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## **Regulation of Microbial Activity and Organic Matter Dynamics by Macroorganisms : Integrating Biological Function in Soil**

**BEARE Michael (1), LAVELLE Patrick (2)**

(1) Crop & Food Research, Ltd. Private Bag 4704, Christchurch, New Zealand

(2) ORSTOM/Université Paris VI, 32 Av. H. Varagnat, 93143 BONDY Cedex, France

In the last 4 decades, much research has been directed at understanding the effects of soil macroorganisms (e.g. plants, earthworms) on soil function, i.e. regulation of microbial activity, nutrient release and organic matter turnover, and soil structure formation. In most cases, the effects of macroorganisms involve direct or indirect interactions with soil microorganisms. As their direct interactions are relatively well studied, recent research has turned to understanding their indirect interactions (through changes in the physical or chemical environment) in soils.

Integrating the interactions of macro- and microorganisms across differing scales of both space and time is a major challenge of this research. One common approach involves soil foodwebs. Foodwebs are composed of fauna and microorganisms linked to each other and organic resources in a trophic network. Although the foodweb approach has been used to quantify temporal changes in biological function (e.g. energy flow), it does not usually account for spatial variability in soil.

Another common approach involves functional domains, i.e. regions within the soil that originate from or are modified by soil organisms to the extent that they influence the activity of other soil organisms (e.g. rhizosphere, drilosphere). This approach provides a means of integrating biological functions at different spatial scales. However, accounting for temporal changes in the function of these domains remains an important limitation of this approach. Solutions are needed to develop practical applications of the functional domain approach to understanding whole soil function.

This paper presents a introduction to the problems of integrating biological function in soil with a particular emphasis on the role that macroorganisms play in regulating microbial activity and organic matter dynamics. The objective of the symposium is to develop new integrated approaches to conceptualizing and quantifying these interactions at different spatial and temporal scales.

**Keywords :** soil microbial activity, organic matter dynamic, macroorganisms, integrating biological function

## **Régulation microbienne, dynamique de la matière organique et macroorganismes du sol: vers une approche intégrée**

**BEARE Michael (1), LAVELLE Patrick (2)**

(1) Crop & Food Research, Ltd. Private Bag 4704, Christchurch, New Zealand

(2)ORSTOM/Université Paris VI, 32 Av. H. Varagnat, 93143 BONDY Cedex, France

Au cours des quarante dernières années, un effet de recherches considérable a été dirigé vers la compréhension des effets des macroorganismes du sol (les « ingénieurs de l'écosystème » tels les plantes ou les vers de terre) sur le fonctionnement du sol. La régulation de l'activité microbienne, la libération des nutriments et le recyclage de la matière organique, et la formation et l'entretien de la structure du sol. Dans la plupart des cas, l'effet des organismes ingénieurs met en jeu des interactions directes ou indirectes avec les microorganismes du sol. Leurs interactions directes étant relativement bien comprises, les recherches récentes se sont intéressées aux interactions indirectes induites par des modifications de l'environnement physique ou chimique dans le sol.

L'intégration des interactions entre macro-et microorganismes à différentes échelles de temps et d'espace est l'enjeu majeur de ces recherches. Une première approche est basée sur l'analyse des réseaux trophiques: basés sur les ressources organiques ils relient la faune et les microorganismes. Cette approche a bien été utilisée pour quantifier les modifications temporelles du fonctionnement biologique (par ex. du flux d'énergie) mais elle ne peut prendre en compte la variabilité spatiale du sol dans l'état actuel des modèles.

Une autre approche communément utilisée considère des systèmes biologiques de régulation, encore appelés domaines fonctionnels: ce sont des régions du sol qui sont créées et modifiées par les organismes ingénieurs et qui influencent l'activité des autres organismes. La rhizosphère des racines ou la drilosphère créée par les vers de terre en sont d'importants exemples. Cette approche permet d'intégrer le fonctionnement biologique à différentes échelles de temps et d'espace. Cependant, la description des changements du fonctionnement de ces systèmes au cours du temps est souvent difficile. La mise en pratique de cette approche dans des modèles de fonctionnement de l'ensemble du sol reste à développer.

Cet article présente le problème de l'intégration des processus biologiques dans le fonctionnement du sol avec un accent particulier mis sur les macroorganismes dans la régulation de l'activité microbienne et la dynamique de la matière organique. L'objectif du symposium est de développer des approches nouvelles pour conceptualiser et quantifier ces interactions à différentes échelles d'espace et de temps.

Mots clés : sol, activité microbienne, dynamique de la matière organique, macroorganisme, fonction biologique intégrée

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## **Regulation of Microbial Activity and Organic Matter Dynamics by Macroorganisms : Integrating Biological Function in Soil**

### **Régulation de l'activité microbienne et de la dynamique de la matière organique par les macro organismes : les fonctions biologiques intégrées du sol**

**BEARE Michael<sup>1</sup> and LAVELLE Patrick<sup>2</sup>**

<sup>1</sup> Crop & Food Research, Ltd. Private Bag 4704, Christchurch, New Zealand and

<sup>2</sup> ORSTOM/Université Paris VI, 32 Av. H. Varagnat, 93143 BONDY Cedex

Since the International Biological Programme (IBP) of the 1970's, considerable research has been directed at describing and quantifying the effects of soil macroorganisms (e.g. plants, earthworms, termites) on the major processes that determine soil function (Lavelle, 1997). These processes include the regulation of microbial abundance and activity, the transformations and turnover of organic matter and nutrients, and the formation and stabilization of soil structure (Andren et al, 1990; Coleman, 1985; Beare et al., 1995; Lavelle, 1997). In most cases, the effects of macroorganisms on soil function involve direct or indirect interactions with smaller soil organisms, particularly microorganisms. These interactions can be positive (e.g. mutualistic, associative) or negative (e.g. competitive, predatory) in function. The importance of direct interactions in regulating soil processes has been the subject of much research. This research has tended to focus in two key areas: 1) the positive interactions between plants and their microbial symbionts (e.g. mycorrhizae, Rhizobium N<sub>2</sub> fixers)(Allen, 1992) and 2) the negative interactions between organisms in detritus foodwebs (Coleman et al., 1983; De Ruiter et al., 1993). Recently, there has been a growing interest in understanding the indirect interactions in soils and whether they confer greater stability and resiliency to soil function (Beare et al., 1995). Indirect effects on soil microorganisms may result from changes in soil physical and chemical environments that are a product of the feeding, burrowing and waste depositing activities of macroorganisms.

In general, the more complex the biotic interactions, the greater the probability that indirect effects will be important to regulating soil function (Price, 1988). To understand these interactions, it is first necessary to understand the factors that constrain biological activity. The factors that constrain the activity of soil organisms depend on the spatial and temporal scales at which they function (Swift et al., 1979). Soil microorganisms (<0.2 mm; including bacteria, fungi, protozoa and nematodes) are constrained by their

ability to: 1) distribute themselves within a compact matrix of loosely connected pores, 2) meet their nutritional requirements in an environment where resources are spatially and temporally unpredictable and of widely varying quality and 3) tolerate extreme and sometimes rapid changes in temperature and moisture. At the other end of the continuum, macroorganisms (>2 mm; including termites, earthworms and macroarthropods) are constrained by their ability to: 1) move within a compact environment, 2) gain adequate nutrition from relatively diffuse, low quality resources, and 3) tolerate extreme changes in moisture.

Although soil microbial communities are numerous and diverse, most are dormant for extended periods of time (Jenkinson and Ladd, 1981). The apparent contradiction between the short generation time of microorganisms (ca 20 h) and their relatively slow turnover time (1 to 1.5 yrs) has been described as the “Sleeping Beauty paradox” (Lavelle et al., 1994). Under this paradox, the “kiss” that awakens dormant microorganisms results from an increase in the availability of suitable resources or microhabitats (Beare et al., 1995). The “kiss” may be delivered by biological or physical forms of “Prince Charming”. Among the biological forms, much emphasis has been placed on the “Ecosystem Engineers” (Jones et al., 1994), i.e. macrofauna capable of mechanically modifying the soil environment (Anderson et al., 1993). Some macrofauna (e.g. earthworms) are also responsible for the deposition of mucus and intestinal byproducts that “prime” the activity of soil microorganisms (Lavelle and Gilot, 1994).

Despite the emphasis on macrofauna, other soil organisms also help to engineer the activity of soil microorganisms. The influence of plant roots in this respect is well known. They establish gradients of moisture and nutrients and release root byproducts (e.g. exudates, etc.) that regulate both the composition and activity of microbial communities (Clarholm, 1985). Though often overlooked, mesofauna also contribute to these processes. They are responsible for the fragmentation of plant litter which increases the surface area for microbial attack and production of organic matter enriched fecal pellets that are enriched in saprophytic microbes. In some soil environments, physical forces may play an equally important, if not dominant, role in awakening dormant microorganism. Rapid wetting of dry soil or thawing of frozen soil can result in mechanical modification of the microbial habitat and increased bioavailability of nutrients and organic substrates that influence microbial activity. The similarities and differences between these “Prince Charming” forces, both biological and physical in origin, are poorly known. Furthermore, their relative importance in specific soil environments is often assumed but rarely demonstrated.

The challenge we face lies in integrating the interactions of macro- and microorganisms across differing scales of both space and time. One of the more common approaches to integrating soil biological function involves the construction of soil foodwebs. Foodwebs are most often composed of micro- and meso-fauna and microorganisms linked to each other and organic resources in a trophic network. This network of direct trophic interactions has been used to describe and quantify the flow of energy and transfer of matter within ecosystems (Coleman, 1985; Clarholm, 1985; Hunt et al., 1987; De Ruiter et al., 1993). In soil, these trophic interactions are most often concerned with the breakdown of organic matter and fluxes of nutrient. Through the use of simulations models, the foodweb approach has been used effectively to quantify temporal changes in biological function. However, a major limitation of the foodweb approach is that it does not usually account for the spatial variability in soil, rather it assumes that these processes occur within a homogeneous matrix. Not surprisingly, some of the more successful applications of the foodweb approach have come from investigations of specific subsystems or functional domains in soil (Santos et al., 1981; Beare et al., 1992; Clarholm, 1985).

Owing to differences in their size, motility and life expectancy, soil organisms function at hierarchically arranged scales of space and time. The composition of biological communities at one hierarchical level (e.g. macroorganisms [earthworms, termites]) influence the distribution of resources and refuges that determine the structure of biological communities at other hierarchical levels (e.g. microorganisms)(Beare et al., 1995). Swift (1984) referred to the species assemblages occupying these resources and refuge patches as "unit communities". The distribution of patches and their associated unit communities ultimately determines the location and rate of interspecific interactions and biogeochemical transformations in soils, factors that are important to determining soil function (Anderson, 1988).

In this paper we use a fairly broad definition of functional domains, i.e. regions within the soil that originate from or are modified by soil organisms to the extent that they influence the activity of other soil organisms. Examples of these include plant litter (detritosphere), roots (rhizosphere) or earthworm burrows (drilosphere). The functional domain approach provides a means of integrating the functions of soil biota at different spatial scales. However, the problem of accounting for temporal changes in the form and, therefore, the function of these domains remains an important limitation of this approach. For example, root channels can persist intact for decades, perhaps even centuries, long after the roots have died. These old root channels often contain the recalcitrant remains of decayed roots. They may also serve as the preferred burrows of

earthworms, enchytraeids and various arthropods. These observations raise the obvious question - at what point does the region surrounding a dead and decaying root cease to be the rhizosphere and become the detritosphere? The organisms that occupy this sphere and the functions they perform are likely to be very different from those found around an actively growing root. Perhaps it is more correctly defined as the rhizodetritosphere. Similarly, are there residual rhizosphere effects that carryover into the "drilosphere" formed when an earthworm occupies an old root channel? Likewise, when does a soil aggregate formed by the casting activity of earthworm cease to be under the influence of the earthworm? Answers to these and other related questions are needed to develop practical applications of the functional domain approach to understanding whole soil function.

This paper presents a general introduction to the problems of integrating biological function in soil with a particular emphasis on the role that macroorganisms play in regulating microbial activity and organic matter dynamics. The objective of the symposium is to develop new integrated approaches to conceptualizing and quantifying these interactions at different spatial and temporal scales.

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