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Carbon input control over soil organic matter dynamics in a temperate grassland exposed to elevated CO_2 and warming

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Abstract

Elevated CO_2 generally increases soil C pools. However, greater available C concentrations can potentially stimulate soil organic matter (SOM) decomposition. The effects of climate warming on C storage can also be positive or negative. There is a high degree of uncertainty on the combined effects of climate warming and atmospheric CO_2 increase on SOM dynamics and its potential feedbacks to climate change. Semi-arid systems are predicted to show strong ecosystem responses to both factors. Global change factors can have contrasting effects for different SOM pools, thus, to understand the mechanisms underlying the combined effects of multiple factors on soil C storage, effects on individual C pools and their kinetics should be evaluated. We assessed SOM dynamics by conducting long-term laboratory incubations of soils from PHACE (Prairie Heating and CO_2 Enrichment experiment), an elevated CO_2 and warming field experiment in semi-arid, native northern mixed grass prairie, Wyoming, USA. We measured total C mineralization and estimated the size of the labile pool and the decomposition rates of the labile and resistant SOM pools. To examine the role of plant inputs on SOM dynamics we measured aboveground biomass, root biomass, and soil dissolved organic C (DOC). Greater aboveground productivity under elevated CO_2 translated into enlarged pools of readily available C (measured as total mineralized C, labile C pool and DOC). The effects of warming on the labile C only occurred in the first year of warming suggesting a transient effect of the microbial response to increased temperature. Experimental climate change affected the intrinsic decomposability of both the labile and resistant C pools. Positive relationships of the rate of decomposition of the resistant C with aboveground and belowground biomass and dissolved organic C suggested that plant inputs mediated the response by enhancing the degradability of the resistant C. Our results contribute to a growing body of literature suggesting that priming is a ubiquitous phenomenon that should be included in C cycle models.

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1 Introduction

The amount of carbon (C) stored in soil results from the input of plant derived materials and the release of C via decomposition of residues and soil organic matter (SOM) pools. Both processes are susceptible to impacts from global climate change. Elevated CO_2 generally increases soil C pools (Luo et al., 2006; Hungate et al., 2009; Jastrow et al., 2005) but has also decreased them (Carney et al., 2007; Langley et al., 2009). Climate warming can potentially enhance or decrease plant productivity (Parton et al., 2007; Wan et al., 2004; Rustad et al., 2001), and thus plant-input mediated effects of warming on C storage can be positive or negative. Furthermore, warming may directly increase heterotrophic soil respiration but can also decrease it indirectly via soil drying (Rustad et al., 2001). There is a high degree of uncertainty on the combined effects of climate warming and atmospheric CO_2 increase on SOM dynamics (Pendall et al., 2004a; Shen et al., 2009), but the direction and magnitude of combined effects are likely to be dependent on ecosystem type (Norby and Luo, 2004). For semi-arid grasslands, models predict strong responses of plant production, soil moisture, N availability and soil C to CO_2 elevation and warming (Parton et al., 2007; Pepper et al., 2005) as well as interactive effects of the combined factors (Pepper et al. 2005).

Through their effects on plant productivity, warming and elevated CO_2 can impact SOM dynamics, both by directly determining inputs and/or by affecting rates of losses (Fig. 1). Increasing CO_2 can positively impact above and belowground biomass (Morgan et al., 2004a; Jastrow et al., 2000; de Graaff et al., 2006) as well as root growth rate and turnover (Allard et al., 2005; Norby et al., 2004). Warmer temperatures can also, in some cases, cause increases or limit above and belowground production and biomass (Belay-Tedla et al., 2009; Rustad et al., 2001; Wan et al., 2005) and root turnover (Wan et al., 2004). A portion of below-ground plant inputs are incorporated into SOM pools (Crow et al., 2009) via root death, slough-off and exudation (Pendall et al., 2004b). The flux of recent plant photosynthate can be a major source of readily microbially available C (Hutsch et al., 2002; Weintraub et al., 2007) and has been found to contribute about

40% of the DOC pool (Högberg and Högberg, 2002; Giesler et al., 2007). Consistently, readily available C for microbes in soil, has been found to be positively correlated with aboveground biomass (Belay-Tedla et al., 2009). Increased exudation of low molecular weight C compounds has been reported for plants under elevated CO_2 (Johansson et al., 2009). However, labile C can stimulate SOM decomposition, an effect known as priming (Dijkstra and Cheng, 2007a; Fontaine et al., 2007; Kuzyakov, 2002), so greater plant inputs can also reduce the stocks of soil C (Pendall et al., 2010). As expected from the relationships between plant biomass, root exudation and labile C availability, priming of SOM decomposition has been found to be correlated to root biomass (Fu et al., 2002) and leaf biomass (Dijkstra et al., 2006) and thus its magnitude could be affected by CO_2 and warming via their effects on plant productivity (Fig. 1).

Studies have shown that global change factors can have contrasting effects for different SOM pools. Cardon et al. (2001) showed that elevated CO_2 retarded the decay of resistant, slow-turnover SOM while it increased the decomposition of labile, fast-turnover SOM. Cheng et al. (2007) observed that under elevated CO_2 more plant derived C was stored in the resistant pool and that its decay rate decreased. In contrast, Gill et al. (2002) found plant growth at increased CO_2 lead to losses in resistant SOM, as measured by mineral-associated soil C. Other studies have observed that elevated CO_2 depletes both resistant SOM as well as fractions dominated by fresh plant derived C (de Graaff et al., 2009; Del Galdo et al., 2006). Because labile and more resistant SOM fractions have different sensitivity to temperature (Davidson and Janssens, 2006) it is likely that the effects of warming will depend on the SOM pool examined (e.g. Belay-Tedla et al., 2009). Soil moisture, which can be affected by CO_2 and temperature may mediate the impact of CO_2 and warming on soil C storage by regulating inputs and outputs (Liu et al., 2009) and moreover, this regulation might not be equivalent for different SOM pools (Garten et al., 2009). To understand the mechanisms underlying the combined effects of multiple global change factors on soil C storage, effects on individual C pools and their kinetics should be evaluated.

We assessed SOM dynamics by conducting long-term laboratory incubations of soils from an elevated CO_2 and warming field experiment, measuring total C mineralization and estimating the size of the labile pool and the decomposition rates of the labile and resistant SOM pools. Incubation experiments provide a more sensitive indicator of SOM responses to climate change than bulk soil measurements (Pendall and King, 2007). In order to examine the role of plant inputs on SOM dynamics we measured aboveground biomass, root biomass, and soil dissolved organic C (DOC) in the field as possible drivers of SOM dynamics (Fig. 1). Soils were collected from the PHACE (Prairie Heating and CO_2 Enrichment) experiment in a semi-arid, native northern mixed grass prairie in Wyoming, USA. The prairie is experimentally exposed to elevated CO_2 (600 ppm) and canopy warming (1.5/3 °C increase during the day/night) in a factorial arrangement. We expected that aboveground production and root biomass would be related to DOC, and microbially available C (measured as total mineralizable and labile C pool) would be regulated by plant biomass and thus would be related to DOC. We hypothesized that total mineralizable C and the proportion of C that is labile would increase with elevated CO_2 due to increased plant inputs. We hypothesized that total mineralizable C and the labile C pool size would not change with warming due to decreased soil moisture offsetting direct warming effects on decomposition, while the combination of elevated CO_2 and warming would increase the microbially available C, assuming soil water was sufficient for nominal plant activity. We anticipated that the decomposability of the labile pool would be lower in elevated CO_2 treatments, where the quality (C/N) of plant inputs is expected to be lower, and that the decomposability of the resistant pool would be related to the availability of plant C inputs due to the priming effect. We expected that CO_2 and warming treatment effects on the resistant pool would be less apparent than on the labile pool, due to longer mean residence time of the resistant pool. Results from these experiments provide information relevant to predicting soil C feedbacks to climate change.

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2 Methods

2.1 Study site

The Prairie Heating and CO_2 Enrichment (PHACE) experiment at the USDA-ARS High Plains Grassland Research Station (1930 m a.s.l.), is located about 10 miles west of Cheyenne, WY, USA (41°11′ N lat, 104°54′ W long). The ecosystem is a northern mixed grass prairie (NMP) with a plant community dominated by the C4 grass *Bouteloua gracilis* (H.B.K) Lag. and two C3 grasses, *Hesperostipa comata* Trin and Rupr. and *Pascopyrum smithii* (Rydb.). About 20% of the vegetation is composed of sedges and forbs. Annual precipitation is 384 mm. Mean air temperatures are 17.5 °C in summer and −2.5 °C in winter, with average maximum July temperature of 27 °C. Soils at the experimental site are Mollisols (fine-loamy, mesic Aridic Argiustoll, mixed Ascalon and Altvan series), with a pH of 7.9 and carbonate content of 1 to 5% below 15-cm depth. Average soil C content is 1.9% at 0–5 cm and 1.3% at 5–15 cm.

The experiment uses Free Air CO_2 Enrichment (FACE) technology (Miglietta et al., 2001) installed in 3.4-m diameter rings to produce an atmosphere with a CO_2 concentration of 600 ±40 ppm in the elevated CO_2 treatments during the growing season. Infrared heaters (Kimball et al., 2008) attached to a frame 1.5 m above the ground increase air temperature by 1.5 °C during daytime and 3 °C at night all year round. NMP is thus exposed to four combinations of CO_2 and temperature (ambient CO_2 and ambient temperature: *ct*; ambient CO_2 and elevated temperature: *cT*; elevated CO_2 and ambient temperature: *Ct*; elevated CO_2 and elevated temperature: *CT*) with five replications. CO_2 enrichment began in April 2006 and heating began in April, 2007.

2.2 Field measurements and sample processing

In each experimental plot, soil volumetric water content is monitored at 10 and 20 cm (Envirosmart sensors, Sentek Sensor Technologies, Stepney, Australia) and soil temperature is continuously monitored at 3 and 10 cm using thermocouples. Daily means

of soil water content and temperature were averaged across the six-week periods prior to soil sampling (Shim et al., 2009). Standing fine root biomass and aboveground plant biomass were assessed at the peak of the growing season (late July, close to the time of soil collection) in 2007 and 2008. Fine roots (<1 mm) were handpicked from soil samples (see below) and they were analyzed for C with a Costech EA 1108 Element Analyzer. Aboveground biomass was obtained by clipping an area of 0.75 m^2 in each plot. In July 2007, April and July 2008 3 soil cores (15-cm deep; 5-cm diameter) were collected from each plot, divided into 0–5 and 5–15 cm depths and composited into one sample. Fresh soils were sieved to 2.0 mm and hand-picked to remove gravels, litter and root material. To obtain a measure of DOC in soil, a 15-g subsample of fresh soil was extracted by shaking in 30 ml of 0.05 M K_2SO_4 for 1 h. Inorganic C was removed from the filtered extract by adding 1 M H_3PO_4 (1 µl per 10 ml of extract). The filtered extract was analyzed for total C (Shimadzu TOC-V_{CPN}, Shimadzu Scientific Instruments, Wood Dale, IL). A subsample of air-dried soil was analyzed for C content after removing carbonates with 1 M H_3PO_4 (Sherrod et al., 2002). Soils were then ground to powder and analyzed with a Costech EA 1108 Element Analyzer.

2.3 Incubations

Fresh, sieved soil (15–20 g) from every plot and depth was placed in a polystyrene beaker which had small holes punched into the bases and pre-combusted glass fiber filters in the bottom for drainage (Townsend et al., 1997). Deionized water was added to each beaker to reach 60% of the soil's field capacity. Each beaker was placed into a 500-ml canning jar with a lid modified to hold a 1.5-cm, blue butyl rubber stopper. Soils collected in April were incubated at 15 °C and those collected in July were incubated at 25 °C to resemble the corresponding field temperatures. Soils collected in 2007 were incubated for ca. 100 days while April and July 2008 soils were incubated for 220 and 270 days respectively. Headspace samples (30 ml) were collected at intervals ranging from 1 (early in the incubation) to 60 days (late in the incubation). Before every sampling event jars were briefly opened to allow equilibration with ambient air and then

closed and flushed with CO_2-free air for 2 min. Incubation periods ranged from 24 to 70 h, to allow approximately 1000 µmol mol^{-1} CO_2 to accumulate. Four empty jars were used as controls for background CO_2 concentration. Headspace samples were analyzed for CO_2 concentration with an infrared gas analyzer (Li-Cor 820, LICOR Inc. Lincoln, NE) calibrated with four standard gases over the concentration range 377–4500 µmol mol^{-1}. To estimate C kinetic parameters, measured CO_2 production rates over time were fitted to a two pool decay model in which a pool of labile C decays exponentially and a pool of resistant C decays at a constant rate (Dijkstra and Cheng, 2007a; Wedin and Pastor, 1993):

$$R_t = R_i \cdot e^{-kl \cdot t} + R_r$$

Where R_t= respiration rate at time t (µg C g $soil^{-1}$ day^{-1}); R_i = initial rate of decomposition of the labile pool (µg C g $soil^{-1}$ day^{-1}); k_l = decay rate of C in the labile pool (day^{-1}); R_r = decomposition rate of C in resistant pool (µg C g $soil^{-1}$ day^{-1}). The size of the labile pool (C_l) was defined as R_i/k_l. Curve fitting was done using the single, 3 parameter exponential decay equation in Sigma Plot 10.0. R_i, C_l and R_r were normalized by dividing the estimated values by total soil C content, measured for each plot and at each depth, to represent the proportion of total C in the labile pool (as µg C soil C^{-1}) and the inherent decomposition rates of the labile and resistant pools (as µg C g soil C^{-1} day^{-1}).

2.4 Statistical analyses

Three-factor ANOVA was used to determine the effects of depth, CO_2 and warming treatments on field soil moisture and temperature, estimated kinetic parameters (size of the labile C pool, the rates of decomposition of the labile and resistant pool), and total C mineralized over the course of the incubation. Each of the three incubations was analyzed as an independent experiment. Aboveground plant biomass, root biomass, DOC and average of daily soil water content means for the six weeks prior to soil sam-

pling were linearly regressed against the estimated pool sizes and kinetic parameters. Significant effects and relationships are reported at $p < 0.05$ unless otherwise stated.

3 Results

3.1 Field treatments effects on soil temperature and moisture

Average soil moisture content ranged from 8 to 17% at 0–10 cm depth, and 12 to 20% at 10–20 cm depth (Table 1). Over the six weeks previous to mid-season sampling in 2007 and 2008 soil water content was significantly greater (by 2.1% water content on average; Table 1) in elevated CO_2 than ambient CO_2 plots ($p = 0.003$ and $p = 0.0003$ for 2007 and 2008 respectively). Elevated CO_2 did not significantly impact soil water content in the weeks before the April 2008 sampling. Warming significantly decreased water content prior to all sampling dates by 2.0% on average ($p = 0.005$ for 2007, $p = 0.02$ for April 2008 and $p = 0.001$ for July 2008; Table 1). No interactions between treatment and depth were observed for soil moisture.

Elevated CO_2 significantly decreased soil temperature by 0.2 °C in the period before sampling in June 2007, 0.6 °C before April 2008 and 0.3 °C before July 2008 ($p = 0.05$, $p < 0.0001$, $p = 0.01$, respectively). Warming significantly increased soil temperature during all periods (Table 1). This effect was dependent on depth before the mid-season sampling date in 2007 and 2008 (significant interaction of warming and depth, $p = 0.0003$ for 2007 and $p = 0.07$ for 2008), as the increase in soil temperature was greater at 3 cm than at 10 cm (2.8 °C vs. 2.1 °C on average in 2007 and 2.1 °C vs. 1.8 °C in 2008). Prior to the April 2008 sampling date, warming increased soil temperature by 1.9 °C independent of depth.

3.2 Plant biomass and DOC

Elevated CO_2 had consistent positive effects on fine root biomass in 2007 and above-ground biomass in 2008 (Table 2). There was no main effect of warming but the com-

bination of elevated CO_2 and warming tended to enhance aboveground biomass in 2007 and fine root biomass in 2008 (marginally significant CO_2 × warming interaction; Table 2). Elevated CO_2 had no detectable effect on DOC while warming tended to increase DOC concentration in 2008 (Table 2). Aboveground plant biomass and fine root biomass were positively correlated (Fig. 2). The concentration of DOC in soil was positively correlated to both aboveground plant biomass and root biomass (Fig. 3).

3.3 Total mineralized C

Significant effects of treatments on total C mineralized were observed in the 0–5 cm soils, and were dependent on the time of soil collection (Fig. 4). In soils from June 2007 warming increased mineralization from ambient CO_2 soils, but had little effect on C mineralization in the elevated CO_2 treatment. Total C mineralized was reduced with warming in April 2008 soils but there was no effect of warming in July 2008 soils. Total mineralized C was positively related to DOC in all sampling dates at depth 5–15 cm ($p = 0.02$, $r^2 = 0.42$ in June 2007; $p = 0.004$, $r^2 = 0.40$ in April 2008; $p = 0.007$, $r^2 = 0.34$ in July 2008) and also at 0–5 cm in April 2008 ($p = 0.03$, $r^2 = 0.25$). In 2007, total C mineralized (at 0–5 cm) was positively related to aboveground biomass ($p = 0.007$, $r^2 = 0.53$).

3.4 Labile C pool and its decomposition rate

In soils sampled at mid-growing season in 2007, 14 months after CO_2 elevation began and 3 months after warming began, the proportion of labile C and its initial decomposition rates showed strong interactive effects of CO_2 and warming in the 0–5 cm layer. Warming increased the proportion of total C that was labile in soils from elevated CO_2 plots but decreased it in ambient CO_2 soils (Fig. 5a). The initial rate of decomposition was lower with warming in ambient CO_2 soils, while it increased under warming in elevated CO_2 soils (Fig. 5d). After nine months, at the beginning of the 2008 growing season, neither CO_2 nor warming had any effects on the labile pool size or its decom-

position rate (Fig. 5b, e). Three months later, at peak biomass, the labile proportion was greater in elevated CO_2 soils and this effect was consistent across depths (Fig. 5c). There was no effect of warming or CO_2 on the labile pool decomposition rate in 2008 (Fig. 5f).

The proportion of labile C (at 0–5 cm) was positively related to shoot biomass ($p = 0.04$, $r^2 = 0.20$) and root biomass ($p = 0.008$, $r^2 = 0.35$) in July 2008, but not at the other two sampling dates. Labile C proportion was not correlated to DOC concentration. The initial rate of decomposition of the labile pool was positively related to soil water content at both depths ($p = 0.04$, $r^2 = 0.34$ at 0–5 cm and $p = 0.03$, $r^2 = 0.39$ at 5–15 cm) in soils from July 2007, but not for the other dates (regression plots not shown).

3.5 Resistant C pool decomposition rate

Although the resistant pool decomposition rate was not significantly affected by CO_2 and warming treatments (Fig. 5g, h, i), significant relationships were observed with the indicators of plant input in both years: it was positively related to aboveground plant biomass, root biomass and DOC in July 2007 and with DOC in July 2008 (Fig. 6).

4 Discussion

Soil organic matter pools result from the balance of inputs from plant biomass and losses via decomposition. Our research demonstrates that positive aboveground productivity responses to global change treatments translate into greater belowground biomass, which enlarged the pools of readily available C (total mineralized C, labile C). Because root exudation is thought to be a rather constant fraction of C fixed in photosynthesis (Pinton et al., 2001) and root biomass (Jones et al., 2009), and root exudation is an important source component of DOC (Högberg and Högberg, 2002; Giesler et al., 2007), DOC was expected to respond to changes in aboveground and

root biomass. DOC was in most cases positively related to total mineralized C, suggesting that it constituted an important component of the microbially available C. This is consistent with previous observations in laboratory incubations (Lagomarsino et al., 2009) and with reduced soil respiration and DOC after the termination of C flow to the roots in field settings (Scott-Denton et al., 2006).

The influence of plant inputs on microbially available C varied across years. Whereas in 2008 the response of the labile C was consistent with increased plant inputs with elevated CO_2 (a positive and consistent effect of elevated CO_2, and positively correlations of July 2008 labile C with above and belowground biomass), in 2007 the observed treatment effects on labile C and total mineralized C suggested that decomposition and turnover also affected pool sizes. Indirect effects of treatments on soil moisture on decomposition of soil C before sampling may have led to this contrasting response. Total precipitation (from the start of the growing season) at the time of soil collection in 2007 was about 60% of that received in 2008 in the same period (Heisler-White, unpublished data) and a more moisture limited system in 2007 would be expected to be more responsive to the drying effects of warming and the moisture enhancing effect of elevated CO_2. In 2007 the strong CO_2 × warming interaction arose because warming strongly stimulated total mineralized C and the proportion of labile C at ambient CO_2, but not at elevated CO_2 (Figs. 4 and 5). The higher total mineralizable C and proportion of labile C in ambient CO_2, warmed plots suggests that warming decreased microbial C use due to soil drying (Liu et al., 2009). It is possible that in elevated CO_2, warmed plots, the drying effect was offset by greater soil moisture due to higher plant water use efficiency under elevated CO_2 (Morgan et al., 2004b), allowing enhanced decomposition with increased temperature (Kirschbaum, 2006). It is noteworthy that the interactive effects of CO_2 and warming only occurred at 0–5 cm, where effect of warming on soil temperature was stronger.

The contrast in the responses of the labile C pool to warming in 2007 and 2008 could have been a result of transient response of heterotrophic respiration to the experimental treatment, which had begun just three months earlier. Various field experiments

have shown that soil respiration initially responds to warming but later returns to pre-warming rates (Oechel et al., 2000; Luo et al., 2001; Eliasson et al., 2005). Substrate depletion due to the direct effect of warming or thermal adaptation by microbes (i.e. altered respiration rates) are competing reasons for this temporal pattern (Bradford et al., 2008). Neither the labile pool or DOC had decreased in warmed treatments by 2008, therefore we suggest microbial adaptation to warming as a potential explanation for the contrast between 2007 and 2008. Assessment of pool sizes from future soil collections will be necessary to confirm whether the 2007 response was a transient effect.

The cumulative mineralized C over the course of a long-term incubation comprises all the labile C released from soil at the beginning of the incubation in addition to the resistant C that was evolved at a slower rate (Pendall and King, 2007). In the present study, warming decreased the total mineralized C in soils from April 2008, but not the size of the labile C pool. Resistant organic matter is more sensitive to temperature than labile organic matter (Vanhala et al., 2007; Davidson and Janssens, 2006); thus the response to warming of the total mineralizable C could be reflecting the response of the resistant pool. We expected that warming would have no main effect on the mineralizable C if the direct enhancement of decomposition was offset by a decrease in soil moisture. Our results suggest that during the winter time, in the absence of any fresh plant inputs, warming was able to deplete the soil mineralizable C (including labile C and more resistant C), possibly because soil moisture was not limiting for decomposition.

Long term soil incubations under optimal soil moisture and temperature conditions and in the absence of live plants allow assessments of changes in SOM pools and kinetics caused by their previous exposure to field treatments. Thus, treatment effects on the rates of decomposition are interpreted as the result of changes in the susceptibility of C pools to decomposition which could potentially be expressed in a field situation. We expected that the decomposition rate of the labile pool would be related to the quality of the roots and DOC, specifically, that rates would be higher in the elevated CO_2 plots, which are have higher C to N ratios (data not shown). We did not find this

to be the case for any of the sampling dates suggesting that other factors controlled the decomposability of this pool. We did not detect any treatment effects of warming or elevated CO_2 on the susceptibility of the resistant pool to decomposition. However, when considering all treatments, the decomposition rate was positively related to plant (above and belowground) biomass and particularly to the concentration of DOC in soil. Greater availability of labile C has been linked to enhanced decomposition of SOM via the priming effect (Fontaine et al., 2007). Priming associated with root derived plant inputs has been termed "rhizosphere priming" (Kuzyakov, 2002). Because elevated CO_2 can promote plant production and thus plant C input to soil, it has been hypothesized to cause SOM depletion (Carney et al., 2007). Studies have found evidence of accelerated decomposition of older OM under elevated CO_2 (Pendall et al., 2003) as well as of smaller pools of total and resistant SOM (Langley et al., 2009), which have been attributed to priming. Other climate factors, however, might contribute to priming by altering the availability of labile C. For example, changes in moisture availability due to either warming or CO_2 could contribute to changes in labile C availability and thus affect the extent of priming (Dijkstra and Cheng, 2007b).

Priming is often assessed by measuring CO_2 fluxes and not directly by assessing C turnover and thus it is difficult to determine whether the C is derived from stable OM or from microbial turnover (Blagodatskaya and Kuzyakov, 2008). We directly assessed the rate of decomposition of the resistant pool under the range of labile C availability generated by the experimental treatments; thus we interpret the positive relationship between decomposition rate, plant biomass and DOC as likely evidence of priming. We speculate that if the increased availability of labile C were to persist over multiple growing seasons in a field situation, the sustained priming could lead to a gradual depletion of the resistant C pool (Carney et al., 2007).

We did not make comparisons of the magnitudes of the estimated rates and pools among the three incubation experiments because some of the environmental conditions and length of incubation differed between them. Our interpretations are thus restricted to the treatment effects observed at different collection times. The choice for

incubation temperatures, 25°C in mid-growing season and 15°C in the beginning of the season incubations had the purpose of representing average soil temperatures at the time of collection so an artificial response to an abrupt temperature change was avoided.

In summary, our study showed that the effects of experimental climate change affected both labile and resistant soil C pools and their intrinsic decomposability, and that these effects were mediated by plant biomass inputs via their effects on available C in the rooting zone. Effects of elevated CO_2 were observed in both study years, but warming effects on soil labile C cycling were observed only in the first growing season, suggesting a transient effect on the microbial response to warming. Long-term, multi-factor global change experiments such as PHACE are needed to better predict feedbacks between SOM cycling and climate change.

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Table 1. Average daily soil water content and temperature at two soil depths over the six weeks period prior to soil collections in 2007 and 2008.

	June 2007		April 2008		July 2008	
Soil water content (%)	0–10 cm	10–20 cm	0–10 cm	10–20 cm	0–10 cm	10–20 cm
ct	10.6 (0.59)	15.6 (1.00)	15.8 (1.18)	19.6 (1.07)	8.9 (0.25)	13.8 (0.82)
cT	9.7 (0.38)	12.7 (0.84)	13.8 (0.45)	15.7 (1.01)	7.9 (0.22)	11.5 (0.72)
Ct	13.0 (0.87)	17.7 (1.35)	16.7 (0.82)	19.3 (1.12)	11.6 (0.63)	16.2 (1.08)
CT	11.5 (0.67)	15.1 (1.30)	16.3 (0.89)	18.0 (1.68)	9.6 (0.57)	13.6 (1.25)
Soil Temperature (°C)	3 cm	10 cm	3 cm	10 cm	3 cm	10 cm
ct	19.0 (0.17)	17.5 (0.16)	3.6 (0.09)	3.5 (0.10)	24.9 (0.15)	23.2 (0.15)
cT	21.6 (0.12)	19.5 (0.06)	5.7 (0.22)	5.1 (0.17)	28.4 (0.11)	25.2 (0.22)
Ct	18.6 (0.10)	17.3 (0.12)	3.3 (0.16)	3.1 (0.11)	24.1 (0.11)	22.7 (0.20)
CT	21.5 (0.20)	19.4 (0.07)	5.4 (0.18)	5.0 (0.11)	27.6 (0.31)	25.0 (0.13)

Values are means with standard error in parentheses. *ct*: ambient CO_2 and ambient temperature; *cT*: ambient CO_2 and elevated temperature; *Ct*: elevated CO_2 and ambient temperature; *CT*: elevated CO_2 and elevated temperature.

Table 2. Above-ground biomass ($g\,m^{-2}$), fine root biomass ($g\,m^{-2}$ of ash-free dry weight in top 15 cm), and dissolved organic C in soil (DOC, $g\,m^{-2}$ in top 15 cm) at the time of peak aboveground biomass in 2007 and 2008.

	Above-ground biomass		Fine root biomass		DOC	
	2007	2008	2007	2008	2007	2008
ct	82.9 (4.0)	87.9 (1.7)	262.6 (27.6)	344.2 (27.4)	3.2 (0.4)	4.4 (0.4)
cT	82.3 (7.5)	89.9 (5.8)	215.1 (25.6)	294.6 (28.1)	2.7 (0.3)	5.3 (0.6)
Ct	82.9 (7.1)	95.7 (8.2)	295.8 (34.6)	342.2 (31.2)	3.1 (0.5)	4.8 (0.5)
CT	113.7 (11.2)	104.8 (4.7)	302.1 (29.5)	441.7 (60.4)	3.2 (0.5)	6.5 (1.0)
ANOVA p-values						
CO_2	0.06	0.005	0.07	0.08	0.64	0.24
Warming	0.07	0.14	0.51	0.53	0.64	0.06
CO_2 × Warming	0.06	0.35	0.39	0.08	0.48	0.56

Values are means with standard error in parentheses. *ct*: ambient CO_2 and ambient temperature; *cT*: ambient CO_2 and elevated temperature; *Ct*: elevated CO_2 and ambient temperature; *CT*: elevated CO_2 and elevated temperature.

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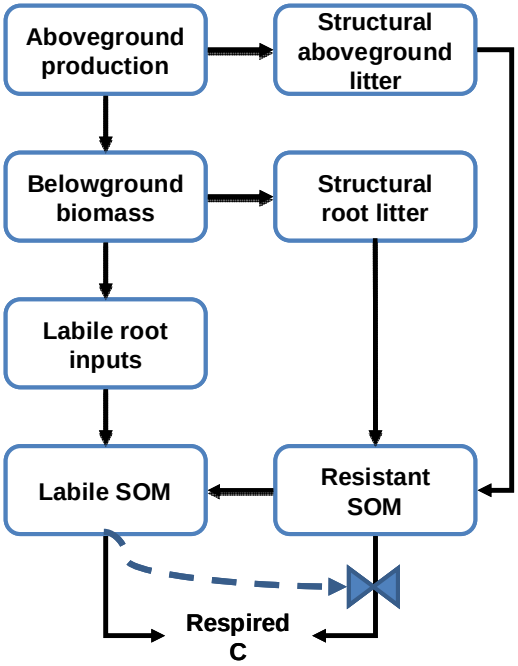

Fig. 1. Effects of warming and elevated CO_2 on soil organic matter (SOM) dynamics via plant production can be direct, by determining inputs to soil or indirect through the regulation of decomposition of soil C pools. Aboveground production and biomass can respond to elevated CO_2 via enhanced photosynthesis and to warming mainly via modifications in the soil water status and/or nutrients availability. Senesced aboveground biomass and production translocated to roots (Belowground biomass) are sources of non-easily degradable litter (Structural aboveground litter and Structural root litter) materials that become part of the Resistant SOM pool. The Belowground biomass is a determinant of the amount of belowground Labile root inputs in the form of exudation, slough-off or labile materials turnover. Recent photosynthates released through roots can constitute a considerable proportion of the dissolved organic C in soil, which in turn, along with other recent labile materials and products of decomposition make up the Labile SOM. As a readily available source of C for microbes, the size of the Labile SOM pool may partly control the decomposition of the Resistant SOM through the priming effect i.e. the observed enhancement of decomposition of resistant SOM associated with a greater availability of C.

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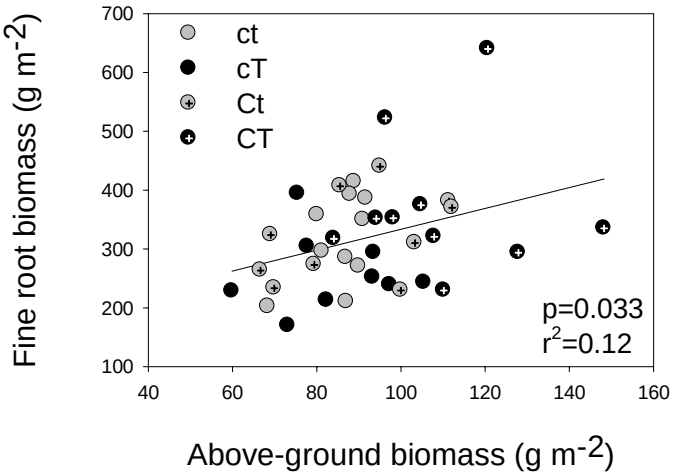

Fig. 2. Linear relationship between above-ground plant biomass and fine root biomass (0–15 cm depth) at the time of peak biomass in 2007 and 2008.

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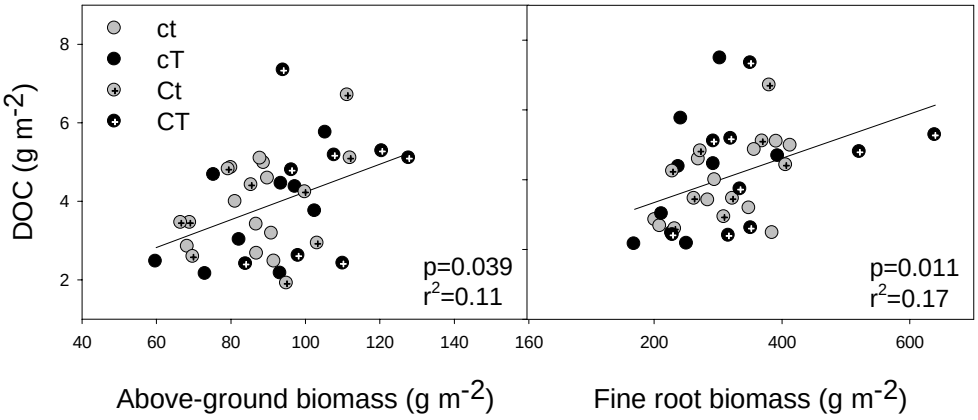

Fig. 3. Linear relationship between dissolved organic C in soil (0–15 cm; DOC) and above-ground plant biomass and fine root biomass (0–15 cm) at the time of peak biomass in 2007 and 2008.

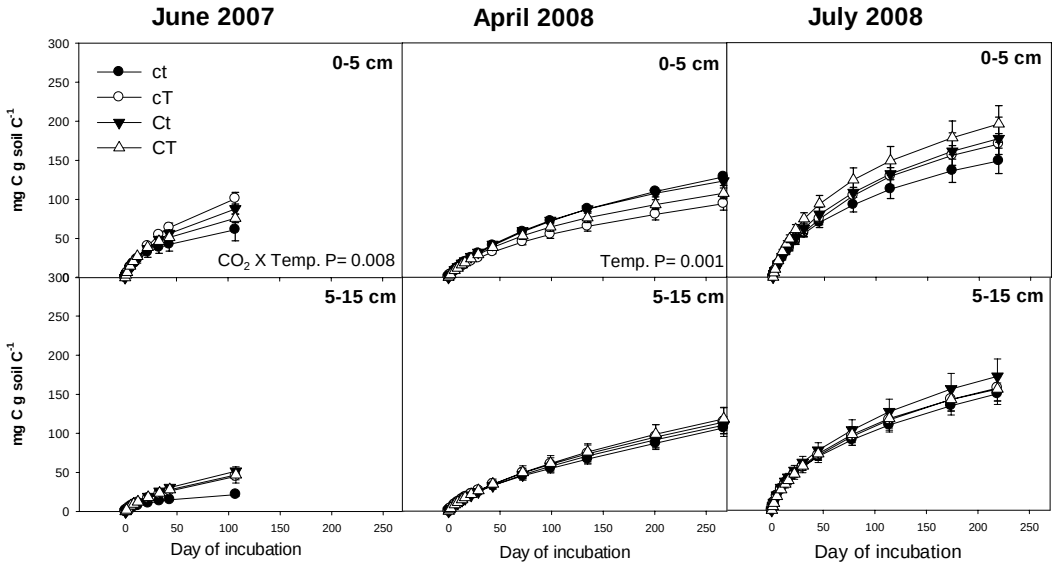

Fig. 4. Total C mineralized per gram of soil C during incubation of soils collected in June 2007, July 2008 (mid-growing season) and at the beginning of the growing season in April 2008. Treatment effects shown are for the final values (2-way ANOVA by depth). Values are means ± standard error. *ct*: ambient CO_2 and ambient temperature; *cT*: ambient CO_2 and elevated temperature; *Ct*: elevated CO_2 and ambient temperature; *CT*: elevated CO_2 and elevated temperature.

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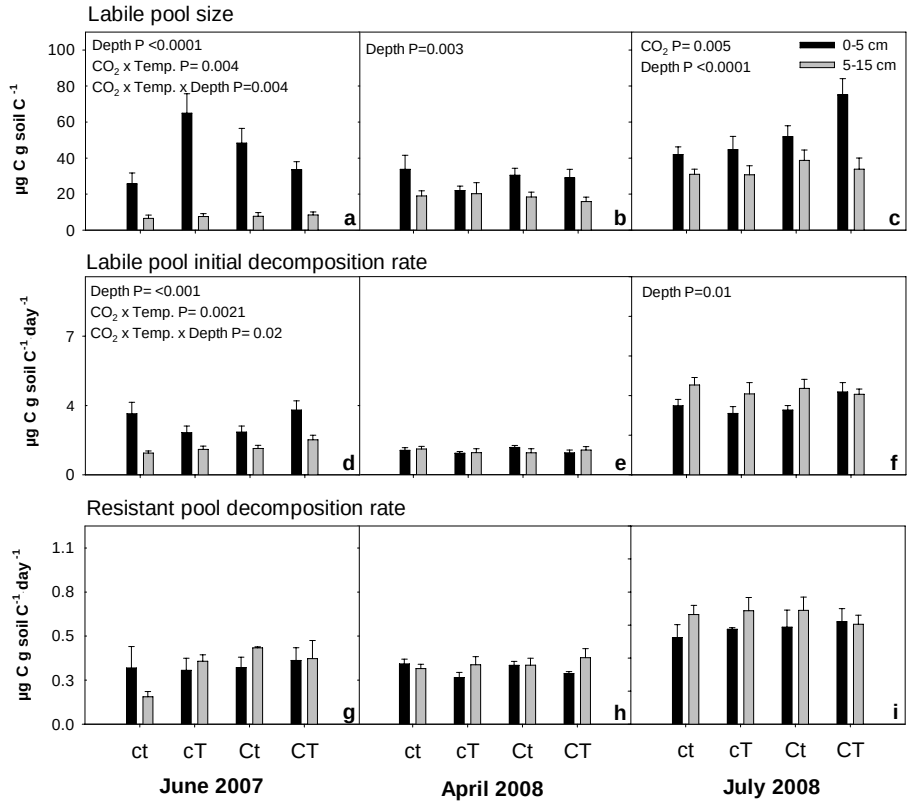

Fig. 5. Proportion of total C in the labile pool size and its initial decomposition rate and decomposition rate of the resistant pool in of soils collected in mid-growing season in July 2007 and 2008 and at the beginning of the growing season in April 2008. Values were estimated through non-linear regression of observed respiration rates during incubation (see Methods). Values are means ± standard error. *ct*: ambient CO_2 and ambient temperature; *cT*: ambient CO_2 and elevated temperature; *Ct*: elevated CO_2 and ambient temperature; *CT*: elevated CO_2 and elevated temperature. p values of treatment effects from 3-factor ANOVA are shown only when effects were considered significant. Incubations of mid-season soils (2007 and 2008) and beginning of season soils took place at 25 °C and 15 °C, respectively.

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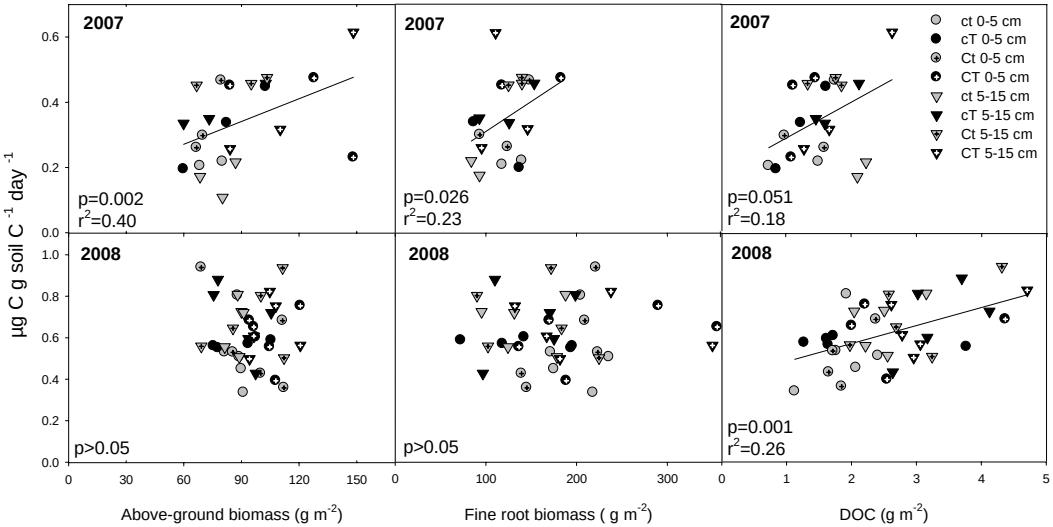

Fig. 6. Linear relationships between the estimated rate of decomposition of the resistant C pool and field measured above-ground biomass, root biomass and dissolved organic C (DOC) for mid-growing season soils in 2007–2008.

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