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Dry-rewetting cycles regulate wheat carbon rhizodeposition, stabilization and nitrogen cycling

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ABSTRACT

Drying and rewetting of soil can have large effects on carbon (C) and nitrogen (N) dynamics. Drying-rewetting effects have mostly been studied in the absence of plants, although it is well known that plant–microbe interactions can substantially alter soil C and N dynamics. We investigated for the first time how drying and rewetting affected rhizodeposition, its utilization by microbes, and its stabilization into soil (C associated with soil mineral phase). We also investigated how drying and rewetting influenced N mineralization and loss. We grew wheat (*Triticum aestivum*) in a controlled environment under constant moisture and under dry-rewetting cycles, and used a continuous ^{13}C-labeling method to partition plant and soil organic matter (SOM) contribution to different soil pools. We applied a ^{15}N label to the soil to determine N loss. We found that dry-rewetting decreased total input of plant C in microbial biomass (MB) and in the soil mineral phase, mainly due to a reduction of plant biomass. Plant derived C in MB and in the soil mineral phase were positively correlated ($R^2 = 0.54$; $P = 0.0012$). N loss was reduced with dry rewetting cycles, and mineralization increased after each rewetting event. Overall drying and rewetting reduced rhizodeposition and stabilization of new C, primary through biomass reduction. However, frequency of rewetting and intensity of drought may determine the fate of C in MB and consequently into the soil mineral phase. Frequency and intensity may also be crucial in stimulating N mineralization and reducing N loss in agricultural soils.

1. Introduction

Drought is predicted to increase in large areas of the world, such as in the Mediterranean and subtropics (Field et al., 2012). Not only a decrease in precipitation is predicted, but also an overall intensification of the hydrological cycle (Huntington, 2006), with longer periods of drought and intense water stress for plants and soil microorganisms, where moisture is one of the primary regulators of their activity (Tezara et al., 1999; Galmés et al., 2006; Bapiri et al., 2010; Colman and Schimel, 2013). Also, in regions where rain is predicted to increase, an increase in evapotranspiration or shift in precipitation patterns could constrain water availability during the growing season (Borken and Matzner, 2009). There is a recent focus on how soil moisture variations affect microbes and the processes mediated by them.

Decreasing soil water content concomitantly increases the portion of oxygen-filled soil pores (Schimel et al., 2007; Manzoni et al., 2012; Moyano et al., 2013), it reduces the mobility of nutrients and dissolved organic carbon (DOC), and disconnects organisms from substrates (Schjønning et al., 2003; Schimel et al., 2007). Microorganisms must be in contact with soil water to remain active and because of their semipermeable cell membrane they need to produce osmolytes to reduce their internal water potential and to avoid dehydration and death when soil moisture is low (Schimel et al., 2007; Borken and Matzner, 2009).

After rewetting of a dry soil usually follows a burst of respiration (up to 500% compared to soil that is continuously wet), the so called "Birch-effect" (Birch, 1958) that can last up to 6 days (Fierer and Schimel, 2002; Li et al., 2010), after which the respiration matches values of the continuously wet soil. The source of this respired carbon (C) has been attributed to microbial material (osmolytes or lysed cells), but also to mobilization of DOC (Schimel et al., 2007; Borken and Matzner, 2009; Butterly et al., 2011; Warren, 2014). Soil rewetting can also increase loss of nitrogen (N) (through leaching or gaseous emissions), often attributed to an

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accumulation of inorganic N during the dry phase (Austin et al., 2004).

Since the early work of Birch (1958), many laboratory incubation studies have been conducted to investigate the impact of drying rewetting on microbial stress response physiology (Schimel et al., 2007) and microbial decomposition of soil organic matter (SOM) in root-free soil (Fierer and Schimel, 2003; Borken and Matzner, 2009; Chowdhury et al., 2011). However, SOM decomposition in natural as well as in agro-ecosystems is also mediated through plant–microbe interactions. Plants can sustain microbial growth and activity through root exudation, which can be as high as 40% of the photosynthesized C (Graystone et al., 1997; Singh et al., 2004). Recent studies proposed this interaction to be important for the stabilization of C in soil (Miltner et al., 2011; Schmidt et al., 2011).

To our knowledge, only one study included rhizosphere effects on C and N dynamics with drying rewetting cycles, highlighting a lack of studies that include plants (Zhu and Cheng, 2013). Plants under drought stress can either increase or decrease root biomass (Dijkstra et al., 2010; Sanaullah et al., 2012) and the allocation of C to microbes (Gorissen et al., 2004; Ruehr et al., 2009; Sanaullah et al., 2011; Zhu and Cheng, 2013; Fuchslueger et al., 2014) depending on plant species and drought intensity. Also plant presence often increased N mineralization, but it is unclear if this increase was caused by root exudation or by intensified drying rewetting cycles with plant presence (Cheng, 2009; Dijkstra et al., 2009). It is also unclear how plant–microbe interactions are altered by alternating cycles of drying and rewetting.

The aim of this study was to assess how the relationships between plants (wheat) and microbes change following multiple dry rewetting cycles at different plant life stages. We addressed the question of how the release and fate of C from rhizodeposition change between drying and rewetting phases, and weather plant–microbe interactions increase N mineralization. We simulated dry rewetting cycles in planted and non-planted pots, where wheat was grown in a ^{13}C–CO_2 depleted atmosphere and a ^{15}N label was applied to the soil. Specifically we hypothesize that (1) wheat reduces rhizodeposition during the drying phase, while after rewetting it increases to higher rates compared to rates at constant moisture, (2) the rewetting phase will cause a burst of microbial growth, extractable organic C (EOC) and enzymatic activity, (3) fluctuations of C rhizodeposition and microbial biomass C (MBC) with dry rewetting cycles will reduce stabilization of C (C associated with soil mineral phase) derived from plants, (4) N mineralization will increase with plant presence through rhizodeposition, and increase with rewetting, and (5) N loss will decrease with plant presence through uptake of mineral N, but increase with rewetting compared to constant moisture.

2. Materials and methods

2.1. Soil collection and processing

Surface soil (0–15 cm) was collected from a grassland at Westwood farm (33°99′88″S, 150°65′26″ E) on the campus of The University of Sydney, Camden (NSW). The grassland, dominated by the C3 grasses *Lolium rigidum* and *Briza subaristata*, was grazed by cattle at moderate stocking rates and was not fertilized. The soil is a Red Kurosol (sand 63%, silt 19% and clay 18%), pH = 5 (1:5 water), C = 5.6%, N = 0.49% and $\delta^{13}C = -21.0‰$.

The soil was sieved (4 mm) and kept at 4 °C until the start of experiment (2 weeks after collection). We filled 2.5 l pots (diameter: 17 cm, height: 15 cm), sealed at the bottom to prevent leaching) with 1.2 kg of dry soil. Half of the pots were planted with *Triticum aestivum* (wheat, cultivar Cranbrook), and we kept all pots at 60% water holding capacity (WHC) for two weeks before starting the dry-rewetting treatment.

2.2. Experimental design

We used 96 pots in this experiment with 2 water treatments: *dry-rewetting* (DR) vs *constant moisture* (CM). Half of the pots were *planted* (P), while the other half had *soil only* (S). Therefore there were 24 pots for each of the 4 treatment combinations. The DR treatment had a drying phase of 21 days at the end of which the soil reached 30% WHC and plants started to show drought stress (yellowing and early senescence of leaves). At this point pots were rewetted to 60% WHC. We harvested 4 pots for each treatment ($n = 4$) one day before and one day after a rewetting event for analysis, with a total of 3 drying and 3 rewetting phases, and 6 harvest dates (on days 20, 22, 41, 43, 62 and 64 after the initiation of the DR treatments, Fig. 1). The rewetting events occurred at different plant life stages: at stem elongation, booting and flowering. The pots were kept in a controlled environment chamber (temperature day/night: 25/11.5 ± 0.5 °C, humidity: 40–60% and atmospheric CO_2: 800 ± 50 ppm). Treatments were randomly assigned to pots in the growth chamber.

2.3. Water management

In the CM treatment, pots were maintained at 60% WHC by watering pots from the top once a day to a target weight. In the DR treatment during the drying phase planted pots dried faster than pots without plants. To maintain the same WHC in the P-DR and S-DR treatments during the drying phase, planted pots were watered to the bottom of the pots through an inlet tube once a day. In this way we maintained a similar drying rate and water gradient (dry at the top, wetter at the bottom) as in the S-DR treatment. All pots were watered with ultrapure water.

We included an *extra* 18 planted pots, 9 with the DR (P-DR) and 9 with the CM treatment (P-CM), that were used to correct total pot weights in the main experiment for accrued fresh plant biomass. These pots were grown two weeks in advance of the main experiment. Three DR and 3 CM pots were harvested every 3 weeks and measured for fresh plant biomass. These weights were then subtracted from the weight of planted pots in the main experiment.

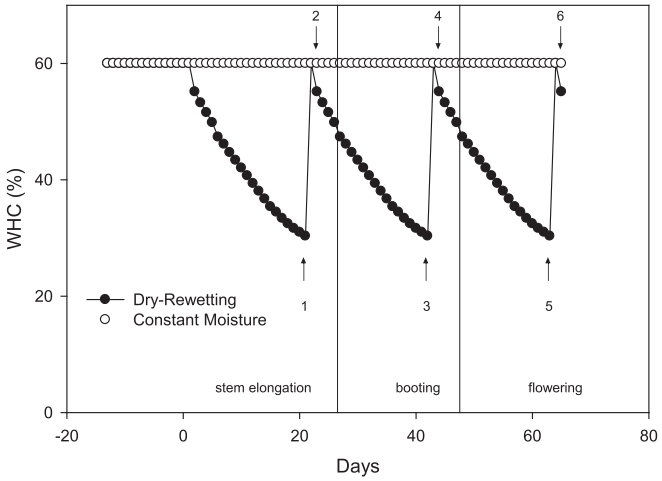

Fig. 1. Water Holding Capacity (WHC) during the experiment calculated from gravimetric soil moisture content. Day 0 represents the start of water treatment. Data points show WHC after watering. Planted and non-planted treatments have the same WHC. Arrows and numbers indicate the harvest number, in each of the section representing different plant life phases (stem elongation, booting and flowering).