



# Digging into the roots of belowground carbon cycling following seven years of Prairie Heating and CO<sub>2</sub> Enrichment (PHACE), Wyoming USA



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## ABSTRACT

Grassland soils are significant carbon (C) sinks as more than half of grassland plant biomass is belowground and roots are the main source of soil C. It is uncertain if grassland soils will continue as C sinks in the future because climate change may affect the dynamic, belowground relationships among crown and root biomass, root chemistry and morphology, and root and soil decomposition, all of which influence C sequestration potential. To better understand future belowground C cycling in semiarid grasslands we analyzed three native species (*Bouteloua gracilis*, *Carex eleocharis*, and *Pascopyrum smithii*) and mixed-grass community crown and root biomass, root chemistry, morphology, and decomposability, and soil organic carbon (SOC) priming following seven years of simulated climate change at the Prairie Heating and CO<sub>2</sub> Enrichment (PHACE) experiment in Wyoming, USA. We found that individual species and the community respond uniquely to the climate change field treatments, indicating that species composition is important when analyzing climate change effects on grassland C cycling. Root biomass in the C3 sedge, *C. eleocharis*, increased under elevated CO<sub>2</sub>, especially when combined with warming. Decomposition rates of roots from warming plots were higher than those from ambient plots for *B. gracilis* and *P. smithii*. Across species, root decomposition rates increased with C and N concentrations. Root morphology was altered as well: *B. gracilis* root diameter increased under warming, and *P. smithii* specific root length and surface area increased under elevated CO<sub>2</sub>. *P. smithii* roots induced short-term, negative SOC priming across all field treatments. Together, our results indicate that grass roots may play a critical role in maintaining soil C stocks in grasslands in the future.

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## 1. Introduction

Grasslands contain more than 10% of the global carbon (C) stock and 98% of that C is in the soil (Jones and Donnelly, 2004; Heinemeyer et al., 2012). The significant amount of C in grassland soils may be attributed to the high root:shoot ratios that characterize grasslands (Mokany et al., 2006). For example, 90% of plant biomass and 67% of NPP in semiarid shortgrass steppe is concentrated belowground (LeCain et al., 2006). Additionally, temperate grasslands contain 17% of the global fine-root pool (less than 2-mm diameter) (Jackson et al., 1997). A large portion of belowground C is also stored as carbohydrates in crowns just below the soil surface

(Milchunas and Lauenroth, 2001). The large quantity of C stored belowground in grasslands makes relationships among biomass, fine-root chemistry, morphology, and decomposition critical, because as CO<sub>2</sub> concentrations and temperatures rise, the dynamics of these components and their impacts on grassland C cycling may change (Silver and Miya, 2001; Hui and Jackson, 2006; de Graaff et al., 2011; White et al., 2012).

Biomass accumulation and plant tissue quality often influence one another, thus changes in biomass in response to climate change may be reflected in root chemistry (Craine et al., 2003). Increases in belowground biomass, root C:N, and longevity often co-occur under elevated CO<sub>2</sub> (van Groenigen et al., 2005; Dijkstra et al., 2010; Pendall et al., 2011; Dieleman et al., 2012). This contrasts with warming treatments, where fine-root biomass decreases or does not significantly change, root C:N generally decreases, and N mineralization increases (Pendall et al., 2011; Dieleman et al., 2012; Carrillo et al., 2014). In an Australian native grassland, elevated CO<sub>2</sub>

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paired with warming increased root biomass, but root C:N responses were dependent on plant functional type and N distribution (Pendall et al., 2011). Therefore, assessing root biomass and chemistry responses to climate change by species may reveal important insights into belowground sources and sinks of carbon.

Known controls over fine-root decomposition include root quality, root morphology, microbial composition, and environment (Silver and Miya, 2001; Vivanco and Austin, 2006; Birouste et al., 2012; Pilon et al., 2013; Bardgett et al., 2014; Smith et al., 2014). Root decomposition may decrease with elevated CO<sub>2</sub> due to an increase in root C:N and/or lignin and suberin concentrations (Gorissen et al., 1995; van Groenigen et al., 2005; de Graaff et al., 2011; Pendall et al., 2011). Also under elevated CO<sub>2</sub>, N-limitation tends to favor roots with large diameters, low specific root lengths (SRL, length per unit mass), and greater root-tissue densities (RTD, mass per volume) (Dieleman et al., 2012). Roots with these characteristics tend to have long lifespans (Bardgett et al., 2014; Reich and Cornelissen, 2014; Prieto et al., 2015). In contrast to elevated CO<sub>2</sub> effects, warming may lower C:N ratios, resulting in accelerated root decomposition (Silver and Miya, 2001; Pendall et al., 2004). The increase in N-availability with warming also appears to favor roots with small diameters, high SRLs, small RTDs, and short lifespans (Dieleman et al., 2012). However, in water-limited ecosystems, where elevated CO<sub>2</sub> increases water content and warming induces soil desiccation (Nowak et al., 2004; Morgan et al., 2011), water-mediated effects might counter N-mediated effects (Dieleman et al., 2012; Pilon et al., 2013; Reich and Cornelissen, 2014). For example, in low moisture ecosystems, root decomposition appears to be accelerated under elevated CO<sub>2</sub> (Allard et al., 2005; Dijkstra et al., 2008; Carrillo et al., 2014). Since both root decomposition and root morphology appear to be impacted by elevated CO<sub>2</sub> and warming, and root morphology appears to influence root lifespan, quantifying both root-morphological traits and root decomposition rates in response to climate change may provide a key link in understanding C transfer from roots to the soil (Eissenstat et al., 2000).

Fine-roots are quite labile relative to SOC and may induce a positive or negative priming effect on SOC decomposition (Mary et al., 1992; de Graaff et al., 2013). Positive priming is an increase, while negative priming is a decrease, in the amount or rate of SOC decomposition (Kuzyakov et al., 2000). Past studies show changes in the amount, quality, and morphology of fine-roots in response to elevated CO<sub>2</sub> or warming (van Groenigen et al., 2005; Morgan et al., 2011; Pendall et al., 2011; Dieleman et al., 2012; Carrillo et al., 2014). Therefore, the effects of increased temperature and atmospheric CO<sub>2</sub> on root dynamics and properties may impact the direction and extent of root-induced priming of SOC, ultimately affecting C storage in grassland soils.

Climate change factors are expected to interactively alter species composition in native plant communities, depending on the resistance or vulnerability of individual species (Zelikova et al., 2014). After prolonged exposure to elevated CO<sub>2</sub> and warming at the Prairie Heating and CO<sub>2</sub> Enrichment (PHACE) experiment, grassland community composition shifted to favor subdominant, C3 species (especially the drought-tolerant sedge, *Carex eleocharis*), at the expense of the dominant C4 species (*Bouteloua gracilis*) (Zelikova et al., 2014; Mueller et al., 2016). We expected that these species shifts could be associated with changes in belowground resource availability, different root traits, and altered soil C cycling. Indeed, elevated CO<sub>2</sub> combined with warming led to lower soil moisture and higher soil inorganic N in comparison with the control treatment (Mueller et al., 2016; Carrillo et al., 2012), larger root biomass and longer, thinner roots at the community-level (Mueller et al., 2016; Carrillo et al., 2014), and enhanced rates of SOC decomposition (Pendall et al., 2013). However, until the end of the

PHACE experiment in 2013 no species-level sampling was conducted belowground.

The objective of this study was to better understand future belowground C cycling in semiarid grasslands by analyzing linkages between climate change effects on belowground biomass with fine-root chemistry, morphology, and decomposition, and SOC priming, particularly at the species-level. We predicted that 1) crown biomass responses to climate change treatments would be similar to root biomass responses for all species; 2) root chemical (C and N concentrations) and morphological responses to climate change treatments would depend on species identity; 3) root decomposition rates and priming of SOC decomposition would be related to root C and N contents and morphology (diameter, specific root length and surface area). We thus expected that intrinsic differences in root traits between native grassland species would mediate soil C cycle responses to climate change (Pendall et al., 2011; Burke et al., 2013).

## 2. Materials and methods

### 2.1. Study site

This experiment was conducted at the Prairie Heating and CO<sub>2</sub> Enrichment (PHACE) experiment located at the USDA-ARS High Plains Grassland Research Station (HPPGRS), 15 km west of Cheyenne, WY (41° 11' N, 104° 54' W; elevation 1930 m) (Carrillo et al., 2011). The PHACE site vegetation is classified as a northern mixed grass prairie composed of grasses and forbs, including a C<sub>3</sub> grass species *Pascopyrum smithii* (Rydb.) A. Love and a C<sub>4</sub> grass species *Bouteloua gracilis* (H.B.K.) Lag., which together comprise 50% of the total aboveground biomass, and a sedge, *Carex eleocharis* L. Bailey (Dijkstra et al., 2010). Annual precipitation averaged 384 mm and average air temperature was −2.5 °C in winter and 17.5 °C in summer (Morgan et al., 2011; Carrillo et al., 2014). The soil was an Ascalon variant loam on the north side of the field site and an Altvan loam on the south side of the field site (Dijkstra et al., 2010; Nie et al., 2013).

### 2.2. Field experiment

The PHACE experiment included twenty, 3.4 m diameter circular plots divided into four combinations of elevated CO<sub>2</sub> and warming, with five replicates of each combination (Dijkstra et al., 2010; Carrillo et al., 2011). The four field treatments included ambient CO<sub>2</sub> and ambient temperature (ct), ambient CO<sub>2</sub> and elevated temperature (cT), elevated CO<sub>2</sub> and ambient temperature (Ct), and elevated CO<sub>2</sub> and elevated temperature (CT). The ambient [CO<sub>2</sub>] was approximately 400 μmol mol<sup>−1</sup> and the elevated [CO<sub>2</sub>] was 600 ± 40 μmol mol<sup>−1</sup> (Morgan et al., 2011). The elevated temperatures were 1.5 °C above ambient during the day and 3.0 °C above ambient at night (LeCain et al., 2015). Free air CO<sub>2</sub> enrichment (FACE) was implemented during the growing season beginning in April 2006; temperatures were elevated year-round with infrared heaters attached 1.5 m above the ground on frames starting in March 2007 (Morgan et al., 2011; LeCain et al., 2015). The experiment was terminated in mid-July 2013, when all samples for this work were harvested.

### 2.3. Field sampling

We collected soil samples from 0 to 5 cm depth by compositing four, 5 cm diameter cores from each of the twenty field plots. The soil was sieved with 2 mm sieves, weighed on site, and then transported back to the lab in coolers. We removed roots and aboveground litter by hand-picking the soil samples and then

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