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Plant and microbial biomarkers suggest mechanisms of soil organic carbon accumulation in a Mojave Desert ecosystem under elevated CO_2

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ABSTRACT

We investigated how properties of soil organic matter (SOM) were altered after 10 years exposure to elevated atmospheric CO_2 concentration ($[CO_2]$) in a Mojave Desert ecosystem, using plant and microbial biomarkers. We focused on roles of *Larrea tridentata*, the dominant evergreen shrub which form islands of fertility, and biological soil crusts which have extensive cover in plant interspace. Soils to 5 cm in depth were collected under *L. tridentata* and plant interspace, and biological soil crusts to 0.5 cm in depth under three cover types, *Pleuraphis rigida*, a C_4 grass, shrubs and plant interspace. Soil organic carbon contents were not significantly different between elevated and ambient $[CO_2]$. However, significantly higher abundance of *n*-alkanes, a major constituent of foliage wax material, occurred in the elevated compared to ambient $[CO_2]$ plots in the soils collected under *L. tridentata*, but no such difference was found in the soils at plant interspace or the biological soil crusts. There was no significant difference in abundance of microbial phospholipid fatty acids between the CO_2 treatments in the soils of either cover types. However, neutral lipid fatty acid abundance was significantly higher under elevated than ambient $[CO_2]$ in the soils under *L. tridentata*, whereas no such significant difference was observed at plant interspace. These results emphasize important roles of the dominant shrubs in SOM formation under elevated $[CO_2]$ in arid ecosystems. Elevated $[CO_2]$ stimulated growth of *L. tridentata* in wet years, and aboveground litter deposition via senescence contributed to SOM formation in islands of fertility. In addition, elevated $[CO_2]$ stimulated soil microbial turnover rates in rhizosphere of *L. tridentata*, which left more soil microbial necromass, a major SOM source. We concluded that responses of dominant shrubs to elevated $[CO_2]$ can stimulate SOM formation in arid ecosystems, but biological soil crusts may have limited capacity.

1. Introduction

Recent studies suggest that arid and semi-arid ecosystems may be important sinks under increasing atmospheric CO_2 concentration ($[CO_2]$) (Poulter et al., 2014; Evans et al., 2014). Semi-arid vegetation growth stimulated by increased precipitation associated with La Niña in Australia could account for 60% of the exceptionally large terrestrial carbon (C) sink observed in 2011 (Poulter et al., 2014). Water availability to vascular plants can be an important factor to determine responses of arid ecosystems under increasing $[CO_2]$. For instance, at the Nevada Desert FACE (Free Air CO_2 Enrichment) Facility (NDFF, Jordan et al., 1999), a 50% increase in $[CO_2]$ doubled new shoot production of the dominant shrub, *Larrea tridentata*, compared to ambient $[CO_2]$ in a high rainfall year (Smith et al., 2000). In the following low rainfall year, however, elevated $[CO_2]$ did not stimulate shoot production of *L. tridentata* (Smith et al., 2000), and dominant shrubs even senesced biomass increased in the previous year (Housman et al., 2006). Following a ten-year experiment at the NDFF, Evans et al. (2014) observed significantly higher ecosystem C under elevated than ambient $[CO_2]$. The greater ecosystem C under elevated $[CO_2]$ was only due to differences in soil organic C (SOC), not in standing above- or belowground plant biomass (Evans et al., 2014), most likely because desert plants could not sustain increased biomass under elevated $[CO_2]$ over long time with precipitation and drought cycles (Newingham et al., 2013). The results of these studies have important implications for terrestrial C dynamics under increasing $[CO_2]$; even though arid and semi-arid ecosystems have relatively low SOC contents, those ecosystems have a substantial storage of SOC because of their extensive coverage of the Earth's surface (IPCC, 2000; Jobbágy and Jackson, 2000; Prentice et al., 2001; Lal, 2004). Globally, the desert biome is estimated to store 112 Pg

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of SOC to 1 m in depth, comparable to that of the boreal forest (112 Pg), temperate deciduous forest (122 Pg) and temperate grassland (105 Pg) (Jobbágy and Jackson, 2000).

One of the unique spatial characteristics of arid ecosystems is islands of fertility (Schlesinger et al., 1990, 1996), where soil C and nutrients concentrate under shrubs relative to plant interspace. These heterogeneous landscapes form when shrubs assimilate nutrients through spatially extensive root systems and concentrate organic C and N through litter deposition and throughfall (West and Skujins, 1977). Greater organic C and N coupled with more favorable moisture conditions associated with shrub canopies results in more pronounced biogeochemical responses to elevated [CO_2] compared with adjacent interspace (Jin and Evans, 2007).

Extensive coverage of biological soil crusts at plant interspace is another unique feature of arid ecosystems. Biological soil crusts, which can constitute up to 70% of living ground coverage (Belnap et al., 2003), consist of numerous organisms, including cyanobacteria, algae, lichens and mosses (Belnap, 2003). Biological soil crusts play multiple ecological roles in arid lands, including providing N via N fixation (Belnap, 2002), prevention of wind and water erosion (McKenna-Neuman et al., 1996) and soil aggregate formation (Belnap, 2003). As biological soil crusts contain photosynthetic organisms (Evans and Johansen, 1999) and their photosynthetic activity can be stimulated under elevated [CO_2] (Lange, 2003), they may be able to contribute to the C sink capacity of arid ecosystems under elevated [CO_2]. However, there is uncertainty in the C sink capacity of biological soil crusts; photosynthetic activity of biological soil crusts is relatively short-lived as they are only active when moist (Lange et al., 1994; Lange, 2003; Austin et al., 2004), and, unlike vascular plants, they do not form extensive structural materials which provide litter as a source of soil organic matter (SOM) (Belnap, 2005).

Quantifications of biomarkers, in combination of their stable isotope probing, can reveal processes of SOM formation, such as potential sources and microbial dynamics. For instance, *n*-alkanes can be used to assess potential SOM sources. *n*-Alkanes are produced by all the primary organisms that can be SOM sources in arid ecosystems, including vascular plants (Bush and McInerney, 2013), non-vascular plants such as algae (Gelpi et al., 1970) and mosses (Dembitsky, 1993), lichens (Zygadlo et al., 1993) and even bacteria and fungi (Jones, 1969; Fisher et al., 1972). *n*-Alkanes produced by those organisms vary in characteristics such as chain length distributions, chain lengths of dominant *n*-alkanes, and ratios of odd-to even-numbered *n*-alkanes, which can help identify dominant sources of *n*-alkanes in soils. Phospholipid fatty acids (PLFAs) can provide biomass of live bacteria and fungi as well as their community structure (Zelles, 1999). Neutral lipid fatty acids (NLFAs) can indicate fungal C utilization patterns (Bååth, 2003) and microbial turnover rates as NLFAs can result from decomposing dead microbes (White, 1993; Bååth, 2003). Thus, quantification and stable isotope probing of these biomarkers can provide insights into processes that are responsive to elevated [CO_2] to better understand whole-ecosystem responses to global change.

In this study, we investigated spatial responses of SOM properties after 10 years exposure to elevated [CO_2] in a Mojave Desert ecosystem. We focused on ***soils*** 0–5 cm in depth located under the dominant evergreen shrub (*Larrea tridentata* (D.C.) Cov.) and plant interspace. We hypothesized that organic C and total N contents would be higher under elevated than ambient [CO_2] in the soils under *L. tridentata*, but not plant interspace (**H1**). In addition, we hypothesized that contents of plant-derived *n*-alkanes (**H2**), microbial PLFA (**H3**) and NLFA (**H4**) in the soils were greater in the elevated than ambient [CO_2] treatment under *L. tridentata*, but not at plant interspace. Potential contribution of ***biological soil crusts*** to SOM dynamics was assessed through measurements of their organic C, total N and *n*-alkane contents and their stable isotope compositions under two plant functional types (shrub and grass) and in the plant interspace. We hypothesized that contents of organic C and total N (**H5**) as well as *n*-alkanes (**H6**) in biological soil crusts would not be significantly different between the two CO_2 treatments because of the limited ability of biological soil crusts to form SOM compared to *L. tridentata*. By testing the specific hypotheses listed above, we explore potential mechanisms behind the higher SOC under elevated than ambient [CO_2] reported by Evans et al. (2014).

2. Materials and methods

2.1. Study site

The Nevada Desert FACE Facility was located 15 km north of Mercury, Nevada, USA (36°49′N, 115°55′W) at an elevation of 965–970 m (Jordan et al., 1999). The site was protected from surface disturbance for the previous 50 years (Jordan et al., 1999). Vegetation was characteristic of *Larrea tridentata-Ambrosia dumosa* desert scrub. Mean annual air temperature and precipitation were 15.5 °C and 144 mm, respectively, from 1998 to 2006 (Nevada Desert Research Center, 2011). Precipitation occurred mostly in a form of rain during winter.

The CO_2 fumigation infrastructure consisted of six, 23-m diameter experimental plots. Three plots (**Elevated**) were fumigated with additional CO_2, and the other three plots (**Ambient**) with ambient [CO_2], and mean concentrations over the life of the experiment were 513 and 375 $\mu L\,L^{-1}$, respectively (Evans et al., 2014). The CO_2 fumigation began April 1997 and ended June 2007. The $\delta^{13}C$ of supplemental CO_2 in Elevated was −5.4‰ until 10 February 2003 when source CO_2 was switched to −32.0‰ for the remainder of the experiment. Dilution with ambient air resulted in $\delta^{13}C$ of CO_2 in Elevated of −7.3‰ and −18.2‰ before and after the source switch, respectively (Schaeffer, 2005). The $\delta^{13}C$ of Ambient treatments was −8‰ throughout the experiment. This ^{13}C-labeling provided us an opportunity to gain insights into biogeochemical processes under elevated [CO_2] via stable isotope probing for three types of biomarkers (i.e., PLFA, NLFA and *n*-alkanes). Specifically, we aimed to assess if the ^{13}C-labeled CO_2 in the elevated [CO_2] plots assimilated by primary producers was incorporated into different components of soils, and, if so, magnitudes of the incorporation.

When the whole ecosystem harvest was conducted in 2006 after the decadal experiment (Evans et al., 2014), there was no significant difference between Ambient and Elevated in plant community characteristics, including total cover, species richness and diversity (Newingham et al., 2013) as well as above- and belowground biomass of vascular plants (Newingham et al., 2014).

2.2. Soils

Soils were collected from the most dominant vegetation cover type (*L. tridentata*, an evergreen shrub, hereafter **LATR**) and plant interspace (**INTR**) on 7 May 2007 for analyses of organic C and total N content and stable isotope composition, *n*-alkanes, NLFA and PLFA. The coverages of LATR and INTR were, on average, 4.9 and 83.4%, respectively, and were not significantly different between the two CO_2 treatments (Newingham et al., 2014). For LATR, three subsamples were collected under canopies of three individual plants at each plot. For INTR, we randomly chose three locations free from any vascular plant, and a subsample was collected from each location at each plot. Three subsamples for each cover type were collected from 0 to 5 cm using a PVC soil corer in each plot. Each subsample was passed through a 2 mm sieve and composited for each plot–cover type combination, and transported to the laboratory on dry ice. Roots were removed and soil moisture was determined after drying a 10-g subsample at 105 °C for 48 h. The remainder of each sample was lyophilized and stored at −40 °C until subsequent analyses.