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Soil carbon responses to past and future CO_2 in three Texas prairie soils

Andrew C. Procter [a, *], Richard A. Gill [b], Philip A. Fay [c], H. Wayne Polley [c], Robert B. Jackson [d, e]

[a] Department of Biology, Duke University, Durham, NC 27708, USA
[b] Department of Biology, Brigham Young University, Provo, UT 84602, USA
[c] Grassland, Soil and Water Research Laboratory, US Department of Agriculture, Agricultural Research Service, Temple, TX 76502, USA
[d] Nicholas School of the Environment, Duke University, Durham, NC 27708, USA
[e] School of Earth Sciences, Stanford University, Stanford, CA, USA

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ABSTRACT

Changes in soil carbon storage could affect and be affected by rising atmospheric CO_2. However, it is unlikely that soils will respond uniformly, as some soils are more sensitive to changes in the amount and chemistry of plant tissue inputs whereas others are less sensitive because of mineralogical, textural, or microbial processes. We studied soil carbon and microbial responses to a preindustrial-to-future CO_2 gradient (250–500 ppm) in a grassland ecosystem in the field. The ecosystem contains three soil types with clay fractions of 15%–55%: a sandy loam Alfisol, a silty clay Mollisol, and a black clay Vertisol. Soil and microbial responses to atmospheric CO_2 are plant-mediated; and aboveground plant productivity in this ecosystem increased linearly with CO_2 in the sandy loam and silty clay. Although total soil organic carbon (SOC) did not change with CO_2 treatment after four growing seasons, fast-cycling SOC pools increased with CO_2 in the two clay soils. Microbial biomass increased 18% and microbial activity increased 30% across the CO_2 gradient in the black clay (55% clay), but neither factor changed with CO_2 in the sandy loam (15% clay). Similarly, size fractionation of SOC showed that coarse POM-C, the youngest and most labile fraction, increased four-fold across the CO_2 gradient in the black clay, but increased by only 50% across the gradient in the sandy loam. Interestingly, mineral-associated C, the oldest and most recalcitrant fraction, declined 23% across the gradient in the third soil type, a silty clay (45% clay). Our results provide evidence for priming in this soil type, as labile C availability and decomposition rate (measured as soil respiration and soil C mineralization) also increased across the CO_2 gradient in the silty clay soil. In summary, CO_2 enrichment in this grassland increased the fast-cycling SOC pool as in other CO_2 studies, but only in the two high-clay soils. Priming in the silty clay could limit SOC accumulation after prolonged CO_2 exposure. Because soil texture varies geographically, including data on soil types could enhance predictions of soil carbon and microbial responses to future CO_2 levels.

1. Introduction

Globally, soils contain about three times as much carbon (C) as the atmosphere and are the largest terrestrial pool of C (Schlesinger, 1997; Jobbágy and Jackson, 2000). Because C cycles between the atmosphere and soil through photosynthesis and respiration, changes in physiological processes could affect atmospheric CO_2 levels by altering soil C pools. Conversely, changes in atmospheric CO_2 could affect soil C storage through changes in plant and microbial activities. Whether soils will be a CO_2 source or sink under future CO_2 levels remains uncertain (Pepper et al., 2005). Some of this uncertainty surrounds the mechanisms by which soils sequester C and the effects of elevated CO_2 on these mechanisms.

There are several hypothetical outcomes for soil C under elevated CO_2. One is an increase in soil C due to CO_2-induced plant growth. Increased plant growth leads to greater rhizodeposition

* Corresponding author. Present address: ORISE/US Environmental Protection Agency, 109 T.W. Alexander Drive, Research Triangle Park, NC 27711, USA. Tel.: +1 205 919 8928.
E-mail address: acprocter@gmail.com (A.C. Procter).

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into soil (Hungate et al., 1997), some of which becomes stabilized as soil organic carbon (SOC) (Fig. 1). Some meta-analyses have found that soil C increases by about 6% in elevated CO_2 experiments (Jastrow et al., 2005; Luo et al., 2006). Alternatively, soil C could decrease as atmospheric CO_2 rises if decomposition rates also increase. Soil CO_2 efflux (soil respiration), a measure of decomposition, commonly increases at elevated CO_2 (Zak et al., 2000; Jackson et al., 2009). Some of this increase could be due to priming, in which labile C released from roots stimulates microbial growth and the decomposition of older soil organic matter (Fu and Cheng, 2002; Carney et al., 2007; van Groenigen et al., 2014). Because older soil organic matter represents the majority of SOC, priming could limit long-term soil C sequestration. Finally, soil C could remain unchanged at elevated CO_2. Increases in plant C input could be balanced by increases in decomposition, or gains in new SOC pools could be offset by losses in older SOC pools (Sayer et al., 2011). The latter mechanism was found in a grassland CO_2 enrichment experiment after four years of CO_2 treatment; the most labile fractions of SOC increased, whereas the most recalcitrant fractions decreased, leading to a negligible increase in total SOC (Gill et al., 2002, 2006). It is also possible that SOC responses to CO_2 are simply too small to detect, which was the conclusion of a recent meta-analysis (Hungate et al., 2009).

When soil C does respond to elevated CO_2, the response shape is not well known. Most CO_2 experiments include only an elevated and ambient treatment, so it is uncertain whether soil C cycling will change linearly as atmospheric CO_2 rises or will instead show a threshold response. Given the large change in atmospheric CO_2 levels that terrestrial ecosystems have experienced during the past 250 years, and the range predicted for this century, it is useful to study ecosystem responses to CO_2 under a range of CO_2 levels. Ecosystem experiments involving a range of CO_2 levels to date include chaparral (Treseder et al., 2003), wheat (Polley et al., 1993) and grasslands (Ross et al., 2000; Gill et al., 2002, 2006). Many of these studies showed an increase in soil C with CO_2 concentration up to ~500–600 ppm, followed by plateau or decline at higher CO_2 concentrations.

Most CO_2 experiments test one soil type, so it is also not clear how soil type influences CO_2 effects on plant productivity, decomposition, and soil C. Soil texture affects productivity and decomposition through factors such as particle surface area and porosity, which influence water holding capacity, cation exchange capacity, and many other factors. Finer-textured (higher silt + clay) soils have greater surface area, allowing greater water and nutrient retention. As a result, they tend to have greater plant productivity in temperate climates (Sala et al., 1988; Reich et al., 1997; Brady and Weil, 2002). Soils with higher silt and clay content also generally sequester more C than sandier soils, with maximum C sequestration at intermediate-to-high values of silt + clay content (>60% silt + clay) (Burke et al., 1989). This occurs because decomposition is generally slowest in the finest-textured soils, where lower O_2 inhibits aerobic microbial processes, and organic matter is physically protected by clay-humus complexing and soil aggregation (Bosatta and Agren, 1997; Krull et al., 2001; Brady and Weil, 2002). SOC content is positively related to soil clay content both at a global scale (Jobbágy and Jackson, 2000) and a landscape scale (Plante et al., 2006). Soil C models typically use clay content or cation exchange capacity to simulate soil texture effects on physical protection of organic C (Krull et al., 2001; Dungait et al., 2012).

We address how soil type affects the responses of productivity and soil C to CO_2, as well as mechanisms behind soil C dynamics. We studied soil C dynamics in a prairie ecosystem on three soils of contrasting texture (sandy loam, silty clay, clay) that were exposed to a continuous gradient of preindustrial-to-future CO_2 levels (250–500 ppm) in the field. We hypothesized that CO_2-induced plant growth would peak on the intermediate (silty clay) or highest-clay (black clay) soil. We expected that these soil types would provide plants with more water and nutrients, allowing higher growth at elevated CO_2. In contrast, we hypothesized that CO_2 stimulation of decomposition would decrease in finer textured soils. Clays physically protect SOC from decomposition, a dampening effect on substrate-induced decomposition with elevated CO_2. In sum, we expected that the CO_2–induced increase in soil C sequestration would be a positive function of soil clay content, with greatest C sequestration in the silty clay or black clay and the least in the sandy loam.

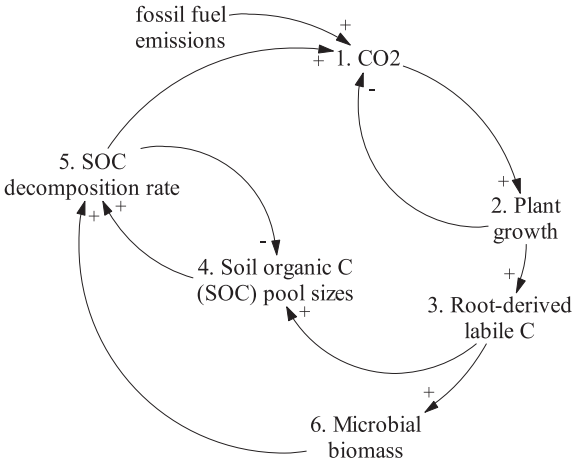

Fig. 1. Conceptual diagram for prairie soil C cycle responses to elevated CO_2. Positive effects are (+) signs, negative effects are (−) signs. Rising CO_2 (1) stimulates plant growth (2), resulting in greater plant C inputs to soil (3) and reduced CO_2 (1). SOC accumulates (4) if plant C inputs exceed decomposition losses (5). SOC decreases if decomposition exceeds plant inputs, possibly as the result of "priming." A priming response involves change in quality or quantity of plant inputs to soil (3), change in microbial biomass (6), and change in decomposition of SOC (5).

2. Materials and methods

2.1. Study system

The research was conducted at the Lysimeter CO_2 gradient (LYCOG) facility operated by the USDA-ARS Grassland Soil and Water Research Laboratory in Temple, TX (Fay et al., 2009, 2012; Polley et al., 2012a). The facility consists of two elongated tunnel-shaped chambers covered in clear plastic. Each chamber is 1.2 m wide and tall and 60 m long. Photosynthesis during daylight and respiration at night were used to create CO_2 gradients. Desired CO_2 concentration gradients were maintained by automatically varying the rate of air flow through chambers in response to changes to photosynthesis (daylight) or respiration rates (night). CO_2 is injected into air entering one tunnel to initiate an elevated to ambient CO_2 gradient (510–380 ppm). Ambient air is introduced into the second tunnel to create an ambient to subambient CO_2 gradient (380–250 ppm). Night-time CO_2 concentrations were regulated at 130–150 ppm above daytime values along each chamber. Cooling coils installed at 5-m intervals along the chambers prevented a temperature gradient from forming. Soil monoliths within chambers were planted with a mixture of perennials – grasses and forbs – representative of the Texas Blackland Prairie located at the site (Table S1). Three soil types were installed along the gradient: a sandy loam Alfisol (Bastsil series) with as much as 15% clay and 60–73% sand in the upper 50 cm, a silty clay Mollisol (Austin series) with up to 45% clay in the upper 50 cm and a black clay Vertisol (Houston series) with as much as 55% clay in the upper 50 cm.

These three soils span much of the clay content range among elevated CO_2 experiments on soil C (Fig. 2, Tables S2 and S3). Bastsil soils (fine-loamy, siliceous, active, thermic Udic Paleustalfs) are made from alluvial sediments and commonly occur on stream terraces. Austin soils (fine-silty, carbonatic, thermic Udorthentic Haplustolls) are found in erosional uplands. Houston Black soils (very-fine, smectitic, thermic Udic Haplusterts) are heavy shrink-swell clays found in lowland areas. Soils were excavated in 2002 as intact monoliths (1 m × 1 m × 1.5 m deep) from sites near the facility, placed into the two chambers, and herbicide was applied to remove existing vegetation. In 2003, a standardized mixture of perennial grasses and forbs was transplanted into the monoliths, representing Texas Blackland Prairie (Table S1). Soils were watered with a metered drip irrigation system using temporal and volume patterns from an average year in central Texas (Fay et al., 2009; Polley et al., 2012a). Mean annual precipitation is 914 mm (1977–2000). The July–August mean maximum temperature is 35 °C, and the December mean minimum is 2.9 °C. CO_2 treatment began in 2006, and typically extends from April–October, the portion of the growing season during which photosynthesis is sufficiently great to maintain the CO_2 gradient.

2.2. Aboveground net primary production (ANPP)

ANPP was measured at the end of each growing season of CO_2 treatment by clipping vegetation to 5 cm height (Polley et al., 2012a). (ANPP data in this paper is from November 2008 and 2009.) Harvested biomass was oven dried for 72 h at 60 °C before weighing. Each following January, harvested biomass was returned to its respective monolith along the CO_2 gradient to minimize harvest effects on element cycling. Biomass was shredded with a wood chipper before it was returned to plots to simulate the effect of late-season mowing.

2.3. Soil sampling and C and N measurement

Soils from the CO_2 gradient were sampled at the end of the fourth growing season of CO_2 treatment (Nov 9, 2009). Soil was cored to 15 cm depth, shipped to Duke University (Durham, NC) and air dried. Soils were broken into an aggregate size allowing passage through a 5.6-mm sieve, then aggregates were passed through a 2-mm sieve to remove roots. Soil C was determined by combustion gas chromatography (NC 2100 Soil analyzer, ThermoQuest Italia, S.p.A., Italy). Air-dried, homogenized soil (50–70 mg) was combusted at 600 °C for organic C and at 1050 °C for total C and total N. Carbonates make up the difference between organic C and total C.

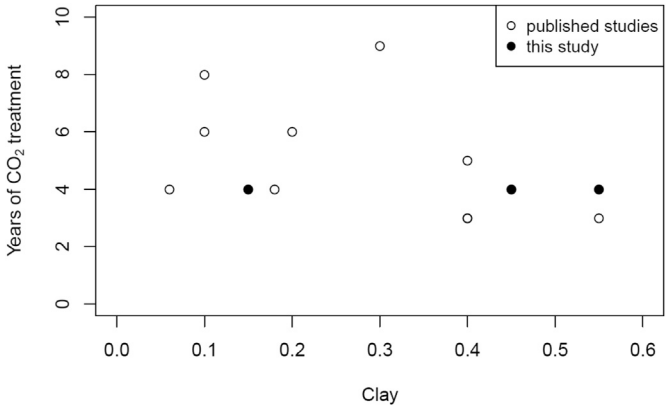

Fig. 2. Soil textures in this study, in the context of eight representative published studies of soil C responses to elevated CO_2. The duration of CO_2 treatment is also shown. Details of each study are listed in Table S2.

Subsamples of the fresh November 2009 soil cores were also shipped to Brigham Young University (Provo, UT) for physical fractionation, which provides a convenient index of soil C fractions of varying age (Gill et al., 2002; Gill, 2007). First, soils were seived to 2 mm to remove root biomass. Soil was then dispersed for 18 h in 0.5 M sodium hexametaphosphate, and the resulting soil slurry was passed through 250 μm and 53 μm sieves. The organic matter collected on these sieves is considered particulate organic matter (POM), and has been shown to have a residence time between a decade and a century, similar to the "slow" or "intermediate" pools in simulation and conceptual models (Six et al., 2002; Gill, 2007; Stewart et al., 2008). Coarse particulate organic matter (POM) C (>250 μm) represents the youngest organic carbon, with residence time shorter than a decade. Fine POM C (53–250 μm) is typically less than a century old. Mineral-associated C (<53 μm) is the most recalcitrant size fraction, centuries to millennia old (Cambardella and Elliott, 1992; Leavitt et al., 1996; Kelly and Burke, 1997). Mineral-associated C was collected from the soil slurry that had passed through the 53 μm sieve. Each fraction was ground, then acid-treated to remove carbonates. Acid treatment represents an alternative to the combustion method for separating organic from inorganic C; both methods yielded similar total organic C. Soil organic C stocks were estimated using organic carbon concentrations from fractionation and bulk density of each soil type.

2.4. Microbial biomass determination

Active microbial biomass in soils across the CO_2 gradient was determined by substrate-induced respiration (SIR), following the methods of Gill et al. (2006) and Gill (2007). SIR is an index of potential microbial activity in the absence of substrate limitation. In preparation for SIR, air-dried soils from the November 2009 cores were re-moistened to 60% field capacity and pre-incubated for 9 days. Two grams of soil were weighed into 40 mL glass vials with septa. Ten milliliters of 4 g L^{-1} autolyzed yeast solution were added to the soil as a substrate, then vials were capped and headspace CO_2 was measured immediately. Headspace CO_2 was measured again at 2 h and 4 h using a LI-6200 portable photosynthesis system and LI-6250 CO_2 analyzer (LI-COR, Lincoln, NE). Respiration rate was determined based on the change in headspace CO_2 over these 4 h. The rise in headspace CO_2 was approximately linear over this time. Between measurements, vials with the yeast-soil slurry were placed on a table shaker at room temperature (21 °C). Microbial biomass was calculated from SIR according to the equation: $SMBC = (40.04 \times CO_2) + 0.37$, where SMBC is soil microbial biomass carbon (μg C g^{-1} soil) and CO_2 is the respiration rate after substrate addition (μL CO_2 g^{-1} soil h^{-1}) (Anderson and Domsch, 1978; Bailey et al., 2002).

2.5. Carbon mineralization incubations

The remaining soil (not subjected to SIR) was pre-incubated for three more days (for 12 days total preincubation), then incubated in the lab for one year to assess long-term carbon mineralization (C_{min}) kinetics from along the CO_2 gradient. A one week pre-incubation before long-term incubation reduces artifacts of previously dried soils (Paul et al., 2001). Soils were maintained in the dark, at ambient (room) CO_2 concentration, with constant moisture and temperature to isolate the effect of native microbial biomass and available carbon on decomposition rates. Soils were incubated at room temperature (21 °C) in 1 pint (473 mL) canning jars with septa added to their lids (Paul et al., 2001; Gill, 2007). Each jar

contained a plastic cup with 40 g (dry mass) soil moistened to 60% field capacity. Field capacity was determined using soil of the same series (Bastsil, Houston, and Austin), from locations that were the source of soils used in the CO_2 gradient (V Jin, pers. comm.) Ten milliliters of water was added to the bottom of each jar (not contacting the soil) to reduce soil drying. Soils were weighed monthly to determine evaporation, and an equivalent weight of water was added back. When jars were not being measured for C_{min}, the septa were removed, and the jars were placed uncapped in a dark cabinet. With septa removed, the lids had a small (~0.5 cm diam.) hole for air exchange, to reduce CO_2 buildup in the jars.

C_{min} rate was calculated based on the rate of CO_2 buildup in jars, measured using a LI-6200 portable photosynthesis system and LI-6250 CO_2 analyzer (LI-COR, Lincoln, NE). Jars were capped, then CO_2 was measured immediately, and again after 2 and 4 h to determine the average rate of CO_2 concentration buildup. Jar headspace air was sampled using a 1 mL glass syringe. C_{min} rate was measured initially at 4 day intervals to day 12, then approximately 12 day intervals to day 74, then approximately 24 day intervals to day 233, with final measurements at day 277 and 365. The long term trend in C_{min} rate was modeled assuming SOC decomposition occurred in two pools (Paul et al., 2001; Gill, 2007):

$$C(t) = C_a{*}\exp(-k_a t) + C_s{*}\exp(-k_s t),$$

Where C(t) is soil C at time t, C_a is the active C pool at time 0, C_s is the slow-cycling C pool at time 0, k_a and k_s are the decay constants for the active and slow pools, respectively. The derivative of the equation is C_{min} rate, which was used to fit the data,

$$C_{min}\ \text{rate} = dC/dt = -k_a C_a{*}\exp(-k_a t) - k_s C_s{*}\exp(-k_s t)$$

We made the simplifying assumption that an additional, recalcitrant C pool contributed little to C_{min} rate. Therefore the model was not constrained to data on total soil C, and the difference between $C_a + C_s$ and experimentally-determined total C represents the recalcitrant C pool. Mean residence time (MRT) for a given pool is the reciprocal (1/k) for its respective decay constant.

2.6. Soil CO_2 efflux (soil respiration)

Soil CO_2 efflux was measured in the field as an index of belowground carbon bioavailability and microbial activity. Soil CO_2 efflux was measured through soil collars, monthly during each year of CO_2 treatment (May–September, 2006-present), using a LI-COR 6400 infrared gas analyzer (LI-COR, Lincoln, NE). The 10-cm deep PVC soil collars are permanently inserted to 7.5 cm depth in the soil (Fay et al., 2009). The collars are near vegetation, but were kept vegetation free to prevent leaf gas exchange from interfering with soil CO_2 efflux measurement. Soil CO_2 efflux represents combined root and microbial respiration.

2.7. Statistical analyses

The relationship between CO_2 concentration and soil variables including organic C, microbial biomass, carbon mineralization, and modeled active and slow C, was analyzed by regression. All statistics were performed in R (R Core Development Team, 2010) with the exception of the SOC physical fraction regressions and the incubation kinetics nonlinear regressions, which were performed in SigmaPlot (Systat Software 2008). The kinetics regression was in the form:

$$C_{min}\ \text{rate} = a{*}\exp(b{*}t) + c{*}\exp(d{*}t),$$

Where $a/b = C_a$ (active C) and $c/d = C_s$ (slow-cycling C).

In this study, sampling was designed to capture the range of CO_2 treatments and soil types. The full CO_2 gradient contains 20 sections, each section containing 4 soil monoliths: two of one soil type and two of another (Table S4). ANPP, soil CO_2 efflux, and SOC physical fractions were measured on 60 monoliths across the CO_2 gradient, consistent with another study (Fay et al., 2012). Regressions on laboratory measurements including microbial biomass, C_{min} rate, modeled SOC pools, and total SOC concentration, were done using section averages (Table S5). In those regressions, each data point is the average of two soil subsamples within a CO_2 gradient section. Actual sample sizes and planned sample sizes differ slightly due to missing samples (Table S5). ANPP, soil CO_2 efflux, and SOC physical fractions had planned sample sizes of n = 16,24,20 (sandy loam, silty clay, black clay) whereas microbial and modeled SOC pools had planned sample sizes of n = 8,10,10 (sandy loam, silty clay, black clay).

3. Results

3.1. ANPP responses to CO_2 and soil type

ANPP increased linearly with CO_2 concentration in the sandy loam (2008: $R^2 = 0.36$, $p = 0.01$, 2009: $R^2 = 0.32$, $p = 0.02$) and the silty clay (2008: $R^2 = 0.36$, $p = 0.002$, 2009: $R^2 = 0.53$, $p < 0.0001$) soils but not the black clay ($R^2 = 0.07$, $p = 0.27$) during the third and fourth seasons of CO_2 treatment, respectively (2008, 2009, Fig. 3). In both years, average ANPP differed among soil types (ANOVA: $p < 0.05$). Sandy loam and black clay each had higher ANPP than silty clay in 2008 and 2009 (Tukey's HSD: $p \leq 0.05$). Based on regressions of 2008–2009 pooled data, ANPP increased from ~400 to 720 g DW m^{-2} across the CO_2 gradient in the sandy loam soil, or by 1.7 ± 0.5 g m^{-2} ppm^{-1} CO_2 (regression slope ± SE). In the silty clay soil, ANPP increased from ~250 to 600 g m^{-2}, or by 1.5 ± 0.3 g m^{-2} ppm^{-1} CO_2. This slope did not differ significantly between sandy loam and silty clay ($p = 0.62$).

3.2. Aboveground and belowground responses compared

In the CO_2 gradient experiment, belowground responses to CO_2 and soil type did not track aboveground responses. The ANPP-CO_2 response was greatest in the sandy loam and silty clay soils (Fig. 3a,b), whereas CO_2 increased active soil microbial biomass most in the black clay (Fig. 4c). Based on regression slope, active microbial biomass increased by 0.42 ± 0.10 μg C g^{-1} soil ppm^{-1} CO_2 in the black clay. Two measures of decomposition rate—C_{min} rate and soil CO_2 efflux—also increased with CO_2 in the two clay soils but did not respond to CO_2 in the sandy soil. C_{min} rate increased by 0.020 ± 0.006 μg C g^{-1} soil d^{-1} ppm^{-1} CO_2 across the CO_2 gradient in the silty clay and by 0.018 ± 0.007 μg C g^{-1} soil d^{-1} ppm^{-1} CO_2 in the black clay. Soil CO_2 efflux increased by 0.010 ± 0.004 μmol m^{-2} s^{-1} ppm^{-1} CO_2 in the silty clay and black clay (Fig. 4c, e, f, Table 1). For C_{min} rate and soil CO_2 efflux, the slope did not differ significantly between silty clay and black clay ($p > 0.8$).

3.3. Modeled SOC pools from one-year incubation

Active (easily-decomposable) soil organic C increased linearly by 75% across the CO_2 gradient in the black clay, as determined by a two-pool exponential model of C_{min} rate (Fig. 5b, Table S6). This soil incubation model was significant for all samples ($p < 0.01$, Fig. S1) but better fit the data from the sandy loam ($R^2 > 0.91$ for each CO_2 level) and black clay soils ($R^2 > 0.83$ for each CO_2 level) than silty clay soil (R^2 as low as 0.75; not shown). Modeled slow-cycling C was not affected by CO_2 treatment. On average, black clay soils lost 6%,

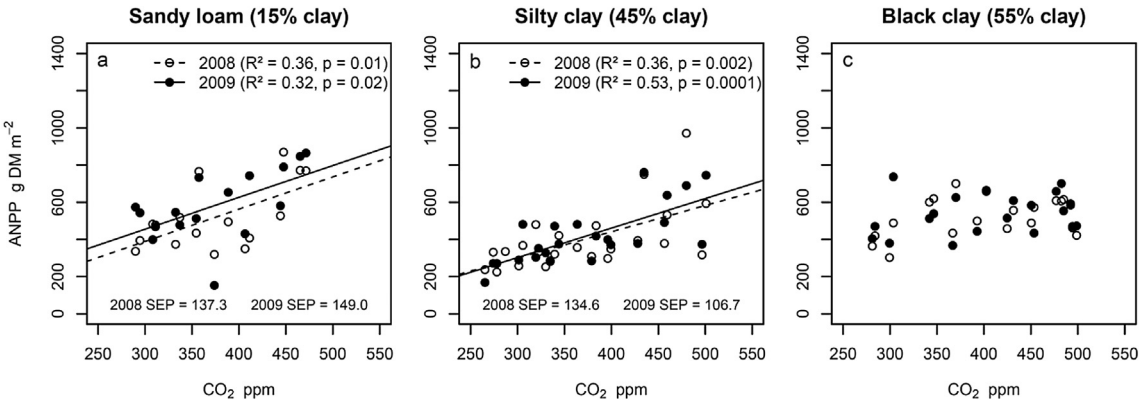

Fig. 3. Aboveground net primary productivity in 2008 and 2009, the third and fourth growing seasons of CO_2 treatment. Linear regressions are significant in the sandy loam (a) and silty clay (b) for both years ($p < 0.05$), but not in the black clay (c). SEP is standard error of prediction.

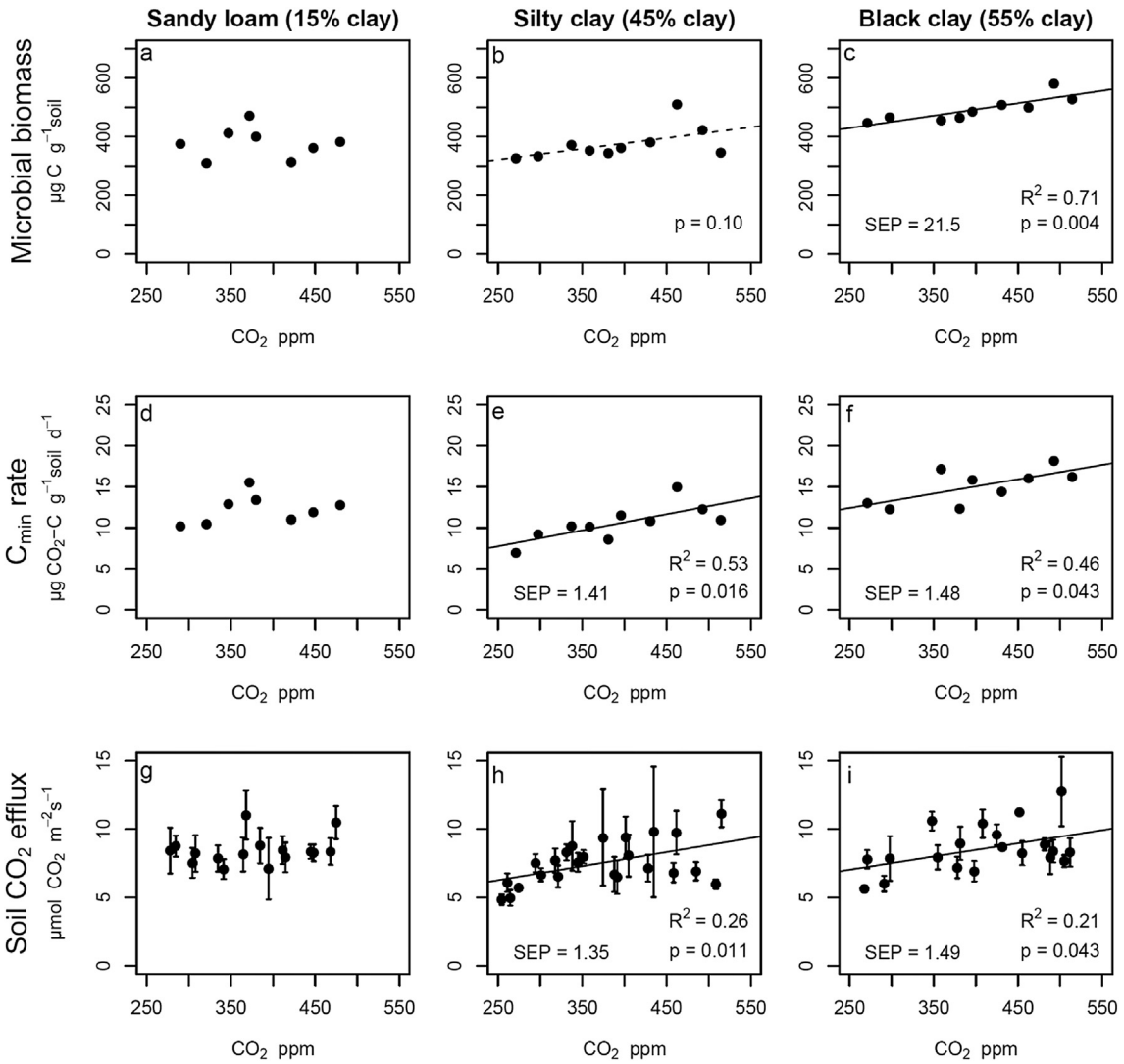

Fig. 4. (a–c) Active microbial biomass measured by substrate-induced respiration (SIR). Microbial biomass had a linear trend with CO_2 in the silty clay (b) and a significant linear increase with CO_2 in the black clay (c). (d–f) Carbon mineralization rate at the start of a one-year soil incubation. (g–i) Soil CO_2 efflux (soil respiration) in the field averaged over the 2009 growing season (May–September, n = 5 for each data point, error bars are standard error).

Table 1
Summary of soil C cycle responses to the CO_2 gradient.

Part of C cycle		Sandy loam 15% clay	Silty clay 45% clay	Black clay 55% clay
C Inputs	ANPP	•+**60%, linear***	•+**40%, linear**	No change
C pools (suggests mechanism)	Total SOC	No change	No change	No change
	Active microbial biomass	No change	Linear trend ($p = 0.1$)	•+**18%, linear**
	Model: active C	No change	Poor model fit	•+**75%, linear**
	Coarse POM-C	•+**50%, linear**	•+**400%, linear**	•+**400%, exponential**
	Mineral-C	No change	•-**23%, linear**	No change
	Model: slow C	No change	Poor model fit	No change
C losses	C_{min} rate	No change	•+**56%, linear**	•+**31%, linear**
	Soil CO_2 efflux	No change	•+**29%, linear**	•+**30%, linear**

*• indicates variables with statistically significant ($p < 0.05$) responses to CO_2 treatment.

silty clay soils lost 12%, and sandy loam soils lost 26% of SOC, as determined by combustion of pre- and post-incubation samples (Fig. 6a). The incubation model estimates for SOC loss, based on cumulative C mineralization, were in a similar range: 6–8% loss in black clay and 15–20% loss in sandy loam (data not shown). Although the black clay had higher decomposition rate by soil mass than the silty clay or sandy loam (Tukey's HSD: $p < 0.03$, Fig. 4d–f), the clay-rich soils had less-bioavailable C and lost a smaller proportion of SOC over long-term incubation (Fig. 6). Consistent with this, decomposition rate increased with clay content and SOC concentration, but the modeled active C pool decreased with clay content (Table S6).

SOC loss over one-year incubation was unaffected by the CO_2 gradient. CO_2 had no effect on SOC loss, measured by combustion (Fig. 6a) or estimated by the incubation model (data not shown; $p = 0.07$ for both measured and modeled loss). In contrast to cumulative SOC loss, initial C_{min} rate g^{-1} SOC increased linearly with CO_2 in the sandy loam and silty clay ($p < 0.05$) implying that CO_2 increased SOC bioavailability (Fig. 6b). Therefore SOC bioavailability increased with elevated

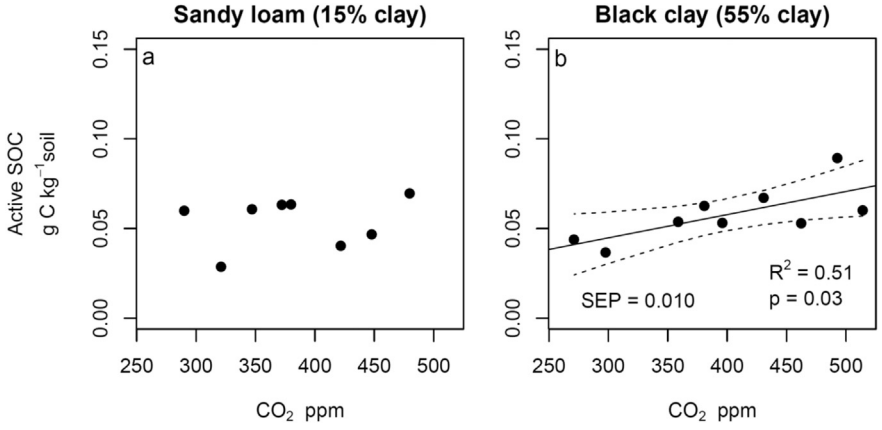

Fig. 5. Active SOC pools in sandy loam (a) and black clay (b) as calculated by the incubation kinetics model. The dotted lines in (b) are the 95% confidence interval for the regression of active SOC vs. CO_2. The modeled slow SOC pools (not shown) had no significant response to CO_2 treatment. Modeled SOC pools for the silty clay are omitted due to poor model fit (R^2 as low as 0.75 compared to $R^2 > 0.83$ for sandy loam and black clay).

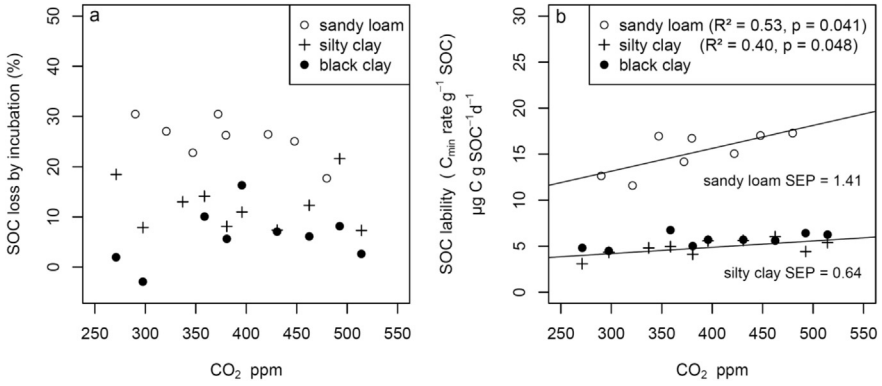

Fig. 6. (a) SOC lost over the one-year incubation (cumulative carbon mineralization), expressed as a percentage of initial SOC. On average, black clay soils lost 6%, silty clay soils lost 12%, and sandy loam soils lost 26% of SOC. SOC loss was determined by combustion of pre- and post-incubation samples. (b) SOC lability based on C_{min} rate g^{-1} SOC at the start of incubation.

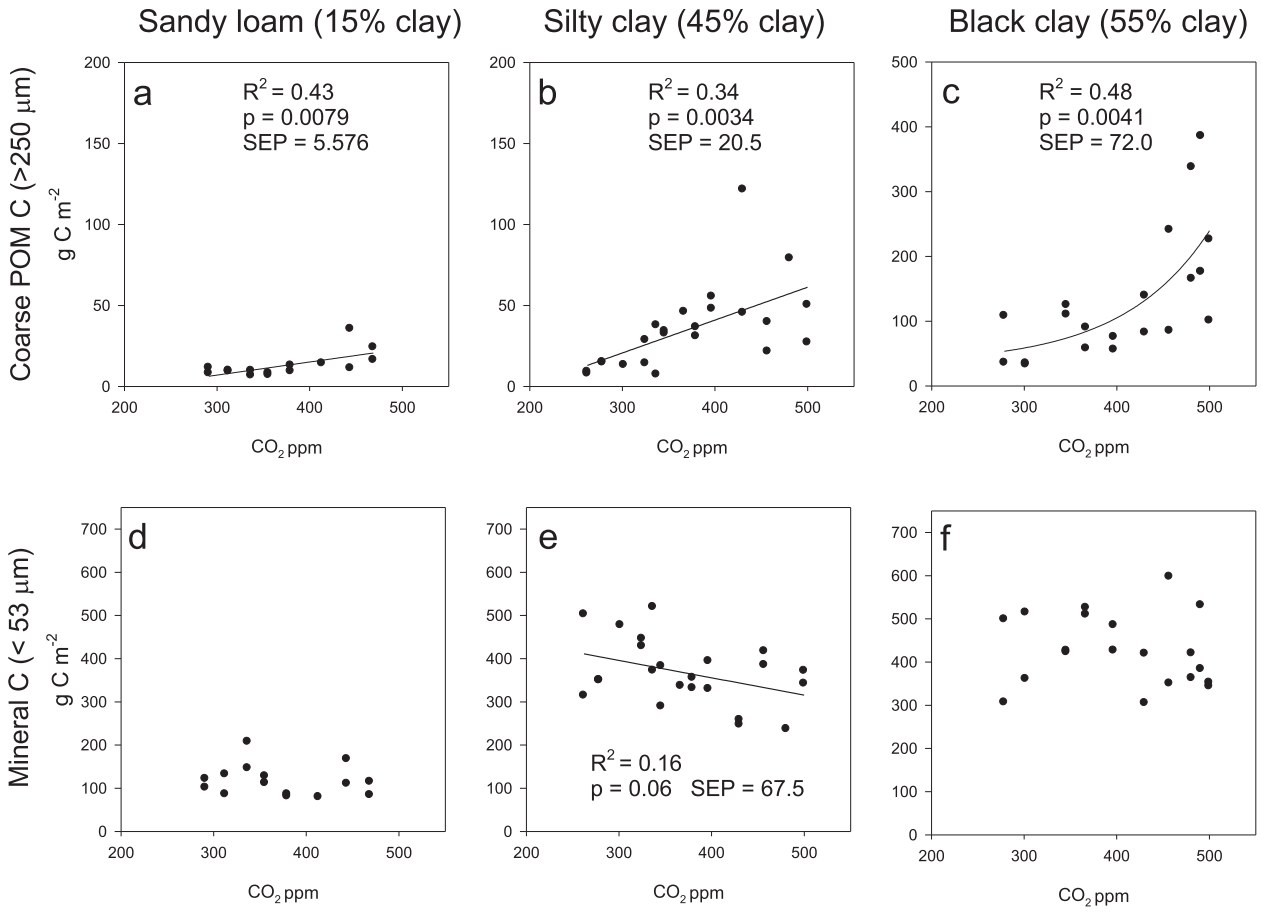

Fig. 7. Organic C in physical fractions of the sandy loam (a, d), silty clay (b, e) and black clay (c, f). Coarse POM C (a–c) represents the youngest, fastest-cycling SOC. The y-scale of (a) and (b) is enlarged to show variation. Mineral C (d–f) represents the oldest and slowest-cycling SOC.

CO_2 only for initial decomposition rate, not cumulative decomposition over a year.

3.4. SOC physical fractionation

In the two clay-rich soils, coarse POM-C increased four-fold across the CO_2 gradient (~50–240 g C m^{-2} in the black clay) but increased by about 50% in the sandy loam (~14–21 g C m^{-2}, Fig. 7a–c). Coarse POM-C represents the youngest, most labile fraction of organic C. Coarse POM-C increased exponentially with CO_2 concentration in the black clay and linearly with CO_2 in the silty clay and sandy loam soils. Fine POM-C is older and less labile than coarse POM-C, and mineral C is the oldest and most recalcitrant fraction. Fine POM-C increased linearly with CO_2 in the sandy loam, but did not respond to CO_2 in the two clay-rich soils (data not shown). Interestingly, mineral C declined 22% across the CO_2 gradient in the silty clay (from ~410 to 320 g C m^{-2}), but did not respond linearly to CO_2 in the other two soils.

4. Discussion

Our study addresses two underexplored areas in how soil organic carbon (SOC) responds to rising atmospheric CO_2: the effect of soil type, and the response shape over a CO_2 concentration gradient. As expected, the bioavailability or decomposability of SOC (C_{min} rate g^{-1} SOC) decreased with soil clay content (Fig. 6). Although we hypothesized that clay physical protection of SOC would also reduce CO_2-induced decomposition, the two clay soils had the most CO_2-induced decomposition, as measured by C_{min} rate and soil CO_2 efflux (Fig. 4d–i). We found no total SOC sequestration after four growing seasons of CO_2 treatment in any soil (Fig. S2). However, labile SOC components defined by incubation or physical fractionation increased with elevated CO_2, particularly in the two high-clay soils as hypothesized (Figs. 5 and 7). Further, soil C priming may have occurred in the silty clay.

4.1. Investigation of potential C priming

Priming is a process whereby the addition of a substrate to soil either increases or decreases microbial decomposition of existing SOC (Kuzyakov et al., 2000). Under CO_2 enrichment, the increase in labile C input from roots could fuel greater microbial biomass, which decomposes more SOC to meet its metabolic needs (Cheng, 1999; Kelley et al., 2011). Evidence for soil C priming under CO_2 enrichment has been seen in a pine forest (Finzi et al., 2006) and a scrub-oak ecosystem (Carney et al., 2007).

In our study, belowground mechanisms consistent with priming occurred in the two clay-rich soils. Labile SOC concentration (Figs. 5 and 7a–c) and decomposition rate (Fig. 4d–i) increased linearly with CO_2 in the silty clay and black clay but showed smaller or negligible CO_2 response in the sandy loam. Active microbial biomass increased linearly with CO_2 in the black clay and increased with a linear trend in the silty clay (Fig. 4b–c), suggesting that the increase in labile C at elevated CO_2 stimulated microbial growth. However, we found evidence for a priming response only in the silty clay soil, in which CO_2 enrichment reduced mineral-associated

SOC (Fig. 7e). A reduction in mineral C could be caused by factors other than priming, such as leaching; however, the increase in labile C and microbial biomass with CO_2 in the silty clay suggest a priming mechanism. CO_2 had no effect on modeled or measured recalcitrant SOC concentration in the black clay soil, despite its increase in microbial biomass. A priming response could become evident in the black clay in later years, or the soil's high clay content may protect organic matter from decomposition and limit priming.

4.2. Aboveground and belowground responses to CO_2 compared

Aboveground and belowground ecosystem responses to the CO_2 gradient were affected differently by soil type. Results did not support our hypotheses that CO_2–induced plant growth would be highest and CO_2-stimulated decomposition lowest in the finest-textured soils. Instead, ANPP increased most with CO_2 in the sandy loam soil (Fig. 3a). This pattern has persisted over four growing seasons, likely due to plant growth from increased soil water potential via reduced plant transpiration at elevated CO_2 (Fay et al., 2012). In contrast, belowground CO_2 effects were largest in the black clay soil, including effects on soil CO_2 efflux as well as on fast cycling C pools such as microbial biomass, modeled active C, and coarse POM-C (Table 1; Figs. 4, 5 and 7a–c). ANPP did not respond significantly to CO_2 in the black clay soil, yet soil CO_2 efflux and C_{min} increased. Although we did not measure root growth, we can assume a root:shoot ratio of 4 for grassland (Jackson et al., 1996; IPCC, 2006). Unless root growth and root (autotrophic) respiration increased with elevated CO_2, this implies that heterotrophic respiration drove the efflux response to CO_2 in this soil. Soil CO_2 efflux, an index of microbial and root metabolism in the field, complements the laboratory index of decomposition, C_{min} rate. Despite increased decomposition rate with CO_2 in the black clay, active C accumulated at elevated CO_2, implying either that CO_2 increased root C inputs more than ANPP, or root C inputs were better protected in high-clay soil, making active C responses more apparent in our assays.

One limitation of our analysis is that, with the exception of soil CO_2 efflux, active soil C responses were measured in soil samples taken at the end of the 2009 growing season. Had the soil been sampled earlier in the growing season, active C responses to CO_2 might have been more pronounced, due to higher photosynthesis and belowground C input. Another uncertainty is the large variation in data points above 400 ppm, particularly in the two clay soils. This variation is seen in silty clay ANPP (Fig. 3b) as well as in both clay soils for soil CO_2 efflux and coarse POM fractions (Figs. 4h and 7b, c). Standard errors of prediction (SEP) were higher in the black clay than the silty loam, indicating greater regression error. In general, the higher variability above 400 ppm in the clay soils may reflect heterogeneity in belowground C inputs or in soil physical characteristics that regulate SOC accumulation, such as aggregation, moisture, or clay content. Additionally, the variability could be a growth effect. Variability could have increased in proportion to plant size at elevated CO_2, as seen in the sandy loam and silty clay, which had the most CO_2-induced plant growth over 2006–2010 (Fay et al., 2012). Variability above 400 ppm reduces our ability to define a CO_2 response shape.

4.3. Other environmental factors in soil C dynamics

Factors such as soil moisture, soil temperature, and plant community composition could explain differences in soil C–CO_2 responses among soil types. Decomposition rates in grassland soil are well known to increase with higher soil moisture and temperature (Mielnick and Dugas, 2000; Epstein et al., 2002). However, the three soils in our experiment experienced similar temperature regimes and the same irrigation regime (Fay et al., 2009). Some difference in decomposition rate may be attributable to water retention differences by soil texture. Contrary to our expectations, soil water potential (plant-available water) was highest in the sandy loam and lowest in the black clay (Fay et al., 2012). In the sandy loam, higher moisture could stimulate decomposition directly through increased microbial activity, or indirectly through higher plant growth and rhizodeposition. Moreover, all three soils experienced increased soil water potential at elevated CO_2 due to reduced plant transpiration (Fay et al., 2012). This water-savings effect was most pronounced in the black clay, and could be a contributing factor as to why microbial biomass and soil CO_2 efflux increased most with elevated CO_2 in the black clay (Table 1). Soil properties such as organic carbon concentration and physical protection of organic matter may limit the role of moisture in decomposition responses, however. Jin et al. (2013) varied soil water content between 25 and 50% of water-holding capacity in a laboratory incubation with the same three soil types. They found that soil and litter decomposition (per kg soil) differed more by soil type than by moisture, with the highest decomposition occurring in the black clay soil. Another possible factor in soil-specific CO_2 responses is the plant community. On the two clay-rich soils, 30–60% of the CO_2-stimulated increase in ANPP is attributed to an increase in the proportion of a C_4 grass, *Sorghastrum nutans*, within the plant community (Polley et al., 2012b). *Sorghastrum* likely outcompeted the drought-adapted C_4 grass *Bouteloua curtipendula* due to higher photosynthetic rate and greater water use efficiency at elevated CO_2 (Fay et al., 2012). We expect that this community change increased *Sorghastrum*'s contribution to root C that entered clay soils at elevated CO_2. Differences in the chemical quality or simply the availability of C from *Sorghastrum* may have contributed to the more pronounced CO_2 responses of C and microbes in the silty clay and black clay soils.

Another possible factor in the observed SOC dynamics is soil nutrient availability. Because we did not fertilize the soils, any nutrient shift along the CO_2 gradient was likely in response to increased plant growth. Across the three soils, plant-available soil inorganic N declined slightly with elevated CO_2 (Fay et al., 2012). This could indicate increased competition between plants and microbes for soil N. Consistent with this, Kelley et al. (2011) found an increase in recalcitrant N-degrading enzymes with elevated CO_2 in the black clay. In a previous CO_2 gradient experiment with the silty clay, Gill et al. (2006) also found decreased soil N availability with elevated CO_2. However, silty clay in the current experiment showed no change in labile (protein) or recalcitrant (chitin) N-degrading enzyme activity with elevated CO_2 (A. Kelley, unpublished data). Although total soil N increased with clay content (Table S3), plant-available soil inorganic N did not differ among the three soils (Fay et al., 2012), suggesting that silty clay had no more N limitation than the other soils. If N limitation contributed to soil C priming in the silty clay, the effect may be subtle. Although we do not have data on soil P, there was no change in alkaline phosphatase enzyme activity with CO_2 in the silty clay soil (A. Kelley, unpublished data). Therefore, there is no evidence connecting soil C priming to P limitation in the silty clay. Alkaline phosphatase activity did increase with elevated CO_2 in the sandy loam, suggesting P limitation (Kelley et al., 2011). This could partly explain the lack of microbial growth with elevated CO_2 in this soil, compared to increased microbial biomass with elevated CO_2 in the clay soils. We did not measure soil K or micronutrients.

4.4. Comparison to other CO_2 experiments: effects of soil type

Field soils vary widely in silt and clay content. US soils range from 11% silt + clay in glacially-derived Minnesota and Michigan

soils to 90% silt + clay in Kansas tallgrass prairie (Zak et al., 1994). Although soil properties are known to influence organic C accumulation, few elevated CO_2 studies have included more than one soil type. Moreover, results from these experiments are mixed. Soil type did not affect soil C sequestration in an annual grassland under elevated CO_2, perhaps because the two soils tested had similar clay content (Luo et al., 1996; Hungate et al., 1997). In contrast, CO_2 enrichment in a beech-spruce ecosystem stimulated greater net C input and retention in an acidic loam than in calcareous sand (Hagedorn et al., 2001, 2003). Our results, like those of Hagedorn et al. (2001, 2003), imply that clay content influenced SOC accumulation by protecting soil organic matter from decomposition. As in their experiment, the sandiest soil in our experiment had the most CO_2-induced plant growth, but the least labile C accumulation, likely because new C was unprotected from decomposition.

There are some caveats in comparing SOC results from our study to others. The physical fractionation method identifies SOC pools based on laboratory procedure, rather than decomposition kinetics. The coarse POM, fine POM, and mineral-associated C fractions may each contain a heterogenous mixture of compounds, meaning the fractions may not completely represent the pools in our incubation model or other incubation-based studies (Wander, 2004; Dungait et al., 2012). We present both fraction and incubation results to give a clearer picture of this disconnect, which is an ongoing area of debate in the literature (Wander, 2004). Another caveat is that the modeled C pool sizes in our study are lower than in other incubation-based studies. In our study, modeled active C is ~0.03–0.07 g kg^{-1} soil in the sandy loam, and 0.03–0.09 g kg^{-1} soil in the black clay. In comparison, active C was 0.13 g kg^{-1} in forest soil (Haile-Mariam et al., 2000), 4 g kg^{-1} in subalpine meadows (Gill, 2007) and 0.5 g kg^{-1} in agricultural soil (Collins et al., 2000). Modeled slow-cycling C in our study was ~2 g kg^{-1} soil in the sandy loam and 3–9 g kg^{-1} in the black clay. Other studies measured slow C as 7–10 g kg^{-1} (Collins et al., 2000; Haile-Mariam et al., 2000; Gill, 2007). Out of simplicity, our model was not constrained to total C, it did not capture a recalcitrant C pool, which may explain these lower estimates. The model ($C_a + C_s$) accounts for only 20% of total SOC, implying that the remaining 80% of SOC is recalcitrant and not influencing decomposition rate.

4.5. Comparison to other CO_2 experiments: shape of CO_2 response

Our study is consistent with others in finding both linear and nonlinear SOC responses to CO_2. In a chaparral experiment, soil C within water-stable aggregates and total soil C increased linearly over 250–650 ppm CO_2 (Treseder et al., 2003). Total SOC increased exponentially along a natural CO_2 gradient in grassland (CO_2 spring; 368–674 ppm), although a linear model also fit the relationship (Ross et al., 2000). In our study, CO_2-response shape differed by soil type and response variable. In the black clay, microbial biomass and modeled active SOC increased linearly with CO_2, whereas coarse POM-C increased exponentially with CO_2. By contrast, most of the SOC pools did not respond to CO_2 in the sandy loam. The only SOC pool which decreased with CO_2 was mineral-associated C in the silty clay.

Our results both support and contrast from those in a previous iteration of the CO_2 gradient experiment (Gill et al., 2006). In that experiment, mesic grassland was exposed to a preindustrial-to-future (200–560 ppm) CO_2 gradient for four years. The grassland had formed on the same soil series (Austin) as the silty clay Mollisol in our current experiment; however, it showed nonlinear rather than linear soil C responses to CO_2. Compared to pretreatment values, total SOC in that experiment declined from ambient to subambient CO_2, and had a small but nonsignificant increase from ambient to elevated CO_2. Soil microbial biomass and soil CO_2 efflux also had nonlinear responses to CO_2, with curves peaking at about 440 ppm CO_2 (Gill et al., 2002, 2006). Our current study also has evidence for a CO_2 response threshold; coarse POM-C curved upward at about 450 ppm CO_2 in the black clay. In contrast to the previous study, microbial biomass and soil CO_2 efflux increased linearly in the black clay. We hypothesize that the drop in microbial biomass and soil CO_2 efflux above 440 ppm CO_2 in the previous study is due to the drop in plant productivity in the same CO_2 range (Polley et al., 2003); whereas in the present study microbial biomass and soil CO_2 efflux mirror the linear increase in plant productivity and labile SOC with CO_2. One consistent result between the two experiments is that CO_2 enrichment increased labile SOC and decreased mineral-associated SOC in the silty clay soil. Therefore, both experiments provide evidence for a priming response to elevated CO_2 in the silty clay soil.

5. Conclusions

In this prairie ecosystem, soil texture had significant effects on soil organic carbon accumulation and its response to CO_2. Higher-clay soils had greater SOC, and the highest-clay soil had the greatest increase in rapidly cycling SOC pools with CO_2 enrichment. We found evidence of priming; SOC loss from recalcitrant organic matter increased at elevated CO_2 for the intermediate-textured silty clay soil only. SOC may be more physically protected from decomposition in the highest clay soil, preventing priming. Although the sandiest soil had the greatest ANPP increase with CO_2, the lack of soil C responses to CO_2 in this soil suggests that 1) soil properties can override plant-mediated CO_2 effects on soil C cycling or 2) belowground plant responses to CO_2 differed from aboveground responses. Our results are consistent with evidence from other studies that CO_2 enrichment accelerates soil C cycling, but we find that CO_2 effects depend significantly on soil texture. Given the wide range of clay content in elevated CO_2 experiments to date (<10% to >50% clay), a better understanding of soil type effects could improve predictions of soil feedbacks on rising atmospheric CO_2.

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Appendix A. Supplementary data

Supplementary data related to this chapter can be found at http://dx.doi.org/10.1016/j.soilbio.2015.01.012.

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