Annals of Microbiology, **52**, 119-131 (2002)

Soil as a biological system

G. PIETRAMELLARA*, J. ASCHER, M.T. CECCHERINI, G. RENELLA

Dipartimento di Scienza del Suolo e Nutrizione della Pianta, P.le Delle Cascine 28, 50134 Firernze, Italy

Abstract - Soil plays a fundamental and irreplaceable role in the biosphere because it governs plant productivity of terrestrial ecosystem, allows the completion of the biogeochemical cycles and microorganisms inhabiting soil degrade, sooner or later, all organic compounds including those more recalcitrant. The main characteristics of soil are the domination of the solid phase, the presence of aqueous and gaseous phase and its capacity of reactions by surface active particles. These characteristics influence the biological processes carried out by the organisms inhabiting soil. A peculiarity of soil as a biological system is that it is a structured, heterogeneous, discontinuous system with organisms living in discrete microhabitats called "hot spots", that represents a small proportion (generally lower than 5%) of the overall available space. The chemical, physical and biological characteristics of these microhabitats differ both in time and space. To explain the capacity of soil to degrade all organic compounds the concepts of "microbial consortia", acquisition of novel degradation pathways by soil microorganisms, "extracellular enzymes" and "enzymatic combustion" were introduced.

Key words: soil structure, biological space, microbial degradation, enzymatic degradation.

INTRODUCTION

The aim of this review is to discuss soil as a biological system, that is its properties, its organisms, the processes carried out by these organisms and the relative kinetics, the main factors affecting these processes, the approaches to simulate and modelling biological processes. It is not possible to prepare an exhaustive review due to the complexity and vastness of the treated matter which exceeds the limits this paper. Therefore, the presentation often summarises the various areas of the topic without a detailed discussion of the underlying mechanisms.

---

* Corresponding author. Phone: +39-0553288200; Fax: +39-0553288200; E-mail: pietra1@unifi.it

MAIN CHARACTERISTICS OF SOIL

The domination of the solid phase
It is a distinctive characteristic of soil respect to other microbial habitats. Solid phase consists of particles of different size made up by living organisms, inorganic (minerals), and organic (plant, animal, microbial residues and humic matter) components, as independent entities and mixed conglomerates.

The capacity of reactions
It depends on the surface area and surface charge of the soil particles. Surface area is a direct result of particle size and shape. Most of the total surface area of soil is due to clay-sized particles (diameter <2 μm) and soil organic matter (especially the humic fraction). Charge in soil is mainly associated with these two fractions, although oxide and hydroxide and even sand and silt size fraction may also contribute. The origin of the charge in soil occurs as a results of *isomorphic substitution* and *ionisation of functional groups* on the surface clay minerals, oxides, hydroxide and organic matter. These two mechanisms give rise to the *permanent charge* and *pH-dependent charge* of soil, respectively (Table 1). The relative contribution of *permanent* and *pH-dependent charge* depends on the composition of soil colloids and on the ionic environment in which the soil has been formed (Bohn *et al*. 1990). Considering what reported above we can define c*olloids* as soil particles which diameter <2 μm, high surface area and surface charge.

TABLE 1 – The charge origin in soil

Mechanisms	Characteristics
Isomorphic substitution	The substitution of one ion by another of similar size but different charge. These substitutions occurs during crystallisation of minerals and the resulting charge is essentially independent of the environmental condition.
Ionisation of functional groups on the particle surface	The gain or loss of H^+ from functional groups, such as hydroxyl, carboxyl, phenolic, and amine groups, on the surface of soil particles. The charge depends on the pH of the soil solution, which regulates the degree of protonation or deprotonation of these groups.

Aqueous and gaseous phase in soil
Soil particles are surrounded by aqueous and gaseous phase, the amount and the composition of these phases fluctuate markedly in time and space. Water films are generally surrounding active particles (colloids). The status of water molecules changes with the distances from the active surface: water molecule is an ordered film adjacent to the charged surface of the soil colloids and this order is lost until water molecules are not held under the attraction of the colloid charges. Thickness of the water film depends on the surface charge value of the colloid. The colloids are present in soil as micro and macro aggregates:

– micro aggregates are clusters of surface active particles;
– macro aggregates are clusters of micro aggregates.

All microorganisms being aquatic organisms are living in water films and their activity depends on the availability of nutrient and energy sources in these water films that surround the surface of solid particles (Stotzky, 1986, 1997). Hattori (1973) has reported that almost 80-90% of the microorganisms inhabiting soil are located on active surface particles; so the distribution of microorganisms in soil is restricted to clay, oxides, hydroxides or organic particles but not sandy or silt particles. The relative hydrophobicity of some soil colloids can be important in modifying the structure of water films and in affecting the interactions of microorganisms with soil colloids (Stotzky, 1986). Hydrophobic regions of lipids, waxes, and hydrophobic moieties in the organic matter can interact with hydrophobic regions of the microbial surfaces or may render hydrophobic inorganic particles, such as clay minerals, when complexes between these inorganic and organic components occur (Stotzky, 1986).

Soil structure is the way in which soil particles are arranged or grouped spatially. Aggregates are formed by particles held together by different types of bonds and those by polysaccharide-base glues are probably the most important. Polysaccharides can be produced by plants (mucigel, mucilage, rhizodeposition) and microbes (exopolysaccharides). Pores of different size are formed in response to the formation of soil structure, and these pores can have different functions (Cambardella and Elliott, 1993; Ladd *et al*., 1996) (Table 2).

TABLE 2 – Type and functions of soil pores

Type of pores	Diameter of pores	Functions
Macro pores	∅ > 2.10-5m	These pores, responsible for the drainage and aeration of soil, are characterised by the presence of roots, micro and meso fauna.
Meso pores	2.10-5m > ∅ > 2.10-7m	These pores contain plant available water, bacteria and root hairs.
Micro pores	∅ < 2.10-7m	These pores are important for the adsorbed and inter-crystalline water.

Adsorption of biological molecules by surface active particles

It is another peculiarity of soil as a biological system. Enzymes can be adsorbed by clay minerals or entrapped by humic molecules maintaining their activity, being protected against proteolysis, thermal and pH denaturation (Nannipieri *et al*., 1996). In this way stabilised extracellular enzymes can be still active under conditions unfavourable for the activity of soil microorganisms (Nannipieri *et al*., 2001). Nucleic acids molecules can also be adsorbed and bound on clay minerals, humic molecules and sand particles, being protected against degradation by nucleases without inhibiting their transforming ability (Khanna and Stotzky, 1992; Paget *et al*., 1992; Pietramellara *et al*., 1997). This fact has important implications on the use of genetically modified organisms in terrestrial ecosystem. Also microorganisms are adsorbed by surface active particles and this adsorption could protect them against predators (Ladd *et al*., 1996).

The mechanisms by which organic molecules are bound to clays, oxides, hydroxides and organic particles determines the strength with which these compounds are held, and the ability of microbes to use organic molecules as substrates.

It has been hypothesised that surface active particles concentrate these substrates at the solid-liquid interface, and this enrichment can support the growth of microorganisms adsorbed on these surfaces. Indeed, particle-size fractionation reveals a concentration of soil organic matter and microbial biomass in the fine silt-size/coarse clay-size materials (Ladd *et al*., 1996). On the other hand Stotzky (1986) discussed that any evidence suggesting that adsorbed organic substrates sustain growth of microorganisms on active surface particle.

Bacteria and fungi are generally the most abundant microorganisms in soil; for example, in a temperate grassland soil the bacterial and fungal biomass amounted to 1-2 and 2-5 t ha-1, respectively (Killham, 1994). Bacteria and fungi are highly versatile, being capable of carrying out almost all known biological reactions. According to Coleman and Crossley (1996), bacteria and fungi are the main decomposers of organic residues entering soil and they differ for the type of growth and exploration of food. Bacteria are the most metabolically significant group of organisms in soil, although fewer in number than viruses and constituting lower biomass than fungi.

Microbial life exists in spot

The first characteristic of soil as a biological system is that soil is a structured, heterogeneous and discontinuous system with organisms living in discrete microhabitats called "hot spots" (Nannipieri *et al*., 1990). The chemical, physical and biological characteristics of these microhabitats differ both in time and space. According to Stotzky (1997) many factors affect microbial life in soil (Table 3).

TABLE 3 – Factors affecting the ecology, activity and population dynamics of microorganisms in soil

– Carbon and energy source	– Temperature	– Oxidation-reduction potential
– Mineral nutrients	– Pressure	– Surfaces
– Growth factors	– Air composition	– Spatial relationships
– Ionic composition	– Electromagnetic radiation	– Genetic of the microorganisms
– Available water	– pH	– Interaction between microorganisms

It is not possible, in this context, to discuss the complex effect of each factor on microbial activities because of the review limits.

The hot spots contain more microbial species than other microbial habitats in soil. The space occupied by organisms is called "biological space" represents a small proportion, generally lower than 5%, of the overall available space. Almost 80-90% of the microbes inhabiting soil is located on solid surface, and the mechanisms by which these micro-organisms interact with soil surfaces are not always clear. Despite of soil is generally poor of nutrients and energy, it contains more microbial species than other microbial habitats. Torsvik *et al*. (1996) calculated a mean number of about 3.8×10^6 bacteria g^{-1} dry weight soil by analysing the reassociation kinetics of complementary strands of DNA extracted from soil. Organisms inhabiting soil are generally grouped according to their size, structure and functions in macrofauna, mesofauna, microfauna, and microbiota (Lee, 1985).

BIOLOGICAL PROCESSES OF SOIL

All known metabolic processes can be carried out by microorganisms inhabiting soil; organic compounds, even those more recalcitrant (synthetic pollutants) are mineralised to CO_2. Synthetic organic pollutants, whose molecular structure differs considerably respect to that of natural compounds, can persist for longer periods of time but then they are degraded (Dobbins *et al*., 1992). Two hypothesis have been postulated for explaining the degradation of more dissimilar organic pollutants:

– acquisition of novel degradation pathways by soil microorganisms based on the occurrence of random mutations followed by selection of microorganisms capable of degrading even synthetic compounds. However the acquisition of a cluster of "degradative" genes on a single genetic unit, such as plasmid or bacteriophage, is generally requested. Indeed, numerous genes involved in the degradation of organic compounds are plasmid-encoded (Nannipieri *et al*., 2000);
– the presence of non specific enzymes capable of carrying out the so called "enzymatic combustion". The lignolytic system of white root fungi is capable to degrading lignin but also polyciclic aromatic hydrocarbons (PAHs) and their derivatives (polychlorinated biphenyl and even dioxin) (Jian and Tso, 1996).

Microbial consortia

Microbial consortia in soil are more efficient in the degradation of compounds than individual microbial species. In a microbial consortium the capabilities of individual species overlap and are integrated in such a way that the consortium, as a whole, has considerably greater potential than do any of the single species on their own (Zeikus, 1983). Bacteria, yeast and fungi are responsible for the initial transformation of the primary substrates (biopolymers, hydrocarbon) to monomers or metabolic intermediates; anaerobic bacteria can transform the intermediates to fermentative and low molecular weight products (Zeikus, 1983).

In the concept of microbial consortia is important the relationship between microbial diversity and microbial function. This relationship is largely unknown. Classical concepts of diversity include species richness (the number of species), evenness (the relative contribution that individuals of all species make to the total number of organisms present) and composition (type and relative contribution of the particular species present) (Griffith *et al*., 1997).

Degradation and polymerisation of organic compound is responsible of the formation of humic molecules characterised by a complex polymeric structure (largely unknown) with aromatic and aliphatic moieties. These molecules are slowly degraded and their age, estimated by radiocarbon dating, can range from 250 to over 3000 years.

As just reported above, the soil functioning depends not only on the compo-

TABLE 4 – Type of interactions among soil microorganisms

Interaction	Characteristics
Neutralism	Neither beneficial nor detrimental effects occur between two partners.
Symbiosis	Two partners are closely associated and both beneficially profit from his association.
Commensalism	Interaction with beneficial effects for one partner whereas the other one is unaffected.
Competition	One or both partners suffer from the presence of the other one.
Amensalism	One species suppresses the other one by producing antibiotics or toxin.
Parasitism	Interaction with beneficial effects for one partner whereas the other one is affected.
Predation	Involve the direct attack of one specie by the other one.

sition of soil microbiota, chemical and physical properties of soil but also on microbial interactions, as reported in Table 4.

In soil interaction between microorganisms is a rare event even when the pore space is saturated with the aqueous phase or where water bridges are present between adjacent microhabitats. In fact also in these cases the movement of bacteria between microhabitats is restricted, as the surface tension of the ordered water around aggregates may be too great to allow passive movement of cells or even active movement by flagellated cells (Stotzky, 1977).

Enzymatic degradation

Many enzymes that usually are active within the cell can also function extracellularly if they do not require cofactors for their activity. Extracellular enzymes in the aqueous soil solution are short-lived due to the combination of adsorption, denaturation and degradation unless they are inglobed and protected by soil colloids. Immobilised enzymes can be used for practical purposes in soil such as to promote the degradation of organic pollutants. The type of support used to immobilised the enzyme should be carefully considered, not only for its property of preserving the activity of the immobilised enzyme, but also for its possible stimulatory or inhibitory effect on the enzyme activity. The immobilised enzyme must be capable of expressing its activity at high level for an extended period of time.

The use of immobilised enzymes present several advantages on microorganisms. They can often withstand environmental extreme conditions that would be lethal to microbial cells. In addition enzymes are not affected by predators and toxins, and may be active even at low substrate concentration.

The enzyme kinetics is described by the Michaelis and Menten equation (Lehninger *et al*., 1993):

$$\mathbf{V = V_{max} [S]/Km + [S] \quad (Eq.\ 1)}$$

where $\mathbf{V_{max}}$ is the maximum reaction rate, **Km** is the Michaelis and Menten constant, expressing the enzyme affinity towards the substrate, and **[S]** is the substrate concentration.

The prevalence of heterogeneous conditions in soil imposes a series of problems on the enzyme kinetics substrate (Nannipieri and Gianfreda, 1998). Intracellular enzymes of microbial cells attached to soil particles or entrapped inside soil aggregates as well as extracellular enzymes adsorbed by clay minerals or entrapped in humic molecules are subjected to a series of *microenvironmental effects* like steric limitations on the interaction between the substrate and the enzymatic active site, different pH conditions respect to the value of bulk soil, and the effect of the charge of the support on the substrate.

The above mentioned examples concerning the enzyme kinetics involve soluble substrates, but substrates are often insoluble in soil (cellulose, starch, lignin, urea etc.). According to McLaren and Skujins (1971) the velocity of enzyme reaction, when the substrate is insoluble, is given by:

$$\mathbf{V = K\,[E_0]\,n \quad (Eq.\ 2)}$$

where **K** is a constant related to the distribution coefficient of the enzyme between the solution and the substrate surface, and **n** is less than unit.

The rate of the enzyme reaction depends on the surface of the insoluble substrate.

The probabilities for microbial cells to detect insoluble substrates by the direct contact are scarce and the release of extracellular enzymes hydrolysing the insoluble substrates present several disadvantages:

– the extracellular enzymes can be degraded by proteases present in the soil environment;
– even if the enzyme reaches the insoluble substrate, the environmental conditions (pH and temperature) can not be optimal for the enzyme reactions;
– even if the enzyme reaction occurs, an opportunistic cell can use the released soluble reaction products.

Considering these problems Burns (1982) proposed a microbial strategy, based on the presence of clay – or humic-enzyme complexes, for the hydrolysis of insoluble substrates to soluble substrates. The presence of the immobilised extracellular enzymes in soil assures the hydrolysis of insoluble substrates and decreases the need to synthesise and release higher amount of extracellular enzymes by microbial cells.

It is noteworthy to say that for most recalcitrant compounds, such as pesticides, the degradation pathways in axenic culture under laboratory conditions are largely unknown, as well as the metabolic intermediates and enzymes involved in most of these pathways (Bollag and Liu, 1990).

THE RHIZOSPHERE

The rhizosphere is the soil surrounding the root and is characterised by a high-number (10-20 times) of microorganisms than bulk soil. This depends by the rhizodeposition, which includes root exudates and root debris (Uren, 2001) (Table 5).

TABLE 5 – Characteristics of the two types of rhizodeposition

Type of rhizodeposition	Components
Root exudates	Aminoacids, proteins, monosaccharides, oligosaccharides, polysaccharides, organic acids, fatty acids, growth factors, flavones, nucleotides and other compounds.
Root debris	Root cap cells and senescent cortical cells.

The flux of organic compounds from roots to soil rhizosphere increase the concentration of available organic carbon, a factor limiting the activity of soil heterotrophic which are largely prevalently over soil autotrophs (Toal *et al.*, 2000).

The following specific compound released from root cells can control the behaviour of specific microorganisms:

- Flavonoids, molecular signals from plant roots to specific bacteria and fungal species (symbiosis between legumes and rhizobia; mycorrhizal infection). According to Hungria and Stacey (1997) more than 4000 flavonoids has been identified in the plant kingdom and some of them function as *nod* gene inducers;
- Siderophores are iron chelating agents secreted in response to iron deficiencies. Siderophores are secreted by microorganisms, whereas phytosiderophores are secreted by graminaceous plants. The competition between plants and microorganisms for iron is very complex being influenced by many factors such as level of siderophores production by the competing organisms, the resistance of siderophores to microbial degradation, the ability of the molecule to solubilise iron by attacking mineral surface, the chelating constants of these complexes and their charge characteristics. Molecular properties can regulate the adsorption of these molecules by soil colloids (Crowley, 2001).

Plant growth promoting rhizobacteria (PGPR)

Plant growth promoting rhizobacteria encompass bacteria with plant growth stimulating activity due to their increase of nutrients (P and N) and then production of phytohormones such as indolacetic acid (IAA), gibberelin and cytokinin-like substances and vitamins. Indirect stimulation can occur due to their control of the soil borne plant diseases phatogens (antagonisms).

Microbiota- fauna interactions

There is an increasing interest on the role of microbiota-fauna interactions in the food chains of soil. Predator – prey interaction between protozoa and bacteria in the rhizosphere can have an impact on plant nutrition due to microbial N immobilisation, and N mineralisation promoted by protozoa predation activity. When bacteria are ingested by protozoa, release of NH_4^+ occurs and this mineral N can be taken up by the plant roots (Clarhom, 1994; Badalucco and Kuikman, 2001).

THE FACTORS AFFECTING MICROBIAL DIVERSITY IN SOIL

In soil the predominance of one or more member groups does not occur because the various microbial species inhabiting soil are spatially separated for most time, being soil moisture generally low (Tiedjie *et al*., 2001). The contact lasts for a very short period immediately after rainfall, when water bridge are formed between various soil conglomerates. The rapid removal of water by gravity would maintain the spatial isolation among the various microbial species inhabiting soil. The presence of a great variety and content of organic compounds is responsible for the formation of a variety of microhabitats supporting the high microbial diversity (Tiedjie *et al*., 2001). Microbial diversity is higher on soil surface than in the deeper soil layers. High or low pH values are determining the prevalence of bacteria or fungi in soil, respectively.

The soil rock fragment fraction, considered inert and of great impediment to the soil tillage, is usually not considered important in soil characterisation (Agnelli *et al*., 2001). The rock fragment fraction represents a water reservoir in soil especially utilisable by fungi (mycorrhiza). This fraction could also protect microorganisms by steric impediment with its irregular surface against predation.

It is well established that different agricultural practices, such as tillage methods, cropping system or manure applications can affect the size, composition and activities of soil microflora. It is important to underline that the minimum tillage is a practice used to minimise the alterations of soil physical characteristics (structure) and microbial equilibrium (Coleman and Crossley, 1996).

MODELLING OF SOIL BIOLOGICAL PROCESSES

It is impossible to monitor each inorganic and organic compound and to quantify the rates of each abiotic reaction in a complex system like soil (Jenkinson 1990; Nannipieri *et al*., 1994; Whitmore and Handayarita, 1997). Today nutrient cycling are quantified in soil by using the holistic approach. The system is partitioned into pools, and fluxes among these pools usually represent physical processes, such as leaching or volatilisation, or abiotic or biotic reactions. Fluxes concerning nutrient transformation include a series of reactions and generally, only changes in the concentrations of the final products are considered. The holistic approach has allowed a better mathematical description of the system with the consequent possibility to simulate processes occurring in soil (Stevenson, 1986).

The current models describing the mineralisation and immobilisation of nutrients are based on the following basic principles:

1. microbial biomass is a significant source of nutrients;
2. microbial decomposition and microbial synthesis occur simultaneously in soil;
3. nutrients in the organic matter are heterogeneous in terms of biological activity because some components cycle very slowly whereas other cycle very rapidly.

For these reasons the models represent soil organic matter as a multiple pool system, and these pools are characterised by different decomposition rates influenced by climatic and main soil properties (Paustian, 2001). Terms as labile, stable, chemically protected organic matter, physically protected organic matter have been used. The terminology is not defined because the physical and chemical significance of the various organic fractions, as well as their functioning, is rather vague. The nutrient quantification has been obtained by monitoring the fate considering stable (^{13}C and ^{15}N) and radioactive (^{14}C) isotopes dynamic than measurements of C mineralisation. Determination of changes in the ^{13}C abundance has allowed to quantify the soil organic matter dynamics in response to changes in agricultural management (Andreaux, 1996; Vittorello *et al*., 1989). Radiocarbon dating of soil organic matter has been useful to define recalcitrant pools, and these data have been used to simulate models of the organic matter in soil (Jenckinson *et al*., 1987; Trumbore *et al.*, 1995).

CONCLUSION

Soil plays a fundamental and irreplaceable role in the biosphere because it governs plants productivity of terrestrial ecosystem, allows the completion of the biogeochemical cycles and microorganisms inhabiting soil degrade, sooner or later, all organic compounds including those more recalcitrant. Soil harbours high population density and enormous microbial diversity under a tremendous range of physical and chemical conditions. Probably the soil microflora is the results of more than 3,5 billions years of evolution (Tiedje *et al*., 2001), and the microbial population inhabiting soil rhizosphere is the result of a coevolution with plant species to which rhizosphere is associated (Biricombe *et al*., 2001).

REFERENCES

Agnelli A., Ugolini F., Corti G., Pietramellara G. (2001). Contrasting the microbial biomass C and the basal respiration of fine earth and highly altered rock fragments of two forest soils from the northern Apennines, Italy. Soil Biol. Biochem., 33 (4-5): 613-662.

Andreaux F. (1996). Humus in world soils. In: A. Piccolo, ed., Humic Substances in Terrestrial Ecosystem. Elsevier, Amsterdam, pp. 45-100.

Badalucco L., Kuikman P.J. (2001). Mineralisation and immobilisation in the rhizosphere. In: Pinton A., Varanini Z., Nannipieri P., eds, The Rhizosphere. Biochemistry and Organic Substances at the Soil-Plant Interface. Marcel Dekker, New York, pp. 159-196.

Biricombe M.J., De Leij F.A., Linch J.M. (2001). The effect of root exudates on rhizosphere microbial population. In: Pinton A., Varanini Z., Nannipieri P., eds, The Rhizosphere. Biochemistry and Organic Substances at the Soil-Plant Interface. Marcel Dekker, New York, pp. 95-140.

Bohn H.L., McNeal B.L., O'Connor G.A., eds (1990). Soil Chemistry. John Wiley & Sons, New York, USA.

Bollag J.M., Liu S.Y. (1990). Biological transformation processes of pesticides. In: Cheng H.H., ed., Pesticide in the Soil Environment. Processes, Impacts and Modelling. Soil Science Society of America, Madison, WI. SSSA Book Ser. 2, pp. 169-211.

Burns R.G. (1982). Enzyme activity in soil: location and a possible role in microbial ecology. Soil Biol. Biochem. 14: 423-427.

Cambardella C.A., Elliott E.T. (1993). Carbon and nitrogen distribution in aggregates from cultivated and native grassland. Soil Sci. Soc. Am. J., 57: 1071-1076.

Clarhom M. (1994). The microbial loop in soil. In: Ritz K., Dighton J., Giller K.E., eds, Beyond the Biomass. John Wiley, Chichester, pp. 221-230.

Coleman D.C., Crossley D.A., eds (1996). Fundamentals of Soil Ecology. Academic Press, New York, USA.

Crowley D. (2001). Function of siderophores in the plant rhizosphere. In: Pinton A., Varanini Z., Nannipieri P., eds, The Rhizosphere. Biochemistry and Organic Substances at the Soil-Plant Interface. Marcel Dekker, New York, pp. 223-261.

Dobbins D.C., Marjorite C.M., Pfaender F. (1992). Subsurface, terrestrial microbial ecology and biodegradation of organic chemicals: a review. Critical Reviews in Environmental Control, 22 (1/2): 67-136.

Griffith B.S., Ritz K., Wheatley R.E. (1997). Relationship between functional diversity and genetic diversity in complex microbial communities. In: Insam H., Rangger A., eds, Microbial Communities: Functional versus Structural Approaches. Springer-Verlag, Berlin, pp. 1-9.

Hattori T. (1973). Microbial Life in Soil. Marcel Dekker, New York.

Hungria M., Stacey G. (1997). Molecular signals exchanged between plants and rhizobia: basic aspects and potential applications in agriculture. Soil Biol. Biochem., 29: 819-830.

Jenckinson D., Shart P.B.S., Raney J.H., Parry L.C. (1987). Modelling the turnover of the organic matter in long-term experiments at Rothamsted. INTECOL Bullentin, 15: 1-8.

Jenkinson D.S. (1990). The turnover of organic carbon and nitrogen in soil. Philosophical Transactions of the Royal Society, London. B329: pp. 361-368.

Jian H., Tso W.W (1996). DNA recombination, plasmid dissemination, enzymatic “combustion” and cell immobilisation: their potential effect on environmental biotechnology. In: Moo-Young M., Anderson W.A., Chakrabarty A.M., eds, Environmental Biotechnology: Principles and Application. Klumer, Dordrecht, Netherlands, pp. 28-37.

Khanna M., Stotzky G. (1992). Transformation of *Bacillus subtilis* by DNA bound on montmorillonite and effect of DNase on the transforming ability of bound DNA. Appl. Environ. Microbiol., 58: 1930-1939.

Killham K., ed. (1994). Soil Ecology. Cambridge University Press, Cambridge.

Ladd J.N., Foster R.C., Nannipieri P., Oades J.M. (1996). Soil structure and biological activity. In: Stotzky G., Bollag J.M., eds, Soil Biochemistry. Vol. 9, Marcel Dekker, New York, pp. 23-78.

Lee K.E., ed. (1985). Earthworms: their ecology and relationship with soils and land use. Academic Press, Sidney, Australia.

Lehninger A.L., Nelson D.L., Cox M.M., eds, (1993). Principles of Biochemistry. Worth Publishers, New York.

McLaren A.D., Skujins J.J., eds (1971). Soil Biochemistry. Vol. 2, Marcel Dekker, New York.

Nannipieri P., Ceccanti B., Grego S. (1990). Ecological significance of the biological activity in soil. In: Stotzky G., Bollag J.M., eds, Soil Biochemistry. Vol. 6, Marcel Dekker, New York, pp. 293-355.

Nannipieri P., Badalucco L., Landi L. (1994). Holistic approaches to the study of populations, nutrient pool and fluxes: limits and future research needs. In: Ritz K., Dighton J., Giller K.E., eds, Beyond the Biomass. John Wiley, Chichester, pp. 231-238.

Nannipieri P., Sequi P., Fusi P. (1996). Humus and enzyme activity. In: Piccolo A., ed., Humic Substances in Terrestrial Ecosystem. Elsevier, Amsterdam, Netherlands, pp. 239-328.

Nannipieri P., Gianfreda L. (1998). Kinetics of enzyme reactions in soil environment. In: Huang P.M., Sanesi N., Buffle J., eds, Structure and Surface Reactions of Soil Particles. John Wiley, New York, pp. 450-479.

Nannipieri P., Falchini L., Landi L., Pietramellara G. (2000). Management of soil microflora. In: Balazas E., Galante E., Lynch J.M., Schepers J.P., Toutant J.P., Werner D., Werry P.A.Th.J., eds, Biological Resource Management Connecting Science and Policy. Springer-Verlag, Berlin, pp. 237-255.

Nannipieri P., Kandler E., Ruggiero P. (2001). Enzyme activities as research tool for microbiological and biochemical processes in soil. In: Burns R.G.,. Dick R, eds, Enzymes in the Environment: Activity, Ecology and Applications. Marcel Dekker, New York.

Paget E., Jocteur-Monrozier L., Simonet P. (1992). Adsorption of DNA on clay minerals: protection against DNase I and influence on gene transfer. FEMS Microbiol. Lett., 97: 31-40.

Paustian K. (2001). Modelling soil organic matter dynamics-global changes. In: Ress R.M., Ball B.C., Campbell C.D., Watson C.A., eds, Sustainable Management of Soil Organic Matter. CABI International, Wallingford, UK, pp. 45-53.

Pietramellara G., Dal Canto L., Vettori C., Gallori E., Nannipieri P. (1997). Effects of air-drying and wetting cycles on the transforming ability of DNA bound on clay minerals. Soil Biol. Biochem., 29: 55-61.

Stevenson F.J., ed. (1986). Cycles of Soil. Carbon, Nitrogen, Phosphorus, Sulphur, Micronutrients. John Widley & Sons, New York.

Stotzky G. (1986). Influence of soil mineral colloids on metabolic processes, growth, adhesion, and ecology of microbes and viruses. In: Huang P.M., Schnitzer M., eds, Interactions of Soil Minerals with Natural Organics and Microbes. Soil Science Society of America, Madison, WI, USA, pp. 305-428.

Stotzky G. (1997). Soil as an environment for microbial life. In: van Elsas J.D., Trevors J.T., Wellington E.M.H., eds, Modern Soil Microbiology. Marcel Dekker, New York, pp. 1-372.

Tiedjie J.M., Cho J.C., Murray A., Treves D., Xia B., Zhou J. (2001). Soil teeming with life: new frontiers for soil sciences. In: Ress R.M., Ball B.C., Campbell C.D., Watson C.A., eds, Sustainable Management of Soil Organic Matter. CABI International, Wallingford, UK, pp. 393-412.

Toal M.E., Yeomans C., Killham K., Meharg A.A. (2000). A review of rhizosphere carbon flow modelling. Plant Soil, 222: 263-281.

Torsvik V., Sorheim R., Goksoyr J. (1996).Total bacterial diversity in soil and sediment communities - a review. J. Ind. Microbiol., 17: 170-178.

Trumbore S.E., Davidson E.A., de Camargo P.B., Nepstad D.C., Martinelli L.A. (1995). Below ground cycling of carbon in forests and pastures of Eastern Amazonia. Global Biogeochem. Cy., 9: 515-528.

Uren N.C. (2001). Types, amounts, and possible functions of compounds released into the rhizosphere by soil-grown plants. In: Pinton A., Varanini Z., Nannipieri P., eds, The Rhizosphere. Biochemistry and Organic Substances at the Soil-Plant Interface. Marcel Dekker, New York, pp. 19-40.

Vittorello V., Cerri C.C., Anderaux F.G., Feller C., Victoria R.L. (1989). Organic matter and natural carbon-13 distribution in forested and cultivated oxisoils. Soil Sci. Soc. Am. J., 53: 773-778.

Whitmore A.P., Handayarita (1997). Simulating the mineralisation of N from crop residues in relation to residue quality. In: Cadish G., Giller K.E., eds, Driven by

Nature-Plant Litter Quality and Decomposition. CABI International, Wallingford, UK, pp. 337-348.

Zeikus J.C. (1983). Metabolic communities between biodegradative populations in nature. In: Slater J.H., Whittenburry R., Wimpenny J.W.T., eds, Microbes in Their Natural Environments. Cambridge University Press, Cambridge, UK, pp. 415-432.