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Interactive effects of precipitation manipulation and nitrogen addition on soil properties in California grassland and shrubland

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ABSTRACT

Soil microbial communities and pools of carbon (C) and nitrogen (N) play an important role in ecosystem responses to precipitation variability and N deposition. In southern California, ecosystem vulnerability to these environmental change drivers may differ for grassland versus shrubland vegetation types. We hypothesized that (1) these vegetation types would differ in their responses to precipitation and N manipulation; (2) reduced precipitation ("drought treatment") would have a negative effect on soil microbial abundance and alter microbial community composition, (3) these changes would be associated with reductions in soil C and N pools, (4) N addition would increase microbial abundance as well as soil C and N pools, and (5) combined drought and N deposition would have offsetting effects on soil properties. We tested these hypotheses at the Loma Ridge Global Change Experiment in southern California. Across vegetation types, we found that microbial biomass based on phospholipid fatty acids declined with drought and N addition. Microbial composition differed more strongly by vegetation type than with environmental change treatments. Added precipitation had little effect on microbial biomass but reduced labile C and N pools; these reductions were mitigated by N addition. Drought reduced labile forms of soil C and N, whereas N addition increased labile soil C pools and all soil N pools. Negative effects of drought and N addition were additive for microbial biomass, which could inhibit soil C cycling if both of these environmental changes occur together. Drought interacted with N addition to significantly increase the most labile N pool under the drought + N treatment, which suggests a build-up of available N under these conditions. These results imply that multiple environmental changes may combine non-additively to affect below-ground microorganisms and soil C and N pools, which may have important consequences for ecosystem services such as productivity, biodiversity, and soil quality in Mediterranean climate regimes of North America.

1. Introduction

Belowground communities in soils are expected to respond to human-induced environmental changes with consequences for soil carbon (C) and nitrogen (N) pools (Bardgett et al., 2008; Ogunseitan, 2005). Large-scale environmental change can produce local effects on soil moisture patterns, N availability, and soil temperature. In addition, changes in plant community composition, C allocation patterns, or the quantity and quality of plant-derived organic matter can alter the supply of C and N to soil as well as the structure and activity of microbial communities involved in biogeochemical processes (Allison et al., 2013; Balser et al., 2010). Shifts in microbial community composition and functioning can also feedback to affect other soil biogeochemical processes (Carreiro et al., 2000; Treseder et al., 2012; Todd-Brown et al., 2012; Henry et al., 2005).

In grasslands and shrublands of southern California, climate change may lead to reductions in winter season precipitation and increases in the duration and severity of drought (Seager and Vecchi, 2010; Cayan et al., 2010). However, precipitation projections are uncertain, and rainfall events may become more extreme with climate change (IPCC, 2013). These changes may have implications for microbial communities and nutrient cycling (Cregger et al., 2012; Castro et al., 2010). For example, Fierer et al. (2013) found a strong correlation between taxonomic diversity of soil microbial communities and precipitation amount. Precipitation changes can also influence soil microbial

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communities and biogeochemical cycles indirectly, via vegetation change (Bragazza et al., 2015; Tiemann and Billings, 2011; Harper et al., 2005). Allison et al. (2013) found that drought reduced litter decomposition directly, through water limitation, and indirectly through changes in microbial population size, community composition, and litter chemistry. Previous studies have shown that increased precipitation can increase soil light fraction C and N, whereas total soil C and heavy fraction C is relatively stable under climate change (Song et al., 2012; Rosenstein et al., 2011).

Nitrogen deposition in some areas of California is among the highest in the United States, with 20 kg ha^{-1} y^{-1} or greater in southern California (Fenn et al., 2010). Nitrogen limits primary production in many terrestrial ecosystems (LeBauer and Treseder, 2008; Niboyet et al., 2011). The effect of chronic N enrichment on soil microbial community structure and activity varies with ecosystem type, duration of N addition, and rate of N addition. Often, N enrichment alters osmotic potentials in soil solution, reduces soil pH and soil magnesium/calcium availability, and alters the availability of soil C and N through aboveground litter production, which could alleviate microbial C limitation (Treseder, 2008; Carreiro et al., 2000; Gutknecht et al., 2012).

The impacts of global change stressors affecting southern California may also depend on vegetation type. Grasslands and shrublands differ substantially in species composition as well as ecosystem C and N dynamics (Wolkovich et al., 2010). Coastal sage shrub species show higher vulnerability to xylem cavitation than chaparral or desert shrubs (Kimball et al., 2014), implying that shrubland species may be particularly sensitive to drought. Such differences in drought or N vulnerability could cause vegetation-specific changes in plant input chemistry or quantity with consequences for soil C and N pools (Harpole et al., 2007; Follett et al., 2012).

In southern California, both precipitation change and N deposition may occur simultaneously. Therefore, we investigated the responses of microbial communities and soil C and N pools to altered precipitation and N deposition with a factorial design in grassland and shrubland vegetation types at the Loma Ridge Global Change Experiment, CA, USA. We hypothesized that (1) The grassland and the shrubland should differ in their soil responses to precipitation and N manipulations; (2) Declining precipitation levels should have a negative effect on soil microbial abundance and soil C and N pools owing to declines in net primary production (Parolari et al., 2012); (3) Changes in microbial community composition are associated with changes in plant community composition under precipitation manipulation (Allison et al., 2013; Parolari et al., 2012); (4) N addition should increase soil microbial abundance, C pools, and N pools based on previous results at Loma Ridge showing that N availability increases above-ground net primary production (Parolari et al., 2012); and (5) Assuming the responses to manipulation are additive, the positive effects of N addition should offset the negative effects of drought in the combined manipulation.

2. Materials and methods

2.1. Field site and experimental design

The Loma Ridge Global Change Experiment is located in the Santa Ana foothills within the Irvine Ranch National Landmark in Orange County, California (33.742 N, 117.704 W, elev. 365 m) on a northeast-facing slope (<10%). Soils are loamy, mixed, thermic *Typic Palexeralfs* sandy loams (California Soil Resource Lab, http://casoilresource.lawr.ucdavis.edu) formed on a several-meter-deep colluvial deposit eroded from sedimentary rock of the Vaqueros formation (Potts et al., 2012). The vegetation at the site is a mosaic of non-native annual grassland (e.g. *Bromus diandrus*, *Avena fatua* and *Lolium multiflorium*) and perennial, drought deciduous shrubland (e.g. *Artemisia californica*, *Salvia melifera*) (Potts et al., 2012). The grass to shrub boundary is not obviously related to differences in soil texture, depth or pH. The grassland and shrubland soils have a consistent texture of 85.3% sand and fine gravel, 7.6% silt, and 7.1% clay, with reduced clay content near the surface presumably due to leaching (Goulden, unpublished data).

The grassland manipulation site is immediately northeast of the coastal sage shrubland manipulation site (Kimball et al., 2014). The sites experience a Mediterranean-type climate, with cool, wet winters and dry, hot summers and annual mean precipitation of 281 mm that falls mostly from November through April (Tustin Irvine Ranch weather 1902–2003 from http://www.wrcc.dri.edu) (Parolari et al., 2012). The timing and size of precipitation events vary markedly both within and between years. Ambient precipitation ranged from 72 mm to 540 mm over the 7 years of the experiment.

Factorial manipulations at Loma Ridge were initiated in 2007 and include altered precipitation and N input. We used a randomized split-plot design with eight replicate blocks in each vegetation type. Three levels of precipitation input were applied within each block: ambient (control), ambient minus 40% (drought), and ambient plus 40% (added) (Fig. 1). Rainfall was excluded from the drought plots with retractable polyethylene roofs that were closed during approximately half of the rain events (closed <5% of the days during a year); this approach reduced potential climate artifacts (measurements show no effect on air temperature or humidity when open) (Parolari et al., 2012; Kimball et al., 2014). Water draining from the roofs was collected in polyethylene tanks for subsequent application to the added precipitation plots using pressure compensated drip tubing. All plots were burned in 2007, shortly after the start of the experiment. Each plot was split lengthwise and half of each plot was fertilized while the other half remained unfertilized. Plots were fertilized with 2 g N m^{-2} immediate-release calcium nitrate (15.5−0−0 + 19% Ca) prior to the growing season and 4 g N m^{-2} 100-day release calcium nitrate during the growing season (Parolari et al., 2012).

2.2. Soil sampling and soil moisture

Soil samples were collected from all of the grassland and shrubland plots on August 20th, 2012. Three replicate cores (2.5 cm diameter and 15 cm deep) were taken from each plot, combined, homogenized, and used for soil analysis. A sub-sample of the homogenized core was frozen and freeze dried for lipid analysis (Microbial ID, Inc., Newark, DE).

The effect of precipitation treatment on volumetric soil water content (q) was measured using Frequency Domain Reflectometry

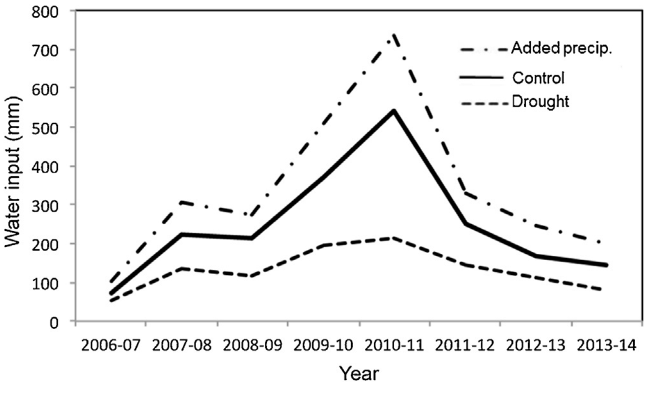

Fig. 1. Annual water input in the control, reduced and added precipitation treatments.