Soil Biology & Biochemistry xxx (2015) 1–15

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Review paper

Microbial hotspots and hot moments in soil: Concept & review

Q3 Yakov Kuzyakov [a, c, d, *], Evgenia Blagodatskaya [a, b]

[a] *Dept. of Soil Science of Temperate Ecosystems, University of Göttingen, Germany*
[b] *Institute of Physicochemical and Biological Problems in Soil Science, Russian Academy of Sciences, Pushchino, Russia*
[c] *Dept. of Agricultural Soil Science, University of Göttingen, Germany*
[d] *Institute of Environmental Sciences, Kazan Federal University, Kazan, Russia*

ARTICLE INFO

Article history:
Received 5 September 2014
Received in revised form
21 January 2015
Accepted 22 January 2015
Available online xxx

Keywords:
C and N cycles
Microbial activities
Priming effects
Microbial successions
Subsoil processes
Active microorganisms
Microbiota-habitat interactions

ABSTRACT

Soils are the most heterogeneous parts of the biosphere, with an extremely high differentiation of properties and processes within nano-to macroscales. The spatial and temporal heterogeneity of input of labile organics by plants creates microbial hotspots over short periods of time – the hot moments. We define microbial hotspots as small soil volumes with much faster process rates and much more intensive interactions compared to the average soil conditions. Such hotspots are found in the rhizosphere, detritusphere, biopores (including drilosphere) and on aggregate surfaces, but hotspots are frequently of mixed origin. Hot moments are short-term events or sequences of events inducing accelerated process rates as compared to the average rates. Thus, *hotspots and hot moments are defined by dynamic characteristics, i.e. by process rates*.

For this hotspot concept we extensively reviewed and examined the localization and size of hotspots, spatial distribution and visualization approaches, transport of labile C to and from hotspots, lifetime and process intensities, with a special focus on process rates and microbial activities. The fraction of active microorganisms in hotspots is 2–20 times higher than in the bulk soil, and their specific activities (i.e. respiration, microbial growth, mineralization potential, enzyme activities, RNA/DNA ratio) may also be much higher. The duration of hot moments in the rhizosphere is limited and is controlled by the length of the input of labile organics. It can last a few hours up to a few days. In the detritusphere, however, the duration of hot moments is regulated by the output – by decomposition rates of litter – and lasts for weeks and months. Hot moments induce succession in microbial communities and intense intra- and interspecific competition affecting C use efficiency, microbial growth and turnover. The faster turnover and lower C use efficiency in hotspots counterbalances the high C inputs, leading to the absence of strong increases in C stocks. Consequently, the *intensification of fluxes is much stronger than the increase of pools*. Maintenance of stoichiometric ratios by accelerated microbial growth in hotspots requires additional nutrients (e.g. N and P), causing their microbial mining from soil organic matter, i.e. priming effects. Consequently, *priming effects are localized in microbial hotspots and are consequences of hot moments*. We estimated the contribution of the hotspots to the whole soil profile and suggested that, irrespective of their volume, the hotspots are mainly responsible for the ecologically relevant processes in soil. By this review, we raised the importance of concepts and ecological theory of distribution and functioning of microorganisms in soil.

© 2015 Published by Elsevier Ltd.

UNCORRECTED PROOF

1. Introduction: definitions and the most important hotspots

1.1. Definitions and concept

The most ecologically relevant biogeochemical processes in soils are microbially mediated. Despite the enormous amount of microbial cells, i.e. 10^7–10^{12} in one gram soil (Watt et al., 2006), their localization is restricted to very small microhabitats comprising much less than 1% of total soil volume (Young et al., 2008) and globally covering merely 10^{-6} % of the soil surface area (Young and Crawford, 2004). Many soil microorganisms tend to form colonies and biofilms and tend to aggregate (Hodge et al., 1998; Ekschmitt et al., 2005), forming microbial hotspots. Consequently, ecologically relevant biogeochemical processes mainly occur in the small volume of soil **hotspots**. We define microbial **hotspots** as small soil volumes with much faster process rates and

* Corresponding author. Dept. of Soil Science of Temperate Ecosystems, University of Göttingen, Germany.
E-mail address: kuzyakov@gwdg.de (Y. Kuzyakov).

http://dx.doi.org/10.1016/j.soilbio.2015.01.025
0038-0717/© 2015 Published by Elsevier Ltd.

Please cite this article in press as: Kuzyakov, Y., Blagodatskaya, E., Microbial hotspots and hot moments in soil: Concept & review, Soil Biology & Biochemistry (2015), http://dx.doi.org/10.1016/j.soilbio.2015.01.025

much more intensive interactions (between pools) compared to the average soil conditions (Fig. 1) (Kuzyakov, 2009, 2010). As microbial activity is limited by various environmental factors and especially by carbon (C) availability (Hodge et al., 2000), microorganisms in soil are mainly in a dormant state (Blagodatskaya and Kuzyakov, 2013). They become active during short hot moments after the limitations are removed. Accordingly, we define microbial **hot moments** as short-term events or sequences of events that accelerate microbial processes as compared to the average rates. Thus, hot moments occur in or lead to the formation of hotspots, but the hotspots do not necessarily disappear at the end of hot moments and may maintain some microbial activity parameters at high level over lengthier periods even after substrate is degraded (Blagodatskaya and Kuzyakov, 2013). *We therefore define the hotspots and hot moments based on dynamic properties, specifically the intensity of processes, i.e. by process rates*, not by the concentration of the substances or any other static properties. Such definitions underline the *dynamic nature of hotspots and hot moments*. These definitions consider the heterogeneity in distribution of locations and the periods of maximal activity of microorganisms in space and time.

Note that previous definitions of hotspots and hot moments were focused mainly on abiotic fluxes (rainfall or erosion events) on much larger scales, e.g. landscape (McClain et al., 2003; Vidon et al., 2010; Leon et al., 2014). The heterogeneity of soil properties on the meso- and macroscales have been frequently described and analyzed statistically earlier (Parkin, 1993; Webster, 2000; Heuvelink and Webster, 2001). However, meso- and macroscales and the related previous definitions of hotspots and hot moments were not focused on microbial processes and were not applicable on the scales from μm to m - the scales relevant for microbial activities and functions at the level of aggregates up to soil profile. Therefore, new concept and definition of hotspots and hot moments relevant for microbial processes is necessary. This review is focused on the spatial and temporal scales comparable with the size and life periods of microorganisms in soil.

The hotspots and hot moments are relevant not only from the perspective of organic matter availability and C limitation, but also from the perspective of other specific factors limiting microbial activity or process rates under particular conditions, including soil moisture, oxygen availability, N excess. This affects many processes such as denitrification, methanogenesis (see below), nitrification, or weathering. Localized input of high N excess (e.g. fertilizer grains or urine of animals) triggers N turnover including strong nitrification (Strong et al., 1997) and denitrification. Therefore, the hotspots and hot moments are not confined to the input of labile C (described below) but have a much bigger impact and broader perspective involving the removal of any limitations of microbial processes.

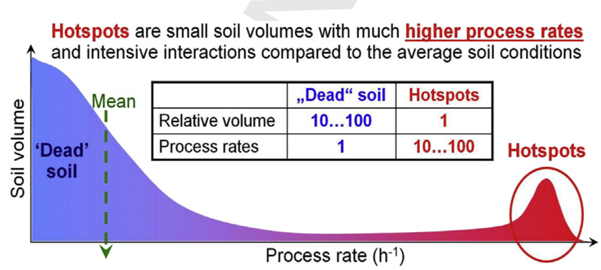

Fig. 1. Concept of microbial hotspots in soil: Hotspots are small soil volumes with much higher process rates and intensive interactions compared to the average soil conditions. The Table inset represents the relative volume and process rates in the hotspots and bulk soil. "Mean" represents the weighted average process rates by soil mixing.

The simultaneous occurrence of numerous hotspots in microhabitats cumulatively affects the dynamics of pools and fluxes and is therefore relevant at higher scales, including the ecosystem scale. The importance of microbial hotspots at the micro-scale level is therefore determined by their relevance to the functions at the higher scales (Blagodatsky and Smith, 2012). Thus, abundant hotspots within a soil volume transforms the environment and extends the hotspots to the hotspheres (Beare et al., 1995) such as rhizosphere or detritusphere, with a high impact at the macroscale. The mechanistic understanding of soil functioning at profile, ecosystem and landscape levels is impossible without quantifying and localizing the hotspots, as well as identifying their origin and formation, their spatial and temporal organization, processes and interactions, along with critical thresholds of intensities necessary for functions at higher scales.

1.2. The most important microbial hotspots in soil

Microbial activity in all soils is limited by labile C (easily available organics) and energy (Blagodatsky et al., 1998; Hodge et al., 2000; Schimel and Weintraub, 2003). Consequently, removing this limitation – the input of labile C – boosts the abundance and activity of microorganisms in soil and produces microbial hotspots. Based on the sources of high input (not the content!) of labile organics and their localization in soil, we emphasize the following hotspot groups (Fig. 2, Table 1):

- Rhizosphere: input of labile root exudates and other less decomposable rhizodeposits at various soil depths (Jones et al., 2004; Hinsinger et al., 2009).
- Detritusphere: input of mainly recalcitrant highly polymeric (Kogel-Knabner, 2002) (but also some labile, low molecular weight) organics as litter, mainly on the mineral soil surface, and upon root death at various depths.
- Biopores: a) input of labile and recalcitrant organics passed through and processed within the hindgut of earthworms (drilosphere) and other soil organisms (mainly invertebrates) at various depths or/and b) formed by deep-growing roots and maintained by roots and burrowing animals (Tiunov and Scheu, 1999, 2004; Brown et al., 2000; Schrader et al., 2007). Also animal feces in soil with the input of labile and recalcitrant organics can be grouped to the biopores.
- Aggregate surfaces: input of organics leached from the detritusphere (e.g. O horizon), from the C rich Ah horizon and partly from the rhizosphere (Kaiser and Kalbitz, 2012). This hotspot group is especially important in deep soil horizons (Fig. 2).

Other locations in the soil have sometimes been mentioned as spots of microbial activities: biochar-sphere (Lehmann et al., 2011), porosphere, drilosphere, guts of soil animals (Mohr and Tebbe, 2006) etc. These locations, however, can be included in one of the above-mentioned hotspots (porosphere consists of biopores and aggregate surfaces, biochar-sphere is partly related to the detritusphere), are of secondary importance and will not be reviewed here separately.

The distribution and importance of the four hotspot groups depend on the ecosystem and soil depth (Fig. 2). Above the mineral soil surface, the detritusphere is the most important hotspot. The density of the rhizosphere is especially high in the top of the Ah (or Ap) horizon. The relevance of biopores and aggregate surfaces for C input in topsoil is marginal compared to the effects of the detritusphere and rhizosphere, but their importance strongly increases with depth (Kautz et al., 2014). The three first hotspots – detritusphere, rhizosphere and biopores – have a *biotic origin*. Only aggregate surfaces have a mainly *abiotic origin*, especially in the

Please cite this article in press as: Kuzyakov, Y., Blagodatskaya, E., Microbial hotspots and hot moments in soil: Concept & review, Soil Biology & Biochemistry (2015), http://dx.doi.org/10.1016/j.soilbio.2015.01.025

Download English Version:

https://daneshyari.com/en/article/8364335

Download Persian Version:

https://daneshyari.com/article/8364335

Daneshyari.com