

6.2.2 The soil system

6.2.2.1 Introduction

The widespread effects of human activities on soils are of global concern because of increased emissions of 'greenhouse' gases, accelerated erosion and desertification, and declining fertility in soils supporting some of the highest population densities in developing countries (World Resources Institute 1992-3). Human-induced soil degradation by wind, water and pollution amounts to about 24% of the inhabited land area of the globe (Oldeman 1994). Changes in climate, atmospheric CO₂ concentrations and UV radiation are affecting soils and vegetation in regions of the world remote from direct effects of human activities (IPCC 1992). Disruption of soil processes from atmospheric pollution, changes in land use, management practices and intensive use of agrochemicals are also affecting freshwater and marine systems as a consequence of increased transfers of sediment, nutrients and toxins from land to water.

Losses of genetic and species diversity below ground resulting from human impacts on the biosphere are largely undocumented in comparison with estimates of extinction rates above ground. Biodiversity in soils, however, is not simply an attribute of the living biota. Unlike above-ground systems, the physical and biochemical properties of dead organic matter (litter and soil organic matter fractions) confer important functional attributes on soils which are integral to biogeochemical cycles. The structural and biochemical characteristics of soils vary both with depth in the profile and in relation to the parent materials, topographic variation, climate gradients and vegetation cover within and between systems. This spatial heterogeneity constitutes a mosaic of sinks and sources for surface water, sediment and trace gases which is important for stabilizing soil processes at aggregate, patch, plot, ecosystem and landscape scales.

The functional importance of biodiversity for the maintenance of soil fertility remains one of the most fundamental gaps in current understanding of terrestrial ecosystems (Swift and Anderson 1993; Anderson 1994). Indeed, the total diversity of the soil biota, as a starting point for this assessment, has not yet been determined for any natural system (Lee 1991). As a consequence of this dearth of comparable information on biodiversity in soils for the different biomes, this review has been developed in the style of a biome essay rather than a cross-biome synthesis as originally intended.

6.2.2.2 Lessons from agriculture

Human impacts on biodiversity. Most of the annual flux of carbon and nutrients in soils from tundra to tropical rain forest occurs in the top 5–10 cm of the profile despite the considerable variation in biomass and primary productivity above ground along this gradient. Structural characteristics of litter cover and the soil surface to a few millimeters depth partition the beneficial or destructive effects of rainfall (Papendick 1994). The animal and microbial communities occupying these critical soil interfaces are highly complex even in natural systems with low biodiversity of plant species. At the molecular and organism level, biodiversity in soils is very high. A single gram of temperate forest soil could contain 10⁹ individual cells comprising 4000–5000 bacterial types, of which less than 10% have been isolated and are known to science (Torsvik *et al.* 1990; Klug and Tiedje 1994). More than 500 species of soil invertebrates have been recorded from a beech (*Fagus sylvatica*) forest (Schaefer and Schauer mann 1990) and new records are still being added to a list of 2500 species of fungi from a nature reserve covering a few hectares in southwest England (Hawksworth 1992). Species richness declines towards the poles but assumptions regarding the simplicity of communities at high latitudes generally ignore the complexity of below-ground systems. Even simple moss tussock communities in the Antarctic Peninsula have complex food webs linking over a hundred species of algae, protozoa, nematodes, tardigrades, collembola and mites plus unknown numbers of fungal and bacteria species (Davis 1981).

Significant loss of biodiversity can occur when natural habitats are modified or converted to intensive permanent cultivation (Paoletti *et al.* 1992; Anderson and Swift 1993; Freckman and Ettema 1993; Lavelle *et al.* 1994). The larger, surface-living invertebrates disappear first with the destruction of litter habitats which provide food and living space. Dead tree boles and branches containing many wood-decomposing invertebrates and fungi can be eliminated under intensive extractive forest management or plantation forestry (Gilot *et al.* 1992). Conversion of tropical forest to tree plantations or smallholder farming

systems can also result in changes in termite communities with the loss of highly diverse humivorous groups and an increase in wood/litter feeders which include damaging pest species (Wood *et al.* 1977). In New Zealand, improvement of temperate pastures with legumes and exotic grasses, eliminated indigenous earthworm species and enabled European lumbricids to become established (Lee 1985). In contrast, European lumbricids maintained marginal populations in US prairies in relation to native *Diplocardia* species because of their intolerance of high summer temperatures (James 1991). However, these exotic earthworms have invaded many mesic habitats where there is a low diversity of indigenous species (Hendrix *et al.* 1992).

Communities of smaller invertebrates live within the highly complex microscopic structure of litter and soil habitats. Anderson (1978) showed that the diversity of mite (Cryptostigmata) species was closely related to microhabitat diversity in organic soils developed under a single tree species. Changes in litter quality or the introduction of plant species with faster decay rates reduces habitat complexity. Improvement of pasture quality to support higher stock densities reduces the thatch of litter on the soil surface and thus the habitat space for the associated micro-arthropod communities (Hutchinson and King 1980), but earthworms living within the mineral soil respond positively to increased grass and dung quality (Knight *et al.* 1992; James 1992).

Mechanical cultivation is highly destructive to most invertebrate groups. The microbiota (nematodes, protozoa, micro-fungi and bacteria) are the main groups surviving in intensively tilled soils (Hendrix *et al.* 1986; Freckman and Ettema 1993). Agrochemicals also reduce the taxonomic and genetic diversity of soil micro-organisms (Domsch *et al.* 1983; Atlas *et al.* 1991). Even so, total biodiversity in agricultural soils is likely to be greater than the total above-ground diversity of plants and animals in the natural systems from which they were derived. The adoption of zero or minimum tillage practices allows the resurgence of biodiversity in agricultural soils provided that sources of colonists are present in habit refugia around the field margins (Hendrix *et al.* 1986).

Ecosystem consequences of human impacts. Most soil organisms are small (<2 mm diameter) and manifest their specific effects at spatial and temporal scales orders of magnitude below those where process measurements are made in most ecological studies (Anderson 1988). As a consequence there is a poor understanding of the links between their proximate roles in biological transformations and processes operating at larger scales and over longer time intervals.

The roles of the soil biota can be described in terms of allogenic and autogenic processes proposed by Jones and Lawton (1995). The allogenic processes, such as carbon

and nitrogen mineralization, are direct products of soil organism metabolism. These are modified by changes in the quality of the resources they are processing as a consequence of changes in plant species composition, CO₂ and N enrichment of plants, or pollution. Autogenic processes involve the modulating effects of organisms where the consequences of their activities, such as removing litter, creating soil macropores or the release of prey from predation, influence mass or energy transfers much larger than their allogenic effects (Anderson 1995).

Microcosm studies have shown that different species and combinations of invertebrates and microorganisms have specific effects on the rates and products of carbon and nutrient fluxes. The feeding activities of collembola, mites, nematodes and protozoa have also been shown to change the composition and activities of bacterial and fungal communities in ways analogous to the effects of herbivores in above-ground communities (reviews by Anderson 1988; Verhoef and Brussaard 1990). The specific nature of allogenic and autogenic effects could be taken to support the 'Rivet Hypothesis' that the removal of each species deletes unique properties from community functions (Ehrlich and Ehrlich 1981; see Section 5.1). However, at an ecosystem level, the attributes of complexity in food webs are not apparent and fumigation treatments, which eliminate much of the biotic diversity in soils, usually show transient effects on soil processes; at least in the short term (Rovira 1976; Ridge 1976; Ingham *et al.* 1986). These results suggests that there is a high level of functional overlap in soil biological processes, with many organisms producing similar metabolic end products able to compensate for changes in community structure. On the other hand, microbial processes such as nitrogen fixation, which are carried out by a group of bacteria with intrinsically low diversity in soils, are susceptible to heavy metal contamination of soils (Brookes and Verstraete 1989). McGrath *et al.* (1988) have shown that the activity of *Rhizobium* associations with white clover (*Trifolium repens*) was drastically reduced by heavy metal concentrations from sewage sludge which were within legislative limits set by the European Community.

The activities of soil fauna are evident at the ecosystem level where functional groups are dominated by one or two species creating persistent artifacts (aggregates, burrows, incorporation of organic matter into soil) which have cumulative effects on soil properties (Anderson 1995). The elimination of earthworms, or the introduction of exotic species with different attributes to the indigenous community, has been shown to alter soil structure, aeration, surface water infiltration, the distribution of organic matter, pesticides and heavy metals, and total crop production (Lee 1985; Lavelle 1988; Clements *et al.* 1991). In Peru, the conversion of forest to improved pasture eliminated most of the soil macrofauna and populations of an exotic tropical

earthworm species, *Pontoscolex corethrurus*, then developed a biomass of 4 t/ha and dominated soil processes (Lavelle and Pashanasi 1989). Termites in semi-arid systems have similar key effects on soil structure and hydrology which can shift from beneficial to deleterious as a consequence of changes in climate or management. In the overgrazed grasslands of Ethiopia, scavenging of the little remaining grass and litter cover by termites leaves soil bare and susceptible to erosion (Wood 1991). Similarly, the bare ground around termite mounds in grassland fallows of West Africa can initiate erosion and land degradation when they reach high densities (Janeau and Valentin 1987). Conversely, the elimination of a single termite species in the Chihuahuan desert altered the soil water balance and resulted in shrubs replacing grass cover in experimental plots over a period of eight years (Elkins *et al.* 1986).

6.2.2.3 Soil organic matter

Components of diversity. Soil organic matter (SOM) contains on average twice the amount of carbon found in vegetation above ground and is a resource of extraordinary physical and biochemical complexity (Theng *et al.* 1989; Anderson 1991). Dead organic matter is essential to the functioning of most natural and derived soils not only as a complex habitat and resource base for a diverse biota, but also because it maintains the physical and chemical integrity of the system. Litter resource types (fruits, leaves, twigs, branches, coarse and fine roots) from species with different chemical compositions and decomposition rates regulate the rates of carbon and nutrient mineralization (Swift and Anderson 1993). Litter cover also protects the soil from wind and rain erosion, and influences water and heat transfer to the underlying soil (Lal 1994). During the process of decomposition, soil organic matter (SOM) is formed which can be chemically or physically stabilized by soil minerals to form different fractions with turnover rates ranging from years to centuries. The whole range of SOM fractions, operationally defined as fast, slow and passive, confer particular attributes on soil such as aggregate stabilization, complexing free aluminium, regulating soil moisture, forming ion exchange complexes and constituting sinks/sources of plant nutrients (Duxbury *et al.* 1989). There are, however, very different time scales over which these effects are manifested. Changes in litter and fast SOM fractions have rapid effects on soil physical processes and nutrient cycling but the slow and passive fractions have turnover rates ranging from decades to millenia. Consequently, the restitution of soil profile characteristics under natural vegetation cover following catastrophic disturbance can effectively operate outside the human time frame.

Ecosystem consequences of human impacts. The effects of changing resource diversity on soil properties fits the asymptotic model of Vitousek and Hooper (1993; see

Figure 5.2-1A) relating species richness to ecosystem functioning. Adding (or removing) resources until all the key resource types are represented has larger effects on a given process than further additions of representatives of those groups. For example, erosion control depends on the amount of litter cover for soil protection rather than the diversity of plant species making up the litter (Mbakaya *et al.* 1988). Similarly, the amount of soil organic matter depends upon the quality and quantity of resource inputs and not on vegetation diversity. Hence SOM accumulation in forests is related to the inherent fertility of the parent soil and not to tree species diversity.

Where resource types are the product of a keystone species the effects of changing diversity can be profound. Davies (1981) has described two Antarctic moss communities: a tall turf community dominated by two moss species and a moss carpet dominated by three species. The decomposition-resistant (low quality) stems of one moss in the tall turf contributed to SOM accumulation to a depth of 2 m under this community against only 0.2 m SOM accumulated under the moss carpet with more rapidly decomposing (high quality) species. Analogous effects on soil carbon pools are associated with changes in landuse between high quality broad-leaf woodlands and low-quality conifer plantations; or the introduction new keystone species with contrasting litter quality into communities with low diversity (Anderson 1991). In Hawaii, organic soils have developed under stands of a single tree species, *Metrosideros polymorpha* which produces a low-quality litter in response to limited N availability. The invasion of the monospecific stands by an introduced nitrogen-fixing tree, *Myrica faya*, which produces a rapidly decomposing litter, has changed the nutrient and organic matter balances of the ecosystem (Vitousek *et al.* 1987). The consequences of these changes for the biodiversity of soil organisms are unknown but are likely to be profound. More gradual increases in litter quality and SOM turnover are occurring over much of Europe where anthropogenic sources of N are saturating forest ecosystems leading to increased nitrate leaching and nitrous oxide emissions (Aber *et al.* 1989; Rosen *et al.* 1992). Conversely, increased C/N ratios in litter as a consequence of CO₂ enrichment of N-limited systems may be increasing carbon storage in SOM on a global scale (Allen 1990; Bazzaz 1990).

6.2.2.4 Functional importance of spatial complexity

Spatial components of biodiversity. Soils under undisturbed vegetation cover have high resilience to natural perturbations, such as storm events, cataclysmic litter inputs and extreme seasonality, so that losses of suspended solids or solutes are usually small in relation to the pools and fluxes within the system boundaries. The mass balance of carbon and nutrients in the system is maintained by transfers between sinks and sources which operate at

different scales from microsites to landscapes (Anderson 1995). Reciprocal processes, which stabilize the overall dynamics of the system, are manifest in soil organism populations (natality/mortality; emigration/immigration), nutrient cycling (mobilization/immobilization), carbon fluxes (plant growth/decomposition), water balances (runoff/infiltration) and soil development (erosion/weathering). These sink/source interactions are considered in other essays in this volume and are only briefly reviewed here.

The balance between processes of nitrogen mineralization/immobilization, and nitrification/denitrification, are important in regulating nitrate leaching and nitrous oxide emissions from soils. These N transfers occur between adjacent bacteria, on gradients within soil aggregates (Groffman *et al.* 1987; Parkin 1987), at the level of resource patches integrated by fungal hyphae on the forest floor (Rayner and Boddy 1988), in forest gaps (Vitousek and Denslow 1986) and between hill-slope and riparian zones of catchments (Peterjohn and Correll 1984; Gregory *et al.* 1991). Sinks and sources for methane similarly exhibit scaling related to aerobic and anaerobic regimes in soils (Crutzen 1991) from microsites within aggregates (King and Adamsen 1992), and between surface and underlying soil horizons (Whalen and Reeburgh 1990) through the patch scales associated with plant communities (Whalen *et al.* 1990) up to the landscape scale (Moore *et al.* 1990).

Hydrological processes are also buffered by spatial heterogeneity of surface water sources and sinks. In rain forest, high intensity storm events, combined with funnelled stemflow as a result of branching patterns of canopy emergents, may create saturated areas around the trunk bases and overland flow downslope from these areas. Exposed roots and buttresses, however, can act as effective barriers to downslope soil wash (Spencer *et al.* 1990). Van Hooff (1982) showed that splash erosion and overland flow in a deciduous woodland was determined by the differential palatability to earthworms of litter from the two tree species. Consumption of the more palatable litter in patches of one tree species in spring caused splash erosion, while patches of the less palatable species, where litter cover remained intact, formed sinks for surface water and sediment so that there were no net losses of sediment across the forest boundary. Soil loss rates are generally low under forest cover but severe erosion can occur in extensive plantations of teak (*Tectona grandis*) where ground cover vegetation is suppressed and the rapidly decomposing leaves give no soil protection from the high kinetic energy of canopy throughfall (Bell 1973).

Spatial heterogeneity of soil properties reduces the amplitude of sediment, solute and trace gas losses from terrestrial systems. Extreme events which exceed sink strengths at local scales may be contained with the patch mosaic sinks at ecosystem or landscape scales. Human activities have major impacts on the heterogeneity of soils

which affect terrestrial, aquatic and atmospheric processes.

Ecosystem consequences of human impacts. Changes in landuse resulting from traditional agricultural practices can increase spatial heterogeneity of ecosystems within the landscape as a consequence of habitat fragmentation. Further intensification of landuse reduces the patch heterogeneity of sources and sinks for trace gases and solutes, and increases the periodicity and amplitude of biogeochemical fluxes within the landscape (Burke and Lauenroth; see 6.2.4). As larger areas of arable agriculture, plantation forestry and pastures come under the same soil management practices and cropping cycles, trace gas fluxes and nutrient leaching can be synchronized across whole landscapes with knock-on effects for atmospheric and aquatic systems on regional and even wider geographic scales.

Extensive development of intensive agricultural practices has increased soil erosion by wind and water in many regions of Europe and North America (Lal 1994; Papendick 1994). The removal of hedgerows and buffer strips, levelling of field systems and intensive tillage have reduced sinks for transported material. Soil channelling and compaction also result in surface runoff exceeding the infiltration capacity and particle retention by the microtopography of inter-rill areas (Boardman 1991). Similarly, Hutsch *et al.* (1993) have shown that sink strengths for methane in agricultural systems are related to the use of inorganic fertilizer (decreased sink) and organic manures (increased sink). Uniform agricultural practices using inorganic fertilizers can therefore reduce sinks for methane across agricultural landscapes (Mosier *et al.* 1991). Atmospheric N deposition also reduces the sink strength of forest soils (Steudtler *et al.* 1989).

6.2.2.5 Summary and relevance to human activities

Soils contain high biological, biochemical and physical complexity which can be defined across all scales from the microscopic to landscape level. The biotic diversity below ground may be orders of magnitude higher than that above ground but total microbial diversity has not been fully documented in any system. Human activities reduce the diversity of species, resources and spatial heterogeneity through changes in land-use and the effects of pollutants but the functional importance of these changes are largely unknown. Processes dominated by a few species representing functional groups are at risk from the direct and indirect effects of human activities. Source/sink dynamics within systems buffer mineral element, trace gas and sediment fluxes. These processes become synchronized with increasing intensity of landuse and reduction of spatial heterogeneity. As a consequence the amplitude and periodicity of biogeochemical fluxes can override sinks within landscapes and result in net transfers between the atmosphere and adjacent systems which would otherwise

be accommodated within system boundaries. It is concluded that there is a high degree of uncertainty over the consequences of reducing biodiversity below ground to undefined threshold levels in any terrestrial systems.

References

- Aber, J.D., Nadelhoffer, K., Steudler, P. and Melillo, J.M. 1989. Nitrogen saturation in Northern forest ecosystems. *Bioscience* **39**: 378–386.
- Allen, L.H. 1990. Plant responses to rising carbon dioxide and potential interactions with air pollutants. *Journal of Environmental Quality* **19**: 15–34.
- Anderson, J.M. 1978. Inter- and intra-habitat relationships between woodland *Cryptostigmata* species diversity and the diversity of soil and litter habitats. *Oecologia* **32**: 341–346.
- Anderson, J.M. 1988. Spatiotemporal effects of invertebrates on soil processes. *Biology and Fertility of Soils* **6**: 216–227.
- Anderson, J.M. 1991. The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecological Applications* **1**: 326–347.
- Anderson, J.M. 1994. Functional attributes of biodiversity in land use systems. In: Greenland, D.J. and Szabolcs, I. (eds), *Soil Resilience and Sustainable Land Use*. 267–290. CAB International, Wallingford.
- Anderson, J.M. 1995. Soil organisms as engineers: microsite modulation of macroscale processes. In: Jones, C.G. and Lawton, J.H. (eds), *Linking Species to Ecosystems*. 94–106. Chapman and Hall, New York.
- Atlas, R.M., Horowitz, A., Kritchevsky, M. and Bej, A.K. 1991. Response of microbial populations to environmental disturbance. *Microbial Ecology* **22**: 249–256.
- Bazzaz, F.A. 1990. The response of natural ecosystems to the rising CO₂ levels. *Annual Review of Ecology and Systematics* **21**: 167–196.
- Bell, T.I.W. 1973. Erosion in Trinidad teak plantation. *Commonwealth Forestry Review* **52**: 233–233.
- Boardman, J. 1991. Land use, rainfall and erosion risk on the South Downs. *Soil Use and Management* **7**: 34–38.
- Brookes, P.C. and Verstraete, W. 1989. The functioning of soil as an ecosystem. *Soil Quality Assessment. State of the Art Report on Soil Quality*. Report to Commission of the European Communities Directorate-General DG XII. Contract EV4A/0008/NL, 41.
- Clements, R.O., Murray, P.J. and Sturdt, R.G. 1991. The impact of 20 years' absence of earthworms and three levels of N fertilizer on a grassland soil environment. *Agriculture Ecosystems and Environment* **36**: 75–85.
- Crutzen, P.J. 1991. Methane's sinks and sources. *Nature* **350**: 380–381.
- Davis, R.C. 1981. Structure and function of two Antarctic terrestrial moss communities. *Ecological Monographs* **51**: 125–143.
- Domsch, K.H., Jagnow, G. and Anderson, T.H. 1983. An ecological concept for the assessment of side effects of agrochemicals on soil microorganisms. *Residue Review* **86**: 65–105.
- Duxbury, J.M., Scott Smith, M. and Doran, J.W. 1989. Soil organic matter as a source and sink of plant nutrients. In: Coleman, D.C., Oades, J.M. and Uehara, G. (eds), *Tropical Soil Organic Matter*. 33–68. University of Hawaii Press, Hawaii.
- Ehrlich, P.R. and Ehrlich, A.H. 1981. *Extinction. The causes and consequences of the disappearance of species*. Random House, New York.
- Ehrlich, P.R. 1991. Population diversity and the future of ecosystems. *Science* **254**: 175.
- Elkins, N.Z., Sabol, G.V., Ward, T.J. and Whitford, W.G. 1986. The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem. *Oecologia* **68**: 521–528.
- Freckman, D.W. and Ettema, C.H. 1993. Assessing communities in agroecosystems of varying human intervention. *Agriculture, Ecosystems and Environment* **45**: 239–261.
- Gilot, C., Lavelle, P., Kouassi, Ph. and Guillaume, G. 1992. Biological activity of soils in *Hevea* stands of different ages. *Acta Zoologica Fennica*.
- Gregory, S.V., Swanson, F.J., McKee, W.A. and Cummins, K.W. 1991. An ecosystem perspective of riparian zones. *BioScience* **41**: 540–550.
- Groffman, P.M., Tiedje, J.M., Robertson, G.P. and Christiansen, S. 1987. In: Wilson, J.R. (ed.), *Advances in Nitrogen Cycling in Agricultural Systems*. 174–192. CAB International, Wallingford.
- Hawksworth, D.L. 1992. In: Solbrig, O.T., van Emden, H.M. and van Oordt, P.G.W.J. (eds), *Biodiversity and Global Change*. 83–93. International Union of Biological Sciences, Paris.
- Hendrix, P.F., Parmelee, R.W., Crossley, D.A., Coleman, D.C., Odum, E.P. and Groffman, P.M. 1986. Detritus food webs in conventional and no-tillage agroecosystems. *Bioscience* **36**: 374–380.
- Hendrix, P.F., Mueller, B.R., Bruce, R.R., Langdale, G.W. and Parmelee, R.W. 1992. Abundance and distribution of earthworms in relation to landscape factors on the Georgia Piedmont, USA. *Soil Biology and Biochemistry* **24**: 1357–1361.
- Hutchinson, K.J. and King, K.L. 1980. The effects of sheep stocking level on invertebrate abundance, biomass and energy in a temperate, sown grassland. *Journal of Applied Ecology* **17**: 369–387.
- Hutsch, B.W., Webster, C.P. and Powlson, D.S. 1993. Long term effects of nitrogen fertilization on methane oxidation in soil of the Broadbalk wheat experiment. *Soil Biology and Biochemistry* **25**: 1307–1315.
- Ingham, E.R., Trofymow, J.A., Ames, R.N., Hunt, H.W., Morley, C.R., Moore, J.C. and Coleman, D.C. 1986. Trophic interactions and nitrogen cycling in a semi-arid grassland soil. II. System responses to the removal of different groups of soil microbes or fauna. *Journal of Applied Ecology* **23**: 615–630.
- Intergovernmental Panel on Climate Change 1992. Houghton, J.T., Callander, B.A. and Varney, S.K. (eds), *Climate Change 1992: The supplementary report to the IPCC Scientific Assessment*. Cambridge University Press, Cambridge.
- James, S.W. 1991. Soil nitrogen, phosphorus and organic matter processing by earthworms in tallgrass prairie. *Ecology* **72**: 2101–2109.
- James, S.W. 1992. Localised dynamics of earthworm populations in relation to bison dung in North-American tallgrass prairie. *Soil Biology and Biochemistry* **24**: 1471–1476.

- Janeau, J.L. and Valentin, C. 1987. Relations entre des termitières *Trinervitermes* spp. et la surface du sol: réorganisations, ruissellement et érosion. *Revue Ecologie et de Biologie du Sol* 24: 637–647.
- Jones, C.G. and Lawton, J.H. (ed.) 1995. *Linking Species and Ecosystems; Fifth Cary Conference, Millbrook, New York, May 8–12, 1993*. Chapman and Hall, New York.
- King, G.M. and Adamsen, A.P.S. 1992. Effects of temperature on methane consumption in a forest soil and in pure cultures of the methanotroph *Methylomomas rubra*. *Applied and Environmental Microbiology* 58: 2758–2763.
- Klug, M.J. and Tiedje, J.M. 1994. Responses of microorganisms to changing environmental conditions: chemical and physiological approaches. In: Guerrero, R. and Pedros-Alio, C. (eds), *Trends in Microbial Ecology*. 371–378. Spanish Society for Microbiology, Barcelona.
- Knight, D., Elliott, P.W. and Anderson, J. M. 1992. The role of earthworms in a managed, permanent pasture in South West England. *Soil Biology and Biochemistry* 24: 1511–1519.
- Lal, R. 1994. Sustainable land use systems and soil resilience. In: Greenland, D.J. and Szabolcs, I. (eds), *Soil Resilience and Sustainable Land Use*. 41–67. CAB International, Wallingford.
- Lavelle, P. 1988. Earthworm activities and the soil system. *Biology and Fertility of Soil* 6: 237–251.
- Lavelle, P., Gilot, C., Fragoso, C. and Pashanasi, B. 1994. Soil fauna and sustainable land use in the humid tropics. In: Greenland, D.J. and Szabolcs, I. (eds), *Soil Resilience and Sustainable Land Use*. 291–300. CAB International, Wallingford.
- Lavelle, P. and Pashanasi, B. 1989. Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). *Pedobiologia* 33: 283–291.
- Lee, K.E. 1985. *Earthworms: Their ecology and relationships with land use*. Academic Press, Sydney.
- Lee, K.E. 1991. The diversity of soil organisms. In: Hawksworth, D.L. (ed.), *The Role of Biodiversity in Agricultural Systems*. 73–88. CAB International, Wallingford.
- Mbakaya, B.S., Blackburn, W.H., Skovlin, J.M. and Child, R.D. 1988. Infiltration and sediment production of a bushed grassland as influenced by livestock grazing systems, Buchama, Kenya. *Tropical Agriculture* 65: 99–105.
- McGrath, S.P., Brookes, P.C. and Giller, K.E. 1988. Effects of potentially toxic metals in soil derived from past applications of sewage sludge on nitrogen fixation by *Trifolium repens*. *Soil Biology and Biochemistry* 20: 415–424.
- Moore, T., Roulet, N. and Knowles, R. 1990. Spatial and temporal variations of methane flux from sub-Arctic/northern boreal fens. *Global Biogeochemical Cycles* 4: 29–46.
- Mosier, A.R., Schimel, D.S., Valentine, D., Bronson, K.F. and Parton, W.J. 1991. Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands. *Nature* 350: 330–332.
- Oldeman, L.R. 1994. The global extent of soil degradation. In: Greenland, D.J. and Szabolcs, I. (eds), *Soil Resilience and Land Use*. 99–118. CAB International, Wallingford.
- Paoletti, M.G., Pimentel, D., Stinner, B.R. and Stinner, D. 1992. Agroecosystem biodiversity: matching production and conservation biology. *Agriculture, Ecosystems and Environment* 40: 3–23.
- Papendick, R.I. 1994. Maintaining soil physical conditions. In: Greenland, D.J. and Szabolcs, I. (eds), *Soil Resilience and Sustainable Land Use*. 215–234. CAB International, Wallingford.
- Parkin, T.B. 1987. Soil microsites as a source of denitrification variability. *Soil Science Society America Journal* 51: 1194–1199.
- Peterjohn, W.T. and Correll, D.L. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. *Ecology* 65: 1466–1475.
- Rayner, A.D.M. and Boddy, L. 1988. *Fungal Decomposition of Wood; Its biology and ecology*. John Wiley, Chichester.
- Ridge, E.H. 1976. Studies on soil fumigation. II. Effects on bacteria. *Soil Biology and Biochemistry* 8: 249–253.
- Rosen, K., Gundersen, P., Tegnhammar, L. Johansson, M. and Frogner, T. 1992. Nitrogen enrichment of Nordic forest ecosystems. *Ambio* 21: 364–368.
- Rovira, A.D. 1976. Studies on soil fumigation. I. Effects on ammonium, nitrate and phosphate in soil and on the growth, nutrition and yield of wheat. *Soil Biology and Biochemistry* 8: 241–247.
- Schaefer, M. and Schauman, J. 1990. The soil fauna of a beech forests – comparison between a mull and moder soil. *Pedobiologia* 34: 299–314.
- Spenser, T., Douglas, I. Greer, T. and Sinun, W. 1990. Vegetation and fluvial geomorphic processes in South East Asian Tropical rain forests. In: Thornes, J.B. (ed.), *Vegetation and Erosion*. 451–469. John Wiley, Chichester.
- Stuedler, P.A., Bowden, R.D., Melillo, J.M. and Aber, J.D. 1989. Influence of nitrogen fertilization on methane uptake in temperate forest soils. *Nature* 341: 314–316.
- Swift, M.J. and Anderson, J.M. 1993. Biodiversity and ecosystem function. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 15–41. Springer-Verlag, Heidelberg.
- Theng, B.K.G., Tate, K.R. and Sollins, P. 1989. Constituents of organic matter in temperate and tropical soils. In: Coleman, D.C., Oades, J.M. and Uehara, G. (eds), *Tropical Soil Organic Matter*. 5–32. University of Hawaii Press, Hawaii.
- Torsvik, V., Goksoyr, J. and Daae, F.L. 1990. High diversity of DNS of soil bacteria. *Applied and Environmental Microbiology* 56: 782–787.
- Van Hooff, P. 1982. Earthworm activity as a cause of splash erosion in a Luxembourg forest. *Geoderma* 31: 195–204.
- Verhoef, H.A. and Brussaard, L. 1990. Decomposition and nitrogen mineralization in natural and agroecosystems: the contribution of soil animals. *Biogeochemistry* 11: 175–211.
- Vitousek, P.M. and Denslow, J.S. 1986. Nitrogen and phosphorus availability in tree fall gaps of a lowland forest. *Journal of Ecology* 74: 1167–1178.
- Vitousek, P.M. and Hooper, D.U. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 3–14. Springer-Verlag, Heidelberg.
- Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D., Matson, P.A. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238: 802–804.
- Whalen, S.C., Reeburgh, W.S. and Sanbeck, K.A. 1990. Rapid

- methane oxidation in landfill cover soil. *Applied and Environmental Microbiology* **56**: 3405–3411.
- Whalen, S.C.** and Reeburgh, W.S. 1990. Consumption of atmospheric methane by tundra soils. *Nature* **346**: 160–162.
- Wood, T.G.** 1991. Termites in Ethiopia: the environmental implications of their damage and resultant control measures. *Ambio* **20**: 136–138.
- Wood, T.G., Johnson, R.A.,** and Ohiagu, C.E. 1977. Populations of termites (Isoptera) in natural and agricultural systems in southern Guinea savannah near Mokwa, Nigeria. *Geo Ecol Trop* **1**: 139–148.
- World Resources Institute** 1992–1993. *Towards Sustainable Development. A guide to the global environment.* WRI, Washington, DC.