frontiers
in Environmental Science

BOOK REVIEW
published: 21 February 2018
doi: 10.3389/fenvs.2018.00010

Book Review: Shifting Paradigms on Soil Microbial Biomass

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Keywords: soil microbiology, biodiversity, fumigation, Jenkinson, history of soil science

A Book Review on

Microbial Biomass: A Paradigm Shift in Terrestrial Biogeochemistry

Kevin R. Tate (London: World Scientific), 2017, 327 pages. ISBN: 978-1-786341-30-3, and cover page given in **Figure 1**.

This book is fundamentally a well-deserved tribute to the late Professor David S. Jenkinson (1928–2011), written by a group of researchers, several of whom, like David Powlson and Philip Brookes, were his long-term collaborators at Rothamsted. During his distinguished career, Professor Jenkinson made many seminal contributions to soil science, in particular to our understanding of the dynamics of soil carbon. In the early 60s, he was among the first researchers to use ^{14}C to study the transformations of organic matter in soils. He carried out pioneering work on the mathematical modeling of organic matter transformations, and his efforts in this context, in collaboration with James Rayner, provided the foundation of the widely-used Rothamsted carbon model, RothC. In a frequently-cited article in *Nature*, published years before most soil scientists perceived the significance of the problem, Jenkinson et al. (1991) proposed the first quantitative assessment of the potential for a "feedback effect" whereby the additional carbon dioxide released from decomposition of organic matter in soils in a warmer world could accelerate climate change.

The book edited by Kevin Tate derives its title and subtitle from another key component of Professor Jenkinson's activities, related to the quantification of soil microbial biomass. Prior to the publication of his landmark 1966 paper on the subject (Jenkinson, 1966), the activity of microorganisms had been acknowledged for some time to be crucial to many processes occurring in soils, a fact that Professor Jenkinson underlined with the now famous description of soil biomass as "the eye of the needle through which all organic matter entering the soil must pass" (Jenkinson, 1977). By the mid-60s, the norm in the soil microbiology literature was to use classical microbiological techniques to identify and count the different species that are present in soils. In parallel, there was also a clear recognition, by at least a number of prominent soil microbiologists (e.g., Rovira and Greacen, 1957; Weber and Gainey, 1962; Griffith, 1965), that to understand the roles microorganisms fulfill in soils, it was necessary to characterize in detail the microenvironments in which they reside. In that respect, Alexander (1964), wrote that "microorganisms apparently in the same habitat are, in fact, often exposed to entirely different environmental influences and population pressures. To understand the forces actually affecting the organisms, a microenvironmental concept rather than the gross macroscopic view of interactions must be adopted."

Bucking these viewpoints, Professor Jenkinson made the bold move to go in exactly the opposite direction. He decided to look at the forest rather than at individual trees, and viewed soil biomass as a black box that he considered to be an integral component of soil organic matter. In addition, he assumed implicitly that a satisfactory description of soil microbial activity could be obtained without having at all to consider microhabitats or microenvironments. Trying to make sense of the

OPEN ACCESS

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Specialty section:
This article was submitted to Soil Processes, a section of the journal Frontiers in Environmental Science

Received: *10 January 2018*
Accepted: *30 January 2018*
Published: *21 February 2018*

Citation:
Baveye PC (2018) Book Review: Shifting Paradigms on Soil Microbial Biomass. Front. Environ. Sci. 6:10. doi: 10.3389/fenvs.2018.00010

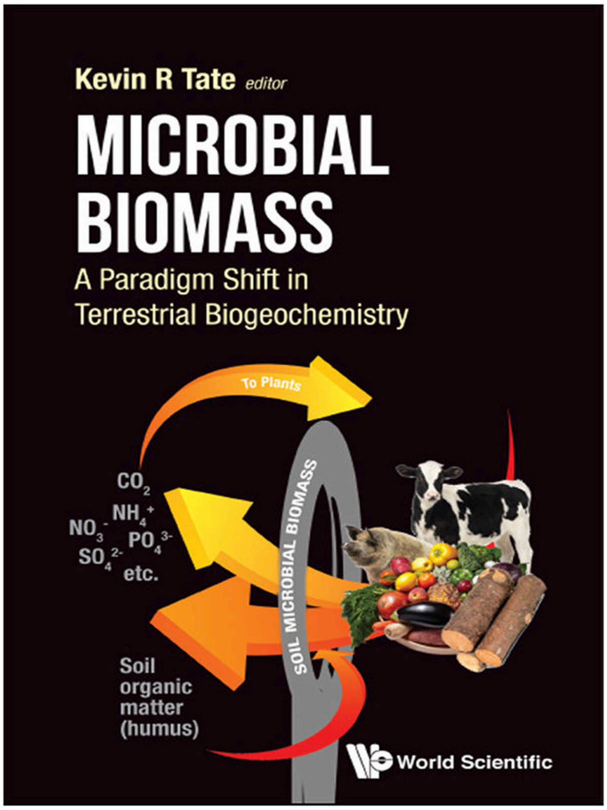

FIGURE 1 | Book cover of Microbial Biomass (Copyright @ 2017 World Scientific, London, United Kingdom. Reprinted with kind permission).

by-then common observation that after partial sterilization of a soil, e.g., using fumigation with chloroform ($CHCl_3$), there was a distinct flush of C and N mineralization, Jenkinson (1966) not only concluded that the origin of this flush was the killing of microorganisms and subsequent release of their intracellular contents in the soil solution. He also ingeniously devised a method by which the amount of CO_2 evolved during this flush could be used to estimate roughly the size of the soil biomass.

The first chapter of the *Microbial Biomass* book, written by Powlson et al. (2017), provides a very interesting, extensive description of Jenkinson's (1966) revolutionary perspectives, as well as of later developments of what became known eventually as the "Chloroform Fumigation-Incubation" and the "Chloroform Fumigation-Extraction" methods, which have since been used extensively in soil microbiological research. Several of the commonly encountered technical difficulties associated with these two methods are discussed, whereas no mention is made of other operational complications, e.g., related to the high sensitivity of these methods to experimental variables like soil moisture (e.g., Ross and Tate, 1984; Ross, 1987; Sparling and West, 1989), which one might find regrettable but can easily remediate by even cursory searching on internet. Curiously, the chapter starts with a slight misrepresentation, since neither the title nor the body of Jenkinson's (1966) article contains the expression "soil microbial biomass," contrary to what Powlson et al. (2017) write. That overzealous slip aside, however, the story the authors tell is extremely compelling.

Aside from this historically-minded introduction, the book contains 9 other chapters, dealing successively with the role of the soil microbial biomass in cycling nutrients (Chapter 2), managing soil microbial biomass for sustainable agro-ecosystems (Chapter 3), microbial biomass and functions in paddy soil (Chapter 4), soil biodiversity and ecosystem functioning (Chapter 5), building predictive models for diverse microbial communities in soil (Chapter 6), dynamic compound-specific stable isotope probing of the soil microbial biomass (Chapter 7), emerging culture-independent tools to enhance our understanding of soil microbial ecology (Chapter 8), microbial ecosystem functions in wetlands under disturbance (Chapter 9), and arctic soil microbial sensitivity to seasonal dynamics and climate change (Chapter 10). All of these chapters have been extremely well crafted and edited, and are most interesting to read.

The subtitle of the book points out, correctly, that Jenkinson's (1966) article caused a paradigm shift in soil microbiology research, and several of the book chapters emphasize the same overall viewpoint. Between the lines, however, various comments here and there in the book seem to suggest as a subliminal message that there is a definite need to revisit whether Jenkinson's paradigm is still meaningful at this point. The first chapter, by Powlson et al. (2017), actually provides very clear pointers in that respect, by describing candidly a number of aspects of the activity of soil microorganisms about which the "soil microbial biomass" perspective has failed to shed any light at all, and which remain largely unresolved to this date. One of the most significant examples in this context is the paradox of soil organic carbon (SOC) mineralization, according to which, in soils with a pH above 5.5, even if 90% of the soil microorganisms are destroyed by $CHCl_3$ fumigation, and the microbial community structure of pre- and post-fumigation populations is vastly different (Domínguez-Mendoza et al., 2014; Chen et al., 2015), SOC mineralization appears unaffected by the fumigation: It continues *at the same rate*, after fumigant removal, once the initial decomposition flush is over (Jenkinson and Powlson, 1976; Wu et al., 1996). As pointed out by Powlson et al. (2017, p.19), "this phenomenon has been known for nearly 60 years but has never been satisfactorily explained, even though $CHCl_3$ fumigation forms the basis for all the widely used methods of measuring soil microbial biomass [...]" To try to come up with an explanation, Kemmitt et al. (2008) proposed a theory, called the Regulatory Gate Hypothesis, which posits formally the abiological transformation of non-bioavailable SOC into bioavailable SOC. The underlying mechanisms causing this transformation are not known, however, and it appears more than likely that to understand them, it will be necessary to gather the kind of detailed microscale information, in particular about microbial habitat properties (Ruamps et al., 2013) and the heterogeneous distribution of SOC, that Alexander (1964) once thought indispensable and now is technically obtainable. Another unanswered question, alluded to by Powlson et al. (2017, p. 35), is related to the fact that soil biomass is commonly observed (based on macroscopic measurements) to have a very low metabolic rate, orders of magnitude lower than that of microorganisms growing exponentially under laboratory conditions, and a very slow turnover rate of about 1.2 years. Yet, overall, it has an ATP concentration and adenylate energy charge (AEC) comparable to those of microorganisms growing exponentially *in vitro*. These conflicting observations have no explanation at present.

One could deduce from this mention by Powlson et al. (2017) of various shortcomings of the soil microbial biomass paradigm that the (perhaps unintended) between-the-lines message of the first chapter of *Microbial Biomass* is that another paradigm shift is needed, not in terms of recognizing that soil biomass has to be included as a component of the total organic matter in soils, which is by now well accepted, but in terms of how soil biomass is described and studied. Other chapters in the book chronicle the fact that this new paradigm shift is in fact already underway. Chapters 3 and 9 (Steenbergh et al., 2017; Stockdale and Murphy, 2017) stress explicitly the need to open up the microbial black box, and they describe several of the spectroscopic and microscopic techniques, like NanoSIMS, Raman microscopy, in-situ hybridization, and single-cell extraction, that major technological advances in the past decade have made available to soil microbiologists to observe *individual* microorganisms in their natural, microscale environments. In his detailed review of modeling efforts, Allison (2017), in Chapter 6, argues that "micron-scale interactions must be considered in macroscale processes," and mentions in that context that recently-developed agent-based models are able to "reveal how social interactions and spatial structure in microbial communities influence biogeochemical processes."

As useful as Jenkinson's perspective may have been at one point in history, half a century ago, when available measurement technologies were too rudimentary to deal quantitatively with the inside of the soil biomass black box, it is clear that recent technological breakthroughs have made the thinking among soil microbiologists evolve in a different direction, and that another change in paradigm is occurring. The chronicling that *Microbial Biomass* provides of this revolution in the making is probably one of the foremost aspects of the book that make it very much worth reading and, in spite of its outrageous price, having in one's library.

AUTHOR CONTRIBUTIONS

The author confirms that he is the sole contributor of this work and that he approved it for publication.

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Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.