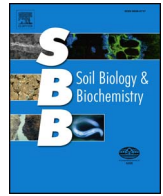




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Citation Classic

A tale of two theories, a chronosequence and a bioindicator of soil quality

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A B S T R A C T

In this Citation Classics commentary, we reflect upon a paper that we published in *Soil Biology & Biochemistry* in 1995 and that provided a critical assessment of the use of the microbial metabolic quotient (qCO_2 or the ratio of microbial respiration to biomass) as a bioindicator of soil quality. This quotient is based on Eugene Odum's 'Theory of Ecosystem Succession' published in 1969 and has been widely used in soil ecology for over 30 years; a higher qCO_2 value is reflective of greater energetic inefficiency of the soil microbial biomass. At the time of our study a strong demand was emerging for easily measured soil quality bioindicators and qCO_2 was an obvious candidate. In our paper we drew on the plant ecological strategy theory of J. Philip Grime by highlighting that, in addition to the two major types of ecosystem identified in Odum's theory ('disturbed' and 'developed'), there is a third type, 'stressed' that is characterized by persistently harsh conditions (e.g., nutrient poor, cold, dry). We measured qCO_2 for soils collected from along the Franz Josef Glacier chronosequence in New Zealand that spans 120,000 years and which includes all three types of ecosystems, going from disturbed to developed to stressed. We found that qCO_2 was least for the developed stage and was similarly high for the disturbed and stressed stages; it was not possible to discriminate between early successional stages characterized by high disturbance and high quality resource inputs from late successional stages characterized by substantial nutrient limitation and poor quality resource inputs. We further reanalyzed data from several publications from which qCO_2 could be calculated and these reinforced our empirical findings. Upon reflecting on our earlier work, we conclude that highly contrasting types of ecosystems that vary in their disturbance regime and stress cannot be arranged to any satisfaction along a unidimensional axis, and that no simple, unidimensional bioindicator (including qCO_2) is capable of adequately summarizing variation of soil quality among ecosystems. However, we also emphasize that despite its limitations as a bioindicator of soil quality, the qCO_2 concept has proven to be highly useful for advancing conceptual understanding of the functioning of the soil microbial community and its contribution to ecosystem processes.

1. Introduction

Over the past three decades there has been much focus on understanding ecosystem 'health', and a key element of this has been an emphasis on the construction of easily measured bioindicators of 'soil quality'. This has been of particular interest in agricultural systems which are focused on maintaining soil fertility and agricultural production (Kibblewhite et al., 2008; Ghani et al., 2003), and in ecological restoration activities which are aimed at the recovery of communities and ecosystem processes impacted by human activities (Kardol and Wardle, 2010). There has been considerable discussion on the value of bioindicators of soil quality, and several commentaries over the past four decades have strongly endorsed the concept (e.g., Sims et al., 1997; Doran and Zeiss, 2000; Karlen et al., 2003; Ritz et al., 2009; Stone et al.,

2016). Furthermore, there has been a recent resurgence of interest in soil quality indicators as governments and policy makers have become more aware of the need to manage soil sustainably and counter soil degradation (FAO, 2015). However, the use of soil quality indicators has also attracted scrutiny (Bastida et al., 2008) and even some significant criticism (Sojka and Upchurch, 1999), on the grounds that many bioindicators are too simplistic to represent the complexity of real ecosystems, and because the link between the bioindicator and the performance of the system (e.g., in terms of soil fertility, sustainable production, or community and ecosystem functioning) is often not apparent.

A landmark advance in understanding soil functioning occurred around 40 years ago through the development of an approach by Jenkinson and Powlson (1976) for the rapid and easy measurement of

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microbial biomass in soils. This (and other related) methodology has now been used in many thousands of studies for illuminating how microbial processes relate to the functioning of terrestrial ecosystems worldwide (Jenkinson and Ladd, 1981; Wardle, 1992; Tate, 2017). While the microbial biomass *per se* has its limitations as a bioindicator (because biomass by itself does not inform on dynamics, turnover or functioning), it has formed the basis of two bioindicators that have enjoyed wide usage. First, the ratio of microbial biomass carbon (C) to organic C gives a measure of the quality of soil organic matter; when quality is higher a greater proportion of C is present in the microbial biomass (Insam and Domsch, 1988; Wardle, 1992). Second, the ratio of soil basal respiration to microbial biomass (hereafter ‘metabolic quotient’ or qCO_2) indicates the inefficiency of the microbial biomass; when the microflora is less efficient a larger proportion of the C that it metabolizes is respired and lost as CO_2 as opposed to taken up by the biomass for tissue maintenance and growth (Anderson and Domsch, 1985).

In this *Soil Biology & Biochemistry* ‘Citation Classic’ commentary, we focus on the second of these indicators, the qCO_2 , with particular reference to our publication on this topic from 23 years ago (Wardle and Ghani, 1995). Specifically, we discuss the theoretical construct for that paper, then describe its development and relevance for understanding the potential of qCO_2 as a bioindicator of soil quality, and finally outline the research directions that have since developed and the broader implications of the work.

2. Theoretical constructs

In our study (Wardle and Ghani, 1995) we drew on two theoretical constructs developed in community and ecosystem ecology. The first of these has its roots in the classic Odum’s Theory of Ecosystem Development (Odum, 1969, 1985). In this theory, succession is regarded not just as a shift in plant community composition over time (which was the prevailing view of succession) but also as a process that involves major shifts in the structure and function of the system, including community energetics, cycling of materials and overall homeostasis. A key element of this theory was the proposition that as succession proceeds and ecosystem development occurs, the ecosystem becomes more energy-efficient and the proportion of C metabolized by organisms that is respired (and thus lost from the ecosystem) should decline. This rationale was applied to soil microbial communities by Anderson and Domsch (1985, 2010), who used the ratio of soil basal respiration to microbial biomass as a measure of microbial efficiency; a microbial community that is less efficient should have a higher rate of respiration per unit biomass. This ratio (i.e., qCO_2) was shown empirically by Insam and Haselwandter (1989) to decline during primary succession over 200 years following glacial retreat in each of two chronosequences, as well as during revegetation, in line with the predictions from Odum’s theory.

Odum’s theory, and the interpretation of qCO_2 based on that theory, recognizes two types of widely contrasting ecosystems: (i) developmental or recently disturbed ecosystem that occur early in succession; and (ii) developed or mature ecosystems that occur later in succession. In our study we drew on a second theoretical construct, which suggests there are actually three broadly contrasting types of ecosystems, based on the plant strategy theory developed for plant ecology by Grime (1977, 1979). Grime’s theory proposed that there are three major plant strategies: (i) ‘ruderal’ (i.e., plants adapted for recently disturbed ecosystems); (ii) ‘competitive’ (i.e., plants adapted for developed ecosystems); and (iii) ‘stress-tolerant’ (i.e., plants adapted for stressed ecosystems, such as nutrient poor, cold, or dry). As such, Grime’s theory is suggestive of three broadly distinct ecosystems, not just two. While unidimensional bioindicators such as qCO_2 can distinguish between disturbed and developed ecosystems, there are serious challenges in using a unidimensional variable to distinguish between three distinct types of ecosystems, especially when they are equally dissimilar. The questions which therefore emerge (and which interested us) are

whether and how unidimensional bioindicators can distinguish among the three types to ecosystems to any level of satisfaction and whether these indicators are useful measures of soil quality and ecosystem performance.

3. Research background and thinking

The research underpinning our study was conducted in the early 1990s when we were both junior research scientists at AgResearch, a New Zealand government research institute that is focused on pastoral agricultural research. Our study was not part of the main research programs that we were funded to work within, but we thought it addressed an interesting topic that merited attention, especially given the growing interest at that time in using easily measured microbial variables as bioindicators of soil quality. Because the study was not expensive or particularly time-consuming to perform, we managed to fit it all around the edges of our core assigned research tasks.

We were interested in how qCO_2 varied across the three types of ecosystems and this required a study system in which these three types were represented. Most chronosequences that had been characterized at the time of our study were comparatively short term (a few hundred years) and therefore contained only the ‘disturbed’ and ‘developed’ stages. However, Odum (1969) noted the possibility of a third stage and asked: ‘*The intriguing question is, do mature ecosystems age, as organisms do? In other words, after a long period of relative stability do ecosystems again develop unbalanced metabolism ...?*’. We both knew through our training in the Department of Soil Science at Lincoln University in New Zealand in the 1980s (DAW took his undergraduate soil science course while at Canterbury University, and AG completed his PhD there) about work by the legendary Professor T. W. (Tom) Walker and his colleagues from that department on a very long term chronosequence that resulted from the progressive retreat of the Franz Josef Glacier (located in the south-west of the South Island of New Zealand) and that spans > 100,000 years (Stevens and Walker, 1970; Walker and Syers, 1976) (Fig. 1). This chronosequence runs for long enough to include not just the ‘disturbed’ and ‘developed’ phases, but also a long subsequent decline or ‘stressed’ phase, in line with the third stage that Odum proposed. This long term decline results from increasing nutrient limitation over millennial timescales due to significant loss of soil phosphorus through weathering and leaching, as well as conversion of the remaining soil phosphorus to increasingly unavailable forms (Walker and Syers, 1976).

We collected soil samples from along this gradient and measured microbial biomass, the ratio of microbial C to total C, and qCO_2 (Fig. 1). We found that the microbial biomass peaked at the intermediate (‘developed’) stages of the chronosequence in parallel with vegetation biomass, while the ratio of microbial C to total C generally declined across the chronosequence, indicative of poorer quality organic matter (and presumably poorer quality litter inputs) as the chronosequence proceeded. Meanwhile, qCO_2 was least for the intermediate (‘developed’) stages and much greater for both the early ‘disturbed’ and late ‘stressed’ stages, and qCO_2 was unable to distinguish between the disturbed and stressed stages (Fig. 1). We concluded that this creates a significant problem with regard to the use of qCO_2 as a bioindicator because similarly high values were obtained for two vastly different types of ecosystems: (i) very early successional ones characterized by heavy disturbance and with high quality resource inputs; and (ii) very late successional ones that have not been subjected to major disturbances for thousands of years and are characterized by substantial nutrient limitation and poor quality litter inputs. This means that, disturbed and stressed conditions promote similar levels of inefficiency of C use by the microbial biomass, but for very different reasons.

The question remained as to whether the results we found were specific to the Franz Josef chronosequence or if were they more generalizable. To test this, we analysed data presented in three previously published papers to show that qCO_2 does not predictably decline during

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