Soil Biology & Biochemistry 42 (2010) 1385–1395

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Review

Considering fungal:bacterial dominance in soils – Methods, controls, and ecosystem implications

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ARTICLE INFO

Article history:
Received 6 December 2009
Received in revised form
7 May 2010
Accepted 11 May 2010
Available online 26 May 2010

Keywords:
Fungal:bacterial
Carbon sequestration
Decomposition
Carbon:nitrogen
Fungi
Bacteria

ABSTRACT

An expectation in soil ecology is that a microbial communities' fungal:bacterial dominance indicates both its response to environmental change and its impact on ecosystem function. We review a selection of the increasing body of literature on this subject and assess the relevance of its expectations by examining the methods used to determine, the impact of environmental factors on, and the expected ecosystem consequences of fungal:bacterial dominance. Considering methods, we observe that fungal:bacterial dominance is contingent on the actual measure used to estimate it. This has not been carefully considered; fungal:bacterial dominance of growth, biomass, and residue indicate different, and not directly relatable aspects, of the microbial community's influence on soil functioning. Considering relationships to environmental factors, we found that shifts in fungal:bacterial dominance were not always in line with the general expectation, in many instances even being opposite to them. This is likely because the traits expected to differentiate bacteria from fungi are often not distinct. Considering the impact of fungal:bacterial dominance on ecosystem function, we similarly found that expectations were not always upheld and this too could be due to trait overlap between these two groups. We explore many of the potential reasons why expectations related to fungal:bacterial dominance were not met, highlighting areas where future research, especially furthering a basic understanding of the ecology of bacteria and fungi, is needed.

1. Introduction

Soil microbial communities are an integral component of many ecosystem processes (Bedard and Knowles, 1989; Zak et al., 2006; Jackson et al., 2007). Because of this, the role of these communities has been studied widely (Waksman et al., 1928; Jackson et al., 2007). Although seemingly straightforward, actually gaining a detailed understanding of these communities regarding their relationship to environmental factors and ecosystem function, and developing methods to accurately assess them has often proven difficult (Barns et al., 1999). The principal contributor to these difficulties is the opaque nature of the soil environment, which makes direct observation of soil communities nearly, if not totally, impossible. Another reason is the high diversity of these communities (Torsvik et al., 2002; Fierer et al., 2007b).

The dominant approach to understanding soil microbial communities has been to simplify the community by dividing it into ecologically meaningful groups (Koch, 2001). Early approaches achieved this via culturing techniques. This method provided the means of functionally classifying microorganisms by selective culturing media, for example distinguishing between cellulose degrading and lignin degrading organisms (Alexander, 1977). Another distinction made within the microbial community is based on the idea of copiotrophs versus oligotrophs where copiotrophs are organisms that thrive under high resource conditions and oligotrophs thrive under low resource conditions (Poindexter, 1981; Koch, 2001; Fierer et al., 2007a). Similar to this is Winogradsky's idea of allochthonous versus zymogenous microbial biomass (Winogradsky, 1924) and r- versus K-selected organisms (Fontaine et al., 2003; Langer et al., 2004; Fierer et al., 2007a). Unfortunately these dichotomous definitions are either incalculable in situ or are determined post-hoc rendering them circular.

One categorization of microorganisms in soil that does not suffer from many of the above shortcomings and that has been widely employed is the division between the major decomposer groups: fungi and bacteria (Waksman et al., 1928; Alexander,

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doi:10.1016/j.soilbio.2010.05.007

1977). It is possible that the original rationale for this separation was pragmatism derived from the early culturing techniques and subsequent staining microscopy employed to study them. Nonetheless, this general division has been maintained in soil ecology and method developments over recent decades (see Section 2.1) have enabled it to continue. This crude and potentially historically contingent approach has provided insight into soil systems leading to concepts that are widely used and discussed in soil ecology today and that are likely to increase in the future (Fig. 1).

The purpose of this review is to examine recent developments with regards to distinctions made between fungal and bacterial dominance. First, in Section 2.1, we briefly discuss some current and prominent methods employed to assess fungal:bacterial dominance. In Section 2.2, we examine some of the major environmental factors that are likely to lead to differences in fungal:bacterial dominance. In Section 2.3, we discuss the relationship between fungal:bacterial dominance and two major ecosystem processes: carbon (C) sequestration and litter decomposition. Finally, we conclude by examining our current understanding of fungal:bacterial dominance and highlight areas where greater knowledge may lead to advances in this concept.

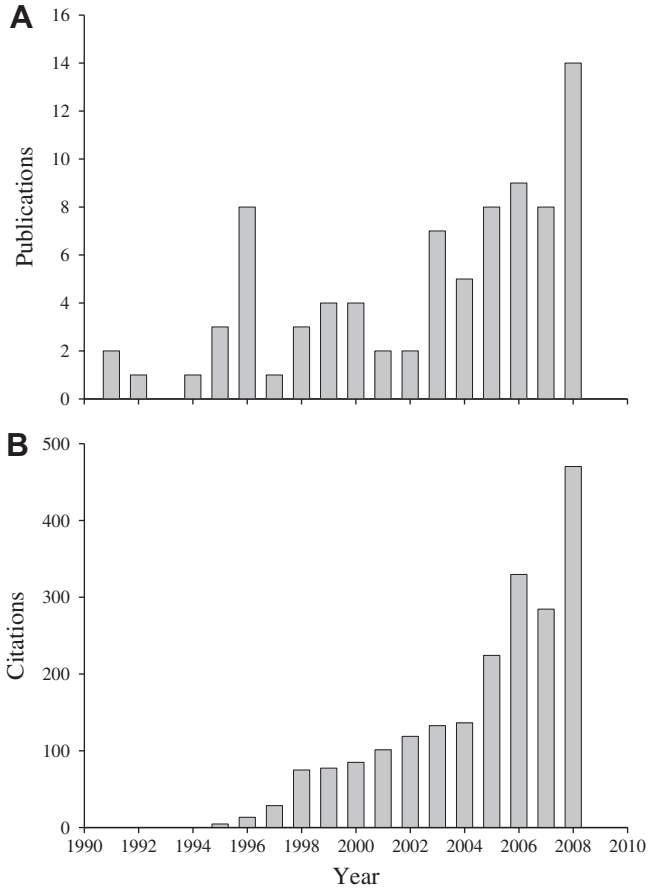

Fig. 1. The prevalence of fungal:bacterial dominance in the literature today showing (A) the number of publications found using the search terms "fungal:bacterial" and "soil" and (B) the number of citations referring to those same publications from 1991 to 2008. Both works specifically related to fungal:bacterial dominance and citations of these works have increased during this period of time. In fact, extrapolating to the year 2015 suggests that articles related to fungal:bacterial dominance will increase ~15 fold and citations of these articles will increase ~8 fold compared to 2008 values. The number of publications and citations were identified using Web of Science. See Supplementary material for the list of articles used in this figure.

2. Review

2.1. Techniques to measure fungal:bacterial dominance

Early techniques used to study soil microorganisms, primarily culture-based, will not be addressed in this review, and instead we will focus on some current and widely applied methods. An array of techniques have been developed that assess fungal:bacterial dominance (Joergensen and Wichern, 2008; Supplementary Table 1). For example, Frostegård and Bååth (1996) used phospholipid fatty acids (PLFAs) that were specific to bacteria and fungi to estimate the biomass of each group in soil. Alternatively, Anderson and Domsch (1973) used selective inhibition with fungal or bacterial specific antibiotics to similarly estimate the substrate induced respiration or SIR biomass of each group (although see Rousk et al., 2009b).

Selective inhibition, PLFA techniques, ergosterol to distinguish fungi from the total microbial biomass, direct observation (*i.e.* microscopy), and the use of fungal/bacterial cell wall derived indicators (*e.g.* chitin and muramic acid) or residues, were recently reviewed by Joergensen and Wichern (2008). They found that across biomes these methods were generally comparable. However, across coarse spatial scales, different measures of whole microbial biomass are often correlated (Wardle and Ghani, 1995) which is not always true at finer scales (*i.e.* within one soil type). This is potentially true for estimates of fungal:bacterial dominance. Another important consideration, particularly for PLFA and ergosterol markers but other measures as well, is the potential confounding inclusion of mycorrhiza in the fungal estimate (Joergensen and Wichern, 2008; also see Section 2.2.2 where the discussion on the mycorrhizal influence on the fungal:bacterial dominance is continued). These biomarkers are also variable within the target groups that make reliable conversion factors hard to obtain. For instance, the concentration of ergosterol in fungal tissue varies between species (Joergensen, 2000; Ruzicka et al., 2000), and there are even a few fungi that lack the lipid [*e.g.* some Zygomycota (Weete and Gandhi, 1999)].

Methods not discussed in Joergensen and Wichern (2008) included DNA and growth-based measures. DNA-based approaches are increasingly being used to measure fungal:bacterial dominance. One approach is quantitative PCR (qPCR). It uses the accumulation of a florescent reporter molecule during the PCR reaction coupled with primers specific to either bacteria or fungi (that typically target the 16S or 18S rRNA gene segments, respectively) to determine fungal:bacterial dominance (Raeymaekers, 2000; Fierer et al., 2005). qPCR represents both a rapid and quantifiable approach to assess fungal:bacterial dominance in soils and is relatively inexpensive when compared to other molecular techniques (Fierer et al., 2005). However, caveats are associated with this technique. Foremost, is that fungal:bacterial dominance, determined via qPCR, may not indicate the abundances of these groups in soil especially on a per biomass basis. Reasons for this include the fact that fungi and bacteria differ physiologically. For instance, fungal cells may include many or no nuclei leading to an over or underestimation of fungal abundance, DNA extraction efficiencies may differ between these two groups, the amplification of genes may not be consistent across all taxa, and multiple copies of the same gene may be found within a single individual (Klappenbach et al., 2000; Martin-Laurent et al., 2001; Smith and Osborn, 2009). Additionally, because DNA is present in both active and inactive cells it may not necessarily be related to a given ecosystem process or response to environmental change (Nocker and Camper, 2009). Fungal:bacterial dominance determined via RNA based or even proteomic approaches may ultimately prove more informative when assessing relationships to environmental