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Soil carbon and nitrogen dynamics throughout the summer drought in a California annual grassland

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ABSTRACT

Drought is common in soil, yet its intensity and immediate effects vary with the timing of precipitation and the depth in the soil profile. We set out to analyze the patterns of soil C and N dynamics through the dry summer in a California annual grassland, and to analyze the processes that control those dynamics. During the dry season, inorganic N, soluble organic matter, and microbial biomass accumulated in soil. Concentrations were generally greater in the surface soil layer (0–10 cm) but increased in both surface and deeper soil (10–20 cm) over the course of the summer. There was a positive relationship between drought length, microbial biomass C and N, extractable C and N, and microbial activity upon rewetting. Upon rewetting of dry soils there was a pulse in nitrate availability (under field conditions) and, in the top 10 cm, a positive correlation between the initial CO_2 pulse released upon rewetting and the drought length. In contrast, below 10 cm there was no correlation between the rewetting CO_2 pulse and drought length. Soils from the top 10 cm and below 10 cm dried under controlled laboratory conditions showed the same CO_2 pulse response to the length of drying as those in the field. These results suggest that the substrates that accumulate during the dry season are relatively labile, and that, in surface soils, biomass/substrate amounts and water availability control their persistence, while in deeper layers, some other factor is more important.

1. Introduction

Dryland ecosystems cover much of the Earth's land surface, including most of the western United States (Gurevitch et al., 2002). These ecosystems have highly variable weather and climate, making them sensitive to climate changes that alter soil water regimes (Strain and Thomas, 1995; Wetherald and Manabe, 2002; Borken and Matzner, 2009). In ecosystems with Mediterranean climates, such as California grasslands, cycles of carbon (C) and nitrogen (N) may be particularly sensitive to shifts in rainfall; the rainy winters support plant growth and C-inputs into soils, but summers are dry and plant C inputs decrease as many plants senesce. In California, the dry season can persist for six months or more without any rain, and during the spring and fall, rains can be intermittent (Silver et al., 2010). Determining how dry conditions affect C and N pools and microbial processes is critical for predicting how biogeochemical processes may shift as regions on Earth become drier in the future (Bonebrake and Mastrandrea, 2010).

Under stress, microbes shift in how they allocate C, energy, and nutrients among growth, resource acquisition, and survival (Williams and Xia, 2009; Schimel and Schaeffer, 2012; Manzoni et al., 2014). Most of what we know about microbial responses to drought and rewetting, however, come from laboratory studies (Kieft et al., 1987; Csonka, 1989; Stark and Firestone, 1995), where soils are disturbed, litter inputs are prevented, variations in moisture due to changing humidity and dewfall are blocked, and where drying and rewetting are accelerated relative to what would occur in nature (Fierer and Schimel, 2002; Miller et al., 2005). How microbes respond to drought under *in situ* conditions is surprisingly unclear (Williams and Xia, 2009; Manzoni et al., 2012) and perhaps contrary to the common understanding of microbial responses to low water potential that had developed from pure culture and lab

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studies (Boot, 2011; Chowdhury et al., 2011; Boot et al., 2013).

The dry season creates antecedent conditions that regulate the pulses of biological activity that occur with the first rains (Xiang et al., 2008; Borken and Matzner, 2009; Evans et al., 2014). Microbes grow quickly under moist conditions, but increasingly, studies suggest that they are also tolerant of the drought stress of summer (Schimel et al., 2007; Lennon et al., 2012). Microbes might even grow during the dry summer, (Treseder et al., 2010; Parker and Schimel, 2011; Homyak et al., 2014) even though soil moisture imposes both direct (lower water potential) and indirect (reduced diffusion of substrate) stress on microbial physiology (Skopp et al., 1990; Or et al., 2007b; Lennon et al., 2012; Manzoni and Katul, 2014).

The annual grasslands of California are an excellent system for studying how drought may affect soil C and N dynamics and microbial processes; live plant inputs are non-existent during the long dry season, allowing us to disentangle whether soil C may vary because of plant-derived C inputs or because of drought-induced changes in soil C. We hypothesized that microbes would persist throughout the summer drought—as measured by shifts in microbial biomass C—but that the balance of physiological stress and breakdown in the hydrological connectivity within the soil matrix would alter the net balance of processes and the fate of C. Specifically, we predicted that soil ammonium (NH_4^+), and organic C and N would accumulate over the summer because microbes would continue to slowly mineralize soil organic matter (SOM), but diffusion limitations reduce would microbial access to resources. Additionally, we hypothesized that in subsurface layers, where moisture is higher and both dead root content and microbial biomass are lower, substrate accumulation and CO_2 respired upon rewetting would be lower than in surface soils.

To test these hypotheses, we analyzed changes in microbial biomass C and N, inorganic N (NH_4^+ and nitrate (NO_3^-)), extractable organic C and N, and the size of the pulse of respiration on rewetting following varying lengths of drought. These studies used both field and laboratory experiments to explore the influences of drought on rewetting responses including: field sampling to evaluate seasonal patterns over two years, focused summer sampling, and soil mesocosms that allowed precise control of experimental conditions.

2. Materials and methods

2.1. Site description

We collected soils over a period of two years from the University of California Sedgwick Reserve. The reserve is located 50 km from the Pacific coast in the Santa Ynez Valley (43°42′30″N, 120°2′30″W). The climate is Mediterranean and characteristic of interior California, with hot dry summers and cool wet winters. Daytime air temperatures average 32–34 °C in summer, and rarely dip below 0 °C at night in the winter (Nahal, 1981). Average yearly rainfall is 380 mm/yr, but can vary widely, with El Niño years often being notably rainy. The soils we sampled are pachic Argixerolls with a sandy clay loam texture and granular structure on nearly flat (less than 2%) slopes with a bulk density of 1.2 g cm^{-3} in the upper 10 cm. Averaged over the course of the study, soil pH did not vary between depths, but total organic C and total N decreased with depth (Table 1). The vegetation is dominated by Mediterranean annual grasses including *Bromus hordeaceous* L., *Avena fatua* L., and *Bromus diandrus* Roth. Three plots (10 × 20 m) were randomly established approximately 100 m apart in the valley bottom of a zero-order watershed emptying into Figueroa Creek. Between June 2007, and October 2009, we collected soils approximately once every two months in 2007 and 2008, and every three months in 2009.

Table 1
Soil pH, total organic C and total N over the study period. Values are shown for two depth increments: 0–10 and 10–20 cm. Values shown and range (minimum and maximum) and mean ± standard deviation.

	pH	Total organic C (mg C g^{-1} dry soil)	Total N (mg N g^{-1} dry soil)	C:N
0-10 cm depth				
Range	6.5 to 8.3	10.2 to 35.3	0.9 to 3.2	8.3 to 14.3
Mean	7.2 ± 0.6	23.3 ± 4.3	2.1 ± 0.4	11.3 ± 1.1
10-20 cm depth				
Range	6.4 to 8.4	9.2 to 26.1	0.2 to 3.5	8.1 to 24.5
Mean	7.2 ± 0.6	15.0 ± 4.0	1.4 ± 0.3	11.2 ± 2.2

At each sampling date, in each plot, four replicate soil cores (5 cm diameter × 20 cm deep) were randomly collected and the soil separated into surface (0–10 cm depth; to capture the grass rooting zone) and subsurface (10–20 cm depth; to exclude most roots) layers (n = 24). Soils were transported to the laboratory for processing, where they were sieved to 4 mm and rocks and roots were removed. Soils were stored at 10 °C prior to extraction with 0.5 M K_2SO_4 to measure inorganic N, extractable organic C and N, and microbial biomass C and N; extractions always occurred within 2 days after sample collection. A subsample was immediately weighed, dried at 80 °C for 48 h, and weighed again to determine gravimetric soil moisture.

2.2. Soil moisture, inorganic N, soluble organic C and N, and microbial biomass C and N

We measured volumetric water content (VWC) of the soil at two depths (20 and 50 cm) within each plot. The VWC probes (EC-5 probes, Decagon Devices, Inc., Pullman, Washington, USA) were installed in February 2008. Data were collected every 5 min, and averaged over an hour, using a datalogger (CR10X, Campbell Scientific, Inc., Logan, Utah, USA). Daily precipitation totals were measured using a tipping bucket rain gauge (TE525WS-L, Campbell Scientific, Inc., Logan, Utah, USA) that is part of a meteorological station maintained by the UCSB Geography Department (IDEAS, Innovative Datasets for Environmental Analysis by Students, www.geog.ucsb.edu/ideas/).

Soil extractable organic C and N, exchangeable NH_4^+, NO_3^-, and microbial biomass C and N were estimated from 10 g soil subsamples extracted using 40 mL of 0.5 M K_2SO_4. Samples were filtered (0.9 μm pore size) prior to freezing and subsequent analysis. Exchangeable ammonium and NO_3^- were analyzed colorimetrically using flow injection analysis (QuickChem, Lachat, Loveland, Colorado). Microbial biomass C and N were measured with a chloroform slurry extraction (Fierer and Schimel, 2002) followed by persulfate oxidation, which oxidizes organic N to NO_3^- and C to CO_2; NO_3^- was analyzed as described above, the CO_2 was measured by the diffusion technique described by Doyle et al. (2004). Microbial biomass was calculated as the difference in organic C or N (total N minus inorganic N) between subsamples with and without chloroform added. No correction for chloroform fumigation efficiency was made (e.g., see Brookes et al., 1985); therefore the data are presented as the microbial "flush" of organic C or N (MBC and MBN) (Hart et al., 1994). Extractable organic C and N were defined as the organic C and N extractable in 0.5 M K_2SO_4 (no chloroform added). We avoid referring to material as dissolved organic C and N (DOC & DON) because soils were dry much of time so soluble material would not have been dissolved *in situ*.