155N: 0438-475X

0038-075C/00/1651-73-86 Soil Science Copyright © 2000 by Lippincott Williams & Wilkins, Inc.

January 2000 Vol. 165, No. 1 Printed in U.S.A.

BAPBA37/1

ECOLOGICAL CHALLENGES FOR SOIL SCIENCE

Patrick Lavelle

Soil Science integrates specific contributions from physics, chemistry, biology, and the human sciences. During the last 2 decades, these approaches, which had primarily developed separately and at different speeds, have been progressively integrated. Ecology has contributed a significant number of integrative concepts and questions, some, such as nutrient cycling and energy budgets, that are rather old, and others, such as soil engineering by macroinvertebrates, the relationship between biodiversity and soil function, and the impact of landscape fractionation, that are more recent.

An important issue common to all disciplines in Soil Science is that of scales. Ecological studies have shown that similar activities, e.g., the building of solid structures by invertebrates for their sheltering or gut transit of soil for digestion, may affect soil function at different scales, affecting the rates of processes in sometimes opposite directions. The concept of functional domains in soil, derived from soil ecological research, defines a scale at which physical, chemical, and biological processes can be studied efficiently in a true multidisciplinary approach. Functional domains are specific sites in soils defined by a main organic resource (leaf litter or soil organic matter), a major regulator, biotic (i.e., an invertebrate 'engineer' or roots) or abiotic (like freezing/ thawing or drying/rewetting alternates), a set of structures created by the regulator (for example, fecal pellets, galleries, or cracks), and a community of dependent invertebrates of smaller size and microorganisms that live in these structures. Functional domains may be physically identified in soils and specifically studied using the different disciplinary approaches. Specific micromorphologic, isotopic, and other techniques allow us to address issues at this scale adequately. Ecological research also provides a theoretical background for management of soils at the larger integrative scales of landscape and regions.

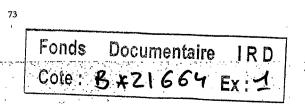
Essential issues for the near future should use this interdisciplinary approach. Sustainability of cropping systems and maintenance of soil ecosystem services depend more on an integrated approach than do the extreme developments in single disciplines in isolation that originated the series of problems we now face: large scale soil erosion, nutrient transfers to neighboring ecosystems, threats of genetically modified organisms, or biodiversity accidents. (Soil Science 2000;165:73-86)

Key words: Functional domains, invertebrates, sustainability, scales, hierarchy.

PEDOLOGY and soil ecology were born at the end of the 19th century with seminal books by Müller (1887) on humus types, Darwin (1881) on earthworm ecology, and Dokuchaev (1889) on soil genesis. Biologists faced with the enor-

Laboratoire d'Ecologie des Sols Tropicaux, Université Paris VI/IRD, 32 rue H. Varagnat, 93143—Bondy Cedex, France. E-mail:lavelle@bondy.orstom.fr mous diversity of invertebrates and microorganism communities focussed their research mostly on classification, basic biology and ecology of soil organisms. This period culminated with the publication of several syntheses on the biology of soil microorganisms and invertebrates (e.g., Kühnelt 1961; Burges and Raw 1967; Dommergues and Mangenot 1970). The next





decade was dominated by the production of enormous datasets on communities of soil microorganisms and invertebrates and their energy budgets as part of the International Biological Programme (Petersen and Luxton 1982). In most cases, the direct participation of invertebrates to C mineralization was estimated to be well below 5 to 10% of the total flux, the remaining 90 to 99% being released by microbial respiration.

At the same time, Swift et al. (1979) produced remarkable synthesis on decomposition processes as perceived through the large datasets published by this time. Bridging soil chemistry with biology, this book laid the ground for new research questions aimed at developing the paradigm that decomposition, as with every process in soil, results from interactions among biological, physical, and chemical components. Bal (1982), on the other hand, using a micromorphological approach, drew attention to the remarkable effects of soil organisms on soil structure, thus linking physical processes to chemical and biological processes of soils; the concept of ecosystem engineering proposed by Jones et al. 1994 had already been considered in these early studies, which showed that biogenic structures produced by invertebrates or microorganisms (e.g., earthworm casts and galleries, arthropod fecal pellets, microbial colonies) comprise a sometimes large proportion, if not all, of the aggregates and macropores dealt with by soil physicists. Present soil ecology is the result of the convergence of these three main approaches.

During these early phases of development, soil ecology has used mainly concepts and paradigms borrowed from other disciplines, and its influence on pedology and ecology has been rather limited, as reflected in the low importance given to soil ecological issues in most textbooks of soil science and ecology and the preference of soil ecologists to publish in their specific disciplinary journals. This trend is being progressively reversed by the formulation of new challenging concepts that propose novel views of soil function and ecological processes in review articles (Coleman et al. 1983; Lavelle et al. 1993; Ohtonen et al. 1997; Beare et al. 1995; Wardle and Giller 1996; Brussaard et al. 1997; Silver 1997; Andren et al. 1999) and textbooks (Coleman and Crossley 1996; Lavelle and Spain 2000). This dynamic is supported by the recognition that practical solutions to environment problems linked to soil use and the maintenance of ecosystem services provided by soils (Daily et al., 1997) clearly need a systematic approach that

considers physical, chemical, and biological processes and their interactions.

The purpose of this paper is to assess progresses and trends in soil ecology in regard to the needs and requirements of general science, soil science in particular, and the needs of societies. Past achievements are reviewed and recent integrative concepts are detailed. Their adaptation to the needs of society and their perceptions by users are discussed.

SOIL SCIENCE, SOIL ECOLOGY AND THE GREEN REVOLUTION(S)

Soil science has always provided the main theoretical background for the scientific development of land use practices (Pedro 1997). This has been the major-if not only-field of application until recently, at times when other services provided by soils (e.g., moderation of water cycling, shelter for seed banks, retention and release of nutrients to plants, decomposition of organic wastes, and recycling of nutrients and regulation of earth's major element cycles) were not accorded the importance they are now. The green revolution that has developed during the past four decades has allowed us to face the highly challenging goal of duplicating food production in less than 30 years and improving per capita food availability in many countries (FAO 1995). This objective has been met by increasing cultivated areas and the use of fertilizers and pesticides, selecting increasingly performing cultivars, and improving the physical preparation of soils by tillage, irrigation, and antierosive devices.

During this period, soil classifications have been developed and used largely to identify the soils best adapted to novel agricultural techniques (Soil Survey Staff 1975; Duchaufour 1977). Although some would address the question of agricultural use directly (e.g., FAO 1978; Sanchez et al. 1982), doubts have sometimes been expressed about the real adaptation of this knowledge to the needs of societies (Dudal 1986). Studies on the chemical fertility of soils and on agricultural machinery and its physical impact have also accompanied this phase (Henin et al. 1960; Seta et al. 1993; Frede et al 1994; Cannell and Hawes 1994; Reicosky and Lindstrom 1995; Entry et al. 1996; Papendick and Parr 1997). The needs of plants for fertilizers and the efficiency of their use have been explored thoroughly to provide adequate fertilization in sometimes highly intensive crops (see reviews by Newman 1997 and Magdoff et al. 1997).

The major inputs of biology during this phase

忡

などの国際

have concerned the relationship between plants and the organisms that interact directly with them. Control of parasites, mainly through direct chemical attacks, has grown very rapidly, leading to a situation where control is reasonable in many instances; however, the cost is a sometimes huge application of a large number of pesticides at relatively short intervals and the continuous creation of new molecules as pests adapt to the currently applied products. There have, however, been some crisis situations in which excessive and inappropriate use of insecticides has resulted in a decline in production (Ooi et al. 1992). Although some progress has been made in the selection of increasingly selective molecules, nontarget effects remain significant for a large number of substances in use, and their transfers to other parts of the ecosystem and landscape and persistence in the environment is a matter of real concern. Of major concern is the effect of nematicides and fungicides, which have had side effects such as the drastic reduction of earthworms and other useful invertebrates in intensive annual crop systems or industrial crops such as Banana or tea garden plantations (Senapati et al. 1994). Finally, the burning debate of the soundness of selecting genetically modified plants resistant to specific herbicides shows clearly that there is an urgent need to reassess the approach to pest management. Research in biological pest management has involved natural microbial and invertebrate enemies of pests as part of biological control strategies. Some rather spectacular successes have resulted from this research, which is progressively associated with chemical approaches into integrated pest management (Waage 1996).

Useful organisms have also been studied to find ways to optimize their activities in the context of highly intensive practices. The field of nitrogen fixation has expended huge efforts to identify and classify microbial N-fixers and isolate the Nif-gene responsible for this fixation (Sprent and Sprent 1990).

At a more practical level, techniques for inoculation of legume roots by locally existing or introduced strains have been developed. There have been significant improvements in legume growth, and N fertilization based on the use of legumes as green manure is developing in favorable circumstances; certain prokaryote-plant associations can routinely fix up to 200 kg N ha⁻¹ per cropping cycle and sometimes more (see e.g., Rinaudo et al. 1983; Toomsan et al. 1995). On a world-wide basis, an overall estimate for biological N-fixation is 10⁵ Mt per year (Sprent 1984). Similar research have been done on mycorrhizae, although the control and manipulation of these almost universal symbionts of plants is still limited.

At the beginning of the 1990s, reports acknowledged the spectacular results of the combination of direct interventions (FAO 1995). They also pointed to the rapid spread of environmental problems that now require solutions to meet the continuous challenge of feeding more people until human populations finally stabilize. As new land to cultivate becomes increasingly rare, soils under cultivation are facing significant physical and chemical degradation while pollution of water tables, freshwaters, seashores and littoral areas, and atmosphere is progressing at alarming rates, especially in countries where intensification has been maximum. A new approach to agriculture, called the second paradigm, has been proposed: rely more on biological processes by adapting germplasm to adverse soil conditions, enhancing soil biological activity, and optimizing nutrient cycling to minimize external inputs and maximize the efficiency of their use (Sanchez 1994). It is recognized increasingly that soils can provide a wide range of ecosystem services; the production of food and fiber is still considered the most important, but it is not soil's only purpose (Daily et al. 1997; Tinker 1997), and the maintenance of soil quality has become a serious issue, leading to the development of systems of soil survey in a large number of developed countries. Issues such as the role of soils in carbon sequestration or as reservoirs of biodiversity have come to the fore, and their study requires holistic approaches. Scales at which soils are considered have become extremely diverse (Wagenet 1998; Lavelle and Spain 1999).

DEVELOPMENT OF SOIL ECOLOGY

At the confluence of soil science and ecology, soil ecology has made its way to become a truly interdisciplinary field of scientific innovation with proper concepts and theories.

Until recently, soil ecologists borrowed concepts and theories from other scientific fields. It soon became evident, however, that important issues of soil ecology would not fit into existing models or paradigms or provide counter examples to currently admitted laws. The excessive importance given by current theoretical ecology to antagonist relationships (predation, parasitism, or competition) rather than mutualistic ones and the relatively little importance given to the quality, and not only the quantity, of food resources as determinants of these relationships have been emphasized (Swift et al. 1979; Lavelle 1983; Price 1984). The foodweb approach to explain ecosystem func-

tioning, widely developed in freshwater systems, has been extended with some success to soils (DeRuiter et al. 1993; Hunt et al. 1987). This approach, however, seems to reach its limits with large organisms (ecosystem engineers, Jones and Shachak 1994) with strong indirect, nontrophic influence on other organisms present (Moore et al. 1993; Anderson 1993; Wardle and Lavelle 1997).

The difficulty of relating biodiversity in soils to soil processes is another indication that all species of soil invertebrates are far from being functionally equivalent. Soil systems seem to be an excellent way to address the important issue of the relationship between biodiversity and ecosystem function (Giller et al. 1997; Brussaard et al. 1997; Freckman-Wall et al. 1997 ; Wardle and Lavelle 1997 ; Hopper et al., in press).

Soil ecology is instrumental to the sustainability of land use practices because solutions to problems of maintenance of soil quality and sustainable production are necessarily global. The success-and problems-of conventional intensive agriculture as practiced at its peak has come from the improvement of each of the individual elements assumed to increase production in a largely reductionist approach. A system approach is now needed to address these elements jointly as compartments that interact as a global model. One such model of crop production would heed closely the relationship between nutrient input and uptake by plants to prevent losses to water and air (Myers et al. 1994); the conservation of soil structure through proper management of organic matter inputs and macroinvertebrate and root activities; and the effects of the different allocations of land to crops and plant covers, including, in some cases, non-crop plants (Hogh-Jensen 1998; Lal 1997).

Concepts and Models

New concepts and models have been proposed during the last decade that will support holistic approaches and serve as a basis for integrated models that will simulate the function of agricultural practices of the next generation.

Scales and hierarchies

The first question faced by ecologists was that of integrating determinants of soil processes into a single comprehensive model. Soil scientists have long recognized that soil formation and function proceed from interactions among climate, bedrock, and living organisms. Swift et al. (1979) then developed the concept that decomposition depends on three elements: (i) organisms (O), (ii) soil physical conditions (P) including climate and bedrock effects, and (iii) resource quality (Q), i.e., the chemical quality of organic matter produced by plants and the network of consumers and decomposers. Human activities were also included as a major effect in these interactions. It was then recognized that these determinants are hierarchically organized since factors operating at large scales of time and space constrain factors that operate at smaller scales (Lavelle et al. 1993; Beare et al. 1995; Wagenet 1998.; Izac 1994). Determinants that operate at the largest scales (i.e., climate and soil properties) constrain those that operate at smaller scales, i.e., the plant community that determines the quality and quantity of organic inputs to the soil, 'macroorganisms' (= macroinvertebrates roots) and microorganisms. However, feedback (or bottom-up) retroactions do exist, with determinants at lower levels of the hierarchy influencing upper levels. Furthermore, this hierarchy is potential and may not be fully operational locally: when climate is not constraining (e.g., in the humid tropics), when soils have no clay minerals such as smectites that strongly influence microbial activities through several mechanisms, and when the organic matter produced is uniform and decomposes easily, microbial activity may be regulated primarily by macroinvertebrates (earthworms and termites) via the biogenic structures that they create (Blanchart et al. 1997). The adoption of this model allowed us to consider jointly factors that had previously been addressed in isolation and to identify the factors of greatest importance.

This is an important step in understanding questions such as the apparent contradiction between soil zoologists and soil scientists in regard to the assessment of invertebrate activities. When the former provided increasing evidence that soil invertebrates had a dramatic influence on the rates and spatiotemporal patterns of soil processes (Anderson et al. 1985; Setälä et al. 1991; Martin 1991; Blanchart et al. 1997), the latter would produce models that simulate the same processes without making any mention of soil invertebrates (see e.g., Parton et al. 1983; Smith et al. 1998). At the scale considered by these models, hot spots of invertebrate and root activities are actually diluted in a soil volume that comprises a majority of almost inactive sites (Anderson 1993). Furthermore, the same factors that determine invertebrate and root activities may also regulate microbial activities. As a result, the inter-

mediate action of macroorganisms is regularly undermined or misunderstood, even when their effects are implicitly contained in some basic soil parameters that they influence in the long term, such as C:N ratios, pH, or bulk density. For example, soil bulk density, which is influenced greatly by macrofaunal activity and dynamics, is considered constant in the CENTURY model of SOM dynamics, one of the highest performing models in this area (Parton et al. 1988). Problems arise when perturbations of invertebrate communities affect soil physical properties and SOM dynamics that could not have been predicted by models, especially when they cannot take into account temporal changes in soil bulk density or C:N ratio.

Soils also present a hierarchical physical and spatial organization, as emphasized in the early synthesis of Tisdall and Oades (1982) and refined further with the introduction of fractal models and the efforts made to explore spatial heterogeneity at different levels using spatial statistics (see e.g., Bartoli et al. 1993). Nowhere in the ecosystem has heterogeneity been better assessed than in soils. This approach has helped to define the levels at which soil processes should be studied. At these levels, functional domains of a particular category of organisms, defined as 'ecosystem engineers', have been identified by ecologists and become the scale at which interdisciplinary approaches have largely developed (Lavelle 1984; Jones et al. 1994; Beare et al. 1995; Lavelle 1997; Lavelle et al. 1997; Beare and Lavelle 1998)

Interactions between micro- and macroorganisms: The Sleeping Beauty and the Ecosystem Engineers

Microorganisms are responsible for more than 90% of the mineralization that occurs in soils (IBP); they are capable of decomposing any kind of natural substrate and multiply in short periods of time, sometimes in a matter of days. The turnover time of their biomass, however, generally varies from 6 to 18 months, which indicates that they are inactive most of the time. This apparent contradictory observation is named the Sleeping Beauty Paradox (Lavelle et al. 1995). The Prince Charmings of the story are macroorganisms and other physical processes that bring microorganisms into contact with new substrates to decompose. Macroorganisms, in turn, are known to have limited proper digestive abilities and rely largely on the ability of microorganisms to digest a wide range of substrates for them (see e.g., Slaytor 1992; Rouland et al. 1991, Barois and Lavelle 1986; Lattaud et al. 1996).

Macroorganisms have been classified into three categories, depending on the type of trophic relationships they have with microorganisms and on the biogenic structures they may produce through their mechanical activities in the soil (Lavelle 1997). The smallest, the protozoa, nematodes, and other microfauna that live in the waterfilled soil pores, are micropredators of microorganisms and do not create any structures. Of a larger size, the nonsocial arthropods and small Oligochaeta Enchytraeidae are litter-transformers that produce organic biogenic structures in the form of fecal pellets. These structures, which serve as incubators for microbial digestion before they are reingested, do not usually last long. They may alter the timing and spatial patterns of decomposition, but they have limited impact on soil physical properties (Hanlon and Anderson 1980). Soil ecosystem engineers are mainly termites, ants, and earthworms, which conduct important mechanical activities and produce organo-mineral biogenic structures. These are solid structures that may persist much longer than the organisms that produce them, and they affect the dynamics of SOM and soil physical processes significantly (see Elkins et al. 1986; Mando and Miedema 1997; Folgarait 1998; Villenave et al. 1999; Blanchart et al. 1999). Through the modifications of the environment and changes in resource availability that they promote, soil ecosystem engineers influence the composition and activity of the smaller organisms (or those of lower functional importance) that inhabit their structures or compete with them for, e.g., surface leaf litter (Marinissen and Bok 1988; Loranger et al. 1998; Decaëns, 1999).

Functional domains in soils

Functional domains are parts of the soil that are influenced by a major biotic or abiotic regulator. They are recognizable in a set of structures (pores, aggregates, fabrics) generated by the regulator that can be physically separated from the soil matrix (Fig. 1)(after Beare and Lavelle 1998). They are colonized by rather specific communities of microorganisms, other invertebrates, and, possibly, roots. They are places where basic processes of soil function operate at specific spatial and temporal scales.

Every structure existing in soils is part of a functional domain. Some functional domains may be closely related, however, and their frontiers difficult to identify with precision.

77

٠ø

LAVELLE SOIL SCIENCE

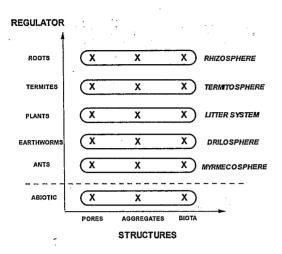


Fig. 1. Functional domains in soils (note that a vertical rather than a horizontal separation of items leads to definition of the porosphere and aggregatesphere (Coleman and Crossley 1996) and soil foodwebs, respectively).

Regulators

Regulators may be biotic or abiotic. Ecosystem engineers such as earthworms, termites, or ants create their own functional domains, i.e., the drilosphere, termitosphere, and myrmecosphere, respectively. Plants create two different spheres of influence in soils, the rhizosphere of roots and the litter system formed by the accumulation of dead leaves and shoots. Biotic functional domains are synonymous with the "biological systems of regulation" described by Lavelle (1984). Abiotic regulators may also create sets of recognizable structures; this is the case for freezing-thawing alternations that create mosaic patterns in soils, or drying/wetting cycles that produce considerable bioturbation and the formation of cracks in soils with swelling clay minerals.

Structures

Functional domains comprise a set of pores, aggregates, and fabrics that have been accumulated by the regulators. They can be described and classified in isolation or at the scale of the whole domain. Biogenic structures considered as extended phenotypes of species (Dawkins 1976) are microsites where taxonomic diversity may influence functional diversity (Lavelle 1996a). A new research approach aims at classifying them into homogenous groups and relating their physical and chemical properties to measurable effects on specific soil processes (Lavelle et al. 1997; Decaëns 1999). Micromorphology, coupled with image analysis or 3D tomography, has proved to be an efficient tool for classifying and quantifying biogenic structures accumulated in the soil (e.g., Lamparsky et al. 1987; Chadoeuf et al. 1994; Binet and Curmi 1992; Jegou et al. 1998).

Communities

Soil ecosystem engineers and abiotic regulators create specific conditions of physical environment and resource availability in their functional domain. As a result, specific communities of organisms from subordinate groups (litter transformers and micropredators) are established in these domains. They form foodwebs, the composition and energy inputs of which are determined by the activities of the regulator.

Processes

Most processes that operate in functional domains are not specific. This is the case for all the transformations linked to C and for nutrient cycles that follow the same pathways and are performed by the same microorganisms everywhere in the soil. Conversely, other processes may be considered highly specific. This is the case for fluxes of energy and matter across foodwebs and priming effects on microbial activities resulting from the production of specific resources such as exudates or mucus in especially active microsites such as the rhizoplane of roots (i.e., a volume approximately 1- μ m thick, in contact with the root surface) or the guts of termites or earthworms (Jenkinson 1966; Lavelle and Gilot 1995).

Scales

Functional domains are places where basic processes of soil function operate following specific spatial and temporal patterns. Processes such as organic matter decomposition may be alternately enhanced or inhibited, depending on the scale of time and space at which they are considered. For example, in the drilosphere (the functional domain of earthworms), mineralization is greatly enhanced in the gut and fresh globular casts, that is to say, in a definite number of small hot spots, during periods of hours to days; in aging casts (which may represent hundreds of tons of aggregates) mineralization is almost nullified as long as the casts retain their structure, which means time scales of months to years (Lavelle 1997). At larger scales, the overall effect of earthworms depends on the balance between shortterm stimulation and longer-term protection. The drilosphere, as with any other functional domain, may still exist and regulate soil processes several

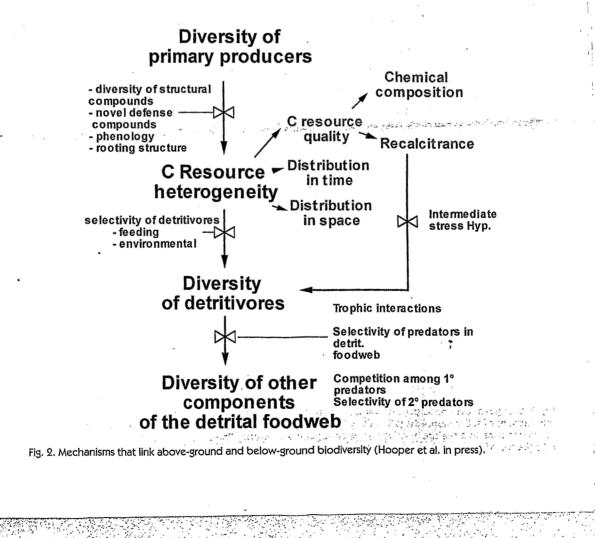
years after the earthworms have been eliminated (Lavelle et al. 1997). This puts new light on the issue of the dynamics of aggregation in natural and managed ecosystems, indicating it is influenced much more by invertebrate activities than currently thought.

NEW CHALLENGES FOR SOIL ECOLOGY

Parts of the conceptual bases of soil ecology are still rather new and need to be refined as their use generalizes. Some present questions of ecology need to be addressed in the context of soils. This is the case for the effects of fragmentation on soil biota communities and populations at local and regional scales. Interactions among soil biota still offer vast opportunities to check the importance of negative (i.e., predation, parasitism, and competition) relationships compared with mutualism. Another important question is the control on process rates via foodwebs: are rates regulated by higher level organisms in the food web (i.e., by predators in a top-down array of determinants) or by a suite of determinants that influence the quality and amount of available organic resources, as suggested by the hierarchical model (Martin et al. 1991; Tayasu et al. 1997; Chen and Wise 1998). Experiments and field observations using isotopic methods constitute an efficient approach to this problem.

The functional significance of biodiversity in soils has been identified as a major scientific concern given the present threats to soil biodiversity (Freckman et al. 1997). Another question relates to the relationship between above- and belowground biodiversity. This question has been now discussed, and research hypotheses have been formulated (Brussaard et al. 1997; Hooper et al. in press) (Fig. 2).

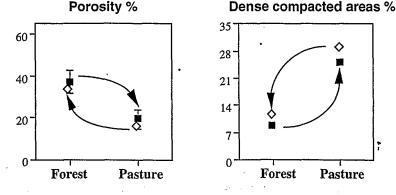
Answers to some of the questions challenging soil science should benefit from recent developments of soil ecology. Modeling SOM dynamics has been a great challenge during the last two decades, and considerable progress have been made; there is still scope for some improvements of predictions and an explicit integration of biological activities (Smith et al. 1998).

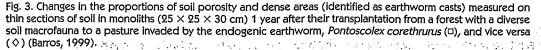


Finally, accurate studies of the dynamics of soils using methods and approaches of soil ecology are likely to provide rather surprising results in the near future. For example, recent studies have shown how trees may transfer silica from deep soil horizons to surface layers through the absorption of this element by roots, transfer to the leaves, and release in decomposing leaves (Lucas et al. 1993). This view, in contradiction to the classical theory of a progressive loss of this element by leaching during soil aging, emphasises the possible strong, bottom-up effects of biota on soil properties in some conditions. The Gaian view of soils and the planet as homeostatic systems regulated by biological activities is finding some support in these results (Lovelock 1993; Lavelle 1996b). Another example comes from recent studies based on micromorphological approaches revealing that, in many soils, most aggregates are formed by invertebrate engineers. Because they are biological structures, they have sometimes surprisingly rapid turnover, and this explains why soil attributes sometimes considered to be rather stable may, in the long term, change at short notice. For example, this is the case for soil macroaggregates when changes in invertebrate communities occur. Disappearance of the invertebrates that produce stable aggregates interrupts the production of new aggregates, and soil aggregation is changed as aging aggregates progressively collapse. In another case, this one reported in Central Amazonia, a compacting earthworm species, Pontoscolex corethrurus, invaded a pasture cleared from the primary forest and produced an excessive amount of large casts. Because these casts were unstable, they col-

lapsed and formed a 5-cm impermeable crust . that created severe limitations to plant growth (Chauvel et al. 1999). Hydromorphy developed below the crust and extended 1 to 2 m in depth, thus changing the entire soil profile in as little as 3 years. During this time, the direct consumption of organic matter by the earthworms and other unidentified mechanisms (possibly methanization) decreased SOM stocks by 18 t/ha in the upper 20 cm of soil. Such events, identified as biodiversity accidents, may occur more frequently than is normally expected. The pullulation of ant nests following abandonment of paddy rice fields to natural fallow in northeast Argentina is another example of a drastic change in soil profile occurring in a very short time when communities of soil invertebrate engineers are disturbed (Folgarait et al. 1998). Interestingly, a disturbance as large as the one observed in the Amazonian soil may revert rapidly when the soil compacted by the activity of a dominant compacting species is re-exposed to the original invertebrate community (Fig. 3).

These fundamental research questions are essential if we are to address larger issues, e.g., the modeling of SOM dynamics or changes in hydraulic soil properties, or understand the bases for sustainable production of agroecosystems and the effect of land use practices. The composition and diversity of soil microorganisms and invertebrate communities is certainly influenced by a wide range of factors that operate at different scales of time and space. Fragmentation of space, colonization abilities of organisms, and their tolerance to different types and intensities of disturbances are essential attributes of populations in





this regard. Understanding the relationship between the diversity of plants and soil biota will also provide essential information for predicting the impact of management options on the composition and activities of invertebrate and other organism populations.

At the next level, it is important to relate the composition and abundance of communities to their effects on physical processes, SOM, and nutrient cycling, their intensity, and persistence in time. A clear understanding of these mechanisms is necessary to design management practices that optimize biological activities and improve the sustainability of the system. Models used to predict the effect of practices will consider various scales of space and time, including the cultivation plot, farm and/or catchment, and region. An example of a conceptual model of that sort is given in Fig. 4 (Mariani, unpublished data). This model explains the interactions between the agrosystem (i.e., the sum of management options chosen), soil attributes (mainly SOM dynamics and physical structure), and soil macrofauna. The aim is to use this model to develop practices that maintain diverse macrofaunal activities at an optimal level to take advantage of their short- and long-term beneficial effects on soil physical structure and SOM dynamics while meeting the requirements of the farmer in terms of productivity and profit. Great importance is given to biogenic structures, i.e., the organomineral structures and voids produced by soil invertebrate engineers, as components of the soil structure that promote suitable properties for plant growth and also as indicators of invertebrate activities. In the long term, invertebrate activities may be absent during given periods of time on parcels of a given size when required by production constraints. Under such conditions, monitoring the soil physical structure, especially the biogenic structures produced by macroinvertebrates, would allow us to determine when the inherited physical effects attributable to past invertebrate activities no longer exist. Different management practices would then be applied to create suitable conditions for invertebrate activities and improve soil conditions. The great challenge is to have accurate indicators to evaluate soil conditions and favorable conditions for fast colonization of the plot. This means that diverse and abundant populations are available in plots adjacent to the area opened to recolonization and that new conditions present in the plot are suitable to attract migrants and to allow rapid growth of their populations. Finally, a number of other ecosystem services provided by soils will come to fruition using the concepts and models that are currently in development.

81

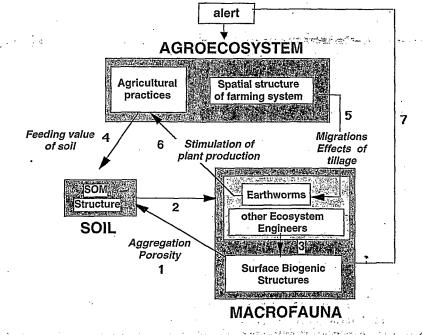


Fig 4. A conceptual model of the type used to predict the effect of practices.

SOIL ECOLOGY ATTITUDES TOWARD ENVIRONMENT AND DEVELOPMENT ISSUES

In a way, ecology may be considered the accountancy of natural systems. Ecosystem research studies energy fluxes and nutrient and matter budgets. Every loss in elements, decrease in process rate or species richness or physical degradation is intuitively considered to be negative. Managed ecosystems always look highly imperfect compared with natural ones, which tend to serve as references for future improvements of artificial systems. The ecological perception of ecosystem functioning has sometimes generated contractive reactions and exaggeratedly conservationist points of view in the face of the poor ecological quality of most agroecosystems. An opposite point of view is supported by agronomists, who look for more artificialization and simplification of the system and evaluate their practices in terms of productivity and profit rather than aesthetic or environmental considerations.

Ecologists are continuously integrating viewpoints from economics and the social sciences and consider the issue of sustainability at levels from water catchments to villages or regions. This new trend is logically derived from the natural enlargement of levels considered as research progresses. International programs have been instrumental in elaborating comprehensive approaches that set human needs and constraints at the center of research approaches. This has been the case, for example, in programs developed by UNESCO (Man and the Biosphere) and by IUBS in its Decade of the Tropics, such as the Tropical Soil Biology and Fertility (TSBF) program (Swift 1986 ; Swift and Woomer 1994). However, this trend has been accelerated greatly by donors who favor direct development and application of research at the farm level through the development of participative research. Increasing difficulties in maintaining research centers and the relatively poor efficiency of transfer to farmers has accelerated this trend. This has led to better consideration of the knowledge of farmers and other soil users, which may be compared with scientific results and/or serve as a basis on which to build.

As awareness of the implications of soil use on global environment is growing, scientific evaluations of their function using Ecological approaches is needed. As soil function is better understood, minimal rates for processes (ex. renovation of soil aggregates, maintenance of porosity) will be identified, budgets for elements will be better established and processes leading to losses (N, P, CO_2 , methane) better understood. Management of organic matter is now considered as essential in any system (fertilisers are better used in the presence of OM) and the maintenance of soil invertebrate engineers is necessary for long term soil conservation. Systemic approach is able to identify the exact trade off among the different constraints: production and financial sustainability, environment protection and soil conservation. As science progresses the uncertainty on processes that gives space to political interpretations is narrowing.

PUBLIC INFORMATION AND TRAINING IN SOIL ECOLOGY

Society in general and farmers as well are frequently ignorant about the role played by soil biota. In a survey of 163 farmers from the state of Vera Cruz (Mexico), 55% ignored the effect of earthworms on soil fertility, 34% recognized their beneficial effect, and 11% considered them harmful, mainly because they mistook them for intestinal parasites (Ortiz et al. 1999). Furthermore, in Congo, where the traditional maala system is one of the few annual cropping systems that enhances earthworm activities, farmers do not seem to be aware of this effect, nor do they acknowledge the importance of soil invertebrates to soil fertility. This ignorance, with some notable exceptions, is surprisingly deep rooted in mythologies and cultures. Societies tend to fear insects and to undermine earthworms. This explains why practices aggressive for soil biota and the environment have, until recently, developed with no limits.

However, these environment-unfriendly practices have led to crises and threats that give space to new technologies. Mad cow disease, fears and fights against GMOs by Indian farmers and consumer unions, and dioxin in Belgian chickens have created interest in ecological technologies based on the use of earthworms and organic wastes that have been largely emphasized by newspapers in Europe and worldwide. Early findings on soil problems caused by lack of diversity have also had large impacts. The effect of invasive earthworms on soil degradation in Amazonia (Chauvel et al. 1999) and the development of new technologies using earthworms to compost domestic wastes (Edwards and Neuhauser 1988) or regenerate degraded soils of tea garden plantations (Senapati et al. 1999) have been widely advertised.

CONCLUSION

In an opening lecture at the last ISSS Congress at Montpellier, Swift (1998) stated: "Soil science has been brilliantly informed by reductionist physics and chemistry, poorly informed by biology, ecology, and geography, and largely uninformed by the social sciences." This sets the ground for the present and future need to further expand interdisciplinary research to face the major problems posed by soil use. Past experiences have shown clearly that interdisciplinary research requires specific interdisciplinary methods and concepts. In the last two decades, soil ecology has participated actively in the development of systemic approaches to soil science. There is still much room for improvement in the concepts and models thus created The next challenge seems to be to integrate adequately economic and sociological parameters in models of soil use; this means adapting scales at which soil science approaches functions to those that matter to individual users and/or to the society (Izac 1993). Another great matter of concern is the rather unsatisfactory transmission of knowledge to stakeholders and practitioners. The approach of soil scientists concerned with this problem (Ruellan 1994) should be supported better in order to accelerate the implementation of the second paradigm in agriculture, that is, to achieve a better integration of basic biological processes (Sanchez 1994), to reach this next paradigm, which will reconcile the ecological and economical sustainability of soil use. The contribution of soil ecology will be to design better artificial systems for the management of natural processes and the invertebrates that have built soil fertility for ages.

ACKNOWLEDGMENTS

This paper has benefited enormously from discussions with soil scientists with many years of experience in various disciplines who will certainly recognize their influence in these pages. I am especially grateful to the TSBF (Tropical Soil Biology and Fertility) program, which has been a unique place for developing and trying new ideas and concepts, to Armand Chauvel his comments on early drafts of this paper, and to Roger Schaefer for reading the proofs.

REFERENCES

Alexandratos, N. 1995. Agriculture mondiale. Horizon 2010. Polytechnica and FAO, Rome.

Anderson, J. M. 1993. Soil organisms as engineers: Microsite modulation of macroscale processes. In Linking Species and Ecosystems. C. G. Jones & J. H. Lawton (eds.). Chapman & Hall, New York, pp. 94–106.

- Anderson, J. M., M. A. Leonard, P. Ineson, and S. Huish S. 1985. Faunal biomass: A key component of a general model of nitrogen mineralization. Soil Biol. Biochem. 17:735-737.
- Andrén, O., L. Brussaard, and M. Clarholm, 1999. Soil organism influence on ecosystem-level processesby passing the ecological hierarchy? Appl. Soil Ecol. 11:177–188.
- Bal, L. 1982. Zoological ripening of soils. 1. The concept and impact in pedology, forestry, and agriculture. 2. The process in two Entisols under developing forest in a recently reclaimed Dutch polder. Pudoc, Wageningen, The Netherlands.
- Barois, I., and Lavelle P. 1986.—Changes in respiration rate and some physicochemical properties of a tropical soil during transit through *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta). Soil Biol. Biochem., 18 (5) 539–541.
- Bartoli F., G. Burtin, R. Philippy, and F. Gras. 1993. Influence of fir root zone on soil structure in a 23 m forest transect: The fractal approach. Geoderma 56 67–85.
- Beare, M., and P. Lavelle. 1998. Regulation of microbial activity and organic matter dynamics by macroorganisms: Integrating biological function in soil. *In* ISSS Congress, Symposium no. 9, Montpellier (CD-Rom).
- Beare, M. H., D. C. Coleman, D. A. Crossley, P. F. Hendrix, and E. P. Odum. 1995. A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. Plant Soil 170: 1–18.
- Binet, F. and P. Curmi 1992. Structural effects of Lumbricus terrestris (Oligochaeta Lumbricidae) on the soil-organic matter system: Micromorphological observations and autoradiographs. Soil Biol. Biochem. 24:1519–1523.
- Blanchart, E., A. Albrecht, J. Alegre, A. Duboisset, B. Pashanasi, P. Lavelle, and L. Brussaard. 1999. Effects of earthworms on soil structure and physical properties. In Earthworm management in tropical agroecosystems. P. Lavelle, L. Brussaard, and P. Hendrix (eds.). CAB International, Wallingford, UK, pp. 139–162.
- Blanchart, E., P. Lavelle, E. Braudeau, Y. Le Bissonais, and C. Valentin. 1997. Regulation of soil structure by geophagous earthworm activities in humid savannas of Cote d'Ivoire. Soil Biol. Biochem. 29:431-439.
- Brussaard, L., V. M. Behan-Pelletier, D. Bignell, V. K. Brown, W. Didden, P. Folgarait, C. Fragoso, D. W. Freckman, V. S. R. Gupta, T. Hattori, D. Hawksworth, C. Klopatek, P. Lavelle, D. W. Malloch, J. Rusek, B. Söderström, J. Tiedje, and V. Ross 1997. Biodiversity and ecosystem functioning in soil. Ambio 26:563–570.
- Burges, A., and F. Raw. 1967. Soil Biology. Academic Press, London.

Cannell, R. Q., and J. D. Hawes. 1994. Trends in tillage

practices in relation to sustainable crop production with special reference to temperate climates. Soil Tillage Res. 30:245-282.

- Chadœuf, J., A. Kretzschmar, M. Goulard, and K. Smettem. 1993. Analysis of the link between earthworm burrows and cracks in the soil. Biometrics, 49:1237-1244.
- Chauvel, A., M. Grimaldi, E. Barros, E. Blanchart, T. Desjardins, M. Sarrazin, and P. Lavelle. 1999. Pasture degradation by an Amazonian earthworm. Nature 389:32--33.
- Chen, B. D., and H. Wise. 1998. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. Ecology.
- Coleman, D. C., C. P. P. Reid, and C. V. Cole. 1983. Biological strategies of nutrient cycling in soil systems. In Advances in Ecological Researches. A. MacFayden and E.D. Ford (eds.). Academic Press, New York, pp. 1–55.
- Coleman, D. C., and D. A. Crossley. 1996. Fundamentals of Soil Ecology. Academic Press, San Diego, CA.
- Daily, G. C., S. Alexander, and P. R. Ehrlich. 1997. Ecosystem services: Benefits supplied to human societies by natural ecosystems. Issues Ecol. 2: 18.
- Darwin, C. 1881. The formation of vegetable mould through the action of worms with observations on their habits. Murray, London.
- Dawkins, R. 1976. The Selfish Gene. Oxford University Press, Oxford, UK.
- Decaëns, T. 1999. Rôle fonctionnel et réponses aux pratiques agricoles des vers de terre et autres ingénieurs Ecologiques dans les savanes Colombiennes. PhD thesis, Paris VI.
- DeRuiter, P. C., J. C. Moore, and H. W. Hunt. 1993. Soil invertebrate/micro invertebrate interactions: Disproportionate effects of species on food web
- structure and function. Vet. Parasitol. 48:247-260.
- DeRuiter, P. C., J. A. Vanveen, J. C. Moore, L. Brussaard, and H. W. Hunt. 1993. Calculation of nitrogen mineralization in soil food webs. Plant Soil 157:263-273.
- Dokuchaev, V. V. 1889. The Zones of Russia (in Russian). Akad. Nauk., Moscow.
- Dommergues, Y., and F. Mangenot. 1970. Ecologie microbienne du sol, Paris.
- Duchaufour, P. 1977. Pedology: Pedogenesis and Classification. Allen and Unwin, London.
- Dudal, R. 1986. The role of pedology in meeting the increasing demands on soils. XIII Conrègèss de l'AISS, 1, AISS, Hamburg, pp. 80–96.
- Elkins, N. Z., G. Z. Sabol, T. J. Ward, and W. G. Whitford. 1986. The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem. Oecologia 68:521-528.
- Entry, J. A., D. W. Reeves, C. B. Backman, and R. L. Raper. 1996. Influence of wheel traffic and tillage on microbial biomass, residue decomposition and extractable nutrients in a Coastal Plain Soil. Plant Soil. 180:129-137. ••••••
- FAO. 1978. Report on the agro-ecological zones pro-· · · ·

ject. Methodology and Results for Africa, Vol. 1. World Soil Resources Report No. 48. FAO, Rome.

- Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: A review. Biodivers. Conserv. 7:1221-1244.
- Freckman, D. W., T. H. Blackburn, L. Brussaard, P. Hutchings, M. A. Palmer, and P. V. R. Snelgrove. 1997. Linking biodiversity and ecosystem functioning of soils and sediments. Ambio 26: 555-562.
- Frede, H. G., R. Beisecker, and S. Gäth. 1994. Longterm impacts of tillage on the soil ecosystem. Z.Pflanzenernähr. Bodenk. 157:197-203.
- Giller, K. E., M. H. Beare, P. Lavelle, A. M. N. Izac and M. J. Swift. 1997. Agricultural intensification, soil biodiversity and agroecosystem function. Applied Soil Ecology. 6:3-16.
- Hanlon, R. D. G., and J. M. Anderson. 1980. Influence of macroarthropod feeding activities on microflora in decomposing oak leaves. Soil Biol. Biochem. 12: 255-261.
- Henin, S., A. Feodoroff, R. Gras, and G. Monier. 1960. Le profil cultural. Principes de physique du sol. Soc. Edit. Ing. Agric., Paris.
- Hogh-Jensen. 1998. Systems theory as a scientific approach towards organic farming. Biol. Agric. Hortic. 16:37-52.
- Hooper, D. U., J. M. Dangerfield, L. Brussaard, D. Wall, D. Wardle, et al. in press. Interactions between above and belowground biodiversity in terrestrial ecosystems: Patterns; mechanisms and feedbacks. Bioscience (in press).
- Hunt, H. W., D. C. Coleman, E. R. Ingham, R. E. Ingham, E. T. Elliott, J. C. Moore, S. L. Rose, C. P. P. Reid, and C. R. Morley. 1987. The detrital foodweb in a shortgrass prairie. Biol. Fertil. Soil 3:57.
- Izac, A. M. 1993. Ecological-economic assessment of soil management practices for sustainable land use in tropical countries. In Soil Resilience and Sustainable Land Use. D.G. I. Szabolcs (ed.). CAB-International Wallingford, UK, pp. 77-96.
- Izac, A. M. N. 1994. On agricultural sustainability and its measurement in small-scale farming sub-Saharan Africa. Ecol. Econ., 11:105–125.

- Jenkinson, D. S. 1966. The priming action. J. Appl. Radiat. Isot. (suppl.):199-208.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. OIKOS 69:373-386.
- Kühnelt, W. 1961. Soil Biology. Faber and Faber, London.
- Lal, R. 1997. Residue management, conservation tillage and soil restoration for mitigating greenhouse effect by CO2-enrichment. Soil Till Res. 43: 81-107.

Lamparski, F., A. Kobel-Lamparski, and R. Kaffenberger. 1987. The burrows of Lumbricus badensis and Lumbricus polyphemus. In A.M. Bonvicini Pagliai and P. Omodeo (eds.). On Earthworms. Mucchi Editore, Modena, pp. 131-140.

34 . 1

Jegou, et al., 1998.

Lattaud, C., S. Locati, P. Mora, and C. Rouland. 1997.

Origin and activities of glucosidic enzymes in gut of the tropical geophagous earthworm *Millsonia anomala* from Lamto (Côte d'Ivoire). Pedobiologia, 41:242–251.

- Lavelle, P. 1983. The structure of earthworm communities. In Earthworm Ecology: From Darwin to Vermiculture J. E. Satchell (ed.). Chapman & Hall, London, pp. 449–466.
- Lavelle, P. 1984. The soil system in the humid tropics. Biol. Int. 9:2–15.
- Lavelle, P. 1996. Diversity of soil fauna and ecosystem function. Biol. Int. 33:3–16.
- Lavelle, P. 1996. Mutualism in soils: A Gaian perspective. In Gaia in Action P. Bunyard (ed.). Floris Books, Edinburgh. pp. 204–219.
- Lavelle, P. 1997. Faunal activities and soil processes: Adaptive strategies that determine ecosystem function. Adv. Ecol. Res. 27:93-132.
- Lavelle, P., D. Bignell, and M. Lepage M. 1997. Global Change and Soil Ecosystem Engineers. Global Change Biology (*in press*).
- Lavelle, P., E. Blanchart, A. Martin, S. Martin, A. Spain, F. Toutain, I. Barois, and R. Schaefer. 1993. A hierarchical model for decomposition in terristrial ecosystems: Application to soils of the humid tropics. Biotropica 25:130–150.
- Lavelle, P., C. Lattaud, D. Trigo, and I. Barois. 1995. Mutualism and biodiversity in soils. In The significance and regulation of soil biodiversity. H. P. Collins, G. P. Robertson and M. J. Klug (eds.). Kluwer Academic Publishers, Dordrecht, pp. 23-33.
- Lavelle, P., and A. V. Spain. 1999. Soil Ecology. Chapman & Hall, London.
- Loranger, G., J. F. Ponge, E. Blanchart, and P. Lavelle. 1998. Impact of earthworm on the diversity of microarthropods in a vertisol (Martinique). Biol. Fertil. Soils 27:21–26.
- Lovelock, J. E. 1993. The soil as a model for the Earth. Geoderma 57: 213–215.
- Lucas, Y., F. J. Luizao, A. Chauvel, J. Rouiller, and D. Nahon. 1993. The relation between biological activity of the rain forest and mineral composition of soils. Science 260:521–523.
- Magdoff F., L. Lanyon, and B. Liebhardt. 1997. Nutrient cycling, transformations, and flows: Implications for a more sustainable agriculture. In Advances in Agronomy, Vol. 60. D. L. Sparks (ed.). Academic Press, San Diego, CA, pp. 1–73.
- Mando, A., and R. Miedema. 1997. Termite-induced change in soil structure after mulching degraded (crusted) soil in the Sahel. Appl. Soil Ecol. 6: 241–249.
- Marinissen, J. C. Y., and J. Bok. 1988. Earthwormamended soil structure: Its influence on Collembola populations in grassland. Pedobiologia 32:243–252.
- Martin, A. 1991.—Short- and long-term effects of the endogenic earthworm *Millsonia anomala* (Omodeo) (Megascolecidae, Oligochaeta) of tropical savannas on soil organic matter, Biol. Fertil. Soils 11:234–238.

- Martin A, A. Mariotti, J. Balesdent, and P. Lavelle. 1991. Soil organic matter assimilation of a geophagous tropical earthworm based on δ¹³C measurements. Ecology 73:118–128.
- Moore J. C., P. C. DeRuiter, and H. W. Hunt. 1993. Soil invertebrate/micro-invertebrate interactions: Disproportionate effects of species on food web structure and function. Vet. Pathol. 48:247–260.
- Müller, P E, 1887. Studien über die naturlichen. Humusformen und deren Einwirkung auf Vegetation und Boden. Berlin, Springer.
- Myers, R. J. K., C. A. Palm, E. Cuevas, I. U. N. Gunatileke, and M. Brossard. 1994. The synchronization of nutrient mineralisation and plant nutrient demand. In The Biological Management of Tropical Fertility. P.L. Woomer and M. J. Swift (eds.). Wiley-Sayce, Chichester, UK, pp. 81-116.
- Newman, E. I. 1997. Phosphorus balance of contrasting farming systems, past and present. Can food production be sustainable? J. Appl. Ecol. 34: 1334-1347.
- Ohtonen, R., S. Aikio, and H. Väre. 1997. Ecological theories in soil biology. Soil Biol. Biochem 29: 1613–1619.
- Ooi, P. A. C., G. S. Lim, T. H. Ho, P. L. Manalo, and J. K Waage. 1992. Integrated pest management in the Asia-Pacific region. In Conference on Integrated Pest Management in the Asia-Pacific region. Kuala Lumpur, Malaysia, 23–27 September, 1991. CAB International/Asian Development Bank.
- Ortiz, B., C. Fragoso, L. Mboukou, B. Pashanasi, J. Kanyonyo ka Kajondo, and B. K. Senapati. 1999. Perception and use of earthworms in tropical farming systems. In Earthworm Management in Tropical Agroecosystems. P. Lavelle, L. Brussaard, and P. Hendrix (eds.). CAB International, Wallingford, UK, pp. 151–166.
- Papendick, R. I., and J. F. Parr. 1997. No-till farming: The way of the future for a sustainable dryland agriculture. Ann. Arid Zone 36:193-208.
- Parton, W. J., D. W. Anderson, C. V. Cole, and J. W. B. Stewart. 1983. Simulation of soil organic matter formation and mineralization in semiarid agroecosystems. In Nutrient Cycling in Agricultural Ecosystems. R.R. Lowrance, R.L. Todd, L.E. Asmussen, and R.A. Leonard (eds.) Athens, GA; Special Publication no. 23 of the Georgia Experimental Station.
- Pedro, G. 1997. La recherche agronomique dans le monde de demain: Valoriser et entretenir durablement l'espace rural et els ressources naturelles. C. R. Acad. Fr. 83:51-106.
- Petersen, H, and M. Luxton. 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39:287-388.
- Price, P. W. 1984. Alternative paradigms in community ecology. In P.W. Price, C.N. Slobodchikoff, and W.S. Gaud (eds.). A New Ecology:Novel Approaches to Interactive Systems. John Wiley, New York, pp. 1–14.

- Reicosky, D. C., and M. J. Lindstrom. 1995. Impact of fall tillage on short-term carbon dioxide flux. In Advances in soil science: Soils and global change. R. Lal, J. Kimble, E. Levine, and B. A. Stewart (eds.). CRC Lewis Publishers, Boca Raton, FL, pp. 177–187.
- Rinaudo, G., B. Dreyfus, and Y. Dommergues. 1983. Sesbania rostrata green manure and the nitrogen content of rice crops and soil. Soil Biol. Biochem. 15:111.
- Rouland, C., F. Lenoir, and M. Lepage. 1991. The role of symbiotic fungus in the digestive metabolism of several species of fungus-growing termites. Comp. Biochem. Physiol. 99A: 657–663.
- Ruellan, A. and M. Dosso. 1993. Regards sur le sol. Fouchier. Paris.
- Sanchez, P.A., W. Couto, and S. W. Buol. 1982 The fertility capability soil classification system: Interpretation, applicability and modification. 27: 283–309.
- Sanchez, P. A. 1994. Tropical soil fertility research: Towards the second paradigm. XVth Congress of AISS, Acapulco, Mexico, July 10--16, 1994. 1:1-24.
- Senapati, B. K., P. K. Panigrahi, and P. Lavelle. 1994. Macrofaunal status and restoration strategy in degraded soil under intensive tea cultivation in India. *In* 15th World Congress of Soil Science, 4a, Acapulco, Mexico, July 1994, pp. 65–75.
- Senapati, B. K., P. Lavelle, S. Giri, B. Pashanasi, J. Alegre, T. Decaëns, J. J. Jimenez, A. Albrecht, E. Blanchart, M. Mahieux, L. Rousseaux, R. Thomas, P. Panigrahi, and M. Venkatachalam. 1999. *In Soil* Earthworm Technologies for Tropical Agroecosystems. *In* The Management of Earthworms in Tropical Agroecosytems. P. Lavelle, L. Brussaard, and P. Hendrix (eds.). CAB International, Wallingford, UK, pp. 189–227.
- Seta, A. K., R. L. Blevins, W. W. Frye, and B. J. Barfield. 1993. Reducing soil erosion and agricultural chemical losses with conservation tillage. J. Environ. Qual. 22:661–665.
- Setälä, H., M. Tyynismaa, E. Martikainen, and V. Huhta. 1991. Mineralisation of C, N, P in relation to decomposition community structure in coniferous forest soil. Pedobiology 35: 285–296. Silver, W. 1997.
- Slaytor, M. 1992. Cellulose digestion in termites and cockroaches: What role do symbionts play? Comp. Biochem. Physiol. 103B:775-784.
- Smith, P., O. Andren, L. Brussaard, M. Dangerfield, K. Ekschmitt, P. Lavelle, M. Van Noordwijk, and K. Tate. 1998. Soil biota and global change at the ecosystem level: The role of soil biota in mathematical models. Global Change Biol. (*in press*).
- Soil Survey Staff. 1975. Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil. Survey U.S.Department of Agriculture, Soil Conservation Service, Washington DC.

- Sprent, J. I. 1984. Nitrogen fixation. *In* Advanced Plant Physiology. M.B. Wilkins (ed.). Longman Scientific & Technical, New York pp. 249–276.
- Sprent, J. I., and P. Sprent. 1990. Nitrogen Fixing Organisms. Chapman and Hall, London.
- Swift, M. J. 1986. Tropical soil biology and fertility (TSBF): Inter-regional research planning workshop. Report of the third Workshop of the decade of the Tropics/TSBF program. Biol. Int., Special Issue 13.
- Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in Terrestrial Ecosystems. Blackwell Scientific, Oxford, UK.
- Swift, M. J., J. Vandermeer, P. S. Ramakrishnan, J. M. Anderson, C. K. Ong and B. A. Hawkins. 1996. Biodiversity and agroecosystem function. In Functional Roles of Biodiversity: A Global perspective. H. A. Mooney, J. H. Cushman, E. medina, O. E. Sala and E. D. Schulze (eds.). John Wiley & Sons Ltd., pp. 261–298.
- Swift, M. J. 1998. In XVIth Congress of the ISSS, Montpellier. (CD-Rom).
- Tayasu, I., T. Abe, P. Eggleton, and D. E. Bignell. 1997. Nitrogen and carbon isotope ratios in termites: An indicator of trophic habit along the gradient from wood-feeding to soil-feeding. Ecol. Entomol. 22: 343–351.
- Tinker, P. B. 1997. The environmental implications of intensified land use in developing countries. Phil. Trans. R. Soc. Lond., B, pp. 1023–1033.
- Tisdall, J. M., and J. M. Oades. 1982. Organic matter and water-stable aggregates in soils. J. Soil Sci. 33:141-163.
- Toomsan, B., J. F. McDonagh, V. Limpinuntana, and K. E. Giller. 1995. Nitrogen fixation by groundnut and soyabean and residual nitrogen benefits to rice in farmers' fields in Northeast Thailand. Plant Soil 175:45-56.
- Villenave, C., F. Charpentier, P. Lavelle, C. Feller, M. Brossard, L. Brussaard, B. Pashanasi, I. Barois, and A. Albrecht. 1999. Effects of earthworms on soil organic matter and nutrient dynamics. *In* Management of Tropical Earthworm Activities. L. B. P. Lavelle P. Hendrix, C. Fragoso, and B.K. Senapati (eds.). CAB-International, Wallingford, UK.
- Waage, J. 1996. Integrated pest management and biotechnology: An analysis of their potential for integration. In Biotechnology and Integrated Pest Management. G. J. Persley (ed.). CAB International, Wallingford, UK, pp. 36–60.
- Wagenet, R. J. 1998. Scale issues in agroecological research chains. Nutr. Cycl. Agroecosyst. 50:23–34.
- Wardle, D., and P. Lavelle. 1997. Linkages between soil biota, plant litter quality and decomposition. In Driven by Nature. G. Cadisch and K.E. Giller (eds.). CAB-International, Wallingford, UK, pp. 107–125.

Wardle, D. A., and K. E. Giller, 1996. The quest for a contemporary ecological dimension to soil biology. Soil Biol. Biochem. 28:1549-1554.