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Soil moisture and plant residue addition interact in their effect on extracellular enzyme activity

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ABSTRACT

Water availability strongly affects soil microbial activity and community composition. In a laboratory incubation we investigated the combined effect of soil moisture potential (−10 kPa, −135 kPa, and <−1500 kPa) and plant residue addition on soil enzyme activities (protease, β-glucosidase, β-glucosaminidase and exocellulase) and phospholipid fatty acid (PLFA) profiles. Soil respiration was positively correlated with soil moisture potential and significantly increased with the addition of residue. In the unamended soil, enzyme activities were little affected by soil moisture potential, nor did they change much over time. The addition of residue, however, significantly increased enzyme activity at each moisture level. Furthermore, all four enzyme activities were considerably higher in the amended dry soil than in amended samples with a higher moisture potential. In contrast, in the amended dry soil, respiration and microbial biomass were reduced compared to the amended samples with a higher moisture potential. The low microbial biomass in the amended dry soil was mainly due to a decrease in Gram-negative bacteria, while the fungal biomass reached similar levels at all water potentials. Therefore, shifts in microbial community composition alone cannot explain the increased enzyme activities in the dry soil. Other factors, such as increased fungal activity, stronger interactions between enzymes and soil particles due to thinner water films, may have contributed to the observed effects. Our results suggest that under dry conditions, potential enzyme activities may be decoupled from microbial biomass and respiration in the presence of substrates.

Introduction

The availability of water is a major factor determining microbial activity in soil. As soils dry, the water potential decreases and microbial activity slows down. In general, studies have found that carbon dioxide (CO_2) evolution (Orchard and Cook 1983; Stott et al. 1986; Quemada and Cabrera 1997), as well as net nitrogen (N) mineralization (Stanford and Epstein 1974; Paul et al. 2003) are reduced under low water potentials. Several interrelated mechanisms affect microbial activity in drying soils. A decrease in water potential concentrates solutes in a smaller volume of water. This forces microorganisms to reduce their internal water potential by accumulating solutes, which is energetically expensive, reducing the energy available for biomass synthesis (Csonka 1989; Schimel et al. 2007). Soil drying also restricts diffusion of substrates towards microorganisms and of waste products and extracellular enzymes away from cells, as the decreasing water potential causes water films to become thinner and increasingly disconnected. Molecules must follow a more tortuous path to diffuse from one point to another, reducing the substrate flux to the cell surface (Griffin 1981; Moldrup et al. 2001).

Microorganisms are not affected equally by low soil moisture potential. As the water potential drops, the diameter of water filled pores decreases. Wong and Griffin (1976) have shown that bacterial movement, which is restricted to water-filled pores and water films, declines sharply as water potential falls. They concluded that it is unlikely that bacteria will actively move at matric potentials approaching −50 kPa. In addition, when water films become thinner, contact between microbes and soil particles becomes more intense, which can lead to adsorption of microbes on particle surfaces (Wong and Griffin 1976). In contrast to bacteria, fungal movement is much less restricted under dry conditions. Hyphal extension occurs at much lower water potentials allowing fungi to bridge air-filled pores and actively explore for nutrients. As the water potential falls, the relative competitive advantage between bacteria and fungi therefore moves progressively towards the latter (Wilson and Griffin 1975; Griffin 1981). In addition, due to their strong cell walls, fungi and Gram-positive (G+) bacteria are in general more tolerant to water stress than Gram-negative (G−) bacteria (Harris 1981). Therefore, low soil

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moisture potentials should select against G− bacteria (Schimel et al. 2007).

While studies generally found a negative effect of low water potentials on CO_2 evolution and N mineralization, the effect on soil enzyme activities is less clear. Criquet et al. (2002) found a strong positive correlation between the annual dynamics of the moisture content of oak litter and the activities of β-glucosidase, β-glucosaminidase and xylanase under Mediterranean conditions. Litter moisture seemed to be the principal factor influencing the activity of extracellular enzymes. These findings were confirmed by Sardans and Peñuelas (2005) who found that the reduction of soil moisture considerably decreased urease, protease and β-glucosidase activity in soil. However, in a field study in furrow irrigated corn, Geisseler and Horwarth (2009a) found increased enzyme activities in the dry surface soil (0–5 cm) despite a decreased microbial biomass compared to the soil below. In a field study carried out in the Negev Desert, Doyle et al. (2006) found that cellulase activity in soil attached to litter bags containing cellulose increased considerably within a few months after the litter bags were buried. The increase in cellulase activity was more pronounced during the dry and hot summer months during which the gravimetric soil moisture content decreased gradually to 1.4% compared to the winter months when the soil moisture content reached 9.4%. However, the opposite seasonal trend was observed when plant litter served as substrate. In a study conducted in the Chihuahuan Desert, Bell et al. (2009) found a negative correlation between gravimetric soil moisture content and the activity of β-glucosidase and β-glucosaminidase in soil sampled in March when soil moisture averaged 4.6%. In contrast, in September, when the soil moisture content was higher (7.1%), the correlation was negative.

The objectives of the present study were (i) to investigate the effect of different soil moisture potentials on soil enzyme activities in the presence and absence of plant residue (ii) to study the relationship between enzyme activities and carbon (C) and N mineralization, and (iii) to determine whether differences in enzyme activity were caused by shifts in microbial community composition.

Material and methods

Soil and plant residue samples

Soil samples were collected in fall 2007 after corn harvest from the 5–20 cm layer of a field under conservation tillage at the UC Davis Long-Term Research on Agricultural Systems (LTRAS) site. Soil enzyme activities in this layer have been found to be relatively low (Geisseler and Horwarth 2009a). The background enzyme activity at the beginning of the experiment was therefore low. The soil is mapped as Rincon silty clay loam (fine, montmorillonitic, thermic Mollic Haploxeralf; Soil Survey Staff 1997). The samples had a pH of 7.2 (determined in a 1:2 soil–water solution; Thomas 1996) and contained 12.3 g C and 1.1 g N kg^{-1} dry soil (dry combustion on a Carlo Erba CNS analyzer NA 1500 series 2). Percentages of sand, silt, and clay were 15%, 53% and 32%, respectively (pipet method; Gee and Bauder 1986). The field moist soil was passed through a 4-mm sieve, spread on a paper in a thin layer, and air-dried at room temperature.

Plant residue consisted of an oats-legume cover crop, harvested in spring 2007 in the same field. The cover crop was composed of 74% oats (*Avena sativa*), 8% legumes (predominantly vetch; *Vicia dasycarpa*) and 18% weeds, dominated by fiddleneck (*Amsinckia* spp.) and common chickweed (*Stellaria media*). The total N content of the cover crop was 13.2 g kg^{-1} and the C to N ratio 31. The cover crop was air dried and ground to pass a 1-mm screen.

Incubation experiment

The soil incubation experiment was carried out with three different initial gravimetric moisture contents, namely 32%, 20.5% and 9%. These treatments will subsequently be called wet, moist and dry, respectively. The gravimetric moisture content of 32% corresponded to 55% water holding capacity, which was chosen to approximately reflect field capacity. Under these conditions, neither water availability nor oxygen supply should restrict microbial activity and decomposition. The lowest moisture content corresponded to 15% water holding capacity. Such low moisture contents were measured at the sampling site in the topsoil under furrow irrigated corn (Geisseler and Horwarth 2009a). A moisture release curve, ranging from −10 to −1500 kPa soil moisture potential, was prepared using a pressure plate apparatus (Klute 1986). At each moisture content, soil samples were incubated with or without the addition of cover crop residue. The amount of residue added was 6.7 mg g^{-1} oven-dry soil, which corresponds to 0.1 mg N g^{-1} oven-dry soil.

To simulate field conditions, where subsoil generally remains moister than topsoil, 20 g of unamended soil was first weighed into a 50 mL centrifuge tube and brought to a moisture content of 32%. 20 g of soil with or without residue were added on top and the moisture content was adjusted to one of the three levels by adding DI water. In order to minimize mass flow of water without inhibiting fungal translocation from one layer to the other, a textural discontinuity was created by separating the two soil layers with a thin layer of coarse sand. Therefore, the centrifuge tubes contained two layers of soil, each about 4 cm thick, which were separated by an approximately 0.5 cm thick layer of sand. The centrifuge tubes with the soil samples were placed into jars containing about 30 mL of DI water to minimize evaporation from the soil. The jars were kept in the dark and at room temperature (22 °C) for the duration of the incubation. After 5, 14, 28, and 56 days, four replicated topsoil samples per moisture-residue combination were destructively analyzed for ammonium (NH_4^+), nitrate (NO_3^-), enzyme activities (protease, β-glucosidase, β-glucosaminidase, exocellulase) and phospholipid fatty acids (PLFA). A total of 96 samples were therefore incubated for this study (3 moisture levels × 2 residue treatments × 4 sampling dates × 4 replicates). Soil moisture content in the two soil layers was determined after 14 and 56 days by drying a sample at 105 °C for 24 h.

Soil analyses

For each treatment, a randomly selected subset of four jars was used for CO_2 measurements. The jars were sealed with lids equipped with rubber septa for gas sampling. Headspace CO_2 was analyzed with a Qubit CO_2 analyzer (model S-151, Qubit Systems Inc., Kingston, Canada). After each analysis, the jars were opened and flushed with ambient air. A blank was used to correct for background CO_2. The ideal gas law was used to calculate the amount of C released based on the CO_2 concentration (Zibilske 1994). The frequency of the CO_2 measurements depended on the microbial activity. Measurements were always taken before the CO_2 in the headspace reached a concentration of 1.5% by volume.

Only the topsoil was used for the other analyses. Samples were extracted with 0.5 M potassium sulfate (5 mL g^{-1} soil; Mulvaney 1996) and the suspension filtered (Fisherbrand, Q5) for the colorimetric analysis of NH_4^+ and NO_3^-. Nitrate was analyzed using a single reagent method (Doane and Horwath 2003). The NH_4^+ concentration was determined using the salicylate method (Verdouw et al. 1978; Foster 1995).

Potential enzyme activities in the topsoil were assayed on soil samples of 1 g. The assay used to determine protease activity was adapted from Ladd and Butler (1972), while β-glucosidase,