SOIL BIOLOGY

A.J. Franzluebbers
USDA–Agricultural Research Service, Watkinsville, GA, USA

Keywords: Actinomycetes, bacteria, biological nitrogen fixation, bioremediation, carbon cycle, earthworms, fungi, microbial biomass, mycorrhizae, nematodes, nitrogen cycle, organic matter, protozoa, rhizosphere

Contents

Summary

Soil biology represents a diverse group of organisms that reside during at least a part of their life cycle in the soil. These organisms vary widely in size from macrofauna > 10

mm in length (earthworms, spiders, beetles, mice, moles, etc.) to micro and mesofauna <10 mm in length (protozoa, nematodes, collembola, etc.) to microscropic forms of bacteria, fungi, and algae. Soil organisms can be primary producers of organic materials (e.g., phototrophic algae and bacteria), but more commonly are heterotrophic consumers of preformed organic materials. These heterotrophic organisms are essential in the cycling of nutrients and transfer of energy following the senescence of plant materials. Soil organisms also play major roles in soil formation and soil structural development by forming biotic pores, transforming soil minerals and organic matter into stable aggregates, and catalyzing mineral weathering processes. Ecologically, soil organisms perform many key environmental functions, including (1) regulation of carbon cycling from plant detritus back to the atmosphere, (2) provision of inorganic nitrogen to plants through decomposition and biological nitrogen fixation, (3) transformation of nitrate via denitrification to mitigate water contamination, (4) biodegradation of natural and synthetic contaminants in soil, and (5) purification of water percolating through soil into groundwater. Soil biology is recognized as a key component along with other soil disciplines for the understanding and development of land management systems by human society to help sustain and improve ecosystem functioning on local, regional, and global scales.

1. Soil organisms

Organisms living in the soil develop an active, diverse, and yet often under-appreciated ecosystem. The soil ecosystem is dynamic and composed of biotic (i.e., plant roots, microorganisms, and macroorganisms) and abiotic components (i.e., mineral particles, water, gases, nutrients, and nonliving organic matter). Soil organisms can be broadly separated into two groups, i.e., microflora and fauna. Microflora are a very diverse group of organisms that are generally "not visible to the unaided eye", i.e., <200 μm. Microflora are classified in the Kingdom Protista, which lack the ability to form distinct tissue or organs for performing specific functions, and include bacteria, actinomycetes, fungi, and algae. Fauna are classified in the Kingdom Animalia and include such diverse organisms as protozoa, nematodes, mites, collembola, arthropods, earthworms, beetles, ants, and termites. Fauna can be further divided by size of body into microfauna (<0.2 mm length, <0.1 mm width), mesofauna (0.2 to 10 mm length, 0.1 to 2 mm width), and macrofauna (>10 mm length, >2 mm width).

Soils can be very different in the diversity of organisms present, but in general fungi dominate the soil biomass with 10^3 to 10^6 colony-forming units g^{-1} soil, while bacteria are most abundant in numbers. Types, numbers, and biomass of organisms vary not only from soil to soil, but also within the same soil type both spatially (i.e., vertically and horizontally due to resource allocation) and temporally (i.e., daily based on plant development and water availability, seasonally based on climatic conditions, and annually based on land use). The basic requirements for life [i.e., a suitable temperature, water, space, time, a terminal electron acceptor (e.g., O_2 for aerobic organisms), an energy source, carbon source, nutrients, and a suitable pH] select for organisms tolerant or capable of activity under the specific set of environmental conditions. An example of depth changes in total soil microbial biomass in a pasture is shown in Figure 1, where plant litter and animal dung deposited at the soil surface provide much of the organic substrates for proliferation of microorganisms. An example of seasonal changes in dung beetle populations in a managed grassland is illustrated in Figure 2.

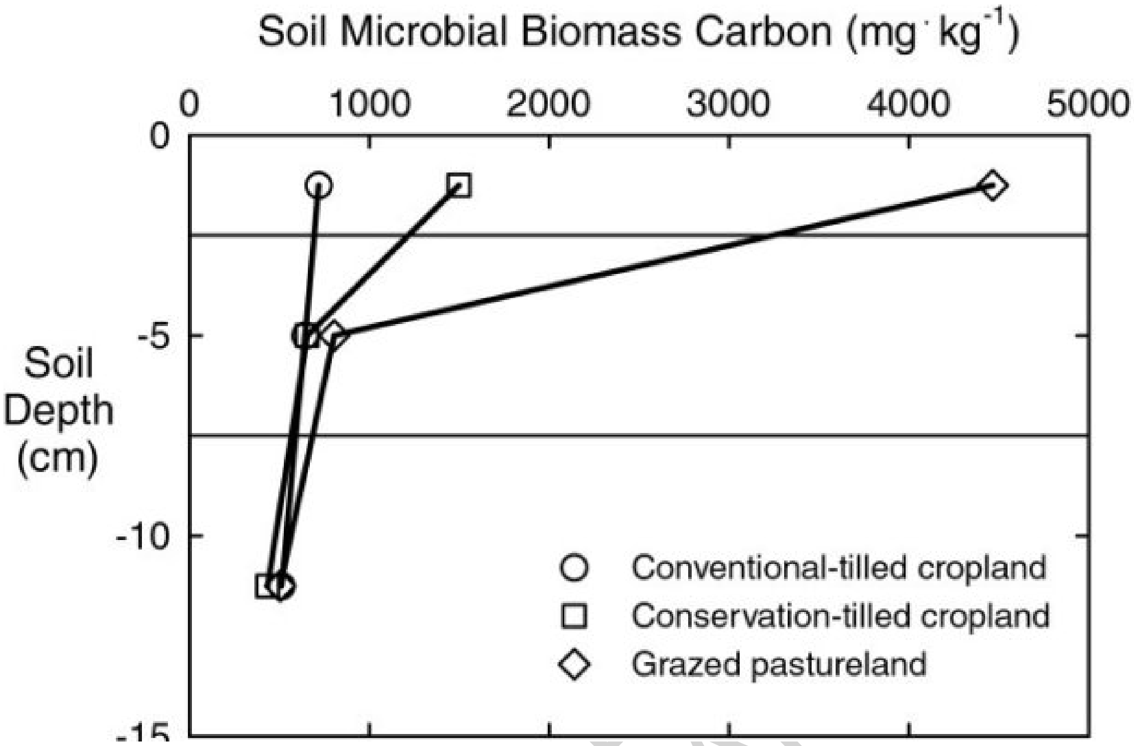

Figure 1. Soil depth distribution of total soil microbial biomass...

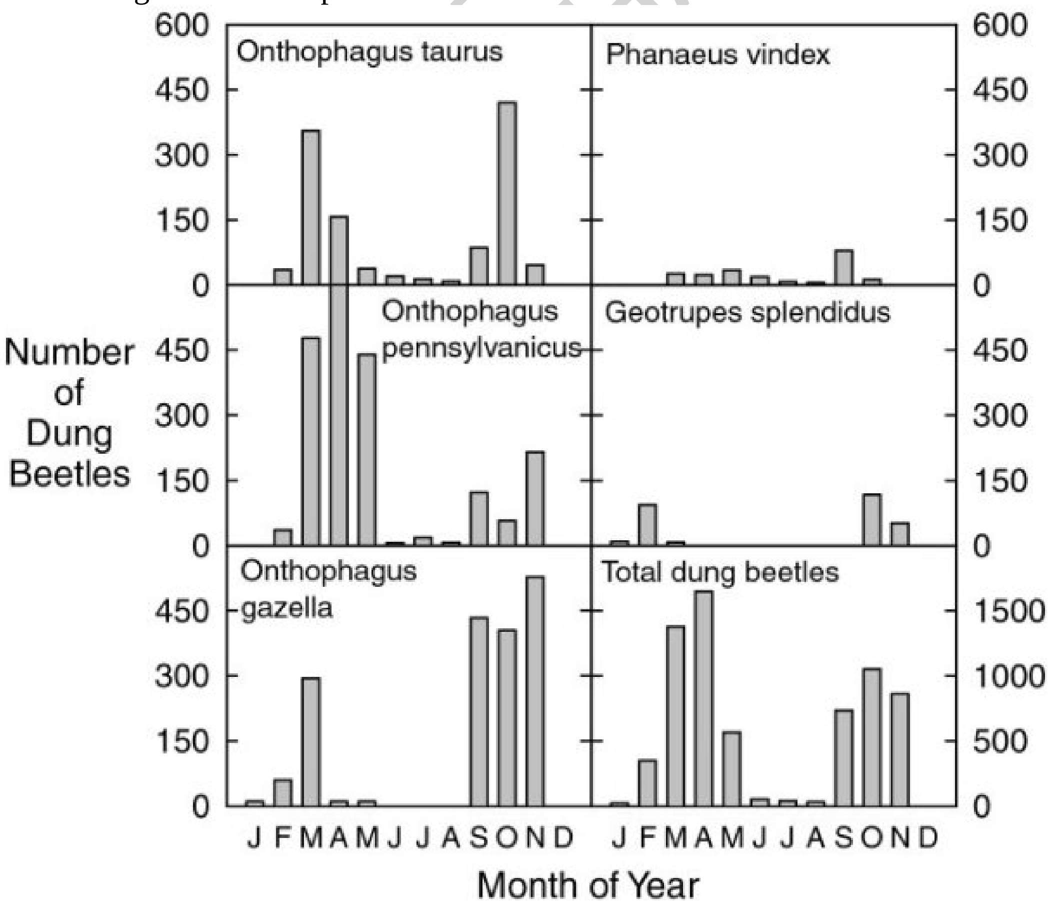

Figure 2. Number of various dung beetles...

Soil microorganisms can be classified ecologically based on growth dynamics. Autochthonous species grow at a slow, steady rate, tend to be indigenous or native species, and undergo dormant stages to resist extinction. Zymogenous species have resistant stages, but become active quickly when food sources become available, such as on senescent roots following rainfall preceded by a long drought. Allochthonous species are invaders of an environment, enter the soil ecosystem through precipitation, manure, sewage, or diseased plant tissue, do not participate in a sustained way to the soil community, and may die off with time.

In addition, soil microorganisms can be classified nutritionally based on the nature of the energy source for generating adenosine triphospate (ATP) and the nature of the principal carbon source used for cell growth (Table 1).

Classification	**Energy source for generating ATP**	**Source of carbon for cell growth**
Photoautotroph	light	CO_2
Photoheterotroph	light	CO_2, simple organic compounds
Chemoautotroph	inorganic compounds	CO_2
Heterotroph	organic matter	organic matter

Table 1. Classification of organisms based on metabolic sources of energy and carbon.

1.1. Bacteria

Bacteria can be found in nearly all soil environments. Bacteria are prokaryotic organisms, defined as cellular organisms without a nucleus. Bacteria vary widely in size (typically 0.5 μm in diameter to 8 μm in length) and shape (typically rod, sphere, or spiral, as well as pleomorphic that change shape during growth). Major groups of bacteria are classified according to shape, cell wall structure (i.e., by gram stain), motility, and metabolic capabilities (Table 2). Depending upon oxygen status of the soil, particular groups of bacteria will proliferate, including obligate aerobes (requiring O_2 to grow), obligate anaerobes (can not grow in presence of O_2), and facultative anaerobes (can grow in presence of absence of O_2).

Group	**Characteristic**
Phototrophs	Utilize light as energy source; including Cyanobacteria
Gram negative chemolithotrophs	Nitrogen or sulfur oxidizers; including *Nitrobacter*
Methanogens	Methane production under anaerobic conditions
Gram negative aerobes	Important in elemental cycling; including *Rhizobium*
Gram negative facultative anaerobes	Including *Escherichia, Salmonella, Klebsiella, Erwinia*
Gram negative anaerobes	Important in elemental cycling; including *Desulfovibrio*
Gram positive cocci	Form irregular clusters; including *Staphylococcus*
Endospore forming rods and cocci	Resist environmental stress; including *Bacillus*

Gliding bacteria	Gliding motility; Form macroscopic fruiting structure
Sheathed bacteria	Morphologically resemble filamentous algae or fungi
Budding and/or appendaged bacteria	Appendages that concentrate metallic oxides
Spirochetes, spirals, and curved bacteria	Helically coiled or spiral morphology
Gram positive asporogenous rod-shaped	Similar to actinomycetes; including *Lactobacillus*
Actinomycetes and related organisms	Form branching filaments; including *Frankia*
Rickettsias	Obligate parasites that lack ATP production capability
Mycoplasmas	Only bacteria to lack cell wall

Table 2. Major groups of bacteria.

In a typical soil environment, bacteria form spores and form microcolonies. Soil conditions that favor heterotrophic bacteria are abundant water (at least 50% of the pore space occupied by water), neutral pH, relatively high temperature (30 to 40 °C), and abundant organic matter.

Cyanobacteria (or formerly blue-green algae) are capable of fixing atmospheric nitrogen. The cyanobacterium, *Anabaena*, forms a symbiotic association with the aquatic fern, *Azolla*. This association is an important mechanism for nitrogen fixation in flooded rice soils.

1.2. Actinomycetes

Actinomycetes give soil its musty or earthy odor through production of geosmin. They are unicellular, aerobic bacteria that resemble fungi in that they produce slender (0.5 to 2 μm diameter), y-branched hyphae, which often fragment and divide as a means of asexual sporulation. Hyphae of actinomycetes are thinner than those of fungi. Actinomycetes develop best under relatively dry and warm conditions and neutral soil pH. Most are heterotrophic, slower growing than most other bacteria (i.e., autochthonous), and utilize organic compounds more resistant to breakdown (e.g., cellulose, pectin, and chitin). Actinomycetes are a source of many antibiotics, including streptomycin, which is produced by one of the most common actinomycetes in soil, *Streptomyces*.

1.3. Fungi

Fungi are typically multicellular (although yeasts are unicellular) eukaryotes that do not contain chlorophyll, but produce a wide variety of spore and resting structures, including mushrooms, sclerotia, conidia, and rhizomorphs. Typical fungi have hyphae of 5 μm in diameter and <100 μm in length, are heterotrophic aerobes, grow from hyphal tips without extracellular enzymes, and predominate in acidic soils (pH<5.5). Many plant pathogens are fungi, but only a few fungi are pathogens. A special group of fungi particularly beneficial in agriculture are those that form a mycorrhizal symbiosis with plant roots, as described later in Section 1.5.

Fungi are split into five major groups:

- Myxomycetes (slime molds), which are morphologically similar to protozoa, i.e., without cell walls in the vegetative state (although spores do contain cell walls). An example is *Physarum*.
- Phycomycetes, which are non-septate and have no specialized spore structure. Examples are *Pythium* and *Rhizopus*.
- Ascomycetes, which are septate with sexual spores in an ascus. An example is *Saccharomyces*.
- Basidiomycetes, which are septate with sexual spores in a basidium. Examples are *Boletus* and *Tricholoma*.
- Deuteromycetes (fungi imperfecti), which are septate with no sexual spores. Examples are *Fusarium* and *Penicillium*.

1.4. Algae

Algae are pioneers that often are the first to inhabit soils following disasters. Algae are photoautotrophic eukaryotes with various pigments and storage products used to distinguish among groups. The most common algae in soil are greens, diatoms, and yellow-greens, which derive inorganic nutrients and water from soil. In soil, most algae grow near or on the surface to capture sunlight for energy, although some can be found at more than a meter depth because they are facultative photoautotrophs obtaining energy from sunlight or inorganic compounds. Algae form various spores. Vegetative forms (2 to 50 μm in size) can be unicellular, colonial, filamentous, folious, tubular, blade-like, or leafy. Algal blooms occur because of their ability to form dormant spores or cysts under unfavorable conditions and then germinate upon return of favorable conditions.

1.5. Mycorrhizae

Mycorrhizae are symbiotic associations between plant roots and fungi. The association is very widespread and beneficial in natural ecosystems as well as in agriculture. Fungi receive carbohydrates and other organic compounds from the plant and fungi provide the plant with enhanced capabilities to acquire nutrients (especially phosphorus and several micronutrients) and water from soil. The smaller diameter of fungal hyphae and extension of these hyphae into surrounding soil increase the surface area of the plant root system so that more nutrients can be extracted from the soil, which is especially important in relatively infertile soils.

There are two general mycorrhizal associations, i.e., endomycorrhizae where fungal colonization is within root cells and ectomycorrhizae where fungal colonization is between cells of the root. The fungal symbiont in endomycorrhizal associations are Phycometes. The most important endomycorrhizae are the arbuscular mycorrhizae, which infect many of the important agronomic crops of the world. Arbuscules are club-like, branched filaments within root cells where the transfer of energy and nutrients takes place. Many arbuscular mycorrhizae also contain vesicles within cells, which contain storage lipids and are probably important for reproduction. Fungal hyphae can extend several centimeters from the root, accessing nutrients and water, decomposing organic matter, and improving soil structure.

Ectomycorrhizae are important to woody plants, especially in the Fagaceae and Pinaceae families. The fungal symbiont in ectomycorrhizal associations are Basidiomycetes, which form mushrooms such as truffles. Fungi do not penetrate root cells in this association, but rather form a mantle around the root and form a web of hyphae (hartig net) between epidermal cells.

Fungal hyphae can extend several meters into the surrounding soil. Hyphae in this association also enhance nutrient uptake, decompose organic matter, and improve soil structure. Many fungal symbionts in the ectomycorrhizal association can be cultured apart from the host plant, while fungi of the endomycorrhizal association are obligate symbionts not cultured apart from host plants.

1.6. Lichens

Lichens are a symbiotic association between fungi and algae or fungi and cyanobacteria. In these relationships, the algae or cyanobacteria are primary producers, capturing energy from the sun and carbon from atomospheric CO_2, and fungi (either ascomycetes or basidiomycetes) are consumers. Fungi provide protection from the environment and obtain inorganic nutrients and growth factors for the association. Lichens grow very slowly, resist direct sunlight, and are able to colonize habitats unsuitable for other microorganisms by producing organic acids to solubilize rock minerals. Some lichens are able to fix atmospheric nitrogen because of the capabilities of cyanobacteria such as *Peltigera* and *Nostoc*.

1.7. Microfauna

Microfauna is a group of small animals (<200 μm length, <100 μm width) including protozoa, rotifers, and nematodes. Protozoa are eukaryotic organisms that are typically motile, single-celled, and nonphotosynthetic. Soil protozoa typically range in size from 25 to 200 μm and are grouped as naked amoebae, testate amoebae, ciliates, and flagellates based on mode of locomotion.

Protozoa proliferate in the surface of moist soils, feeding on bacteria and other soil organisms especially near the roots of plants. Cysts are formed during dormancy as a result of depletion of food source or soil drying. Number of protozoa in a surface soil is often inversely related to number of bacteria, i.e., high population following consumption and decreasing quantities of bacteria.

Rotifers can be found in soils that are continually moist, but are typically aquatic organisms and, therefore, not a major soil organism.

Nematodes (also called roundworms, threadworms, or eelworms) are some of the most numerous multicellular organisms in a wide range of soils. They proliferate in the water-filled pores of soil, as do protozoa and rotifers. The rhizosphere is a particularly active area for nematode proliferation. Most nematodes are saprophytic, i.e., feeding on decaying organic matter. Other nematodes feed on bacteria, fungi, plant roots, and other nematodes.

1.8. Mesofauna

Mesofauna is a group of organisms (0.2 to 10 mm length, 0.1 to 2 mm width) including tartigrades, collembola, and mites. Tartigrades (or water bears) range in size from 0.05 to 1.2 mm. They have similarities to both nematodes and microarthropods with bilateral symmetry having four pairs of legs. Tartigrades have cryptobiotic capabilities, i.e., undergoing dormancy induced by environmental stress and reactivating up to several years later. They are found typically in the top few centimeters of soil, feeding on algae, other microorganisms and particulate organic matter.

Collembola (or springtails) are small (0.2 to 5 mm in length), primitive insects. Many species jump by means of a furcula attached to the bottom of the abdomen. Most collembola eat decaying vegetation and fungi, although they have also been observed to consume nematodes and plant roots throughout the soil profile.

Collembola are opportunistic microarthropods (r-strategy), capable of rapid individual and population growth when conditions are favorable. They may be important biological control agents for crops by consuming pathogenic fungi. Eggs are laid in groups, and therefore, populations occur in aggregations rather than at random. Collembola can be important food sources for predacious mites, beetles, and ants.

Mites are some of the most abundant microarthropods in many soils. Soil mites are a very diverse assemblage of spiders, divided into four major groups, i.e., oribatids, prostigmatics, mesostigmatics, and astigmatics. Oribatid mites are often most numerous in soils, are morphologically distinct between juvenile and adult stages, reproduce relatively slowly (k-strategy), and typically feed on detritus and fungi.

Unlike most other microarthropods, oribatid mites have a calcareous exoskeleton. Prostigmatic mites feed on fungi, algae, and other soil organisms. Fungal-feeding prostigmatics are r-stategists, capable of rapid response to shifts in resources. Mesostigmatic mites are not particularly abundant in soil and are mostly predators of nematodes and other microarthropods. Astigmatic mites are the least common mites in soil and are found primarily in moist soil high in organic matter.

Other mesofauna that are less numerous, but present in many soils are protura (wingless insects lacking antennae and eyes that live near plant roots and litter), diplurans (elongate, delicate insects with long antennae and two abdominal cerci that feed either on decaying vegetation or predacious on nematodes, collembola, and enchytraeids), pseudoscorpions (small scorpions lacking tails and stingers that feed on nematodes, microarthropods, and enchytraeids), symphylids (white, eyeless, elongate, many-legged invertebrates resembling centipedes that feed on vegetation and soft soil animals), pauropoda (colorless, many-legged insects with branched antennae that feed on fungi and other soil organisms), and enchytraeids (or potworms, similar to earthworms, except smaller, that feed on fungi and possibly algae, bacteria, and other soil organisms).

-
-
-

Bibliography

Alexander M.A. (1994). Biodegradation and Bioremediation. 302 pp. San Diego, CA, USA: Academic Press [An excellent description of the processes and technologies of bioremediation].

Brussard L., Kooistra M.J. (1993). Soil Structure/Soil Biota Interrelationships. 829 pp. Amsterdam, Netherlands: Elsevier [A thorough review of established and innovative methods of soil ecological study and assessment at the microscopic scale].

Coleman D.C., Crossley D.A.Jr. (1996). Fundamentals of Soil Ecology. 205 pp. San Diego, CA, USA: Academic Press [A very good description of the types of organisms in soil, their interactions with the soil environment, and the processes they mediate].

Crossley D.A.Jr., Coleman D.C., Hendrix P.F., Cheng W., Wright D.H., Beare M.H., Edwards C.A. (Eds). (1991). Modern Techniques in Soil Ecology. 510 pp. Amsterdam, Netherlands: Elsevier [A recent compilation of methods describing soil microbial and faunal characteristics under various conditions].

Darbyshire J.F., (Ed). (1994). Soil Protozoa. 209 pp. Wallingford, Oxon, UK: CAB International [The only recent publication that describes in detail the types and activities of soil protozoa].

Dindal D.L. (1990). Soil Biology Guide. 1349 pp. New York, NY, USA: Wiley Press [Extensive classification key to the most common organisms found in soil].

Doran J.W., Coleman D.C., Bezdicek D.F., Stewart B.A. (1994). Defining Soil Quality for a Sustainable Environment. 244 pp. Madison, WI, USA: Soil Science Society of America [A collection of perspectives on defining soil quality, identifying soil quality indices, and assessing the biological importance of soil quality].

Paul E.A., Clark F.E. (1996). Soil Microbiology and Biochemistry. 340 pp. San Diego, CA, USA: Academic Press [Textbook devoted to the classical study of soil microbiology and its role in the environment].

Sylvia D.M., Fuhrmann J.J., Hartel P.G., Zuberer D.A. (1998). Principles and Applications of Soil Microbiology. 550 pp. Upper Saddle River, NJ, USA: Prentice-Hall [Excellent textbook devoted to the comprehensive coverage of soil microbiology].

Weaver R.W., Angle J.S., Bottomley P.S. (Eds). (1994). Methods of Soil Analysis, Part 2: Microbiological and Biochemical Properties. 1121 pp. Madison, WI, USA: Soil Science Society of America [Describes why and how procedures are used by soil scientists for the investigation of soil microbial properties].

Biographical Sketch

Alan J. Franzluebbers has been a Research Soil Ecologist with the U.S. Department of Agriculture–Agricultural Research Service in Watkinsville, Georgia, USA since 1996. He has a Ph.D. in soil science from Texas A&M University and graduated with a M.S. and B.S. in agronomy and horticulture from the University of Nebraska. He served one year as a Canadian Government Visiting Fellow in Beaverlodge, Alberta, Canada in 1995. He is the lead scientist for a base-funded project entitled "Enhancing soil-water-nutrient processes in Southern Piedmont pasture and crop systems". His scientific interests are in developing sustainable pasture and crop management systems and determining their impacts on the soil environment. Biochemical and biophysical properties of soils are of special interest. He has authored/coauthored 65 peer-reviewed publications and 101 non-peer-reviewed proceedings and abstracts. Alan serves as Joint-Editor-in-Chief of *Soil & Tillage Research*, is an associate editor of *Soil Science Society of America Journal*, and has served as a subject editor for *Soil Biology & Biochemistry*. He has been a reviewer of >300 manuscripts in 18 different agricultural and environmental journals.