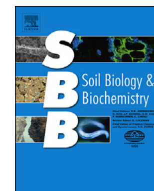
Soil Biology & Biochemistry 96 (2016) 229–237

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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



Rhizosphere shape of lentil and maize: Spatial distribution of enzyme activities

Bahar S. Razavi [a, *], Mohsen Zarebanadkouki [b], Evgenia Blagodatskaya [c, d], Yakov Kuzyakov [a, c]

[a] *Department of Agricultural Soil Science, University of Göttingen, Göttingen, Germany*
[b] *Division of Soil Hydrology, University of Göttingen, Göttingen, Germany*
[c] *Department of Soil Science of Temperate Ecosystems, University of Göttingen, Göttingen, Germany*
[d] *Institute of Physicochemical and Biological Problems in Soil Science, Pushchino, Russia*

A R T I C L E I N F O

Article history:
Received 7 January 2016
Received in revised form
23 February 2016
Accepted 29 February 2016
Available online 10 March 2016

Keywords:
Rhizosphere extent
Spatial pattern
Enzyme distribution
Soil zymography
Lentil and maize

A B S T R A C T

The rhizosphere, the small soil volume that surrounds and is influenced by plant roots, is one of the most dynamic biological interfaces on Earth. Enzymes, produced by both roots and microorganisms, are the main biological drivers of SOM decomposition. *In situ* soil zymography was applied to test hypotheses that 1) the spatial pattern of rhizosphere activity is enzyme-specific and 2) the distribution of enzyme activity along the roots is dependent on root system and plant species. Lentil (*Lens culinaris*) and maize (*Zea mays* L.), two species with contrasting root physiology, were chosen to test their effects on spatial distribution of activities of β-glucosidase, cellobiohydrolase, leucine-aminopeptidase and phosphatase.

The extent of the rhizosphere for each enzyme and plant species was estimated as a function of distance from the root. For the first time, we demonstrated plant-specific patterns of exoenzyme distribution: these were uniform along the lentil roots, whereas in the rhizosphere of maize, the enzyme activities were higher at the apical or proximal root parts. We conclude that the shape and extent of the rhizosphere for enzyme activities is plant species specific and varies due to different rhizosphere processes (e.g. root exudation) and functions (e.g. nutrient mobilization abilities). The extension of enzyme activity into the rhizosphere soil was minimal (1 mm) for enzymes responsible for the C cycle and maximal (3.5 mm) for enzymes of the phosphorus cycle. This should be considered in assessments and modeling of rhizosphere extension and the corresponding effects on soil properties and functions.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

The rhizosphere, as a soil volume surrounding living roots, represents one of the most dynamic habitats and interfaces on Earth (Hinsinger et al., 2009; Kuzyakov and Blagodatskaya, 2015). The rhizosphere effect is typically most intense at the root surface (termed the rhizoplane) and extends several millimeters out into the soil (Dazzo and Gantner, 2012). The spatial distribution of the rhizosphere is a dynamic function of the soil matrix and plant properties, including root morphology, microbial colonization, nutrient uptake, root exudation and rhizodeposition (Neumann and Römheld, 2002; Dazzo and Gantner, 2012). Activity of microorganisms in the rhizosphere is strongly affected by root exudates and other rhizodeposits (Parkin, 1993; Högberg and Read, 2006; Oburger et al., 2014). Plants release about one third of their photosynthetic products in the form of rhizodeposits into the soil (Kuzyakov et al., 2003) providing the basis for the establishment of plant-microbial interactions (Bais et al., 2006). Rhizodeposits include root cap and border cell loss, death and lysis of root cells, gaseous losses, passive and active release of solutes (root exudates) and gelatinous material at the surface of roots (mucigel) (Curl and Truelove, 1986; Hinsinger et al., 2009; Jones et al., 2009). Root exudation stimulates microbial activity (Kuzyakov and Domanski, 2000; Hinsinger et al., 2009), production of extracellular enzymes (Asmar et al., 1994) and, thus, SOM decomposition (Cheng and Coleman, 1990). However, the higher enzyme activity of the rhizosphere than of root-free soil depends not only on microbial activity but also on the direct release of enzymes by roots or by lysis of root cells (Jones et al., 2009; Marinari et al., 2014).

* Corresponding author.
E-mail address: brazavi@gwdg.de (B.S. Razavi).

http://dx.doi.org/10.1016/j.soilbio.2016.02.020
0038-0717/© 2016 Elsevier Ltd. All rights reserved.

The plant plays an important role in selecting, enriching and stimulating the functional groups of microorganisms depending on its root physiology and exudate constituents (Asmar et al., 1994; Fontaine et al., 2007; Blagodatskaya et al., 2009). Thus, root exudates affect microbial community composition, and their corresponding ability to utilize various C and nutrient sources (Kuzyakov, 2002; Frank and Groffman, 2009). Microbial diversity differs between the rhizospheres of plant species (Kowalchuk et al., 2002; Valentinuzzi et al., 2015), cultivars (Averill and Finzi, 2013) or even along the roots (Schmidt and Eickhorst, 2014) and over the course of root development (Remenant et al., 2009; Philippot et al., 2013; Schmidt and Eickhorst, 2014). Similarly, exoenzyme activity is a function of the morphological and physiological attributes of microbial and plant species and root type (Grierson and Adams, 2000). Enzymes, produced by both roots and microbes, are the main biological drivers of SOM decomposition (Nannipieri et al., 2007). Enzyme activity in the rhizosphere reflects plant-microbial interactions and is a sensitive indicator for changes in microbial community composition, activity and function (Baldrian, 2009; Nannipieri et al., 2012).

The exoenzyme activities of plant species may vary, depending on root morphology, rhizodeposition, and interactions with microorganisms (Grierson and Adams, 2000). However, a clear understanding of the variation and distribution along and around the roots still is lacking. Furthermore, it is not clear whether the enzyme activities follow the patterns of root exudation (mainly concentrated at the root tips) (Pausch and Kuzyakov, 2011), or rhizodeposition along the root (Neumann and Römheld, 2000), or whether it is mainly dependent on the nutrient uptake strategy of the plant. For the latter, both 1) nutrient acquisition solely at the root tip and 2) along the whole root length have been proposed (Schnepf et al., 2008; Hinsinger et al., 2011). Such specific patterns have not yet been analyzed or discussed for the spatial distributions of enzymes in the rhizosphere.

Due to complex microbial community structures and diversity, the evaluation of enzyme activities in the rhizosphere requires consideration of the spatial variability along and radially outward from the roots (Pinton et al., 2001). This calls for studies on the spatial distribution of rhizosphere enzymes in undisturbed samples (Mackie et al., 2014; Kuzyakov and Blagodatskaya, 2015). The spatial distributions of enzyme activities in soil have been investigated by destructive methods for different root zones and root proximities (Tarafdar and Jungk, 1987; Kandeler et al., 2002). However, these approaches only provide one-dimensional distributions (Tarafdar and Jungk, 1987; Gahoonia and Nielsen, 1991; Marinari et al., 2014). Consequently, our knowledge about rhizosphere enzyme activities remains limited. The development of *in situ* and non-invasive techniques for measurement of root enzyme activities could alleviate these difficulties. Visual approaches and advanced analytical tools such as functional gene probes (Naseby and Lynch, 1998), histochemical techniques (Shaykh and Roberts, 1974; Gahan, 1984; Joner et al., 2000), electron microscopy of soil sections (Ladd et al., 1996), nano-sensors (Rodríguez-Lorenzo et al., 2012), root window-based approaches (Dinkelaker et al., 1997; Grierson and Comerford, 2000; Dong et al., 2007), and zymography (Spohn et al., 2013a) have opened new avenues to reveal the origin, location and distribution of enzyme activities in soil.

Zymography, a non-destructive *in situ* technique for two-dimensional imaging, now offers an opportunity for visualization of enzyme activities -spatial and temporal- in soil and in the rhizosphere (Spohn and Kuzyakov, 2013, 2014; Vandooren et al., 2013). We applied *in situ* soil zymography by placing substrate-saturated membranes in direct contact with roots and soil (Dinkelaker et al., 1997; Grierson and Comerford, 2000; Dong et al., 2007). We used this technique to test the hypothesis that spatial patterns of activity of various enzymes vary along the root and depend on the plant species. To cover a broad range of functions, we studied the spatial distribution of enzymes involved in decomposing soil organic materials: cellulose (e.g. β-glucosidase and cellobiohydrolase which are commonly measured as enzymes responsible for consecutive stages of cellulose degradation); proteins (e.g. leucine aminopeptidase, which hydrolysis L-peptide bonds) and phosphorous-containing organic compounds (e.g. acid phosphatase, which catalyzes the hydrolysis of organic P compounds to phosphate esters), (Eivazi and Tabatabai, 1988; Asmar et al., 1994). Lentil (*Lens culinaris*) and maize (*Zea mays* L.), species with contrasting physiology and root morphology, were chosen to test their effects on enzyme activity distribution. The lentil, a member of the Fabaceae, was selected as a plant with a tap-root system and is a nitrogen-fixing legume crop (Erskin et al., 2009, 2011). Maize was selected because of its fibrous root system and is an important non-legume crop. Both plants are very important agricultural crops for food and fodder production and can be grown on a broad range of soils.

We aimed at quantitative imaging of enzyme activities in soil as a function of distance along and outward from the root to clarify 1) whether spatial distributions of enzyme activity show enzyme-specific patterns along the root, 2) whether enzyme activity is associated mainly with root tips, and 3) to estimate the extent of the rhizosphere for each enzyme and plant species as a radial distance from the root.

2. Materials and methods

2.1. Sample preparation

Soil samples were taken from the top 10 cm of the Ap horizon of an arable loamy Haplic Luvisol, located on a terrace plain of the river Leine in the north-west of Göttingen, Germany. The soil consisted of 7% sand, 87% silt, 6% clay, with a bulk density of 1.4 g cm^{-3}, a water content of 30% at field capacity, a pH of 6.5, total carbon of 12.6 g C kg^{-1}, and total nitrogen of 1.3 g N kg^{-1} (Kramer et al., 2012; Pausch et al., 2013).

We grew sixteen maize (*Z. mays*) and sixteen lentil (*L. culinaris*) plants, each in a separate rhizobox with inner dimensions of 12.3 × 12.5 × 2.3 cm. The rhizoboxes were placed horizontally with one side open (like a door) and then soil was slowly and continuously poured into the rhizoboxes through a 2 mm sieve to achieve a uniform soil packing and to avoid soil layering. The open side was then closed, the samples were turned vertically, and they were gently shaken to achieve a stable soil packing (Carminati, 2013). Maize and lentil seeds were germinated on filter paper for 72 h. Then one seedling was planted in each rhizobox at a depth of 5 mm. During 3 weeks of growth, the rhizoboxes were kept inclined at an angle of 50° so that the roots grew at the vicinity of the lower wall of the rhizobox due to gravitropis. The samples were kept in a climate chamber with a controlled temperature of 20 ± 1 °C and a daily light period of 16 h with photosynthetically active radiation intensity of 300 μmol m^{-2} s^{-1}. During the growth period, the soil water content was maintained at 60% of the water holding capacity by irrigating the soil from the bottom with distilled water.

2.2. Soil zymography and imaging procedure

After cultivating maize and lentil plants for 3 weeks, zymography was applied as an *in situ* technique to study the spatial distribution of exoenzymes around the roots. We followed the protocol proposed by Spohn and Kuzyakov (2013) with slight modifications, and in combination with the root-window approach (Dong et al., 2007). Visualization of enzyme activities consisted of using membranes saturated with 4-methylumbelliferone (MUF)-

Download English Version:

https://daneshyari.com/en/article/2024366

Download Persian Version:

https://daneshyari.com/article/2024366

Daneshyari.com