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Soil aggregation: Influence on microbial biomass and implications for biological processes

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ABSTRACT

Our 1988 paper, describing the effects of cultivation on microbial biomass and activity in different aggregate size classes, brought together the 'aggregate hierarchy theory' and the 'microbial biomass concept'. This enabled us to identify the relationships between microbial and microhabitat (aggregate) properties and organic matter distribution and explain some of their responses to disturbance. By combining biochemical and direct microscopy based quantification of microbial abundance with enzyme activities and process measurements, this study provided evidence for the role of microbial biomass (especially fungi) in macroaggregate dynamics and carbon and nutrient flush following cultivation. In the last ten years environmental genomic techniques have provided much new knowledge on bacterial composition in aggregate size fractions yet detailed information about other microbial groups (e.g. fungi, archaea and protozoa) is lacking.

We now know that soil aggregates are dynamic entities – constantly changing with regard to their biological, chemical and physical properties and, in particular, their influences on plant nutrition and health. As a consequence, elucidation of the many mechanisms regulating soil C and nutrient dynamics demands a better understanding of the role of specific members of microbial communities and their metabolic capabilities as well as their location within the soil matrix (e.g. aggregates, pore spaces) and their reciprocal relationship with plant roots. In addition, the impacts of environment and soil type needs to be quantified at the microscale using, wherever possible, non-destructive '*in situ*' techniques to predict and quantify the impacts of anthropogenic activities on soil microbial diversity and ecosystem level functions.

1. Perspective

The paper "*Distribution of microbial biomass and its activity in different soil aggregate size classes as affected by cultivation*" was published in 1988 (Gupta and Germida, 1988). The research we reported was one of the early studies that integrated measurements of microbial biomass (MB), abundance of microbial communities, biochemical activities, process rates and organic matter (OM) concentrations in an attempt to identify relationships with microhabitat (aggregate) properties and explain their responses to disturbance. We used a wide range of analytical methods considered modern at the time to quantify various properties. While those methods allowed the identification of links between the location of bacteria and fungi and the spatial changes in biological processes and C and nutrients in soils, they were not suitable to identify specific phenotypic and functional associations of microbial communities. Recent developments in ecogenomic (DNA/RNA), isotopic and spectroscopic techniques allow us to measure the distribution and changes in specific genera or groups/communities of microorganisms (both total and active as well as taxonomic and functional groups) in various parts of aggregates and pore spaces and to determine their role in soil functional processes in relation to OM composition (Davinic et al., 2012). However, we are still unable to determine the metabolic capabilities and activity of microorganisms within aggregates and pore spaces and their interactions with one another – and thus their importance to functions at an ecosystem level. Such in-depth understanding of the complex relationships between microbial diversity (especially functional communities) and habitat characteristics is necessary not only to enhance and manage biological functions for agricultural

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production, but also to identify management options that promote soil C sequestration. Our knowledge of how soil aggregate structure and the location of microorganisms within the aggregate impacts on microbial community resilience to environmental stress is limited. Understanding the functional resilience of the soil microbial community is extremely important to predict impacts of anthropogenic activities. Currently, most research is conducted using separated aggregate fractions. It is clear, however, that the connectivity between aggregates and associated pore network spaces, both intra and inter-aggregate spaces, is an important aspect that needs to be considered in order to effectively integrate and interpret micro-scale information. Such investigations will require the use of '*in situ*' assessment techniques.

2. Background to our work on aggregates

Prior to the 1970s, soil aggregate research focused mainly on the physical processes involved in aggregate formation. It was generally accepted that polysaccharides were associated with structural stability, and aggregates were complex organisations of soil particles and organic materials (Emerson, 1959; Edwards and Bremner, 1967). Edwards and Bremner (1967) also suggested that particles of clay-polyvalent metal-organic matter (C-P-OM) bond to form micro-aggregates and that macro-aggregates consist of complexes of C-P-OM where polyvalent metals help bind clays to humified OM. In a series of papers from 1972 to 1978, Tisdall and Oades proposed their 'aggregate hierarchy theory' for soil structure and OM, which consists of three physical units: macro-aggregates, micro-aggregates and primary particles. They also postulated differing roles for roots, fungi and bacteria in the formation and stabilization of aggregates. The model explained, to some degree, how aggregate formation and stabilization were affected by chemical, plant, microbial and physical processes. Contrary to previous beliefs, Tisdall and Oades (1982) proposed that roots and soil fungi (especially mycorrhizae) bound the smaller aggregates into stable macro-aggregates. They hypothesized that roots and mycorrhizal hyphae bring together and stabilise smaller aggregates and soil particles initially by entanglement and adhesion. They also suggested that tillage would have a greater destructive impact on larger aggregates more than micro-aggregates. Their work concentrated on the structural aspects of aggregation which postulated that different hierarchical stages of aggregate formation and stabilization are influenced by different groups of transient (organic materials that can be rapidly decomposed by microorganisms e.g. polysaccharides), temporary (agents that can build-up in the presence of plants and persist for months e.g. roots, hyphae, bacteria and algae) and persistent (aromatic humic materials and polymers) binding agents based on their temporal persistence.

During this intensive period of research it was thought the structural heterogeneity of soils influenced microbial diversity and function, sometimes limiting plant access to carbon and nutrients. Using conventional culture techniques, Hattori and Hattori (1976) reported on the distribution of bacteria and fungi in different aggregate size fractions and within different locations of large aggregates, and suggested possible relationships between an organism's location and its metabolic functions – such as denitrification. Similarly, culture-based studies by McCalla et al. (1957) reported that fungi appeared to be highly effective in stabilizing soil aggregates. Inevitably these culture-based methods failed to clearly demonstrate how biophysical interactions between soil particles and microorganisms yield structurally sound aggregates.

Electron microscopy observations of non-tangential thin sections or frozen-etch preparations revealed that the size and fine structure of microbial cells in soils were often different from that of their laboratory cultivated counterparts: specifically that cells were generally <1 μm in diameter and a majority were so-called '*dwarf*' forms less than 0.5 μm in diameter (Bae et al., 1972; Bae and Casida, 1973; Balkwill and Casida, 1973). Although these studies described the physical appearance of microbial cells in natural soil environments, sample preparation methods did not allow identification of their precise location. In contrast, Foster et al. (1983) presented a series of scanning and transmission electron microscopy pictures of the rhizosphere environment using intact samples of roots and soils. These studies were mainly about understanding plant-pathogen-microbe interactions related to soil-borne diseases. Nevertheless, the photographs and their interpretation provided many ideas and a strong impetus for our use of microscopic methods to study the location of soil microorganisms in aggregates impacted by cultivation.

By the mid-1980s, aggregates had been identified as focal points for biota–physicochemical interactions and biogeochemical processes. It was hypothesized that stable aggregates provided an optimum habitat for microorganisms, which in turn would support highly active biological- and biochemical-mediated (primarily using extracellular enzymes) transformations of dead biomass, organic carbon and key nutrients such as N, P and S. Elliott (1986) extended the size based aggregation concept by incorporating changes in the concentration of C, N and P to explain the effect of cultivation on C and N turnover. He observed that micro-aggregate classes contained lower concentrations of C, N and P than macro-aggregates and that the C to N and P nutrient ratios were narrower. Elliott's paper also presented evidence showing that cultivation decreased the OM that binds together micro-aggregates into macro-aggregates providing protection and was the source of nutrients released upon cultivation. In a review, Burns and Davies (1986) postulated that cultivation causes the breakage of microbial filaments and root hairs, destroys stable soil pores and increases aeration, all processes stimulating the decomposition of released binding materials. Elliott (1986) postulated that differences in C, N and P dynamics in the different aggregates could be explained based on the biological and biochemical mineralization hypothesis (McGill and Cole, 1981); however, he did not present any direct evidence for the underlying biological mechanisms.

3. Our research

Based on Elliott's work and earlier microscopy studies of bacteria and fungi in soil, we hypothesized the differential location of bacteria and fungi within soil aggregates, and suggested that disturbance due to cultivation would influence aggregate stability and the nutrient mineralization processes. This idea required that we linked the presence of biota to the physical habitat characteristics in order to understand mechanisms of both biochemical (mobilized by periplasmic and extracellular hydrolases controlled by end product supply) and biological (mineralized as a result of C oxidation to provide energy) mineralization of nutrients, especially for S which is processed through both the mechanisms (McGill and Cole, 1981). Furthermore, we attempted to link the dynamics of microbial biomass turnover with the physical location of the microbiota within aggregates and their contribution to nutrient (C, N and S) transformations (Tiessen and Stewart, 1983; Voroney and Paul, 1984). We integrated measurements related to the chemical characteristics of OM, populations of microorganisms, enzyme activities and process measurements to provide a comprehensive story. Through the use of fluorescence and electron microscopy we were able to give an *in-situ* description of the distribution of fungi and bacteria within aggregates and provide visual evidence for the involvement of fungal hyphae in aggregation.

As expected, 69 years of cultivation decreased microbial biomass (MB), microbial respiration and enzyme activities.

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