Soil biology, soil ecology, and global change

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Summary. This overview paper addresses aspects of scaling in space and time, and scaling in relation to micro- and macrohabitats. Ecological processes in soils are examined for possible generalizations about processes and organisms, across a wide range of different habitats. Problems of scaling in space and time that have an important impact on processes associated with global change are outlined.

Key words: Global change – Scaling – Hierarchies – Soil organisms – Soil processes

Scaling in space

In the last decade of the twentieth century, there is an ever-increasing awareness of the need to integrate studies of organismal activities and the biotic diversity extant in a wide range of different ecosystems. This is being pursued in various national networks, such as the Long Term Ecological Research program (LTER), and international networks, such as the SCOPE and IGBP research efforts which extend across most continental land masses on the surface of the earth.

The situation at the end of the twentieth century is one of moderate success; we have been concerned with levels of resolution ranging from the microscale, within soil aggregates, through the mesoscale, within m^2 quadrats of study, to the macroscale, of events on given landscape units. We need additions at very small levels, within aggregates, or even at the level of clay platelets, which can be effectively scaled up to regional and global levels. The most satisfying approach to this almost overwhelming array of organisms, processes, and levels of resolution is to consider the phenomena in terms of levels of origin and their ultimate effects.

Examples of the global influence of soil processes include the products of denitrification, such as N_2O, N_2,

and the global accumulation of CO_2, CH_4, and associated C-cycle gases (Melillo et al. 1989; Mosier et al. 1991). For the C cycle in particular, plant and ecosystem responses (Mooney et al. 1991) and the question of the missing 1–2 gigatonnes (disparity between annual inputs and outputs from the atmosphere) is of concern to the scientific community (Scharpenseel et al. 1990).

Global change and regional research efforts

Large-scale field and process studies. As part of several integrated measurement programs, it has been necessary to undertake large-scale (regional–continent wide) field and process studies. These efforts require collaboration across many disciplines, including remote sensing, atmospheric physics, meteorology, and several biological and soil science disciplines, too.

There are several studies underway, including (1) Hydrologic Atmospheric Pilot experiment (HAPEX), concentrating on energy and water balance studies on large regional scales; (2) International Global Atmospheric Chemistry program, involving rates of exchange between representative tropical biological environments and the atmosphere; and (3) one of the more noteworthy experiments operating over a wide range of spatial scales, FIFE, the First ISLSCP Field Experiment, conducted at the Konza Prairie Research Natural area, in collaboration with NCAR, NOAA, and NSF.

For the latter experiment, several levels of resolution have been required to reach research objectives, and at various levels of interaction (Fig. 1), including surface flux stations, and automated meteorological sites monitor surface fluxes and near-surface meteorological conditions; NOAA providing nine satellite scans at a resolution of about 1 km^2; a National Aeronautics and Space Administration (NASA) C-130 plane traversing at 5000 m above ground level, taking scanner and sun photometer data; a NASA helicopter hovering above preselected sites at 250 m above ground level, acquiring radiometric data; and a NCAR King Air device collects eddy correlation data at 160 m above ground level. This array feeds in spot

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NOAA-9

FIFE
15:17
June 4th, 1987

NASA C-130

NASA H-1

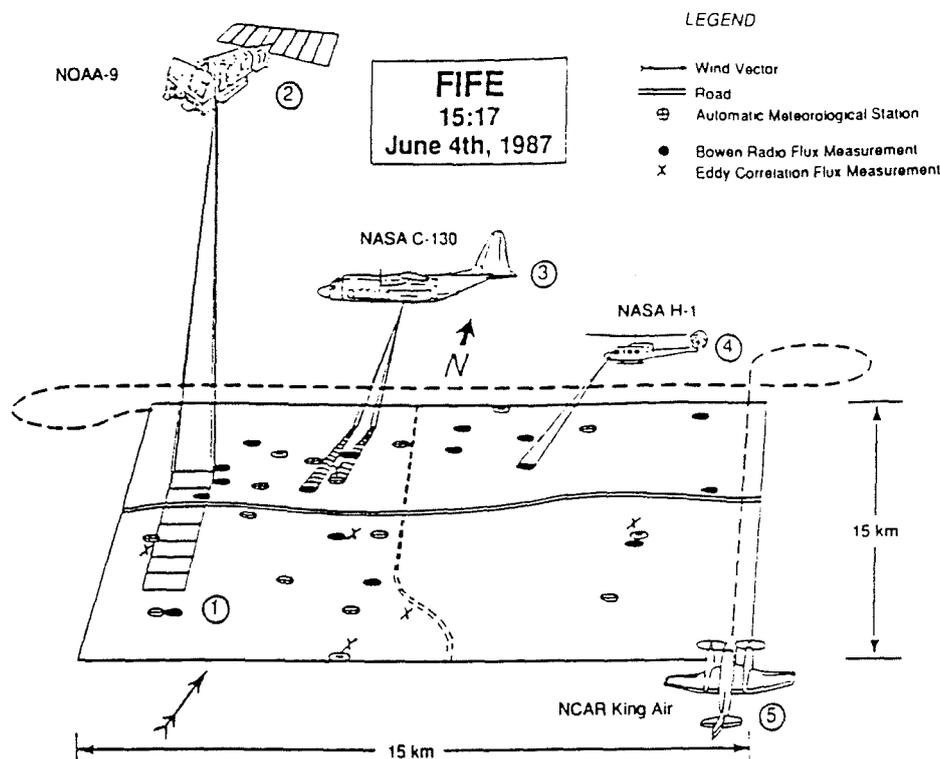N

15 km

NCAR King Air

15 km

Fig. 1. Hierarchical array of measurements taken as part of the First ISLSCP Field Experiment (FIFE) on Meteorological and Net Primary Production studies at the Konza Prairie Research Natural Area, in 1987 (from Risser 1990). *NASA*, National Aeronautics and Space Administration; *NOAA*, National Oceanic and Atmospheric Administration; *NCAR*, National Center for Atmospheric Research

measurements from collections made within a grid of ca. 225 km square, giving information that can be used to calculate various process measurements, and increments of biomass, particularly with ongoing experiments on spring or fall burning, and cattle grazing.

Further examples of approaches to broadening our scales of resolution and scope of investigation to a landscape and regional scale are covered in a recent paper by Wessman (1991).

Mesoscale

On a mesoscale, a holistic view is necessary in finding loci of activity. Thus Vance and Nadkarni (1990) examined the nature and extent of canopy organic matter in Costa Rican tree canopies (Table 1). They found that canopy organic matter was fully as dynamic as the active organic matter fraction in soil (Parton et al. 1988), and may be a key factor in N and P cycling in these ecosystems with high standing-crop plant biomass and low amounts of labile N and P.

Soil as the chief organizing center for ecosystem function

We can perhaps draw an analogy between the operation of a computer and the operation of an ecosystem. To operate a computer one has to have a disk operating system (DOS) that is either inserted as a floppy disk or built into the machine as part of a hard drive. In a somewhat analogous way soils are the organizing center for terrestrial ecosystems and sediments, likewise in aquatic ecosystems. Major functions such as P and R (community production and respiration) and recycling are controlled by the rate at which nutrients are released by decomposition

Table 1. Microbial biomass concentrations in canopy organic matter (COM) and forest-floor (FF) horizons H and A1, Costa Rica

Sample	Biomass C	Biomass N	Biomass C as percentage of total organic C
	(μg g^{-1} soil)		
COM	2650a $\pm$ 330	340a $\pm$ 70	0.71
FF-H	2670a $\pm$ 170	320a $\pm$ 20	0.99
FF-A1	1950a $\pm$ 30	220a $\pm$ 20	1.3

Means $\pm$ SE, $n = 4$. Values designated by different letters are significantly different at $P = 0.05$. From Vance and Nadkarni (1990)

in the soil and litter horizons and transported to the photosynthetic layers of the ecosystem.

In soils that are poor, either because of geological history, as in rain forests developing on sand, or because of abuse by humans, as in the eroded soils of Piedmont, USA, mycorrhizas or other mutualonts are major, perhaps obligate, partners with roots in maintaining the flow of nutrients to the green biomass. It has recently been shown that mycorrhizas are efficient at extracting nutrients from both mineral and organic sources and passing them to plants (Read 1991). Learning how to measure the output of nutrients from the recycling center in a holistic manner, and understanding how it is controlled might be considered as two major objectives for future research. Certainly, we cannot really scale up to a global hierarchical level without better knowledge about the decomposition and detrital food chains in major ecosystem types that comprise the global landscape.

Soil structure, microscale phenomena

The need for an appreciation of soil structure has been emphasized by several soil scientists/soil biologists.

Romell (1930) commented: "It is more and more generally recognized that a natural soil, like a living organism, must be studied as a whole to get a correct idea of its responses." Other authors compared soil structure to a dwelling. Burger (cited in Jacot 1936) observed that "agricultural soil" may be compared "to an unorganized mass of building material, whereas the natural forest soil, with its definite, stable organization, is like a house built from this material." Jacot (1936) likened many physicochemical analyses to blowing up a large apartment house, and reporting its constituents as so much bricks, mortar, etc., but noted: "natural soil is as highly organized as a huge apartment house and as well tenanted." One of the major developments of the last decade has been the use of minimum tillage or no-tillage approaches to agroecosystem research and management, which has brought soils subjected to agricultural activities more closely in line with natural soils.

On a microscale, physicochemical interactions are important at the level of clay platelets and other soil primary particles. Soil physics and biology interact at the level of microbial activity and root–faunal interactions in micro- and macroaggregates. These have been well reviewed by Tisdall and Oades (1982) and Oades (1988). Other reviews that include a wider range of soil biota have been presented by Foster (1985) and Elliott and Coleman (1988). Some of the still unanswered questions at the microscale are concerned with the interactions among "legacies" of previous organismal actions, such as the deposition of fecal pellets, which markedly alter several elemental cycling processes in the vicinity (Pawluk 1987). These questions have provided the focus for several current research studies around the world in an experimental agroecosystem context. For example, Hendrix et al. (1990) and Coleman et al. (1989) studied changes in soil aggregate stability and organic matter persistence at microsites in an agricultural landscape. Recent work in Europe (Andrén et al. 1990; Brussaard et al. 1990) has also examined these processes.

One of the recurring global themes is the extent to which human-influenced systems, whether forested or agricultural, can be managed to retain or even enhance aspects of structural complexity that are of cardinal importance for long-term ecosystem stability. For much of our research in terrestrial ecosystems, we try to find ways of successfully integrating a large number of processes into an overall environmental matrix. One of the more successful integrative constructs has been the watershed, which uses water movement as the chief integrating variable. Situated in a topographic matrix, this enables us to consider the contributing factors of parent material, geomorphological processes, and so forth. Numerous studies in the LTER network have used this approach (Swank and Crossley 1988; Swanson and Sparks 1990; Franklin et al. 1990).

Scaling in time

Like scaling in space, scaling in time requires the development of methods, in this case to handle sequences on either end of the existing time-scale, which ranges from minutes to years and centuries. There are events that occur at the split-second level, in very disparate microsites, such as volatilization of N_2O and N_2 during denitrification, and leaf ammonia volatilization (Groffman and Tiedje 1989; Mosier et al. 1991). On the long-range end of the time-scale, questions of organic matter accumulation and the formation of kerogens, etc., are of considerable interest and should be extended to the immobilization, or lack of it, of organic C and N in various deposits, and sedimentary rock. These concerns are an important interface with global geochemistry (Scharpenseel and Becker-Heidmann 1990).

Some of the global C-cycle questions directly concern the effects of soil biota and of the soil organic matter "pool" on the rate of accumulation of organic C over the shortterm span of the next few decades. Scharpenseel and Becker-Heidmann (1990) have estimated the amount of C in the pedosphere as about 2000 petagrams (10^{15} g), with annual fluxes, in and out, of about 60 petagrams (Fig. 2). As reported by Prinn (personal communication) some recent conjectures suggest that up to 3 petagrams per year of the often-quoted "missing C" in the global C cycle may be entering the soil organic matter pool (pedosphere minus biosphere = ca. 1200 petagrams). Inasmuch as this estimate has come from an inference that it must be there, because it cannot be traced anywhere else, it is important to discuss the ways in which these measurements might be taken. Does the soil C pool receive inputs in a uniform fashion across all regions and biomes, or does the input occur more extensively in a few sites? If the entire pool is ca. 1200 petagrams, and a net addition of 3 petagrams per year is postulated, how soon should there be a significant increase in the global mean value? These are some of the questions for which soil ecologists can help provide the answers.

Viewed more generally, soils operate over a large range of time-scales, which may be characterized as fast, intermediate, and slow. Stewart et al. (1990) characterized variables such as soluble salts or microbial growth as highly dynamic, varying within a season, microbial/faunal interactions as intermediate, whereas organic matter levels have time dimensions of decades to centuries,

Table 2. Grouping of soil-related processes and components based on time

| Highly dynamic	Dynamic	More static, slow
Soluble nutrients	Adsorbed nutrients	Nutrient reserves in minerals
Active or soluble organic matter	Labile organic matter adsorbed to clay	Chemically stabilized organic matter
Solution and movement of soluble components	Weathering of carbonate minerals	Weathering of silicates and clay minerals
Microbial growth	Micro-fauny and meso-fauna Plant growth	Vegetation (forest)

From Stewart et al. (1990)
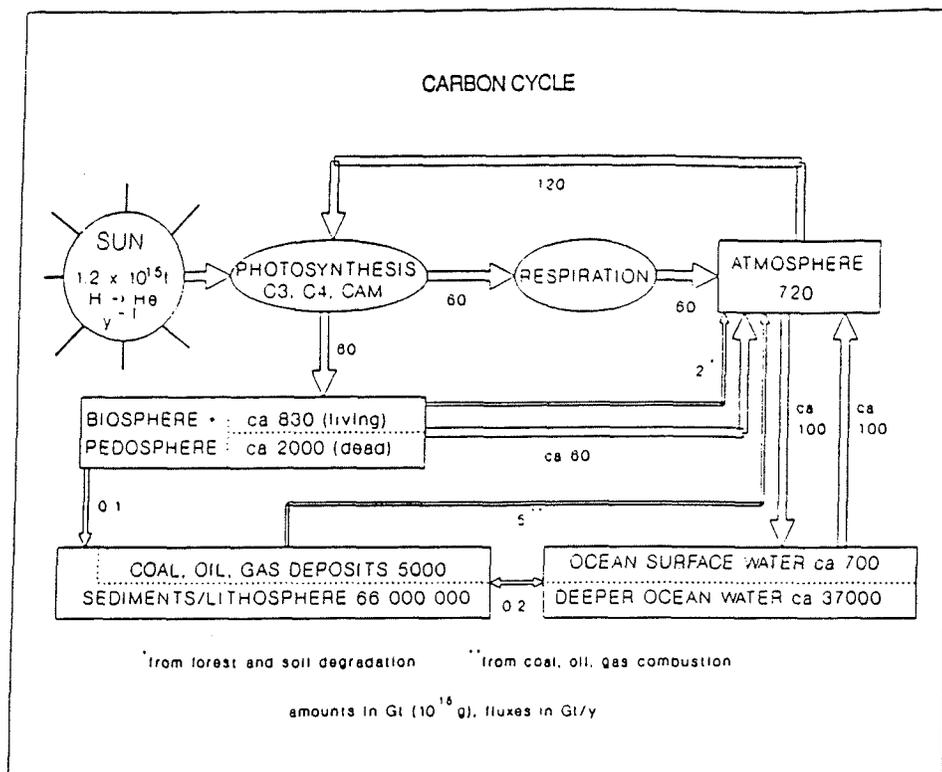
Fig. 2. C compartments in biochemical and geochemical cycles, showing C in standing crop and annual fluxes into and out of the biosphere and the pedosphere (from Scharpenseel and Becker-Heidmann 1990)

with clay weathering occuring over millennia in arid or semiarid climates (Table 2).

A hierarchical view of soil ecology

Hierarchical approaches to ecological research have aroused increasing interest over the last decade (Allen and Starr 1982; O'Neill et al. 1986). A number of studies have referred to ways of organizing research in landscapes and regions. A number of levels of resolution can be organized in a landscape context, using ecosystem-level criteria, such as movement of water and materials within a watershed (Fig. 3). The conceptual diagram (Fig. 3) ranges from an entire watershed at the widest scale down to microsites on roots and leaves, and even lower, to ways in which the chemical composition of leaves, roots and organic matter can be determined analytically. Thus there are numerous processes, arranged in more of a level-of-resolution fashion (Fig. 4), that can be studied in a comparative fashion. As discussed below, we most often compare processes between stands of vegetation or across watersheds, particularly when following integrating variables, such as water flow, which influences nutrient and POM and DOM exports. If one were more concerned with air pollutants or gaseous losses of NO_x or CH_4, we would work at a wider, more regional or airshed-level of resolution (Haines and Swank 1988).

Habitat variability in soil ecology

One of the guiding principles in soil studies has been the theory of soil formation, with various factors originally proposed by Dokuchaev (1879) and more formally organized by Jenny (1941). A few years ago, Coleman et al. (1983) reformulated these factors in the context of pro-

cesses in ecosystems. As shown in Fig. 4, a wide range of human-influenced and other, less affected ecosystems are considered.

The above approach incorporates the unity of purpose that various processes have in common across many ecosystems. We also wish to consider the reverse, namely, what processes are different, across ecosystems, and are these traceable to any of the major soil-forming factors, and if so which ones are most prominent in contributing to these differences? What aspects of ecosystem function at the site, watershed, or landscape level are amenable to comparison using readily available techniques? A few researchers have used this approach, as outlined below.

Habitat variability as related to ecosystem processes

Example of cross-site comparisons. In a series of experiments, the structural and functional inter-relationships of belowground food webs were compared across three different semiarid vegetation types, lodgepole pine (*Pinus contorta* subsp. latifolia), mountain meadow (*Agropyron smithii*), and shortgrass prairie (*Bouteloua gracilis*). The site and soil characteristics were similar, with all having a sandy loam texture, a pH of 5.5–6.5, and a mean annual precipitation ranging from 400 mm (prairie) to 600 mm in the other two sites. Mean annual temperatures were 10, 4, and 0 °C for the prairie, forest, and meadow sites, respectively (Coleman et al. 1990). Net primary production, decomposition rates, and extractable N in soil were measured at each site after the application of 60 g sucrose-C per m^2 and 15.4 g ammonium nitrate-N per m^2. The densities of food web groups were measured after treating litter in litterbags with carbofuran and
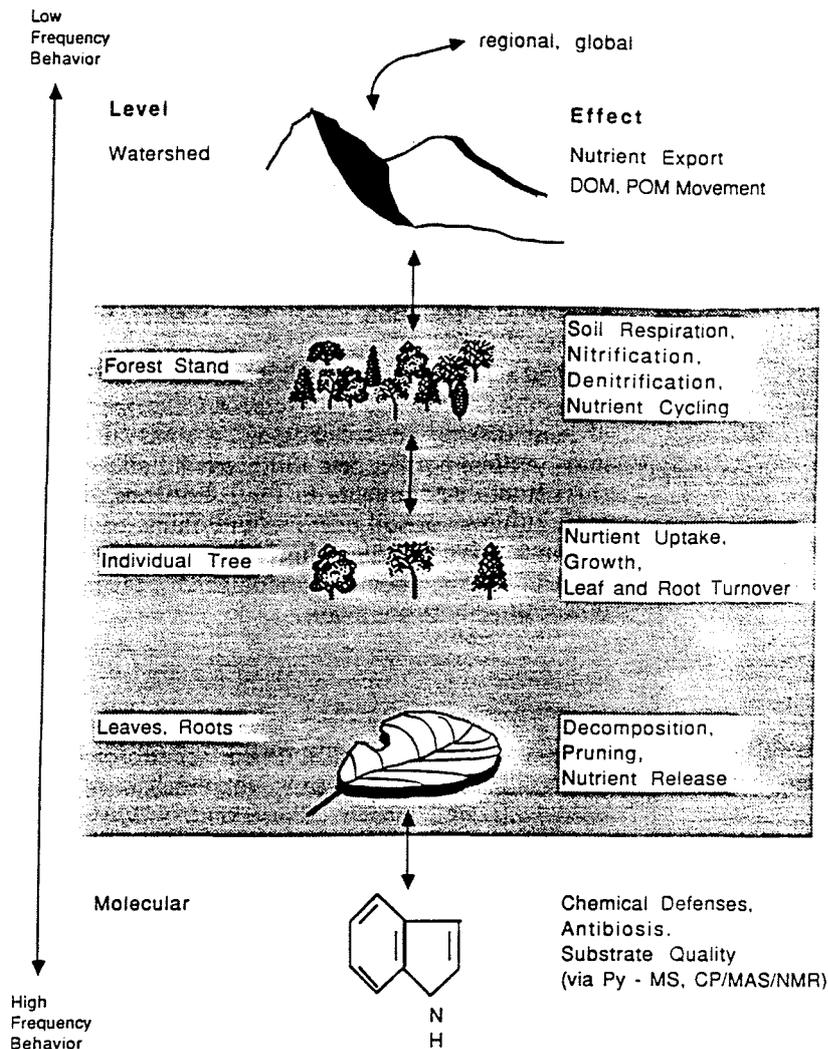
HIERARCHICAL VIEW OF SOIL BIOLOGY

Fig. 3. Hierarchical view of soil biology ranging from a molecular level up to watersheds and beyond. The soil-related levels of resolution are stippled, to highlight the central organizing function of soil processes. In some cases, feedbacks from vegetation and soil interactions reverberate back down to the molecular level, and flows should be viewed as potentially going both ways. *DOM*, Dissolved Organic Matter; *POM*, Particulate Organic Matter; *PY—MS*, Pyrolysis Mass Spectrometry; *CP*, Cross-Polarized; *MAS*, Magic Angle Spinning; *NMR*, Nuclear Magnetic Resonance

dimethoate biocides to reduce numbers of microarthropods and nematodes.

The results (Ingham et al. 1989, Coleman 1990) showed that reduction of microbial predators in systems with high densities of fauna (forest) led to increased decomposition rates. In systems with low faunal numbers, e.g., prairie, the reduction of fauna slowed decomposition rates. The litter with the narrowest C:N ratio, blue grama, decomposed most rapidly in all three ecosystems. The litter with the widest C:N ratio (pine needles) decomposed most slowly in the forest, but not in the two grasslands. In the pine forest, litter decomposed most rapidly during the winter, when the litter was covered and protected by a layer of snow ca. 80–90 cm deep. In contrast, the litter decomposed most rapidly during the brief wet spring period. The N concentration in all litters in a given ecosystem increased to a certain, ecosystem-dependent level.

Features of the detrital food web were also of interest. In terms of biomass, the two grasslands were dominated by bacteria, whereas the forest was much more fungal-dominated. This was mirrored by the dominant microbivores; bacterial-feeding nematodes were most abundant in the grasslands while fungivorous microarthropods, particularly Oribatids in the family Oppiidae, were most numerous in the pine forest. After addition of the nematicide and acaricide, the responses were quite different in the various ecosystems. In the bacterial-dominated grassland, the reduced nematode numbers had no apparent effect on bacterial densities because soil protozoa increased in a compensatory fashion following the decrease in bacterivorous nematodes. The fungal biomass increased, as did soil organic N. In the forest, following biocide application to the litter, the total fungal biomass decreased, but inorganic N levels increased. This was in spite of a reduction of the total Acari to less than half of the numbers in control bags. The mountain meadow was most resilient to disturbance, as it returned to control numbers more rapidly than either the prairie meadow or the forest.

Other information in Ingham et al. (1989) and Hunt et al. (1988) further indicates that there are some important spatial variables of interest here, including the considerable litter layer in the forest, which increases the
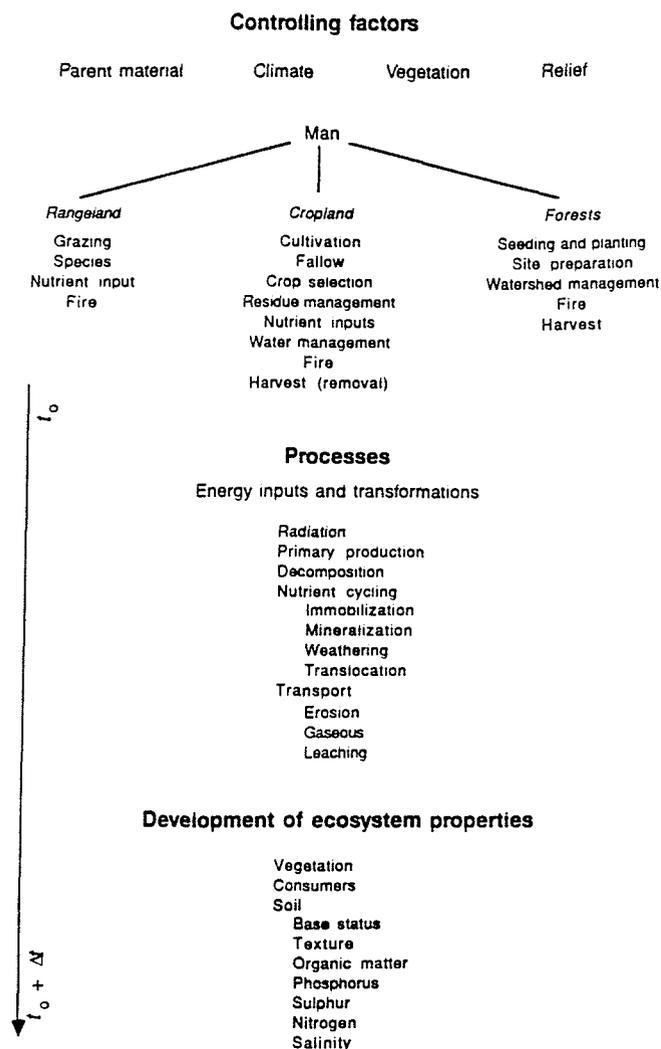
Controlling factors

Parent material   Climate   Vegetation   Relief

Man

Rangeland	Cropland	Forests
Grazing	Cultivation	Seeding and planting
Species	Fallow	Site preparation
Nutrient input	Crop selection	Watershed management
Fire	Residue management	Fire
	Nutrient inputs	Harvest
	Water management	
	Fire	
	Harvest (removal)	

t_o

Processes

Energy inputs and transformations

Radiation
Primary production
Decomposition
Nutrient cycling
  Immobilization
  Mineralization
  Weathering
  Translocation
Transport
  Erosion
  Gaseous
  Leaching

Development of ecosystem properties

Vegetation
Consumers
Soil
  Base status
  Texture
  Organic matter
  Phosphorus
  Sulphur
  Nitrogen
  Salinity

$t_o + \Delta t$

Fig. 4. Factors that influence soil development, over time, influence ecosystem properties (from Coleman et al. 1983)

amount of fungal hyphal material and accompanying mesofaunal abundances. Thus all biotic groups were ca. 10-fold greater in the forest than in the grassland. An interesting finding is that when N concentrations were examined in live grass shoots and pine needles collected 1 year after application of the C and N as described above, N concentrations were between 0.5 and 0.7 greater in the N-added plots than in the controls. The only significant decrease in N concentration versus controls was in new terminal buds of the lodgepole pine (Hunt et al. 1988).

Our study totally omitted any explicit inclusion of mycorrhizal activities, although other studies (C. P. P. Reid, personal observation) showed considerable amounts of ectotrophic mycorrhizas in the O1 and O2 layers of our forest site.

Mycorrhiza and root process studies, some comments.
We need to develop a more wide-ranging perspective on nutrient cycling, and transport from sources in soil, both inorganic and organic, into mycorrhiza. Frank reported, in 1885, that ectomycorrhizal roots are formed most abundantly in the O1 and O2 horizons (particularly the H horizon). Frank assumed that these mycorrhiza gained access to organic N. Melin and Nilsson (1953) demonstrated that small organic N molecules, such as amino acids, are absorbed by mycorrhiza, and transferred to the host plant. The possibility of taking up polymeric forms of N has received little attention.

Recent studies by Read (1987) and Abuzinadah and Read (1986) have demonstrated considerable uptake of these compounds, particularly in some of the low pH conditions characteristic of a number of sites with ericaceous vegetation. This was further reviewed by Dighton (1991).

When ^{15}N is incorporated in humus or humified materials, it is not moved via mycorrhiza. There are more labile and heterogeneous N sources, such as microbial biomass, animal corpses, etc. Both ericoid and ectomycorrhizal roots predominate in the F horizons, and so the rapid turnover of soil microbes and fauna could provide N sources for mycorrhizal fungi. Further, organic N, once taken up, does not remain immobilized in the hyphae, but moves directly to the plant.

Mobilization of C from decaying materials: Saprophytic competence?

Ponge (1990) scrutinized a 25-cm² chunk of pine litter which had an admixture of bracken (*Pteridium aquilinum*) and moss (*Pseudoscleropodium* sp.). There were large amounts of two mycorrhizal fungi, *Cenococcum* and *Hyphodontia* spp. Using a light microscope, Ponge made observations on litter consumption by these fungal species in the advanced stages of decomposition of several substrates in this little microcosm. The two mycorrhizal species exploited the F layer in a non-random way. Fecal masses, mainly from lumbricid and enchytraeid worms were undoubtedly preferred, with the mycelial mat embedding and spreading through them, and also various animal cadavers, such as numerous soil microarthropods. How does this behavior affect tree nutrition? In poor soils, where most mycorrhizal root tips are located in the Ao or F horizon, many nutrients are in an organic form and confined to the litter and humus layers. Ponge (1990) suggested that when nutrients are confined to decaying fragments, mycorrhizal fungi are an obligate partner in tree nutrition. Considering forest strategies, Meyer (personal communication in Ponge 1990) hypothesized that trees with an obligate ECM compete better in soil with a holorganic humus layer, unlike pioneer trees without obligate mycotrophy, which are more successful in mineral soils.

Do mycorrhizal fungi really act directly on plant litter as decomposers? This is reminiscent of the Gadgil and Gadgil (1975) hypothesis on the possible suppression of litter-decomposition fungi by mycorrhizal fungi. Ponge's direct observations showed only some penetration of epidermal cells of the *Pteridium* sp. (bracken) by *Cenococcum* sp. hypae, but no plant cell lysis. The *Hyphodontia* sp. seemed to benefit from the general melange of other decomposer hyphae, and perhaps took up organic N from various substrates in the microcosm.

Finally, there is the question of antagonism between mycorrhizal fungi and other soil organisms. This brings together the spatial and temporal aspects in an interesting way. Ponge, in earlier work (1985), reported an extensive development of bacterial colonies on the outside and inside of pine needles in the L layer, i.e., in the absence of a dense mycorrhizal mycelial mat. In the F layer, in contrast, bacterial colonies were much less numerous, and there was considerable lysis of colonies. These antibiotic properties occur in several genera of Basidiomycetes., so that is perhaps expected. Ponge thus described a food web, reporting that some genera, such as *Verticicladium* and *Marasmius*, can penetrate needles on their own, and digest lignocelluloses. Others, including *Cenococcum* and *Hyphodontia* can penetrate needles only after tunnelling by soil animals, such as Phthiracarid mites, presumably. Studies on consumers of mycorrhizal hyphae are very scarce indeed, with only those by Riffle (1967), and others summarized by Ingham (1988). More general observations on "mycorrhizosphere" biotic interactions have been reviewed by Garbaye (1991).

Concluding remarks

In summary, it is possible to induce and repress various types of decomposition and nutrient cycling processes by a variety of biochemical and biophysical activities in various soil profiles. Although we cannot yet foresee how much more work is needed to better understand and forecast some of these processes, we need this work to proceed apace under field conditions, along with the more large-scale integrative studies mentioned elsewhere in this paper.

This paper has ranged over more than a dozen levels of resolution, and perhaps omitted several topics that need coverage. It is apparent that we require considerable wisdom and wit to adequately scale both downward and also upward, using the "macroscope" so well described by Odum (1971).

As noted by the National Research Council committee report on global change (Risser 1990), much is unknown in the realm of soil processes and global change. The committee commented that in the realm of global change symptoms (vital signs), soil process information is very poor, with a series of coordinated observation networks being desirable.

It is high time that the biologists, chemists, pedologists, and climatologists got together to put a truly effective synthesis into motion.

References

Abuzinadah RA, Read DJ (1986) The role of proteins in the nitrogen nutrition of ectomycorrhizal plants: I. Utilization of peptides and proteins by ectomycorrhizal fungi. New Phytologist 103:481–493

Allen TFH, Starr TB (1982) Hierarchy. Perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois

Andrén O, Lindberg T, Paustian K, Rosswall T (eds) (1990) Ecology of arable land: Organisms, carbon and nitrogen cycling. Ecol Bull (Copenhagen) 40

Brussaard L, Coleman DC, Crossley DA Jr, Didden WAM, Hendrix PF, Marinissen JCY (1990) Impacts of earthworms on soil aggregate stability. Trans 14th Int Cong Soil Sci 3:100–105

Coleman DC, Reid CPP, Cole CV (1983) Biological strategies of nutrient cycling in soil systems. Adv Ecol Res 13:1–55

Coleman DC, Brussaard L, Beare MH, Hendrix PF, Hassink J, Heijnen CE, Marinissen JCY (1989) Microbial–faunal interactions as they influence soil organic matter dynamics. In: Hattori T, Ishida Y, Maruyama Y, Morita RY, Uchida A (eds) Recent advances in microbial ecology. Japan Scientific Societies Press, Tokyo, Japan pp 175–179

Coleman DC, Ingham ER, Hunt HW, Elliott ET, Reid CPP, Moore JC (1990) Seasonal and faunal effects on decomposition in semiarid prairie, meadow and lodgepole pine forest. Pedobiologia 34:207–219

Dighton J (1991) Acquisition of nutrients from organic resources by mycorrhizal autotrophic plants. Experientia 47:362–369

Dokuchaev VV (1879) Short historical description and critical analysis of the more important existing soil classifications. Trav Soc Nat St Petersburg 10:64–67

Elliott ET, Coleman DC (1988) Let the soil work for us. Ecol Bull (Copenhagen) 39:23–32

Foster RW (1985) In situ localization of organic matter in soils. Quaest Entomol 21:609–633

Franklin JF, Bledsoe CS, Callahan JT (1990) Contributions of the Long-term Ecological Research program. BioScience 40:509–523

Gadgil RL, Gadgil PD (1975). Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata*. NZ J For Sci 5:33–41

Garbaye J (1991) Biological interactions in the mycorrhizosphere. Experientia 47:370–375

Groffman PM, Tiedje JM (1989) Denitrification in north temperate forest soils: Spatial and temporal patterns at the landscape and seasonal scales. Soil Biol Biochem 21:613–620

Haines BL, Swank WT (1988) Acid precipitation effects on forest processes. In: Swank WT, Crossley DA Jr (eds) Forest hydrology and ecology at coweeta. Springer-Verlag, New York, pp 359–366

Hendrix PF, Crossley DA Jr, Blair JM, Coleman DC (1990) Soil biota as components of sustainable agroecosystems. In: Edwards CA, Lal R, Madden P, Miller RH, House G (eds) Sustainable agricultural systems. Soil and Water Conservation Society, Ankeny, Iowa, pp 637–654

Hunt HW, Ingham ER, Coleman DC, Elliott ET, Reid CPP (1988) Nitrogen limitation of production and decomposition in prairie, mountain meadow and pine forest. Ecology 69:1009–1016

Ingham ER, Coleman DC, Moore JC (1989) An analysis of food web structure and function in a shortgrass prairie, mountain meadow and lodgepole pine forest. Biol Fertil Soils 8:29–37

Ingham RE (1988) Interactions between nematodes and vesiculararbuscular mycorrhizae. Agric Ecosyst Environ 24:169–182

Jacot AP (1936) Soil structure and soil biology. Ecology 17:359–379

Jenny H (1941) Factors of soil formation. McGraw-Hill, New York

Melillo JM, Steudler PA, Aber JD, Bowden RD (1989) In: Andreae MO, Schimel DS (eds) Exchange of trace gases between terrestrial ecosystems and the atmosphere. Wiley, Chichester, pp 263–280

Melin E, Nilsson H (1953) Transfer of labelled nitrogen from glutamic acid to pine seedlings through the mycelium of Boletus variegatus (S.W.) Fr. Nature (London) 171:434

Mooney HA, Drake BG, Luxmoore RJ, Oechel WC, Pitelka LF (1991) Predicting ecosystem responses to elevated CO_2 concentrations. BioScience 41:96–104

Mosier A, Schimel D, Valentine D, Bronson K, Parton W (1991) Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands. Nature (London) 350:330–332

Oades JM (1988) An introduction to organic matter in mineral soils. In: Weed SB, Dixon JB (eds) Minerals in the soil environment, 2nd edn. Soil Sci Soc Am, Madison, Wisconsin, pp 187–259

Odum HT (1971) Environment, power, and society. Wiley/Interscience, New York

O'Neill RV, DeAngelis DL, Waide JB, Allen TFH (1986) A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey, pp 253

Parton WJ, Stewart JWB, Cole CV (1988) Dynamics of carbon, nitrogen, phosphorus and sulfur in cultivated soils: A model. Biogeochemistry 5:109–131

Pawluk S (1987) Faunal micromorphological features in moder humus of some western Canadian soils. Geoderma 40:3–16

Ponge JF (1985) Étude écologique d'un humus forestier par l'observation d'un petit volume: II. La couche L_2 d'un moder sous *Pinus sylvestris*. Pedobiologia 28:73–114

Ponge JF (1991) Ecological study of a forest humus by observing a small volume: I. Penetration of pine litter by mycorrhizal fungi. Eur J For Pathol 20:290–303

Read DJ (1987) In support of Frank's organic nitrogen theory. Angew Bot 61:25–37

Read DJ (1991) Mycorrhizas in ecosystems. Experientia 47:376–391

Riffle JW (1967) Effect of an *Aphelenchoides* species on the growth of a mycorrhizal and a pseudomycorrhizal fungus. Phytopathology 57:541–544

Risser PG (1990) Trace gases and nutrient fluxes, a working group report. National Research Council, Washington, DC

Romell LG (1930) Forest soil research in relation to forestry with particular reference to the northeast. J For 28:841–848

Scharpenseel HW, Becker-Heidmann P (1990) Overview of the greenhouse effect: Global change syndrome, general outlook. In: Scharpenseel HW, Schomaker M, Ayoub A (eds) Soils on a warmer earth. Elsevier, Amsterdam, pp 1–14

Scharpenseel HW, Schomaker M, Ayoub A (eds) (1990) soils on a warmer earth. Elsevier, Amsterdam

Stewart JWB, Anderson DW, Elliott ET, Cole CV (1990) The use of models of soil pedogenic processes in understanding changing land use and climatic change. In: Scharpenseel HW, Schomaker M, Ayoub A (eds) Soils on a warmer earth. Elsevier, Amsterdam, pp 121–131

Swank WT, Crossley DA Jr (1988) Forest hydrology and ecology at Coweeta. Springer-Verlag, New York

Swanson FJ, Sparks RE (1990) Long-term ecological research and the invisible place. BioScience 40:502–508

Tisdall JM, Oades JM (1982) Organic matter and waterstable aggregates in soils. J Soil Sci 33:141–163

Vance ED, Nadkarni NM (1990) Microbial biomass and activity in canopy organic and the forest floor of a tropical cloud forest. Soil Biol Biochem 22:677–684

Wessman CA (1991) Remote sensing of soil processes. Agric Ecosyst Environ 34:479–493