

Mineralization of native soil organic matter is not regulated by the size, activity or composition of the soil microbial biomass—a new perspective

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Abstract

Soil organic matter is extensively humified; some fractions existing for more than 1000 years. The soil microbial biomass is surrounded by about 50 times its mass of soil organic matter, but can only metabolize it very slowly. Paradoxically, even if more than 90% of the soil microbial biomass is killed, the mineralization of soil organic matter proceeds at the same rate as in an unperturbed soil. Here we show that soil organic matter mineralization is independent of microbial biomass size, community structure or specific activity. We suggest that the rate limiting step is governed by abiological processes (which we term the Regulatory Gate hypothesis), which convert non-bioavailable soil organic matter into bioavailable soil organic matter, and cannot be affected by the microbial population. This work challenges one of the long held theories in soil microbiology proposed by Winogradsky, of the existence of autochthonous and zymogenous microbial populations. This has significant implications for our understanding of carbon mineralization in soils and the role of soil micro-organisms in the global carbon cycle. Here we describe experiments designed to determine if the Regulatory Gate operates. We conclude that there is sufficient experimental evidence for it to be offered as a working hypothesis.

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1. Introduction

Humified soil organic matter is a globally important repository of carbon (C), comprising about 1550 Gt (Lal, 2004). The size of the soil organic matter pool is determined by the rate of input of fresh organic matter, the proportion of added C that is humified and the rate of efflux of C via gaseous losses of CO₂ and CH₄, erosion and leaching of dissolved organic C. An improved understanding of these fluxes is vital if we are to increase our awareness of how soil management affects soil fertility (e.g. water holding capacity, nutrient cycling and soil structure) and C sequestration. Currently there is considerable interest in the effects of changes in mineralization rates

on feedbacks within the global carbon cycle (Cox et al., 2000; Freibauer et al., 2004; Lal, 2004).

The C derived from soil organic matter that is used by microbes is either mineralized to CO₂ (and CH₄ in anaerobic soils) or it is put to anabolic use in production of biomass (new or maintenance) or egested as cellular metabolites (e.g. enzyme production). The soil microbial biomass mineralizes humified soil organic matter at a remarkably constant rate over long periods, even when fresh substrate is not supplied (e.g. Joergensen et al., 1990). Soil organic matter is stabilised to varying degrees and by various mechanisms. Its complex, random chemical structure makes it a substrate that does not yield a sufficient return of useful monomers from investment in enzyme synthesis (Sollins et al., 1996; Allison and Vitousek, 2005). It may also be chemically stabilised, via the formation of organo-mineral associations with clay minerals and/or metal oxides (Wiseman and Püttmann, 2005; Eusterhues

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et al., 2003; Schulten and Leinweber, 2000) and physically protected by incorporation into aggregates (Pulleman and Marinissen, 2004). Soil organic matter may be considered as the sum of fractions of varying recalcitrance, ranging from inert to refractory to very labile. The refractory fraction may form 10–60% of soil organic C and may be up to several thousand years old (Falloon and Smith, 2000).

This paper is concerned with the mineralization of soil organic matter, rather than the mineralization of fresh organic inputs. The current understanding is that mineralization of soil organic matter is governed by several concurrent processes: (1) destabilization via oxidation/hydrolysis, desorption and diffusion and (2) the size, community composition and metabolic activity of the microbial biomass (Ekschmitt et al., 2005; Fontaine and Barot, 2005).

In the bulk, non-rhizosphere soil, the soil microbial biomass (biomass) is normally limited by availability of C and/or N (Vance and Chapin, 2001), and nutrient sources must be derived from in-situ sources (the native soil organic matter, microbial turnover) or from soluble substrates leaching from upper horizons. From this point of view, dissolved organic matter is an especially important fraction of the soil organic matter pool. It is thought that substrates must pass through the dissolved phase to reach and pass through microbial membranes (Marschner and Kalbitz, 2003). The dissolved organic C pool is extremely dynamic, with some components of the low molecular weight fraction being at very low concentrations but turning over more than ca. 4000 times annually (Boddy et al., 2007).

Because mineralization is performed by the microbial biomass, it is often assumed that the process is at least partly regulated by its size, specific activity or composition (Marschner and Kalbitz, 2003; Fontaine and Barot, 2005). However, reflection on early work on the fumigation–incubation (FI) method to measure biomass (Jenkinson, 1966; Jenkinson and Powlson, 1976) challenges this. This work demonstrated that soils which were fumigated with chloroform, followed by fumigant removal and aerobic incubation, evolved a flush of CO₂ as the recolonizing population mineralized the fumigant-killed biomass. After around 4 days, once that flush was past, the C mineralization rate returned to the same rate as that in the nonfumigated soil. However, the recolonizing population in the fumigated soil was much smaller than that in the nonfumigated soil. Jenkinson and Powlson (1976) reported that it was around 20% of the original population 53 days after fumigation, while Lin and Brookes (1996) measured 10–40% of the initial nonfumigated value 10 days after fumigation. During the initial 0–10-day period after the flush, the biomass is only a few percent of the initial pre-fumigation value. The biomass-specific respiration rate was therefore very much higher in the fumigated than nonfumigated soils. Furthermore, chloroform fumigation does not measurably alter the mineralization, or extractability, of other, non-biomass,

soil organic matter fractions (Jenkinson and Powlson, 1976).

It is remarkable therefore that the rate of mineralization of humified soil organic matter is the same in fumigated and nonfumigated soils, despite the very much smaller recolonizing population in the fumigated soil and its very different specific activity and community structure (Zelles et al., 1997; Degens, 1998). The significance of this has hitherto been overlooked.

How can this small, structurally distinct population mineralize the soil organic matter pool at the same rate as the large, complex community in nonfumigated soil? The long established paradigm is that a population of autochthonous micro-organisms metabolizes the recalcitrant fraction of organic matter, reproducing slowly, whilst a zymogenous population metabolizes labile organic matter, only growing when fresh substrate becomes available and becoming dormant when a fresh substrate becomes exhausted (Winogradsky, 1924). A useful discussion of the terminology is given by Langer et al. (2004). However, if there is a discrete fraction of the microbial biomass for which it is energetically viable to use humified soil organic matter, albeit at an exceedingly slow rate, why have the autochthonous micro-organisms not evolved better strategies to utilize it and so better exploit this niche?

Freeman et al. (2001) demonstrated that in waterlogged soil the limitation of oxygen prevented the action of polyphenol oxidase which acted as a ‘latch’ on the mineralization of organic matter. When this limitation was removed, rates of organic matter mineralization increased. However, the present paper is concerned with the mineralization of soil organic matter in freely draining mineral soils.

We propose the ‘Regulatory Gate’ hypothesis to explain the observed phenomenon. This hypothesis considers that the mineralization of soil organic matter is a two-stage process. Firstly, non-bioavailable humified soil organic matter is altered by an abiological process(es) to become bioavailable organic matter. This process is independent of, and cannot be altered by, microbial activity. The second step is the mineralization of this trickle of, now bioavailable, soil organic matter by the soil microbial biomass. Possible mechanisms involved in the conversion of non-biologically available to biologically available soil organic matter may include:

- (1) chemical oxidation or hydrolysis,
- (2) diffusion from inaccessible soil pores or aggregates,
- (3) desorption from the solid phase,
- (4) action of extracellular stabilised enzymes.

Here we report experiments designed to test the Regulatory Gate hypothesis. Experiment 1 examined the microbial community size, structure and activity for 62 days following fumigation. Experiment 2 determined whether bioavailable C accumulated in moist soil in the absence of a living microbial biomass. In Experiment 3 we

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