



THE WORLD BENEATH OUR FEET: SOIL BIODIVERSITY AND ECOSYSTEM FUNCTIONING

DIANA H. WALL

Natural Resource Ecology Laboratory, College of Natural Resources,
Colorado State University, Fort Collins, Colorado 80523

ROSS A. VIRGINIA

Environmental Studies Program, Dartmouth College,
Hanover, NH 03755

ECOLOGICAL SERVICES PROVIDED BY SOIL BIODIVERSITY

THE IMPORTANCE of soil fertility as a national resource was aptly noted by Franklin D. Roosevelt: "The nation that destroys its soils destroys itself" (Roosevelt 1937). Since then, the importance of soils and the organisms within them for many vital ecosystem processes has been identified, for example, cleansing of water, detoxification of wastes, and decay of organic matter. Indeed, it is now recognized that the functioning of soils, the dark material beneath our feet, is critical for the survival of life on the planet in its present form. Almost every phylum known above the ground exists below the surface of the ground (Brussaard and others 1997). Soil biota include the microorganisms (bacteria, algae, and fungi), protozoa (single-celled animals), microscopic invertebrates that are less than 1 mm long (such as rotifers, copepods, tardigrades, nematodes, and mites), larger invertebrates up to several centimeters long such as those easily seen by the naked eye—ants, snails, earthworms, spiders, termites and so on, and vertebrates. One cubic meter of soil can harbor millions of species of microorganisms and microscopic invertebrates—organisms whose identities and contributions to sustaining our biosphere are largely undiscovered.

Life in soil is recognized as an important part of Earth's overall biodiversity, yet few studies measure the taxonomic diversity of soil or the relationship of soil biodiversity to ecosystem structure and function (Pimentel and others 1997; Swift and Anderson 1994). Understanding of the relationship between biodiversity and ecosystem function in soils is critically needed if we are to manage and predict

the impacts of human activity on ecosystems effectively and ensure soil sustainability.

Species in soils perform ecological services that directly control the sustainability of human life. Soil microorganisms and invertebrates (such as fungi, bacteria, nematodes, and earthworms) provide for the purification of air and water, for the decay and recycling of organic matter and hazardous wastes, and for soil fertility. Soil organisms mediate critical ecosystem processes, particularly those in biogeochemical cycling (Swift and Anderson 1994; Matson and others 1987). Soils store vast amounts of carbon, and it is the biota in soils that most influences local and global processes involving the cycling of carbon and nitrogen, including several greenhouse gases (Coleman and Crossley 1996; Huston 1993). The organisms in soil—through their direct, indirect, and modifying effects on these ecosystem processes (Lavelle and others 1995)—provide humans with numerous services (table 1). Pimentel and others (1997) valued the function of soil biodiversity at \$25 billion per year on the basis of the contributions of soil biodiversity to topsoil formation in agricultural lands; this value would increase considerably if natural terrestrial systems were included.

A single ecosystem service, such as the generation and renewal of soil and soil fertility (table 1), involves many ecosystem processes and countless organisms representing diverse phyla. These range from large vertebrates to invertebrates and smaller macrofauna such as earthworms and ants that channel through the soil, algae living on the soil surface, and microorganisms involved in the decay of organic matter (Pankhurst and Lynch 1994). The decay of a small animal (such as a piglet) in the soil requires many phyla and can involve 100–500 species of Arthropoda (Richards and Goff 1997). Knowledge of the succession of species participating in the decay of humans is used in forensic medicine to determine the time of death (Goff 1991). Information on the number and types of soil species and phyla required to decompose plant material or invertebrates might be avail-

TABLE 1 Some Ecosystem Services Provided by Soil Biota

Biota Ecosystem Services
Regulation of major elemental cycles
Retention and delivery of nutrients to plants
Generation and renewal of soil, and soil fertility
Detoxification and decomposition of wastes
Modification of the hydrological cycle
Mitigation of floods and droughts
Translocation of nutrients, particles, and gases
Regulation of atmospheric trace gases (production and consumption)
Regulation of animal and plant populations
Control of potential agricultural pests
Foundation of life from which humanity has derived elements of its agricultural, medicinal, and industrial enterprises

Source: Modified from Daily (1997).

able, but the data from many isolated field studies and from taxonomic work have not been synthesized.

Soil organisms contribute to the detoxification of pollutants on a global and a local scale—for instance, detoxifying the pollutants in our yards, farms, golf courses, and parks. These organisms, through their metabolism, are critical to detoxifying and purifying many pollutants before they are leached into groundwater and reach aquatic ecosystems (Abrams and Mitchell 1980; Sayler 1991). Finding environmentally sound ways to use organisms to renew polluted soils and decompose the garbage in our landfills is a growing industry (bioremediation) that depends on the ecosystem services of soil organisms (Sayler 1991).

Ecosystem services such as the mitigation of floods and droughts through prevention of soil erosion, the buffering and modification of the hydrological cycle and the translocation of nutrients, particles, and gases are a result of many species accomplishing different, but linked, tasks. For example, soils are a temporary habitat for predominantly aboveground organisms (such as vertebrates, lizards, rabbits, gophers, and birds) (Anderson 1987) and invertebrates (such as ants, spiders, and beetles) that move through the soil acting as cultivators or bioturbators, some species ingesting soil and others burrowing in and moving it. Those activities affect soil porosity, the retention of soil water and its movement vertically and horizontally, the transfer of materials throughout the soil profile, and the hydrological cycle. Soil bioturbators, while changing the physical and chemical environment of the soil, also transfer other, smaller organisms and soil particles within the soil, constantly creating new soil aggregates and new surfaces as habitats for microorganisms and facilitating topsoil formation. In this way, the soil biota “plows” the soil, mixing organic matter and nutrients essential for life throughout the soil profile.

Soil organisms have long been recognized as essential for agricultural food production. Nitrogen-fixing bacteria, mycorrhizal fungi, and rhizobacteria that have beneficial relationships with plants, in consort with the decomposers, supply elements essential for plant growth. In addition, through predator and prey interactions and parasitism, soil organisms control vast numbers of agricultural pests (insects, microorganisms, and fungi) (Kerry 1987). For example, the Steinernematid and Heterorhabditid nematodes that parasitize insects above and in the ground are used as a biological control of armyworms, carpenter worms, flea beetles, crown borers, cutworms, cockroaches, leaf miners, mole crickets, root weevils, stem borers, and white grubs (Kaya 1993). Many invertebrate species yet to be discovered are expected to have enormous potential as biological control agents.

SOIL BIODIVERSITY ASSESSMENT

Despite the essential nature of services provided by the soil biota, the systematics of the majority of these organisms has not been determined. Information is lacking on how species' abundance, distribution, and interactions influence ecosystem functioning and whether there are key taxa essential for ecosystem processes. Our ecological knowledge is insufficient to make needed inferences about factors controlling the distribution and activity of the species of soil biota

over broad geographic ranges and whether removal or introduction of species alters ecosystem processes. The identification of individual soil organisms to the species level is severely hampered because

- the sheer abundance of soil biota is overwhelming to describe—1m² of a pasture can contain 10 million nematodes, 45,000 oligochaetes, and 48,000 mites and collembola (Overgaard-Nielsen 1955);
- few scientists have soil taxonomic or soil ecological expertise; estimates are that only 3% of the world's scientists study microscopic and invertebrate organisms in soils;
- in situ identification of most soil organisms is difficult, so sampling and extraction techniques must be used to remove the organisms from soil, and these techniques should not affect the features used to identify and describe the individuals;
 - organisms range in size from microscopic to macroscopic;
 - organisms can have many different structures during their life cycle;
 - methods of sampling and identification must vary with the size of the taxonomic group, for example, earthworms and bacteria (Hall 1996; Oliver and Beattie 1996); and
- promising molecular techniques for most soil organisms are still in their infancy (Blair and others 1996; Hall 1996).

Together, those factors often make the identification and enumeration of soil biota seemingly an insurmountable obstacle for soil research. Perhaps the most important part of this problem is that the decline in human resources in taxonomy overall as a result of diminished institutional support for systematic research, particularly by agricultural and natural resource agencies, has been especially severe for soil taxa (Brussaard and others 1997; Freckman 1994).

There is a poor understanding of the ecological roles played by soil species. Factors contributing to the dearth of knowledge are many and include the following:

- The diversity of soil organisms spans many phyla (from microorganisms to arthropods to vertebrates), and this makes interactions and ecological roles difficult to assess.
- The temporal (seasonal and annual population changes) and spatial scale of the soil habitat that is relevant for an organism (from soil aggregate to landscape) varies among groups.
- Soil species can live at considerable depths (Freckman and Virginia 1989; Silva and others 1989), or can be restricted to microhabitats such as near the surface of roots (rhizosphere).
- The specific taxa participating in soil food webs can change with the soil physiochemical environment, the quality of organic matter, plant species diversity, landscape characteristics and climate. All these make it difficult to compare the ecological roles of soil taxa in different ecosystems.

Other than for earthworms, termites, and other larger soil invertebrates, the use of species composition in ecosystem studies is not yet widespread, because the taxonomy of nearly all groups is incomplete, and for most species only the adult stage is described. As a result, the approach to studying the link between organisms and ecosystem processes has been to place soil organisms in functional groups at a gross level—for example, considering all oribatid mites and springtails that feed on fungi to be fungivores, all mesostigmatid mites to be predators of other microfauna, and so on. The taxonomic and ecological limitations of this approach have been emphasized (Moore and others 1996; Walter and others 1988). We lack knowledge of the feeding strategies of more than 90% of the soil biota.

There is only baseline knowledge of the soil biodiversity in a few ecosystem types, mainly those with high economic value—agricultural, grazing, and forestry (Daily 1997; Pimentel and others 1997). The soil biodiversity estimates of those types generally exclude aboveground organisms that have only one phase of their life cycle in soil or that use the soil as a habitat. Groups of invertebrates, such as wasps and bees, or vertebrates (Anderson 1987; Ingham and Detling 1984; Naiman and Rogers 1997) are studied primarily by “aboveground scientists”, and the interchange of information about the functions of such organisms between these scientists and soil ecologists is rare. Some vertebrates, a group generally thought of as living predominantly aboveground, live entirely in the ground. For example, Caecilians (Wake 1983), one species of which was found living at a depth of 30 ft. We note that the recent summaries of taxonomic progress in the major soil biotic groups, which we have outlined below, do not include these predominantly aboveground organisms (Brussaard and others 1997; Groombridge 1992; Hawksworth and Ritchie 1993; O'Donnell and others 1994; Systematics Agenda 2000 1994). A brief assessment of the summaries and methods for studying soil organisms follows. We discuss the groups of soil organisms in order of increasing body size.

Viruses, Bacteria, and Fungi

There have been dramatic advances in the methods for assessing bacterial and fungal biodiversity, although no method can give the “best” quantitative estimate of diversity, because for these taxa and such invertebrates as the nematodes, the reproductive biology of the groups does not permit the application of a “species concept” (de Leij and others 2000; Zak and Visser 1996). For those groups, characteristics to define species are genetic, ecological, chemotaxonomic, and physiological (Snelgrove and others 1997). Molecular methods and chemosynthetic approaches are expanding our knowledge of bacterial and fungal diversity and of trophic relationships with soil invertebrates (Anderson 1975; Hawksworth 1991). Fungi and other microorganisms can be combined into functional groups on the basis of differences in the enzymes required to use particular carbon compounds (for example, cellulose, lignin, and sugar) (Zak and Visser 1996). The specificity of analysis has increased, allowing functional groups to be separated at finer levels of resolution, and enabling the types and numbers of microorganisms and their rates of use of primary and secondary compounds to be analyzed (Zak and Visser 1996). Another method, relying on biochemical markers of diversity termed

FAME (fatty acid, methyl esterase) profiles the relative abundance and diversity of broad groups of microorganisms (Stahl and Klug 1996). Viruses are rarely considered even though they can be potential biological control agents for soilborne pathogens of plants or plant pests. The importance of these microorganisms to ecosystem function is detailed in Lynch and others (this volume).

Microfaunal and Mesofaunal Invertebrate Groups

These groups are Protozoa, Rotifera (wheel animals), Tardigrada (water bears), Nematoda (roundworms), Acari (mites), and Collembola (springtails). No method extracts all taxa, and methods vary widely in their ability to extract these organisms from soil quantitatively and qualitatively. Many groups can be classified to the species level on the basis of morphological characteristics. More molecular methods are becoming available for classification and for assessing interspecific and intraspecific variation on a geographic basis (Avanzati and others 1994; Courtright and others in press; Oliver and Beattie 1996)

Macrofaunal Invertebrate Groups

These include Arachnida, Chilopoda, Diplopoda, Insecta, Annelida (segmented worms), and Mollusca (see figure 1). They can be more easily classified to the species level, and their ecological roles are known in general (Brown and Gange 1990). In temperate regions, their ecological roles include direct processing of organic matter, predatory regulation of population size, modification of soil structure, and production and consumption of atmospheric gases, such as methane. Organisms that cannot be readily identified to the species level include enchytraeid worms, many of the larger mites, some spiders, larval beetles and larval flies. Knowledge of these soil taxa varies dramatically between different locales, and only a few locations have well-described invertebrate macrofauna. Stable-isotope techniques have been used successfully to study trophic relationships and interactions in freshwater habitats and have great promise in soils (Barios and Lavelle 1986; Boutton and others 1983), particularly if extended to the microfauna.

CURRENT ESTIMATES OF SOIL BIODIVERSITY

Almost all aboveground phyla have representatives in soils, but there are no global assessments of the biodiversity in soils and only a few global estimates of individual taxonomic groups (Brussaard and others 1997). In figure 1, we present our estimate of soil biodiversity described to date on the basis of the lit-

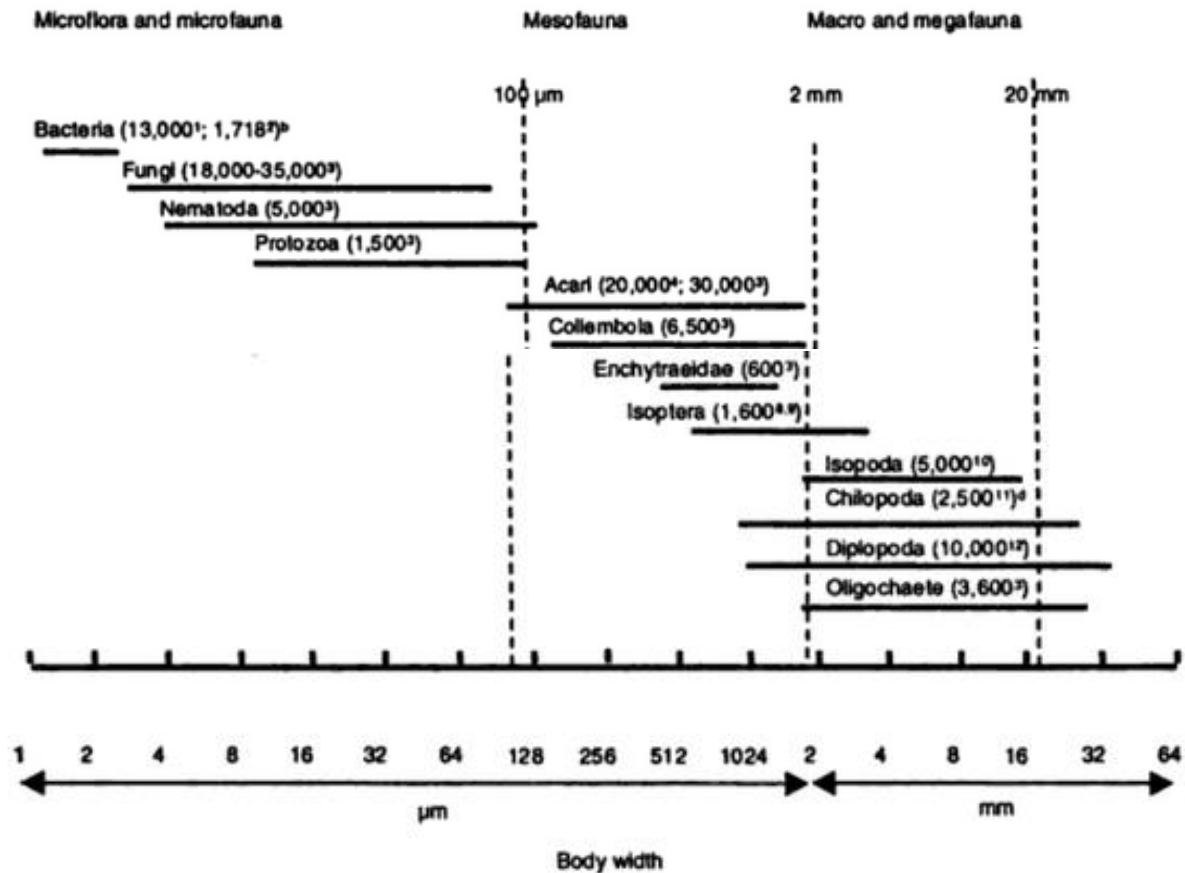


FIGURE 1 Size classification of organisms in the decomposer food web of soils^a, by body width (based on Swift, Heal and Anderson 1979), with number of species described to date for each group.

(a) Species in litter and decaying logs are included in the estimate of soil-dwelling species. (b) Torsvik and others (1994) measured 4,000 independent bacterium-sized genomes in 30 g of forest soil, using DNA analysis. They calculated that this equated to 13,000 species. In a review of Torsvik's study, Dykhuizen (1998) suggested that there could be as many as 500,000 species in the soil sample. Those numbers of species based on DNA analysis are much higher than those described from traditional bacterial isolation and culturing techniques (for example, the 1,718 according to Akimov and Hattori 1996) because culturable bacteria might represent only 0.1–1% of the species in a population. (c) Maddison (1995) gives the number of total described Diplura species (800). Because most Diplura are found in soil, we assumed this number to equal the number of soil-dwelling species. (d) Hoffman (1982a) gives the number of total Chilopoda species described (2,500). Because Chilopods are found only in soil, leaf litter, rotting wood, and caves, we assumed this number to equal the number of soil-dwelling species.

¹Torsvik and others 1994.

²Akimov and Hattori 1996.

³Brussaard and others 1997.

⁴Walters, personal communication.

⁵Ravlin 1996a.

⁶Maddison 1995.

⁷Scheller 1982.

⁸Bignell, personal communication.

⁹Bignell and Eggleton 1998.

¹⁰Brusca 1997.

¹¹Hoffman 1982a.

¹²Hoffman 1990.

Collembolla, 20,000–24,000 (Ravlin 1996b); Diplura, 1,647 (Ravlin 1996a); Enchytraeidae, 1,200 (Behan-Pelletier, personal communication); and Isoptera, 3,000 (Bignell and Eggleton 1998). In other groups, some of the species live outside the soil; estimates of total species in these groups include bacteria, 1,000,000; fungi 1,500,000; algae, 400,000; Nematoda, 1,000,000; protozoa, 200,000 (Hammond and others 1995); acari, 348,500–900,000 (Walter, personal communication; Walter and others 1998); and Diplopoda, 50,000–60,000 (Hoffman 1982b, 1990). These estimates of total existing species could be low; the soil component of biodiversity has traditionally been underappreciated and poorly described relative to aboveground species because of soil organisms' abundance and microscopic size and the dearth of soil taxonomists. The gulf between the numbers of species already described in soils and the projections of total numbers of species confirms what has already been heralded by others (Andre and others 1994; Wilson 2000; May 2000): that microscopic groups—such as bacteria, fungi, nematodes (Baldwin and others 2000; Bernard 1992), acari (Behan-Pelletier and Bisset 1993), Symphyla, and Enchytraeids (Healy 1980) are desperately in need of taxonomic and ecological attention.

The broad groups listed in figure 1 probably all have a global distribution. Information has not been synthesized to make general statements about diversity and geographic distribution (Brussaard and others 1997; Dighton and Jones 1994). For example, Lavelle and others (1995) analyzed earthworm community assemblages containing 8–11 species across 53 global climatic locations and found that neither species richness nor species diversity increased with decreasing distance from the tropics. However, they noted changes in the proportion of species feeding on soil and litter with decreasing latitude. That might not be unusual; Hammond (1995) noted that, for seasonally dry ecosystems, the increase in floristic diversity is not necessarily paralleled by an increase in the terrestrial diversity of invertebrates, fungi, or microorganisms.

There are more biogeographic assessments for individual groups listed in figure 1 on the political and regional scale than on a global scale (Brussaard and others 1997; Folgarait 1996; Pearce and Waite 1994). Species distribution patterns are influenced by chemical and physical factors—such as soil texture, organic matter, and soil moisture—as well as by climate and vegetation (Anderson 1975; Swift and others 1979; Wright and Coleman 1993). For example, some species of earthworms and Enchytraeids in the Oligochaetes rarely occur in deserts (Dash 1990; James 1995); and in the United States, where there are six indigenous genera of earthworms, the species distribution has been limited geographically (to such areas as those not affected by the Wisconsin glaciation, forests, mud flats, and riparian areas) (James 1995; Reynolds 1995).

On the basis of political boundaries, Coomans (1989) listed 228 terrestrial nematode species in Belgium, and Behan-Pelletier and Bissett (1993) estimated North American soil arthropods as follows: isopods, 92 described, 62 undescribed; chilopods, 850 described, 400 undescribed; diplopods, 850 described, 400 undescribed; pauropods, 70 described, 47 undescribed; symphyla, 33 described, 22 undescribed; spiders, 1,700 described, 250 undescribed; Opilionids, 235 described, 250 undescribed; acari, 2,500 described, 14,500 undescribed; and

Protura, 26 described, 104 undescribed. Lindquist and Behan-Pelletier (personal communication) estimate that the totality of described and undescribed species represents 10% of the world's total soil arthropods. Lawton and others (1996) in a Cameroon tropical-forest study, identified 115 species of termites and 432 nematode morphospecies in 185 genera. More than 90% of the nematodes remain unidentified because costs for further descriptions by taxonomists are expensive and time-consuming.

There is no compilation of endemic species in soils, but there are summaries of the endemic species in some groups listed in figure 1, such as earthworm species in the United States (James 1995). It is likely that in ecosystems that have endemic species and low species diversity, such as in soils of the Antarctic dry valleys, the species are more vulnerable to loss by disturbance, but whether their loss would affect ecosystem function must be confirmed through experimentation (Freckman and Virginia 1998).

EFFECT OF DISTURBANCE ON SOIL BIODIVERSITY

Whether the presence or absence of a single soil species can affect ecosystem structure or function (for example, such biogeochemical processes as rates of decomposition and plant production) is largely unresolved (Beare and others 1995) except for agroecosystems, in which a single species becomes noted as a crop pest, affecting transfer of nutrients and plant production (Brussaard and others 1997; Swift and Anderson 1994). The effects of introductions of soil species on ecosystem functioning constitutes a new field of study by aboveground ecologists, but it is a well-established field among agriculturalists. An example of the introduction of an alien species from Asia into a natural ecosystem in the United States is the earthworm species *Amyntas hawayanus*, which reduced New York forest-floor organic matter and increased water runoff and soil erosion (Burtelow and others 1998). The effects of introductions of alien species into fields have been studied by agriculturalists worldwide because of the potential devastating economic loss to crops (Cotten and Riel 1993; Swift 1997). Of growing importance is research on the introductions of soil organisms that might enhance plant productivity while protecting plants from pests (Cook 1993).

Better known, however, are the quarantines to restrict movement of soil biota and plant pests and thereby prevent the spread of exotic or established soil-pest species. The European Community lists nine plant-parasitic nematode species that are targeted in the hope of prohibiting introduction into Europe (EEC Council Directive 77/93/EEC, see Cotten and Riel 1993); California has 25 nematode species listed in its quarantine regulations. Despite such efforts, even the tightest regulations have been only partially successful. The US Department of Agriculture, with millions of dollars allocated to prevent the spread of *Globodera rostochiensis* (the potato cyst nematode) from Long Island, NY, where it became established in 1941, was unsuccessful in preventing its spread to other North American areas (figure 2). A second species of the potato cyst nematode, *Globodera pallida*, has not established itself in the United States but since 1972



FIGURE 2 Global dispersal of the potato cyst nematodes *Globodera rostochiensis* (diagonal lines) and *G. pallida* (stippling) from their centers of origin in the Andes of South America (based on Evans and Trudgill 1992).

has spread from its place of origin in the Andes of South America to New Zealand and globally (Wood and others 1983). It appears that the quarantine measures slow movement of the pest but in the long run is unable to prevent its introduction.

Although there has been no synthesis of the effects of the loss of individual soil species, the loss of entire functional groups has been shown to influence ecosystem function. For example, loss of taxa that are symbiotic with plants, such as the mycorrhizal fungi, can affect plant community structure. Re-establishment of plants on mine spoils or young volcanic soils can be slowed if mycorrhizal fungi are not present (Allen 1991). What is difficult to assess is the importance of the interactions of functional groups or individual species with other soil biota in the food web and how these perhaps less noticeable interactive effects influence ecosystem processes.

Soil biodiversity is adversely affected by human-induced disturbances that can be classified as physical (plowing, desertification, and landfill), chemical (air pollutants, fertilizers, chemical spills, and pesticides), changes in plant diversity (introductions of plants, changing from natural to managed systems, and changing plant species in agroecosystems), and environmental changes, such as climate alteration. Most observed changes in the diversity of soil biota after disturbance have been recorded at the level of the functional group (Brussaard and others 1997; Coleman and Crossley 1996) or at taxonomic levels, such as family (Andren and others 1995). On the basis of such results, several groups are recognized as useful indicators of soil disturbance; nematodes might be the most widely studied of such indicators (Blair and others 1996; Bongers 1990; Niles and Freckman

1998), although Lawton and others (1998) found that few organism groups, whether aboveground or in the ground, were effective indicators of habitat fragmentation.

The physical changes from disruptions of the soil environment include plowing, erosion, and desertification, which induce changes in the soil profile, soil texture, amounts and types of soil organic matter, soil chemistry, and microclimate (temperature, moisture, aeration, and release of carbon, nitrogen, and other greenhouse gases). Like aboveground organisms, soil-dwelling species have habitat preferences, and disruption of their soil habitat changes the community composition (Freckman and Ettema 1993; Freckman and Virginia 1989). The number of species of soil-dwelling termites and nematodes found in the Cameroon discussed earlier (Lawton and others 1998) declined with soil disturbance, even though deforestation can also increase the amount of woody debris for termite consumption. The termite species produce methane, but how their responses to disturbance affected methane production locally or globally is unknown. Erosion of the top inch of soil can also remove many microorganisms and smaller invertebrates. Chemical disturbances—such as caused by fertilizers, oil spills, heavy metals, and pesticides—have adverse effects on biotic function and species richness in soils (Brussaard and others 1997; Korthals 1997; Niles and Freckman 1998). Changes in plant diversity in cropping systems have been used for centuries to reduce the population densities of host-specific soil parasites.

The effects of global change on soils have been summarized (Ingram and Wall-Freckman 1998: see reviewer comment 26); they can alter soil biodiversity and ecosystem processes directly and indirectly. Norby (1997) suggested that effects of global change on the soil biota can result in feedbacks that could increase cycling rates of nutrients, resulting in increased emissions of CO₂ to the atmosphere. Direct effects of temperature could influence the duration of the life cycle of organisms and affect quantities and biomass of prey, food sources, and predators.

RESEARCH PRIORITIES AND CONCLUSIONS

Among the most pressing research needs is increased training of ecologists and taxonomists to work on the natural history and identification of soil-dwelling organisms. Only with this knowledge can we determine how to manage soils sustainably around the globe. Programs such as the Tropical Soil Biology Fertility Program (Swift 1997b), which has been going on for 11 years, are using international experiments that incorporate available information on soil biota and ecosystem processes to develop sustainable soil management in tropical agriculture. Increased knowledge of the relationship of biodiversity in soils to plant species diversity and the physical and chemical environment might allow us to predict hot spots of soil diversity by using the tools of remote sensing and geographic information systems and thus contribute to better predictions for land management. Information about soil biotas alone and their interactions with plants will contribute to testing and developing the ecological theory needed to predict the response of natural systems to disturbance (Ohtonen and others 1997). Knowledge of the

TABLE 2 Scientific Disciplines Necessary for Soil-Ecology Research

Biology and Taxonomy	Soil Science
Vertebrate zoology	Pedology
Invertebrate zoology	Soil chemistry
Entomology	Soil physics
Nematology	Soil ecology
Microbiology	Geology
Bacteriology	Hydrology
Mycology	Micrometeorology
Virology	Ecosystem science
Plant sciences	Landscape ecology
Agronomy and botany	Biogeochemistry
Plant pathology	
Plant physiology	
Ecology	
Taxonomy	
Molecular biology	
Informatics	

natural history of a soil biota, such as types of physiological changes in plant hosts caused by pest species, could help to reduce crop damage on a regional scale. For example, differences in transpiration flows between winter-wheat fields infected and not infected by the soil nematode *Heterodera avenae* can be noted with thermal infrared radiometry (Rivoal and Cook 1993). The spread of the pest, which is the most important in wheat fields of Australia and causes damage to 50% of the wheat fields in Europe, could be more effectively controlled with techniques based on knowledge of the natural history of the species. Today, our knowledge of this relatively well-studied species has enabled us to use its obligate fungal parasites for effective biological, rather than chemical, control in some regions (Rivoal and Cook 1993). Without increased resources for training in soil biodiversity and ecology, we will never be able to discover (or realize) the full extent of the benefits that the life in our soils can offer.

Recently, soil ecologists have assessed the priorities for research (Brussaard and others 1997; Ingram and Wall-Freckman 1998; Klopatek and others 1992; Wall-Freckman and others 1997), some of which are as follows:

- development of new techniques, improvement of current techniques, standardization of techniques for sampling and analysis, and informatics to enhance the database on soil biodiversity;
- development of interdisciplinary (table 2) and international cross-site experiments with predictive models to quantify the relationship of soil biodiversity to critical ecosystem processes on various spatial scales (see Freckman 1994 for examples of experiments, <http://www.nrel.colostate.edu/soil/lifeinthesoil.html>); a

basis for this work is being led by the UK (<http://mwnta.nmw.ac.uk/soilbio/>) and is being considered by other nations; and

- development of syntheses of the distributional patterns of soil biodiversity globally and regionally to understand the effects of global change on endemic and introduced species and to predict better how soils should be maintained for sustainable use; included is a proposed synthesis by a subcommittee of the Scientific Committee on Problems of the Environment that will examine the interrelationship of species biodiversity and functional groups aboveground to the below-surface realm, soils, and freshwater and marine sediments (Wall-Freckman and others 1997).

ACKNOWLEDGMENTS

The authors are grateful to Gina Adams for her research and critical comments. DHW particularly acknowledges the continued enthusiastic encouragement of Wren Wirth, Hal Mooney, D.C. Coleman, and D.A. Crossley Jr. The support of National Science Foundation grants OPP 91-20123, DEB 96-26813, and OPP 92-11773 is appreciated.

REFERENCES

- Abrams BJ, Mitchell MJ. 1980. Role of nematode-bacterial interactions in heterotrophic systems with emphasis on sewage sludge decomposition. *OIKOS* 35:404-10.
- Akimov V, Hattori T. 1996. Towards cataloguing soil bacteria: preliminary note. *Microbes Environ* 11:57-60.
- Allen MF. 1991. *The ecology of Mycorrhizae*. Cambridge UK: Cambridge Univ Pr.
- Anderson DC. 1987. Below-ground herbivory in natural communities: a review emphasizing fossorial animals. *Quar Rev Biol* 62(3):261-86.
- Anderson JM. 1975. Succession, diversity, and trophic relationships of some soil animals in decomposing leaf litter. *J Anim Ecol* 44:475-94.
- Andre HM, Noti M-I, Lebrun P. 1994. The soil fauna: the other last biotic frontier. *Biod Cons* 3:45-56.
- Andren O, Bengtsson J, Clarholm M. 1995. Biodiversity and species redundancy among litter decomposers. In: Collins HP, Robertson GP, Klug MJ (eds). *The significance and regulation of soil biodiversity*. Plant and Soil 170(1) Dordrecht The Netherlands: Kluwer Acad Publ. p.141-51.
- Avanzati AM, Baratti M, Bernini F. 1994. Molecular and morphological differentiation between steganacarid mites (Acari: Oribatida) from the Canary Islands. *Biol J Linn Soc* 52:325-40.
- Baldwin JG, Nadler SA, Wall DH. 2000. Nematodes: pervading the earth and linking all life. In: Raven PH, Williams T (eds). *Nature and human society: the quest for a sustainable world*. Washington, DC: National Academy Press. p 176-91.
- Barios I, Lavelle P. 1986. Changes in respiration rate and some physicochemical properties of a tropical soil during transit through *Pontoscolox corethurus*. *Soil Biol Biochem* 18(5):539-41.
- Beare MH, Coleman DC Jr, Hendrix PF, Odum EP. 1995. A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. In: Collins HP, Robertson GP, Klug MJ (eds). *The significance and regulation of soil biodiversity*. Plant and Soil 170(1) Dordrecht The Netherlands: Kluwer Acad Publ. p 5-22.
- Behan-Pelletier VM, Bisset, B. 1993. Biodiversity of Nearctic soil arthropods. *Canad Biod* 2:5-14.
- Bernard EC. 1992. Soil nematode biodiversity. *Biol Fertil Soils* 14:99-103.
- Bignell DE, Eggleton P. 1998. Termites. In: Calow P (ed). *Encyclopedia of ecology and environmental management*. Oxford UK: Blackwell Scientific. p 742-4.
- Blair JM, Bohlen PJ, Freckman DW. 1996. Soil invertebrates as indicators of soil quality. In: Doran J, Jones A (eds). *Methods for assessing soil quality*. Madison WI: Soil Science Society of America. p 273-91.

- Bongers T. 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83:14–19.
- Boutton TW, Arshad MA, Tieszen LL. 1983. Stable isotope analysis of termite food habits in East African grasslands. *Oecologia* 59:1–6.
- Brown VK, Gange AC. 1990. Insect herbivory belowground. *Adv Ecol Res* 20:1–58.
- Brusca R. 1997. Isopoda. Grice Marine Biological Laboratory, University of Charleston. Available at <http://phylogeny.arizona.edu/tree/eukaryotes/animals/arthropoda/crustacea/isopoda/isopoda.html>. Last accessed October 26, 1998.
- Brussaard L, Behan-Pelletier VM, Bignell DE, Brown VK, Didden W, Folgarait P, Frago C, Wall-Freckman D, Gupta VVSR, Hattori T, Hawksworth DL, Klopatek C, Lavelle P, Malloch DW, Rusek J. 1997. Biodiversity and ecosystem functioning in soil. *Ambio* 26 (8):563–70.
- Burtelaw A, Bohlen PJ, Groffman PM. 1998. Influence of exotic earthworm invasion on soil organic matter, microbial biomass and denitrification potential in forest soils of the northeastern US. *Appl Soil Ecol* 9(1–3):197–202.
- Coleman DC, Crossley Jr DA. 1996. Fundamentals of soil ecology. San Diego CA: Academic Press. p 205.
- Cook RJ. 1993. Making greater use of introduced microorganisms for biological control of plant pathogens. *Ann Rev Plant Path* 31:53–80.
- Coomans A. 1989. Oversight van vrijlevende nematofauna van België. In: Wouters K, Baert L (eds). Invertebrates of Belgium symposium papers. Brussels Belgium: Institut Royal des Sciences Naturelles de Belgique. p 43–56.
- Cotten J, Riel HV. 1993. Quarantine: problems and solutions. In: Evans K, Trudgill DL, Webster JM (eds). Plant parasitic nematodes in temperate agriculture. Wallingford UK: CABI. p 566–93.
- Courtright EM, Freckman DW, Virginia RA, Frisse LM, Vida TT, Thomas WK. In press. Nuclear and mitochondrial DNA sequence diversity in the Antarctic *Scottinema lindsayae*. *Nematology*.
- Daily GC. 1997. Natures services: societal dependence on natural ecosystems. Washington DC: Island Pr. p 392.
- Dash MC. 1990. Oligochaeta: Enchytraeidae. In: Dindal DL (ed). Soil biology guide. New York NY: J Wiley. p 311–40.
- de Leij FAAM, Hay DB, Lynch JM. 2000. Investment in diversity: the role of biological communities in soil. In: Raven PH, Williams T (eds). Nature and human society: the quest for a sustainable world. Washington, DC: National Academy Press. p 242–51.
- Dighton J, Jones HE. 1994. A review of soil biodiversity. London UK: Royal Commission on Environmental Pollution.
- Dykhuizen DE. 1998. Santa Rosa revisited. Why are there so many species of bacteria? *Antonie van Leeuwenhoek* 73:25–33.
- Eisenbeis G, Wichard W. 1987. Atlas on the biology of soil arthropods. New York NY: Springer-Verlag.
- Evans K, Trudgill DL. 1992. Pest aspects of potato production. Part 1—Nematode pests of potatoes. In: Harris PM (ed). The potato crop: the scientific basis for improvement. London UK: Chapman & Hall. p 445.
- Folgarait PJ. 1996. Latitudinal variation in myrmecophytic *Cercropia*. *Bull Ecol Soc Amer* 77:143.
- Freckman DW. 1994. Life in the soil. Soil biodiversity: its importance to ecosystem processes. Fort Collins CO: NREL, Colorado State University.
- Freckman DW, Ettema CE. 1993. Assessing nematode communities in agroecosystems of varying human intervention. *Agric Ecosys Environ* 45:239–61.
- Freckman DW, Virginia RA. 1989. Plant feeding nematodes in deep-rooting desert ecosystems. *Ecology* 70:1665–78.
- Freckman DW, Virginia RA. 1998. Soil biodiversity and community structure in the McMurdo Dry Valleys, Antarctica. In: Priscu J. Ecosystem dynamics in a polar desert. The McMurdo Dry Valleys, Antarctica. Washington DC: American Geophysical Union. p 323–36.
- Goff ML. 1991. Comparison of insect species associated with decomposing remains recovered inside dwellings and outdoors on the island of Oahu, Hawaii. *J Foren Sci* 36(3):748–53.
- Groombridge B (ed). 1992. Global biodiversity: status of the Earth's living resources. World Conservation Monitoring Center. London UK: Chapman & Hall.
- Hall GS. 1996. Methods for the examination of organismal diversity in soils and sediments. Wallingford UK: CABI. p 307.

- Hammond PM. 1995. Described and estimated species numbers: an objective assessment of current knowledge. In: Allsopp D, Colwell RR, Hawksworth DL (eds). *Microbial diversity and ecosystem function*. Wallingford UK: CABI. p 29–71.
- Hammond PM, Hawksworth DL, Kalin-Arroyo MT. 1995. Chapter 3. Magnitude and distribution of biodiversity: 3.1. The current magnitude of biodiversity. In: Heywood VH (ed). *Global biodiversity assessment*. Cambridge UK: Cambridge Univ Pr. p 113–38.
- Hawksworth DL. 1991. The fungal dimension of biodiversity: magnitude, significance, and conservation. *Mycolog Res* 95:641–55.
- Hawksworth DL, Ritchie JM. 1993. *Biodiversity and biosystematic priorities: microorganisms and invertebrates*. Wallingford UK: CABI.
- Healy B. 1980. Records of Enchytraeidae (Oligochaeta) from western France and Pyrenees. *Bull Mus Nation Hist Nat Paris Ser (2) A*:421–43.
- Hoffman RL. 1982a. Chilopoda. In: Parker SP (ed). *Synopsis and classification of living organisms*. New York NY: McGraw-Hill. p 681–8.
- Hoffman RL. 1982b. Diplopoda. In: Parker SP (ed). *Synopsis and classification of living organisms*. New York NY: McGraw-Hill. p 689–724.
- Hoffman RL. 1990. Diplopoda. In: Dindal DL (ed). *Soil biology guide*. New York NY: J Wiley. p 835–60.
- Huston M. 1993. Biological diversity, soils, and economics. *Science* 262:1676–80.
- Ingham RE, Detling JK. 1984. Plant-Herbivore interactions in a North American mixed-grass prairie. *Oecologia* 63:307–13.
- Ingram J, Wall-Freckman D. 1998. Soil biota and global change. Special issue, preface. *Global Change Biology* 4(7):699–701.
- James SW. 1995. Systematics, biogeography, and ecology of Nearctic earthworms from eastern, central, southern and southwestern United States. In: Hendrix PF (ed). *Earthworm ecology and biogeography*. Boca Raton FL: Lewis Publ. p 29–52.
- Kaya HK. 1993. Entomogenous and entomopathogenic nematodes in biological control. In: Evans K, Trudgill DL, JM Webster (eds). 1993. *Plant parasitic nematodes in temperate agriculture*. Wallingford UK: CABI. p 565–91.
- Kerry BR. 1987. Biological control. In: Brown RH, Kerry BR. *Principles and practices of nematode control in crops*. Sydney Australia: Acad Pr. p 233–63.
- Klopatek CC. 1992. The sustainable biosphere initiative: a commentary from the US Soil Ecology Society. *Bull Ecol Soc Amer* 73(4):223–7.
- Lavelle P, Lattaud C, Trigo D, Barois I. 1995. Mutualism and biodiversity in soils. In: Collins HP, Robertson GP, Klug MJ (eds). *The Significance and regulation of soil biodiversity*. Plant and Soil 170(1). Dordrecht The Netherlands: Kluwer Acad Publ. p 23–33.
- Korthals GW. 1997. Pollutant-induced changes in terrestrial nematode communities. PhD thesis. Landbouwniversiteit te Wageningen.
- Lawton JH, Bignell DE, Bloemers GF, Eggleton P, Hodda ME. 1996. Carbon flux and diversity of nematodes and termites in Cameroon forest soils. *Biod Cons* 5:261–73.
- Lawton JH, Bignell DE, Botton B, Bloemers GF, Eggleton P, Hammond PM, Hodda M, Holt RD, Larsen TB, Mawdsley NA, Stork NE, Srivastava DS, Watt AD. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in a tropical forest. *Nature* 391:72–6.
- Maddison, David. 1995. Diplura. Department of Entomology, University of Arizona. Available at <http://phylogeny.arizona.edu/tree/eukayotes/animals/arthropoda/hexapoda/diplura/diplura.html>. Last accessed 26 October 1998.
- Matson PA, Vitousek PM, Ewel JJ, Mazzarino MJ, Robertson GP. 1987. Nitrogen transformations following tropical forest felling and burning on a volcanic soil. *Ecology* 68(3):491–502.
- May RM. 2000. The dimensions of life on earth. In: Raven PH, Williams T (eds). *Nature and human society: the quest for a sustainable world*. Washington, DC: National Academy Press. p 30–45.
- Moore JC, Coleman DC, DeRuiter PC, Freckman DW, Hunt HW. 1996. Microcosms and soil ecology: critical linkages between field studies and modelling food webs. *Ecology* 77:694–705.
- Naiman RJ, Rogers KH. 1997. Large animals and system-level characteristics in river corridors: implications for river management. *BioScience* 47(8):521–9.
- Niles RK, Freckman DW. 1998. From the ground up: nematode ecology in bioassessment and ecosystem health. In: Barker KR, Pederson GA, Widham GL (eds). *Plant-nematode interactions*. Agronomy Monograph. Madison WI: Amer Society of Agronomy, Crop Science Society of America, and Soil Science Society of America. p 65–85.

Norby R. 1997. Inside the black box. *Nature* 388:522–3.

O'Donnell AG, Goodfellow M, Hawksworth DL. 1994. Theoretical and practical aspects of the quantification of biodiversity among microorganisms. *Philos Trans Roy Soc London* 345:65–73.

Ohtonen R, Aikio S, Vare H. 1997. Ecological theories in soil biology. *Biochemistry* 29:1613–9.

Oliver I, Beattie AJ. 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecol Appl* 6(2):594–607.

Overgaard-Nielsen C. 1955. Studies on Enchytraeidae 2: field studies. *Natura Jutlandica* 4:5–58.

Pankhurst CE, Lynch JM. 1994. The role of the soil biota in sustainable agriculture. In: Pankhurst CE, Doube BM, Gupta VVSR, Grace PR (eds). *Soil biota management in sustainable farming systems*. Melbourne Australia: CSIRO. p 3–9.

Pearce MJ, Waite B. 1994. A list of termite genera with comments on taxonomic changes and regional distribution. *Sociobiology* 23:247–62.

Pimentel D, Wilson C, McCullum C, Huang R, Dwen P, Flack J, Tran Q, Saltman T, Cliff B. 1997. Economic and environmental benefits of biodiversity. *BioScience* 47(11):747–57.

Ravlin FW. 1996a. Diplura (Diplurans). Department of Entomology, Virginia Polytechnic Institute and State University. Available at http://www.gypsymoth.ento.vt.edu/~ravlin/insect_orders/diplura.html. Last accessed 26 October 1998.

Ravlin FW. 1996b. Collembola (Springtails). Department of Entomology, Virginia Polytechnic Institute and State University. Available at http://www.gypsymoth.ento.vt.edu/~ravlin/insect_orders/collembola.html. Last accessed 26 October 1998.

Reynolds JW. 1995. Status of exotic earthworm systematics and biogeography in north America. In: Hendrix PF (ed). *Earthworm ecology and biogeography*. Boca Raton FL: Lewis Publ. p 1–28.

Richards EN, Goff ML. 1997. Arthropod succession on exposed carrion in three contrasting tropical habitats on Hawaii island. *J Med Entomol* 34(3):328–39.

Rivoal R, Cook R. 1993. Nematode pests of cereals. In: Evans K, Trudgill DL, Webster JM (eds). *Plant parasitic nematodes in temperate agriculture*. Wallingford UK: CABI 210–59.

Roosevelt FD. 1937. Speech as United States President. Letter to all State Governors, requesting implementation of Standard State Soil Conservation District Laws.

Saylor G. 1991. Contribution of molecular biology to bioremediation. *J Hazard Mat* 28:13–28.

Scheller U. 1982. Symphyla. In: Parker SP (ed). *Synopsis and classification of living organisms*. New York: McGraw-Hill. p 96–102.

Silva S, Whitford WG, Jarrell WM, Virginia RA. 1989. The microarthropod fauna associated with a deep rooted legume, *Prosopis glandulosa*, in the Chihuahuan desert. *Biol Fertil Soils* 7:330–5.

Snelgrove PVR, Blackburn TH, Hutchings PA, Alongi DM, Grassle JF, Hummel H, King G, Koike I, Lamshead PJD, Ramsing NB, Solis-Weiss V. 1997. The importance of marine sediment biodiversity in ecosystem processes. *Ambio* 26(8):578–83.

Stahl PD, Klug MJ. 1996. Characterization and differentiation of filamentous fungi based on fatty acid composition. *Appl Env Microbiol* 62(11):4136–46.

Swift MJ. 1997. Soil biodiversity, agricultural intensification and agroecosystem function in the tropics. *Appl Soil Ecol* 6:1–108.

Swift MJ. 1997. Ten years of soil fertility research—where next? In: Bergstrom L, Kirchman H (eds). *Carbon and nutrient dynamics in natural and agricultural tropical ecosystems*. Wallingford UK: CABI. p 303–12.

Swift MJ, Anderson JM. 1994. Biodiversity and ecosystem function in agricultural ecosystems. New York NY: Springer-Verlag. p 25.

Swift MJ, Heal OW, Anderson JM. 1979. *Decomposition in terrestrial ecosystems*. Oxford UK: Blackwell Scientific Pr. *Systematics Agenda 2000*. 1994. Charting the biosphere. A consortium of the American Society of Plant Taxonomists, Society of Systematic Biologists, and the Willi Hennig Society, in cooperation with the Association of Systematists Collections. Available from: *Systematics Agenda 2000*, Dept. of Ornithology, American Museum of Natural History.

Thematic Issue: soil biota and global change. 1998. *Global change biology*.

Torsvik V, Goksoyr J, Daae FL, Sorheim R, Michalsen J, Salte K. 1994. Chapter 4. Use of DNA analysis to determine the diversity of microbial communities. In: Ritz K, Dighten KE, Giller (eds). *Beyond the biomass*. Chichester UK: Wiley. p 39–48.

Wake MH. 1983. *Gymnopsis multiplicata*, *Dermophis mexicanus*, and *Dermophis parviceps* (Soldas, Suelda con Suelda, Dos Cabezas, Caecilians) 400–1. In: Janzen DH (ed). 1983. *Costa Rican natural history*. Chicago IL: Univ Chicago Pr. p 816.

Wall-Freckman D, Blackburn TH, Brussard L, Hutchings PA, Palmer M, Snelgrove PVR. 1997. Linking biodiversity and ecosystem functioning of soils and sediments. *Ambio* 26(8):556-62.

Walter DE, Hunt HW, Elliott ET. 1988. Guilds or functional groups? An analysis of predatory arthropods from shortgrass steppe soil. *Pedobiologia* 31:247-60.

Walter, DE, Krantz J, Lindquist E. 1998. <http://phylogeny.arizona.edu/tree/eukaryotes/animals/arthropoda/arachnida/acari/acari.html>.

Wilson EO. 2000. The creation of biodiversity. In: Raven PH, Williams T (eds). *Nature and human society: the quest for a sustainable world*. Washington, DC: National Academy Press. p 22-9.

Wood FH, Foot MA, Dale PS, Barber CJ. 1983. Relative efficacy of plant sampling and soil sampling in detecting the presence of low potato cyst nematode infestations. *New Zeal J Exp Agric* 11:271-3.

Wright DH, Coleman DC. 1993. Patterns of survival and extinction of nematodes in isolated soil. *OIKOS* 67:563-72.

Zak J, Visser S. 1996. An appraisal of soil fungal biodiversity: the crossroads between taxonomic and functional biodiversity. *Biod Cons* 5:169-83.