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Effects of organic amendment on soil aggregation and microbial community composition during drying-rewetting alternation

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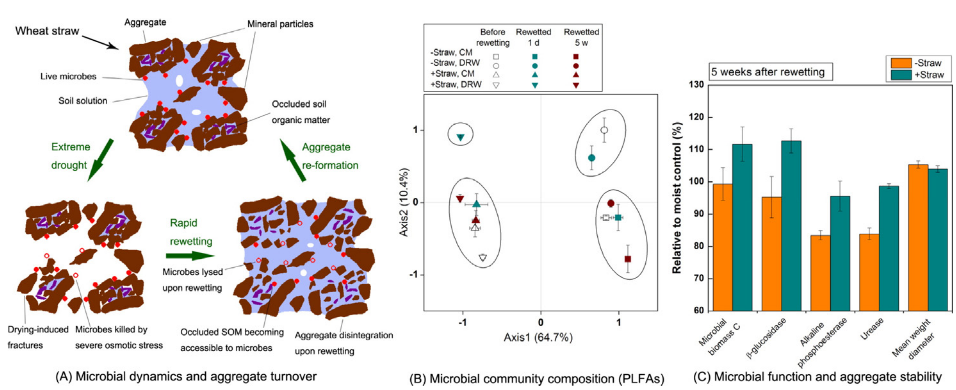
HIGHLIGHTS

- We tested the effects of straw addition and DRW on microbial community and aggregation.
- Straw improved soil aggregation and microbial community resistance to drought.
- Straw addition increased hydrolase activities and their resilience after rewetting.
- Post-rewetting nutrient acquisition drove colonization of heterotrophic communities.
- Straw amendment favored soil functional stability during drying and rewetting.

GRAPHICAL ABSTRACT



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ABSTRACT

The alternation of drying and rewetting events could dramatically affect the biological and structural properties of soil and consequently influence nutrient transformation. To examine whether organic amendments could improve the resistance and resilience of microbial function (extracellular enzyme activities), community composition (phospholipid fatty acids), and soil structure to drying-rewetting alternation, cropland soils with or without wheat-straw amendment were allowed to desiccate in a microcosm for two months, followed by moist incubation for five weeks, and continuously moist treatments were maintained at 50% water holding capacity during the entire period, as a control treatment. Straw amendment increased microbial biomass, extracellular enzyme activities, the relative abundance of fungal groups, dissolved organic carbon, and proportion of large macroaggregates (>2000 μm), but decreased mineral nitrogen and available phosphorus. The drying-rewetting treatment increased microbial biomass carbon and β-glucosidase activities by 10% and 13% in straw-amended soils, respectively, but not in unamended soils, and decreased the urease and alkaline phosphomonoesterase activities by >15% in unamended soils, but not in amended soils. The contents of fungi, actinomycetes, *Pseudomonas* spp., and *Bacillus* spp. decreased with drying, and more so with the subsequent rewetting, but recovered by the end of the experiment. The drying-rewetting treatment caused a decrease in the nitrate content in both soils (>10%) and an increase in the macroaggregates of straw-amended soils (~8%). These results indicated that improved soil aggregation, as a result of straw amendment, protected microbial communities from drought stress and that nutrient acquisition promoted the post-rewetting colonization of heterotrophic communities characterized by hydrolase production, which consequently facilitated aggregate re-formation. Thus, straw amendment

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positively contributed to aggregate turnover and to both microbial and enzymatic responses to drying-rewetting events, which suggests that straw amendment is favorable to maintain soil function under conditions of increasing rainfall variability.

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1. Introduction

In arid and semi-arid ecosystems, the temporal distributions of rainfall are highly uneven, and, thus, water availability is one of the essential factors driving soil processes. For example, surface soils commonly experience gradual drying followed by rapid rewetting events, as a result of evapotranspiration and irrigation or rainfall. These drying-rewetting (DRW) events can alter microbial activities (Göransson et al., 2013; Wang et al., 2014), soil aggregation (Cosentino et al., 2006), organic matter decomposition (Morillas et al., 2013), and nutrient transformation (Schönbrunner et al., 2012). Meanwhile, microbial community composition and function have also been reported to change with experimental manipulation of soil moisture (Fierer et al., 2003a; Yuste et al., 2011). This has attracted great attention during the last few decades, in the context of climate change and increasing variability in rainfall patterns (Greve et al., 2014).

Interestingly, bacteria and fungi have been reported to be differently affected by soil DRW, owing to their contrasting structure and physiology, which results in differences in the microbial community composition of soils under different water regimes (Fierer et al., 2003a; Kaisermann et al., 2013; Kakumanu et al., 2013). Such shifts in microbial communities can alter carbon (C) sequestration and litter decomposition (Strickland and Rousk, 2010), and can even result in positive feedback to climate change (Nie et al., 2013). In fact, microorganisms rarely mediate nutrient transformation directly. Rather, they are involved in most nutrient cycling through extracellular enzymes that they secrete. Therefore, shifts in microbial communities as a result of climate change might further affect enzyme production and ultimately affect primary productivity and nutrient cycling (Burns et al., 2013). Moreover, enzyme activities per se are vulnerable to moisture conditions (Alarcón-Gutiérrez et al., 2010). Furthermore, it is well known that microorganisms, particularly fungi, play an important role in aggregate formation; however, in contrast, soil structure largely contributes to the distribution of microorganisms in soil matrix and their response to environmental conditions (Hattori, 1988). The drying or watering of aggregated soils generally results in fractures along failure zones and, therefore, decreased aggregation (Denef et al., 2001; Six et al., 2004), which may alter the habitat wherein microorganisms are heterogeneously distributed.

The application of organic residue is a common agronomic approach for improving soil fertility in field management. Previous studies have shown that organic amendment increases soil microbial biomass and the activity of extracellular enzymes (Hueso et al., 2011; Pan et al., 2016; Peng et al., 2016), enhances soil water holding capacity (WHC), porosity, and water infiltration rate (Hargreaves et al., 2008), and has positive effects on soil aggregation (Cosentino et al., 2006). Therefore, soil amendment with manure compost could potentially alleviate the effects of severe drought on microbial community composition (Hueso et al., 2012).

Although it is likely that organic substrates provide an external source of energy and nutrients for microbial colonization and metabolic adjustment under unfavorable conditions (Griffiths and Philippot, 2013), the microbial communities of grassland soils are resistant and resilient to fluctuations in rainfall, regardless of compost amendment (Ng et al., 2015). The chemical nature of amended compost, such as its C composition, may contribute to the contrasting results, since sheep manure compost was used in the former study and municipal green waste in the latter and since C composition influences the physicochemical and biological interactions of soil organic matter within the soil matrix and determines its stability and accessibility to soil microbial communities (Kögel-Knabner et al., 2008). In contrast, crop residues, which are widely used in practical field management, possess lower microbial biomass, enzyme activities, and mineral nutrients than compost and are much less mature (Cox et al., 2001), and these differences may contribute to the distinct influences of organic compost and crop residues on microbial responses to moisture stresses.

The responses of microbial community composition and aggregates to water stresses can strongly affect soil functions; yet, little is known about the influence of crop residues on the resistance and resilience of microbial communities, aggregation, and soil functions during drastic moisture fluctuations. Accordingly, the aim of the present study was to determine: (i) the effects of crop residue amendment on microbial parameters and soil aggregation during DRW alternation and (ii) the relationships between microbial community composition, enzyme activities, and soil aggregation.

2. Materials and methods

2.1. Soil and wheat straw

Soil samples (0–20 cm) were taken from a wheat-corn rotation field located in Shouguang, Shandong Province, eastern China (N 36°46′35″, E 118°49′09″). The climate was semi-arid with mean annual precipitation of 650 mm. The soil was a silt loam with a texture of 29.7% sand, 60.6% silt, and 9.7% clay (Mastersizer 2000 Laser Grainsize, Malvern Instruments Ltd. UK). It contained 18.4 g kg^{-1} organic C, 1.59 g kg^{-1} total nitrogen (N), 0.59 g kg^{-1} total phosphorus (P), a C/N ratio of 11.6 and a pH of 7.9 (1:2.5 soil:water ratio). The fresh soil samples were homogenized, sieved (<2 mm), and stored at 4 °C. Wheat straw was collected after wheat harvest from the same field from which soil samples were obtained. The wheat straw was air-dried and ground to <0.5 mm. Only stems and leaves were used, containing 483.5 g kg^{-1} organic C, 7.3 g kg^{-1} total N, 0.52 g kg^{-1} total P and a C/N ratio of 66.2.

2.2. Experimental design

Soil samples (500 g, oven-dry basis) were placed in 1 L plastic pots, and half of them were amended with wheat straw at the rate of 10 g kg^{-1} and mixed thoroughly. The resulting soils were then moistened to 50% WHC and pre-incubated for 30 d to minimize the priming effect, and to allow soils to equilibrate. Thereafter, half of the amended and unamended soil samples were maintained at 50% WHC, and half were left unwatered. After 60 d, the dried soils were quickly rewetted to 50% WHC, and all the soils were incubated for another 5 weeks at 50% WHC. All the pots were incubated at 25 °C in the dark, and soil moisture was monitored during the incubation period by periodical weighing the pots. Soil samples were also taken after 0, 7, 14, 30, and 60 d of the drying and on days 61, 63, 67, 75, and 95 (that is, 1, 3, 7, 15, and 35 d after rewetting). The 100% WHC of the amended and unamended soils was determined as the gravimetric water contents of soils saturated and allowed to drain over 6 h in a Buchner funnel (Miller et al., 2005), and the length of the 60-d drying period was used because it is a common condition during winter and spring in northern China, as well as during the summer and autumn of some years, as a result of limited rainfall. Therefore, our experiment was composed of the following treatments and their combinations: (i) with or without straw amendment (i.e., amended or unamended)

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