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Increased belowground carbon inputs and warming promote loss of soil organic carbon through complementary microbial responses

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ABSTRACT

Current carbon cycle-climate models predict that future soil carbon storage will be determined by the balance between CO_2 fertilization and warming. However, it is uncertain whether greater carbon inputs to soils with elevated CO_2 will be sequestered, particularly since warming hastens soil carbon decomposition rates, and may alter the response of soils to new plant inputs. We studied the effects of elevated CO_2 and warming on microbial soil carbon decomposition processes using laboratory manipulations of carbon inputs and soil temperature. We incubated soils from the Aspen Free Air CO_2 Enrichment experiment, where no accumulation of soil carbon has been observed despite a decade of increased carbon inputs to soils under elevated CO_2. We added isotopically-labeled sucrose to these soils in the laboratory to mimic and trace the effects of increased carbon inputs on soil organic carbon decomposition and its temperature sensitivity. Sucrose additions caused a positive priming of soil organic carbon decomposition, demonstrated by increased respiration derived from soil carbon, increased microbial abundance, and a shift in the microbial community towards faster growing microorganisms. Similar patterns were observed for elevated CO_2 soils, suggesting that the priming effect was responsible for reductions in soil carbon accumulation at the site. Laboratory warming accelerated the rate of the priming effect, but the magnitude of the priming effect was not different amongst temperatures, suggesting that the priming effect was limited by substrate availability, not soil temperature. No changes in substrate use efficiency were observed with elevated CO_2 or warming. The stimulatory effects of warming on the priming effect suggest that increased belowground carbon inputs from CO_2 fertilization are not likely to be stored in mineral soils.

1. Introduction

The terrestrial carbon (C) cycle regulates atmospheric CO_2 concentrations through a balance between photosynthetic uptake and respiratory release from plants and plant residues sequestered in soils. Rising atmospheric CO_2 and concomitant global warming are likely to alter this balance by modifying the rates of these uptake and release processes, with unknown implications for long-term soil C storage. Higher atmospheric CO_2 concentrations fertilize plant C uptake, resulting in greater plant productivity that is transferred to soils in the form of increased litterfall, root biomass, and root exudation (Liu et al., 2005; Norby et al., 2005; Pregitzer et al., 2008; Phillips et al., 2011). However, it is unclear whether these enhanced inputs increase soil C storage (Norby and Zak, 2011), because elevated CO_2 also stimulates respiratory losses of C from plant tissues and soils (Drake et al., 2011).

In addition, climate warming is likely to erode stores of soil organic carbon (SOC) by increasing decomposition rates (Hopkins et al., 2012); however, the warming effect may be limited by the amount of substrate available for decomposition (Melillo et al., 2002). Through its interaction with substrate availability, warming has the potential to alter the response of soils to additional plant inputs in a high CO_2 world. Ecosystem-scale manipulations of CO_2

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and temperature have shown that the combination of these two drivers has a different effect on SOC turnover rates and soil microbial community composition than either treatment alone (Gray et al., 2011; Gutknecht et al., 2012; Nie et al., 2012).

Prior to ecosystem-scale experimental tests, it was predicted that additional C taken up by forests under elevated CO_2 would be stored in soils (e.g., Harrison et al., 1993); however, data from the Free Air CO_2 Enrichment (FACE) experiments have shown a mixed response (de Graaff et al., 2006). Despite consistent stimulation of plant productivity across forested FACE sites (Norby et al., 2005), increased C allocation belowground under elevated CO_2 has actually resulted in less accrual of C to soil stores in some experiments (e.g., Talhelm et al., 2009).

Given higher litter inputs under elevated CO_2 (eCO_2), observed reductions in SOC formation can only be explained by decreased retention of new C inputs to soil, or an acceleration of SOC decomposition rates. Specifically, eCO_2 may increase the fraction of C inputs lost from soils through respiration by changing the efficiency of microbial processes, such as the proportion of C allocated to respiration vs. growth (Ziegler and Billings, 2011). In contrast, eCO_2 may increase decomposition outputs from SOC via the rhizosphere priming effect, whereby additions of easily degradable C exuded by roots stimulates microbial activity and results in greater SOC turnover (Kuzyakov et al., 2000; Carney et al., 2007; Cheng et al., 2013). Higher root exudation rates have been observed under eCO_2 (Phillips et al., 2011), as have increased soil respiration rates (Pregitzer et al., 2006); however, the many sources of soil respiration make the detection of the priming effect in an intact ecosystem extremely challenging (Hopkins et al., 2013; Phillips et al., 2013). Nevertheless, both explanations— reduced microbial efficiency and rhizosphere priming— invoke changes in microbial metabolism as drivers for reductions in SOC under eCO_2; thus, better understanding of the microbial drivers of SOC decomposition is needed to assess the effect of CO_2 fertilization on soil C storage (Billings et al., 2010).

The effect of climate warming on the C balance of soils is also mediated by microbial decomposition— warming rapidly stimulates microbial metabolism, and results in nearly instantaneous increases in microbial respiration (Dijkstra et al., 2011). In the long term, however, warming may hasten substrate limitation for microorganisms (e.g., Melillo et al., 2002—field; Fissore et al., 2008—laboratory), and alter the temperature response of microbial respiration rates (Thiessen et al., 2013). It remains unclear whether observed decreases in the temperature sensitivity of microbial respiration over the course of long-term soil warming experiments is due to the direct effect of temperature on microbial physiology, such as through reduced substrate use efficiency (Bradford et al., 2008), or whether the decrease is owed to indirect effects of warming on microbial substrate supply (Dungait et al., 2012).

In this study, we combine short-term manipulations of temperature and substrate supply in a laboratory incubation experiment of soils from a decade-long CO_2 fertilization experiment. We used a combination of C isotope labels, respiration measurements, and microbial biomarker analysis to study the response of microbial processes to eCO_2 and warming. Soils were taken from the Aspen FACE experiment, where eCO_2 exposure had altered the amount and ^{13}C and ^{14}C isotope signature of plant-derived C inputs to soils for more than 10 years. In the laboratory, we warmed soils and added isotopically-labeled sucrose to mimic root exudation, further enabling us to track incorporation of new C inputs, and to monitor the effects of changing substrate availability on the temperature response of respiration. Our goal was to determine how global change effects on microbial community composition and activity might affect the decomposition process, and in turn, the fate of soil C stores in the future.

We evaluated the plausibility of a rhizosphere priming effect in eCO_2 soils by adding isotopically-labeled sucrose to soils in the laboratory. Sucrose and its monomers are a common component of root exudate (Grayston et al., 1996) that can induce priming effects (de Graaff et al., 2010), and are readily available to most heterotrophic soil organisms (Killham and Prosser, 2007). We hypothesized that sucrose addition would induce a positive priming effect, exemplified by increases in respiration of soil-derived C and microbial abundance relative to soils receiving water alone. We also examined the effect of eCO_2 and sucrose addition on microbial community composition to determine whether they were consistent with a priming effect. We tracked incorporation and respiration of added sucrose as a measure of microbial function, which allowed us to determine the effect of eCO_2 on microbial substrate use. We hypothesized the eCO_2 soils would retain a lower proportion of new C inputs, demonstrated by less incorporation of the sucrose $\delta^{13}C$ label into microbial biomass per unit of CO_2 respired. We also investigated the relationship between substrate availability and the warming response by using respiration of added sucrose as a proxy for substrate availability. We monitored respiration of added sucrose, using the ^{13}C and ^{14}C label, and compared temperature treatments on the basis of amount of sucrose respired rather than length of time of the experiment. We hypothesized that any apparent interactions between warming and substrate supply, e.g., higher temperature sensitivity in the sucrose addition treatment, would result from differences in amount of C available to microbes, not to changes in microbial substrate use.

2. Methods

2.1. Free air CO_2 enrichment

We studied soils from the Aspen FACE experiment near Rhinelander, WI, USA (45°40.5′N, 89°37.5′W), which was designed to study the effects of eCO_2 on a newly planted stand of deciduous trees (Dickson et al., 2000). In eCO_2 plots, CO_2 concentrations were raised during the growing season by 200 μmol mol^{-1} above background levels for 11 years (1998–2009). The CO_2 used in the experiment was derived from fossil sources, and thus had a distinct C isotope signature from background air (Pregitzer et al., 2006). Hence the SOC isotopic signature records incorporation of C into soils in eCO_2 plots over the 11-year duration of the experiment. C fixed by photosynthesis and delivered belowground in eCO_2 plots in 2009, the year of sampling, was depleted in its C isotope signature by −12‰ in $\delta^{13}C$ and −340‰ in $\Delta^{14}C$ relative to C fixed in ambient CO_2 plots (Table 1a).

2.2. Aspen FACE site

We sampled soils where the vegetation type was an aspen clonal monoculture plantation (*Populus tremuloides* Michx.). The soils are classified as mixed, frigid Alfic Haplorthods with sandy loam A horizons. After a decade of eCO_2, net primary productivity (NPP) was enhanced by an average of 26% over the aCO_2 control plots, with a 34% stimulation of litterfall and a 15% stimulation of fine root production (Zak et al., 2011). After trees were planted in 1997, SOC contents increased linearly in both eCO_2 and ambient CO_2 (aCO_2) control plots (Talhelm et al., 2009), but after a decade of eCO_2, SOC contents did not differ significantly between the CO_2 treatments (Hofmockel et al., 2011).

2.3. Soil sampling and processing

In July 2009, we sampled soils from 3 replicate eCO_2 plots, and 3 replicate aCO_2 plots. After removal of surface litter, soils were