice of sowing white clover with the last crop has become very general; only a few apathetic and indolent agriculturalists or men who are firmly wedded to old opinions and customs, neglect this practice."

It took the work of Sprengel in 1826, Liebeg in 1840, and Boussingault in 1841 (see Feller *et al.*, 2003b) to found the concept of mineral nutrition of plants. However, modern organic agriculture still credits soil organic matter with properties other than nutrient supply, water and nutrient retention, complexation, and aggregation. Humic constituents in small quantities continue to be investigated for their effect on plant respiration as does the use of specific plant- and microbial-derived molecules as information signals for plant and microbial interactions (Vaughn, 1985; Bais *et al.*, 2004).

Berzelius, first in 1806 and later in the 1830s, described the dark, black, and lighter yellow humic compounds and showed their interactions with metals. Field experiments carefully conducted in 1834 by Boussingault, considered the father of modern scientific agronomy, analyzed the C, H, O, N, and mineral inputs in manure relative to those in subsequent plant parts grown on manured soils. In 1826 and 1837, Sprengel found that the C content of humus is 58%, described the most important characteristics of humates (its salts), and studied their decomposition and solubility characteristics. The Russian scientist German, in 1837, still believed that humus was a direct source of plant nutrition, but found that cultivated soils contained less humus than virgin ones and attempted to obtain scientific confirmation of the value of rotations. This was a prelude to modern-day sustainable agriculture and the questions arising today regarding soil C and global change. He also was the first to question whether humic acids were chemically individual compounds. The large number of fractions he, and later others, identified as constituents of humus was not found to be reproducible and this led to a general questioning of the usefulness of soil organic matter fractionation. Danish scientist Müller (see Wilde, 1946) further defined the solubility and characteristics of humics in his book "Natural Forms of Humus" and developed the concepts of Mull and Mor in forest soils. Mull horizons had earthworms and fungi, whereas earthworms were absent from Mor soils.

Dokuchaiev, the founder of Western soil science, recognized the involvement of the five interacting factors of soil formation (parent material, vegetation, organisms, climate, and time) in the development of rich, high-organic-matter, chernozemic soils. Other scientists in this productive period include Kostychev, who in 1886 suggested that products synthesized by bacteria participated in the production of humic substances (see Kononova, 1961). Hebert in 1892 and Dehérain in 1902 developed the concept of humus formation as the interaction of lignin and proteinaceous substances. Büchner is credited for his pioneering work in enzymology by disrupting yeast cells to produce a cell-free system capable of alcoholic fermentation. This later led to the many investigations of enzyme reactions in soils.

During the period of 1908–1930, Shreiner, Shorrey, and their co-workers used large-scale extraction equipment to isolate 40 identifiable organics including hydrocarbons, sterols, fats, organic acids, aldehydes, carbohydrates, and organic P and N compounds. These studies gained a great deal of attention because of their precision, but may have detracted from the overall study of soil organic matter as a natural entity. They were a prelude to Waksman's detailed studies on the proximate analysis of organic matter in which he rejected the concepts of humic and fulvic acids. However, Tyurin in his 1937 book (see Kononova, 1961) on the organic matter of soils and Springer in 1934–1935 (see Kononova, 1961) regarded Waksman's denial of the existence of specific humic soil compounds as unfounded and incorrect, and claimed that proximate analysis, as suggested by Waksman, would not stand the test of time in that it characterized only a small fraction of humus. However, some mistrust of humic acid characterization, generated by Waksman's criticisms, continues today in Western soil science, although humic acid chemistry is well accepted in aquatic research in both marine and freshwater environments.

The translation of earlier Russian volumes entitled "Soil Organic Matter, Its Nature, Its Role in Soil Formation and Soil Fertility" (Kononova, 1961) described organic matter much as it is defined today and brought together literature on the role of physical, chemical, and biological factors of soil formation and its effect on cultivation. Stevenson's 1994 book entitled "Humus Chemistry" recognized the role of humic and fulvic acids and humic fractionation and delineated today's knowledge of organic C, N, P, and S transformations. Aiken *et al.* (1985) in "Humic Substances in Soil, Sediment and Water" recognize the similarity of humic substances in soils, sediments, and water. They describe methods, such as NMR and pyrolysis mass spectrometry, for studying this series of complex, and still difficult to study, soil organic matter constituents that form such an important component of present-day sustainable agriculture and global change investigations.

Nitrogen is important as a constituent of soil organic matter, as a nutrient in soil fertility, in water pollution, and in trace-gas, radiative forcing in global change. It thus continues to receive a great deal of attention. It took a great deal of research and many publications to delineate the processes of N_2 fixation and N immobilization, mineralization, plant uptake, and denitrification. The reviews edited by Bartholomew and Clark (1965), Stevenson (1982), and Mosier *et al.* (2004) delineate the use of instrumentation, tracers, and inhibitors in determining the processes and rates in soils. In 1943, Norman and Werkman labeled soybeans with ^{15}N. Addition of the labeled residue to soil showed that 26% of the tagged N was recovered by a subsequent crop. Work with both ^{15}N and ^{13}C by Broadbent and Norman in 1946, and Broadbent and Bartholomew in 1948 (see Jansson, 1958; Paul and Van Veen, 1978), established the principles for the use of soil tracers. The equations of Kirkham and Bartholomew (1955) for mineralization–immobilization and the epic work of Jannson (1958) on soil N dynamics should be required reading for anyone today contemplating tracer studies.

The advent of tracers in the 1940s came at a time when the principles affecting plant decomposition had been reasonably established. Harmsen and van Schreven (1955) summarized the early work on the effects of environmental factors and the possibility of soil biota turnover in subsequent releases of N as follows:

> "The study of the general course of mineralization of organic N was practically completed before 1935. It is surprising that many of the modern publications still consider it worthwhile to consider parenthetical observations dealing with these entirely solved problems."

These authors then pointed out that the relationships between C and N and the effects of environmental factors had to be determined for each soil type, indicating that the underlying controls were not understood nor could the dynamics of resistant compounds be measured.

Libby developed the ^{14}C dating technique in 1952. It was used for peats, buried soil profiles, and soil pedogenesis by Simonart and Mayaudon in 1958, Simonson in 1959, and Tamm and Ostlund in 1960 (see Paul and Van Veen, 1978). In 1964, Paul and co-workers carbon dated soil organic matter fractions to calculate their mean residence times. The further interpretation of carbon dating by Scharpenseel, and Stout and Rafter (see Goh, 1991), did a great deal to establish pools and fluxes for modeling purposes. Decomposition experiments with plant residues with laboratory-enhanced ^{14}C contents provided much information on the effects of soil type and climate management in studies by Sorensen in 1967, Jenkinson and Rayner in 1977, and Sauerbeck and Führ in 1968 (see Paul and Van Veen, 1978). Differences in naturally occurring ^{13}C resulting from C3 ↔ C4 plant vegetation switches and from enhanced CO_2 experiments are now being effectively utilized to answer global change and soil and ecological sustainability questions involving soil organic matter (Coleman and Fry, 1991; Boutton and Yamasaki, 1996).

The use of tracers allows one to also measure nontracer soil C and N. There is continual turnover of organic matter during decomposition, and tracer experiments often show more soil C and N being released than can be determined in the absence of the tracer. Some of today's authors are mistakenly calling this priming. Fontaine *et al.* (2004) credit Löhnis as defining priming in 1926 as an increased availability of nutrients due to higher microbial activity resulting from the addition of substrate. With the use of tracers, Broadbent and Bartholomew (1948) also defined priming as the increased mineralization of unlabeled soil organic matter constituents in the presence of available fertilizer N or labeled plant residues. Replacement by the tracer of nontracer C or N during normal soil dynamics must be taken into consideration before priming is said to occur. It is hoped that today's authors will read the original literature and not erroneously redefine what was established many years ago. Priming does occur. We must, however, use a mass balance approach together with the tracers to determine that it is a net release of the nutrients from soil organic matter and not a normal exchange of the tracer for nontracer isotopes during microbial growth and product formation.

There are excellent reviews on soil N, such as Bartholomew and Clark (1965), Stevenson (1994), and Mosier *et al.* (2004). These contain discussions of the significance of fixed ammonia as part of total soil N, especially with regard to depth, in clay soils. Today's literature seems to have forgotten this constituent. It is hoped that in the next 10 years, we will not read a spate of papers that claim to have newly discovered this not necessarily active, but important, N component.

Fred *et al.* (1932), Stewart (1975), and Graham (2000) have reviewed N_2 fixation. Prosser (1986) and Norton (2000) reviewed nitrification, whereas N losses, especially those leading to pollution and global warming, have been covered in Robertson (2000) and Groffman (2000). Publications such as "Biogeochemistry" (Schlesinger, 1997) and "Geomicrobiology" (Ehrlich, 1996) cover related areas of nutrient cycles and exchange in soils, freshwater sediments, and the vadose zone. The fact that the processes and process controls are similar in all environments is heartening for our level of knowledge. These controls lead to a rather similar composition for organic matter in most aerobic terrestrial soils. Modeling, such as that used by Jenkinson and Rayner (1977), is now an integral part of soil biochemistry used to test concepts and extrapolate information to different landscapes and for future predictions. Whether the ability to develop reasonably descriptive models based primarily on soil organic

FIGURE 1.2 A dog's eye view of decomposition and soil organic matter formation. Copyright 1962; reprinted by permission of United Feature Syndicate, Inc.

matter dynamics, but not soil population data, can be attributed to the great redundancy of microbial populations or to the fact that our models are not yet accurate enough to require population input data is yet to be determined. The 10-volume, edited series entitled "Soil Biochemistry" initiated by McLaren and Peterson (1967) has since been coedited by Paul and Ladd and by Stotsky and Bollag. It has brought together information on biologically related soil processes and components, nutrient cycles, and enzymes. It has also covered extraterrestrial life, soil enzymes, and pollutants as they affect soil organisms and the environment. The best way to summarize this section on soil biochemistry is to republish the cartoon from the comic strip Peanuts that was included in the first volume of the "Soil Biochemistry" series (Fig. 1.2).

IN PERSPECTIVE

The soil microbiologist, ecologist, and biochemist must be aware that their organisms and processes are affected by soil type, vegetation, landscapes, and management. Forestry and rangelands are a very important component of our studies. Wilde (1946), in his very readable book "Forest Soils and Forest Growth," quotes the following from the Kalevala, the National Epic of the Finns, dated to approximately 900 BCE, showing that early man recognized the interaction of soil type and vegetation.

> Seeds upon the land he scatters,
> Seeds in every swamp and meadow,
> Forest seeds upon the loose earth,
> On the firm soil he plants acorns,
> Spreads the spruce seeds on the mountains,
> And the pine seeds on the hill-tops,
> In the swamps he sows the birches,
> On the quaking marshes alders,
> And the basswood in the valleys,
> In the moist earth sows the willows,
> Mountain ash in virgin places,
> On the banks of streams the hawthorn,
> Junipers on knolls and highlands;
> Thus his work did Pellerwoinen. . . .

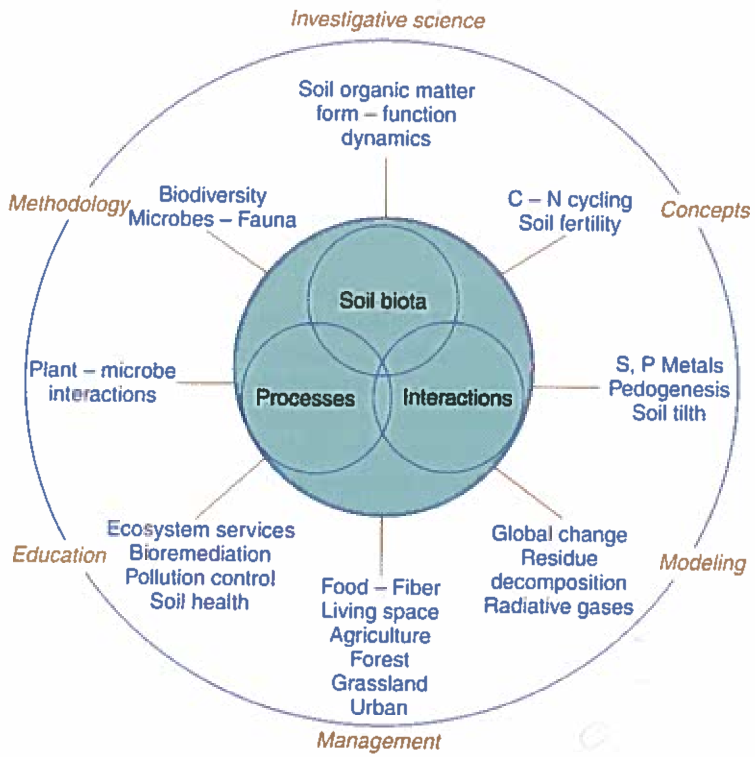

FIGURE 1.3 The interplay of soil biota, interactions, and processes in investigative science and management.

The great biodiversity of soil biota in both macro and micro forms, and the important questions that need to be answered, indicate to me that many of the new concepts in our field will come via the study of the physiology and ecology of soil organisms, as well the processes they mediate relative to soil nutrient transformations and global biogeochemical cycles. This text, therefore, has chapters on the physiology–biochemistry of organisms as well as on ecology in an attempt to enhance the understanding required to provide a foundation for the interdisciplinary approaches that will continue to provide exciting new concepts in our field. It is hoped that the individual chapters will provide new breakthroughs, concepts, methods, and ideas, as well as more individualized references. Figure 1.3 shows the interdependence of soil microbiology, ecology, and biochemistry, some of its fields of study, and some of its applications.

The last chapter in this volume will provide an oversight of the individual chapters and, it is hoped, provide insights into the future.

This edition is dedicated to that great soil microbiologist, F. E. Clark, whose keen insight and clear writing were such a joy to read in many early publications, as well as in the first two editions of "Soil Microbiology and Biochemistry."

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2

THE SOIL HABITAT

R. P. VORONEY

At first sight nothing seems more obvious than that everything has a beginning and an end and that everything can be subdivided into smaller parts. Nevertheless, for entirely speculative reasons the philosophers of Antiquity, especially the Stoics, concluded this concept to be quite unnecessary. The prodigious development of physics has now reached the same conclusion as those philosophers, Empedocles and Democritus in particular, who lived around 500 BCE and for whom even ancient man had a lively admiration. (Svante Arrhenius, Nobel Lecture, 1903)

INTRODUCTION

Soil is the naturally occurring, unconsolidated mineral and organic material at the earth's surface that provides an environment for living organisms. Recently, it has been referred to as the earth's "critical zone" and as deserving special status, because of its role in controlling the earth's environment and thus affecting the sustainability of life on the planet. This concept, that the earth's physicochemical properties are tightly coupled to the activity of the living organisms it supports, was proposed in the early 1970s by James Lovelock as the Gaia hypothesis. He theorized that the Earth behaved as a superorganism, with an intrinsic ability to control its own climate and chemistry and thus maintain an environment favorable for life. However, it is only microorganisms that have proven they can sustain the biosphere and can do so even without larger organisms.