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Warming induced changes in soil carbon and nitrogen influence priming responses in four ecosystems

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ABSTRACT

Soil contains the largest terrestrial pool of carbon (C), but how this pool will be affected by global change remains unknown. Warmer temperatures generally increase soil respiration, while additional C inputs from plants to soil can increase or decrease soil C decomposition rates through a phenomenon known as priming. Priming occurs when soil organic matter (SOM) decomposition rates change in response to a fresh substrate, though the mechanisms underlying priming are poorly understood. Here, we measured priming in four ecosystems during a seven-week incubation with weekly glucose additions. Soil was collected from field warming experiments in the four ecosystems, so our experiment assessed the influence of long-term warming on priming. All treatments exhibited negative priming (reduced SOM decomposition) after the first substrate pulse. Subsequent substrate pulses elicited variable responses, and the effect of long-term warming on priming was ecosystem-dependent. Priming was correlated with changes in soil C and N in response to warming: ecosystems that lost soil C and N over nine years of experimental warming exhibited low rates of priming (decreased SOM decomposition), while ecosystems that gained soil C and N in response to warming had high priming. Consequently, priming may accelerate C losses in ecosystems that exhibit warming-induced C increases, and vice versa, thus partially buffering soil C content against change.

1. Introduction

Soils contain twice as much carbon (C) as the atmosphere and three times as much as all terrestrial vegetation (Ciais et al., 2013). Therefore, understanding how this C pool will respond to changes in temperature is vital for predicting how terrestrial ecosystems will feed back to future climate change. Increased atmospheric carbon dioxide (CO_2) concentration is causing higher global temperatures (Hartmann et al., 2013) and C fixation rates in plants (Curtis and Wang, 1998; De Graaff et al., 2006), but how these factors will interact together to affect terrestrial C-cycling remains uncertain.

Warming can increase soil C losses by stimulating respiration (Dalias et al., 2001; Rustad et al., 2001), though these short-term losses may be offset by long-term acclimatization of respiration (Luo et al., 2001; Oechel et al., 2000), decreased microbial biomass (Frey et al., 2008) and reduced soil moisture suppressing microbial activity (Allison and Treseder, 2008). A recent meta-analysis tested whether soil C loss in response to warming was proportional to soil C stocks, suggesting that ecosystems with high soil C pools (e.g., arctic and tundra) showing the largest soil C losses (Crowther et al., 2016). Warming can also influence soil C balance by altering plant productivity and community composition. Some studies report that warming can increase plant inputs (Cowles et al., 2016; Rustad et al., 2001; Wu et al., 2011a), though others have found that this response can diminish over time (Wu et al., 2012). Shifts in plant communities under warmer climates are also often reported (Wu et al., 2012; Xu et al., 2015; Zhou et al., 2011), and these changes can alter ecosystem C balance in a number of ways including altering the stoichiometry of organic inputs to the soil (Carrillo et al., 2017; Xu et al., 2015), nitrogen (N) cycling (Wu et al., 2012), and microbial community composition (Carrillo et al., 2017). Changes in the quantity and quality of C inputs to soil is known to alter C-cycling dynamics, a phenomenon known as 'priming.'

Priming is defined as a change in native soil organic matter (SOM) decomposition in response to fresh inputs (Kuzyakov, 2010). Despite the potentially large role priming can play in altering terrestrial C-cycling (Carney et al., 2007; Cheng, 2009), few studies have directly measured priming in response to warming (Ghee et al., 2013; Zhu and Cheng, 2011). Additionally, most studies assess priming effects after a single substrate pulse, an unlikely scenario in natural environments that receive continuous or pulsed inputs via root exudates and plant litter.

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Priming responses were affected by whether the same amount of substrate was added as a single pulse, repeated pulses, or continuous additions (Hamer and Marschner, 2005; Hoyle et al., 2008; Qiao et al., 2014). Therefore, to more accurately understand how ecosystems may respond to changing C inputs as a result of climate change, more repeated or continuous C pulse studies are required.

The focus of this study was to measure priming after repeated C amendments in four ecosystems, and to assess how long-term warming would influence those effects. The four ecosystems, situated along an elevation gradient in Northern Arizona, USA, included grass-dominated areas in mixed conifer and ponderosa pine forests, a pinyon-juniper woodland and a cool desert grassland. We predicted that warming would decrease C and N stocks, with greater losses in colder ecosystems (Crowther et al., 2016; Kirschbaum, 1995), and that priming would correlate negatively with these changes in soil nutrients. We reasoned that more labile compounds would be selectively degraded during the nine-year warming treatment, resulting in a pool of relatively more recalcitrant SOM in ecosystems with greater losses and that this more recalcitrant pool would be less susceptible to priming effects (Blagodatskaya et al., 2011a).

2. Materials and methods

2.1. Site description and warming treatment

Field sites were located in Northern Arizona, USA, along the C. Hart Merriam Elevation Gradient (http://www.mpcer.nau.edu/gradient; Table 1). Sites included four ecosystems: mixed conifer forest, ponderosa pine forest, pinyon-juniper woodland, and cool desert grassland. In 2002, intact plant-soil cores, 30 cm in diameter and 30 cm deep, were extracted from grass-dominated areas in each ecosystem, placed in PVC cylinders and either re-planted in the same ecosystem ("ambient" treatment) or transplanted to the next one lower in elevation as an ~3 °C warming treatment ("transplanted" treatment; Wu et al., 2011b). The warmed cores from the grassland ecosystem were transplanted to the Great Basin desert site. To compensate for lower precipitation in the transplanted mesocosms, rainfall collectors were used to add additional precipitation to simulate the rainfall of the native ecosystem. Rainfall collectors were located adjacent to the experimental plots, avoiding shading effects or other possible changes to the light environment. See Blankinship et al. (2011); Wu et al. (2011a, 2011b) for more complete site descriptions as well as a detailed description of the warming treatment design.

2.2. Soil C and N

In August 2011, soil (0–15 cm) from 6 to 7 replicate mesocosms of the ambient and transplanted treatments was collected and homogenized. Soils were sieved (2 mm mesh) and stored at 4 °C for less than a week prior to the start of the incubation (see details below). Subsamples (n = 3) of each homogenized soil sample were oven dried at 105 °C, ground with a mortar and pestle, and analyzed for total C and N using a Carlo Erba NC2100 elemental analyzer configured through a CONFLO III to a DELTA V Advantage mass spectrometer (Thermo Fisher Scientific, West Palm Beach, FL USA). Additional subsamples (n = 5) were extracted with a 0.1 M K_2SO_4 solution to measure extractable C and N. Briefly, 50 mL of 0.1 M K_2SO_4 was added to approximately 15 g dry weight soil, shaken for 1 h, and then filtered using a Whatman #1 filter. The filtered extracts were subsequently dried at 60 °C, ground and analyzed for C and N as described above.

At the end of the experiment, subsamples of soil from the incubations described below were analyzed for total C and N, as well as extracted with a 0.1 M K_2SO_4 solution to measure extractable C and N as described previously.

Table 1
Site characteristics of the five ecosystems along the C. Hart Merriam elevation gradient near Flagstaff, AZ, USA.

Ecosystem	Elevation (m)	MAT* (°C)	MAP* (mm)	Soil C (g m^{-2})	Soil N (g m^{-2})
Great Basin Desert	1556	12.8	127.3	–	–
High Desert Grassland	1760	12.6	169.6	2378.6	200.9
Pinyon-Juniper Woodland	2020	10.8	272.0	2041.7	184.4
Ponderosa Pine Forest	2344	8.9	392.8	2596.6	160.4
Mixed Conifer Forest	2620	6.6	543.3	6626.5	506.7

MAT, Mean Annual Temperature; MAP, Mean Annual Precipitation.
* Based on weather station data from 2002 to 2010 (http://perceval.bio.nau.edu/MPCER_OLD/gradient/).

2.3. Incubation experiment

Approximately 40 g dry weight soil was weighed into specimen cups. Water was added to bring the moisture content to 60% of field capacity, after which the cups with soil were placed in 470 mL airtight Mason jars. Half of the samples (n = 5) received 250 μg C g^{-1} soil once a week as 100 μL of a glucose solution (U-^{13}C glucose; $\delta^{13}C$ = 1369‰) for seven weeks, while the remaining samples received an equal amount of deionized water (non-amended controls). The quantity of amendment was chosen as it is approximately 1.5 times previously measured microbial biomass C of the ecosystems, which has been shown to induce priming responses (Blagodatskaya and Kuzyakov, 2008), and is within estimates of plant exudation rates (Cheng and Gershenson, 2007; Nguyen, 2003). After each glucose or water addition, soils were stirred to distribute the substrate. Jars were incubated at room temperature (~23 °C) in the dark.

Headspace samples were removed through a septum two and five days after each weekly glucose or water amendment and analyzed for $\delta^{13}CO_2$ using a Picarro G2101-i CO_2 cavity ring-down isotope spectroscope (Picarro Inc., Sunnyvale, California, USA). Immediately afterwards, jars were opened for approximately 30 min, re-sealed, and two additional gas samples were taken to determine CO_2 concentrations using a LI-COR 6262 CO_2/H_2O gas analyzer (LI-COR Biosciences Inc. Lincoln, NE, USA). One sample was taken at t = 0 (~30 min after closing the jars to allow soil and headspace atmosphere to re-equilibrate) and one approx. 2 h later. We calculated respiration from these measurements.

The use of isotopically labeled glucose allowed us to partition CO_2 released in the amended samples into glucose-derived CO_2 and native SOM-derived CO_2 using a mass balance equation:

$$C_{SOM} = C_{total}\,(\delta_{total} - \delta_{glucose})/(\delta_{SOM} - \delta_{glucose}) \quad (1)$$

where C_{SOM} is the respiration rate (μg C h^{-1} g^{-1} dry weight soil) of native SOM, C_{total} is the measured respiration rate (μg C h^{-1} g^{-1} dry weight soil) from glucose-amended samples, δ_{total} is the $\delta^{13}C$ signature of CO_2 from glucose-amended samples, $\delta_{glucose}$ is the $\delta^{13}C$ signature of the glucose solution (1369‰), and δ_{SOM} is the averaged $\delta^{13}C$ signature from the native SOM measured from the non-amended control samples. Percent priming was then calculated as:

$$\%\ \text{priming} = (\text{SOM-C}_{glucose} - \text{SOM-C}_{non\text{-}amended})/\text{SOM-C}_{non\text{-}amended} * 100 \quad (2)$$

where SOM-$C_{glucose}$ is the CO_2 production rate (μg C h^{-1} g^{-1} dry weight soil) from native SOM in glucose-amended samples and $SOM_{non\text{-}amended}$ is the CO_2 production rate (μg C h^{-1} g^{-1} dry weight soil) from SOM in non-amended control samples. Priming was expressed in terms of percentages to standardize measurements from ecosystems with