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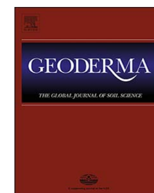

Effects of maize roots on aggregate stability and enzyme activities in soil

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ABSTRACT

Soil aggregation and microbial activities within the aggregates are important factors regulating soil carbon (C) turnover. A reliable and sensitive proxy for microbial activity is activity of extracellular enzymes (EEA). In the present study, effects of soil aggregates on EEA were investigated under three maize plant densities (Low, Normal, and High). Bulk soil was fractionated into three aggregate size classes (> 2000 μm large macroaggregates; 2000–250 μm small macroaggregates; < 250 μm microaggregates) by optimal-moisture sieving. Microbial biomass and EEA (β-1,4-glucosidase (BG), β-1,4-*N*-acetylglucosaminidase (NAG), L-leucine aminopeptidase (LAP) and acid phosphatase (acP)) catalyzing soil organic matter (SOM) decomposition were measured in rooted soil of maize and soil from bare fallow. Microbial biomass C (C_{mic}) decreased with decreasing aggregate size classes. Potential and specific EEA (per unit of C_{mic}) increased from macro- to microaggregates. In comparison with bare fallow soil, specific EEA of microaggregates in rooted soil was higher by up to 73%, 31%, 26%, and 92% for BG, NAG, acP and LAP, respectively. Moreover, high plant density decreased macroaggregates by 9% compared to bare fallow. Enhanced EEA in three aggregate size classes demonstrated activation of microorganisms by roots. Strong EEA in microaggregates can be explained by microaggregates' localization within the soil. Originally adhering to surfaces of macroaggregates, microaggregates were preferentially exposed to C substrates and nutrients, thereby promoting microbial activity.

1. Introduction

Intensive agriculture often leads to decreases in soil carbon (C) stocks and reduces the quality of soil organic matter (SOM) (Paz-Ferreiro and Fu, 2016). The alterations to soil C stocks could have further impacts on the global C cycle (Nie et al., 2014). Soil microorganisms are one of the important biotic drivers regulating the soil C cycle. In terrestrial ecosystems, microbially mediated SOM decomposition constitutes a major part of soil C losses along with abiotic factors (Kaiser et al., 2010). Therefore, even minor changes in microbial decomposition of SOM due to intense agricultural practices may substantially impact the global climate via carbon dioxide (CO_2) efflux to the atmosphere.

Extracellular enzyme activities (EEA) are good indicators of microbially mediated SOM decomposition and are highly sensitive to environmental changes (Burns et al., 2013; Mganga et al., 2015; Sinsabaugh et al., 2005). Depending on their functions, enzymes are divided into several groups, of which oxidoreductases and hydrolases are especially relevant for SOM decomposition (Tischer et al., 2015). Among these enzymes, β-1,4-glucosidase (BG) cellulose de-polymerization, releasing two moles of glucose per mole of cellobiose (disaccharide of cellulose) (Turner et al., 2002). Degradation of various organic N compounds in soil, including proteins and chitin, are catalyzed by the hydrolyzing activities of L-leucine aminopeptidase (LAP) and β-1,4-*N*-acetylglucosaminidase (NAG), respectively (Sanaullah et al., 2011), releasing N for microbial and plant uptake. Extracellular activity of acid phosphatase (acP) in soil is associated with P mineralization through hydrolysis of organic phosphate compounds (Goldstein et al., 1988; Nuruzzaman et al., 2006).

Activities of extracellular enzymes are triggered by the presence of plants and are usually higher than in bulk soil. Release of labile substrates (i.e. root exudation) by living roots into soil enhances EEA (microbial activation hypothesis; Cheng and Kuzyakov, 2005, Kumar et al., 2016, Zhu et al., 2014). Availability of labile C from root exudation increases the microbial demand for other nutrients such as nitrogen (N) and phosphorus (P). The microbial activation enhances SOM decomposition via mining for N and P (Kuzyakov and Xu, 2013).

Soil aggregation is another factor affecting SOM decomposition as well as nutrient cycling because microbial communities and their activities differ between aggregate size classes (Caravaca et al., 2005; Duchicela et al., 2012; Gupta and Germida, 2015). Soil aggregation physically protects SOM by making it inaccessible for microbial

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mineralization. Aggregation strongly regulates aeration, nutrient retention, and erosion (Blankinship et al., 2016) and controls the sequestration of plant-derived organic matter by occlusion into macro- and microaggregates (Lagomarsino et al., 2012; Tian et al., 2015). Based on observations, it has been identified that C content increase with increasing aggregate size classes from micro- to macroaggregates. Moreover, microaggregates constitute relatively old and recalcitrant C than macroaggregates (Six et al., 2004). Therefore, the quality of C contained within microaggregates or macroaggregates regulates the microbial community structure and associated activity (Bach and Hofmockel, 2014; Hattori, 1988).

Soil macro- (> 250 μm) and microaggregates (< 250 μm) are responsible for the heterogeneous distribution of microorganisms (Blaud et al., 2012) and therefore may affect the associated EEA. The impact of aggregate size class on EEA is inconsistent: increase, decrease or no change have been obtained. One of the possible reasons may be the methods of aggregate size fractionation (Allison and Jastrow, 2006; Dorodnikov et al., 2009a; Fang et al., 2016; Shahbaz et al., 2016). For instance, application of conventional wet- and dry sieving may substantially modify easily soluble and desiccation-sensitive enzyme molecules, and cause their redistribution from one aggregate size class to another (Dorodnikov et al., 2009a). In contrast, the proposed 'optimal moisture sieving' method was developed to minimize biases from the above-mentioned factors on EEA. The method is based on a moisture content that limits mechanical stress, to induce maximum brittle failure along natural planes of weakness in the bulk soil (Dorodnikov et al., 2009a; Kristiansen et al., 2006). This technique involves neither complete drying nor water saturation, which are respectively necessary for dry and moist sieving. Due to the optimal moisture level, macroaggregates do not disrupt completely and the microaggregates located on surfaces of macroaggregates or along natural planes of weakness are preferentially separated. This fraction comprises the free microaggregate size class, distinct from the microaggregates located inside macroaggregates (Bossuyt et al., 2005; Six et al., 2004).

In the present study, the response of EEA catalyzing the decomposition of C (BG and NAG), N (NAG and LAP), and P (acP) compounds was determined in three aggregate size classes. For this, a modified 'optimal moisture sieving' technique was used to separate bulk soil into large macroaggregates (> 2000 μm), small macroaggregates (2000–250 μm), and free microaggregates (< 250 μm). Our previous findings have shown increased enzymes activities in the rhizosphere soil as compared to bare fallow, driven by labile C inputs from roots (Kumar et al., 2016). Increase in root density will also change the distribution of the three aggregate size classes. Therefore, the following research question was addressed: could the optimally fractionated aggregates explain the effects of rhizosphere on microbial biomass distribution and measured EEA? We hypothesized that (i) EEA is higher in aggregates of planted soil than that of bare fallow, as microorganisms are fueled with C and energy-rich labile substrates by rhizodeposition; (ii) EEA is higher in free microaggregates than macroaggregates as the former should be preferentially exposed to root exudates, water and oxygen flows.

2. Materials and methods

2.1. Experimental setup

The experiment was established on a haplic Luvisol in an agricultural field (51°29′37.2″N and 9°55′36.9″E), which belongs to the research station "Reinshof" of the Georg-August-University Göttingen, Germany. Soil properties are as follow: total C (1.41 ± 0.04%), total N (0.16 ± 0.002%), pH (7.2 ± 0.01), soil bulk density (1.2 ± 0.2 g cm^{-3}).The experimental field was divided into 16 plots, each with an area of 5 × 5 m. To avoid any neighboring effects, the plots were separated by 2 m-wide buffer strips, which were kept vegetation-free throughout the experiment. A gradient of three plant densities (low, normal and high) was established in the field with completely randomized design. For this, maize was sown in plots with a plant density of 16 plants m^{-2}. When the plants were approximately 10 cm high, the plots were thinned according to the plant density gradient. Plots were thinned to 6 plants m^{-2} for low plant density; 10 plants m^{-2} for normal plant density; and 16 plants m^{-2} were left as high plant density. Four plots were kept vegetation-free throughout the experiment as control.

2.2. Soil and plant sampling

Soils were collected when the plants entered into the reproductive state (72 days after planting (DAP)) from a depth of 5–15 cm assuming maximum root growth and root exudation during plant vegetative stage (Kumar et al., 2016). This soil depth corresponded to the highest root biomass (data not presented). For soil sampling, the upper 0–5 cm soil layer was carefully removed and soil from 5 to 15 cm was collected between maize rows with a border spade. After delivery to the laboratory, soils were immediately sieved through an 8-mm sieve. A 5 g sub-sample was dried at 60 °C for 3 days to determine soil moisture content. The remaining soil was used for aggregate size fractionation. To determine shoot biomass, two plants from each plot were cut at the base, dried at 60 °C for 3 days, and weighed. Based on plot size and plant density of the respective treatment, shoot biomass was scaled up to g dry weight m^{-2}. For the total root biomass, which could not be directly quantified, the root-to-shoot ratio was used to scale measured shoot biomass to root biomass in units per area (i.e. g dry weight m^{-2}). The root-to-shoot ratio under normal plant density was 0.11 (97 DAP) and did not differ significantly between low, normal, and high plant densities at the end of the field experiment (130 DAP). The ratio was within the range of the data reported by Amos and Walters (2006), showing that the main changes of root-to-shoot ratio in maize occur within the first 60 days after planting.

2.3. Aggregate size fractionation

Aggregates of three size classes were isolated by the method described by Dorodnikov et al. (2009a) with modifications. In order to minimize disturbance to microbial activities, soils were cold dried at 4 °C to approximately 10% gravimetric water content (Bach and Hofmockel, 2015). For this, soil samples were placed in a container and spread into a thin layer. All stones and visible roots were hand-picked. Once the desired condition was achieved, approximately 700 g soil was transferred to a nest of sieves (2 mm and 0.25 mm). The nest was bolted onto a vibratory sieve shaker AS200 (Retsch, Germany) and shaken for 3 min, 2 times. Aggregates remaining on the 2 mm sieve were classified as large macroaggregates (> 2000 μm), aggregates passing through the 2 mm sieve but remaining on the 0.25 mm sieve were classified as small macroaggregates (2000–250 μm), and the remaining soil materials which passed through the 0.25 mm sieve were classified as microaggregates (< 250 μm) (Fig. 1). From each aggregate size class, soil was weighed to determine the mass distribution and mean weight diameters (MWD) of aggregates. Mean weight diameter was calculated after John et al. (2005):

$$MWD = \sum (Weight\%of\ sample\ remaining\ on\ sieve \times Mean\ inter-sieve\ size) \div 100$$

where mean inter-sieve size is the average of the two sieve sizes through which the aggregates have passed and on which the aggregates have remained after sieving.

Thereafter, post-sieving moisture content, total C and N, microbial biomass C and N, and maximal potential extracellular enzyme activities of C-, N-, and P-degrading enzymes were measured. For moisture content, a soil subsample was dried at 60 °C for 3 days. Total C and N contents were estimated with an Elementar Vario EL analyzer

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