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Faster turnover of new soil carbon inputs under increased atmospheric CO_2

Kees Jan van Groenigen[1,2] | Craig W. Osenberg[3] | César Terrer[4] | Yolima Carrillo[5] | Feike A. Dijkstra[6] | James Heath[7] | Ming Nie[8] | Elise Pendall[5] | Richard P. Phillips[9] | Bruce A. Hungate[1]

[1]Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK

[2]Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ, USA

[3]Odum School of Ecology, University of Georgia, Athens, GA, USA.

[4]AXA Chair Programme in Biosphere and Climate Impacts, Department of Life Sciences, Imperial College London, Ascot, UK

[5]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia

[6]Centre for Carbon, Water and Food, School of Life and Environmental Sciences, The University of Sydney, Eveleigh, NSW, Australia

[7]Lancaster Environment Centre, Lancaster University, Lancaster, UK

[8]Ministry of Education Key Lab for Biodiversity Science and Ecological Engineering, The Institute of Biodiversity Science, Fudan University, Shanghai, China

[9]Department of Biology, Indiana University, Bloomington, IN, USA

Correspondence
Kees Jan van Groenigen, Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK.
Email: kj.vangroenigen@exeter.ac.uk

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Abstract

Rising levels of atmospheric CO_2 frequently stimulate plant inputs to soil, but the consequences of these changes for soil carbon (C) dynamics are poorly understood. Plant-derived inputs can accumulate in the soil and become part of the soil C pool ("new soil C"), or accelerate losses of pre-existing ("old") soil C. The dynamics of the new and old pools will likely differ and alter the long-term fate of soil C, but these separate pools, which can be distinguished through isotopic labeling, have not been considered in past syntheses. Using meta-analysis, we found that while elevated CO_2 (ranging from 550 to 800 parts per million by volume) stimulates the accumulation of new soil C in the short term (<1 year), these effects do not persist in the longer term (1–4 years). Elevated CO_2 does not affect the decomposition or the size of the old soil C pool over either temporal scale. Our results are inconsistent with predictions of conventional soil C models and suggest that elevated CO_2 might increase turnover rates of new soil C. Because increased turnover rates of new soil C limit the potential for additional soil C sequestration, the capacity of land ecosystems to slow the rise in atmospheric CO_2 concentrations may be smaller than previously assumed.

KEYWORDS
isotopes, meta-analysis, respiration, roots, soil carbon, turnover

1 | INTRODUCTION

Because soils are one of the largest natural sources of the greenhouse gas CO_2 (Raich & Schlesinger, 1992), they play a crucial role in determining the future trajectory of climate change. Yet, the response of soil C dynamics to future atmospheric conditions remains uncertain. Numerous studies have found that rising CO_2 concentrations stimulate plant growth (Ainsworth & Long, 2005). If the resulting increase in soil C input increases the size of the soil C pool, soils may slow the rise in atmospheric CO_2 concentrations (Thornton, Lamarque, Rosenbloom, & Mahowald, 2007). However, long-term changes in soil C stocks are determined by the balance between the input of new organic matter to soil pools and the decomposition of soil organic matter (Hungate, Jackson, Field, & Chapin, 1995). Many CO_2 enrichment experiments do not directly measure C fluxes or the fate of recently added plant detritus vs. soil organic matter that is already present, possibly limiting their predictive power for the response of soil C stocks to rising atmospheric CO_2 (Cardon et al., 2001). A recent meta-analysis used a data–model assimilation approach to show that CO_2 enrichment increases decomposition rates of both new plant inputs and soil organic matter (Van Groenigen, Qi, Osenberg, Luo, & Hungate, 2014). However, without separate measurements of both these C pools, estimates of decomposition rates could in theory be affected by the structure of the soil C model used to analyze experimental data (Georgiou, Koven, Riley, & Torn, 2015; Van Groenigen, Xia, Osenberg, Luo, & Hungate, 2015).

The dynamics of different C pools can be assessed through isotopic labeling, in which the isotopic composition of the totality of recently fixed C differs from pre-existing soil C (hereafter "old soil C"). With this approach, we can determine the amount of soil C derived from the cumulative plant inputs since labeling began (i.e., "new soil C"; Balesdent, Mariotti, & Giullet, 1987; Keith, Oades, & Martin, 1986). A similar approach enables us to determine what fraction of total soil CO_2 respiration is derived from decomposition of old C (Rochette, Flanagan, & Gregorich, 1999), and these results can be combined to assess the net C storage in an ecosystem (Pendall, King, Mosier, Morgan, & Milchunas, 2005). Results vary from studies that use isotopic labeling to quantify CO_2 effects on soil C dynamics, making it difficult to infer global responses from individual experiments. A quantitative synthesis of results across a wide range of studies can overcome this problem. Thus, we used meta-analysis (Osenberg, Sarnelle, Cooper, & Holt, 1999) of results from 28 published studies to (i) summarize the effect of atmospheric CO_2 enrichment on new and old C stocks in mineral soil, on soil respiration rates and soil C input rates, and to (ii) explore the factors that shaped the responses to CO_2 enrichment.

2 | METHODS

2.1 | Data collection

We extracted results for soil C content and CO_2 fluxes from atmospheric CO_2 enrichment studies conducted in the field, in growth chambers, or in glass houses. For studies reporting new soil C contents, we also extracted data on soil C input proxies. We used Web of Science (Thompson Reuters) for an exhaustive search of journal articles published before June 2016, using search terms "CO_2" for article title, and "soil AND carbon" and "isotop* OR label*" for article topic. To be included in our dataset, studies had to meet several criteria:

1. Studies needed to include at least two CO_2 treatments: ambient (between 350 and 400 ppmV) and increased (550–800 ppmV).
2. Plants and soils needed to have distinctive isotopic composition in each of the treatments. Such differences in isotopic composition were established in one of two ways. First, experiments exploited the difference in C_3 and C_4 plants; the abundance of ^{13}C relative to ^{12}C is less in plant tissue than in atmospheric CO_2 due to isotope discrimination, with C_4 plants discriminating less than C_3 plants (Farquhar, Ehleringer, & Hubick, 1989). Thus, growing C_3 plants on soil developed under C_4-vegetation (or vice versa) creates a difference in isotopic signature between plants and soil. Second, some experiments grew plants under an atmosphere with CO_2 that had a different composition from atmospheric CO_2 under natural conditions. This was achieved through ^{13}C or ^{14}C labeling of CO_2 in glass houses, growth chambers, or field experiments. In all cases, the contribution of each source to the total soil C pool was calculated using an isotopic mixing model with two end members, that is, new plant material and old soil C (Balesdent et al., 1987; Keith et al., 1986). Using the same approach, the contribution of old soil C respiration to soil CO_2 efflux was determined as well (Rochette et al., 1999). Because root respiration and CO_2 derived from new C input have a similar isotopic signature, isotopic labeling usually cannot distinguish between the contributions of these two sources to soil CO_2 efflux. As such, we did not quantify CO_2 production derived from the decomposition of new soil C.
3. Plants needed to be labeled using methods that distributed the isotope among all plant parts. Therefore, we excluded studies that applied a single pulse of ^{14}C–CO_2 or ^{13}C–CO_2 to plants, because this approach results in a distribution of labeled C that does not correspond to the distribution of total C across different plant parts (Kuzyakov & Domanski, 2000).
4. Means and sample sizes had to be available for both ambient and increased CO_2 treatments to be included in our dataset. Estimates of variance were tabulated when available but were not required for inclusion in the analysis.

We found 31 papers that met our requirements. One study was excluded because no new soil C input was detected in either the control or the increased CO_2 treatment. Another study was excluded because it assumed temporal variation in the old soil C end member; this approach prohibited direct comparisons with new and old C stocks in other studies in our dataset. Finally, one study was excluded because low image resolution prevented extraction of graphical data (see Data S1). Of the remaining 28 papers, 18 papers

reported new soil C stocks; 18 papers reported soil C input proxy data; 14 papers reported old soil C respiration rates; and seven papers reported old soil C stocks (Table 1).

We extracted final observations on soil C contents (only one experiment reported soil C data for more than one time point). Although this was not a requirement for a study to be included in our dataset, all soil C measurements in our dataset were from mineral soil layers. We averaged observations of old soil C respiration rates over time. For each study, we also tabulated experimental duration, plant species, and the type of experimental facility that was used to increase CO_2 concentrations. Experiment duration (i.e., the time period during which soil C input was isotopically labeled) varied between 6 days and 4 years (Table 1, Data S2–S5).

2.2 | Soil C input proxies

For each study, we chose the proxy that we assumed was most indicative of net primary productivity (NPP), while taking into account the experimental design (Table 1). In studies on newly seeded plants that lasted less than one growing season, the incorporation of aboveground litter in mineral soil was likely to be minimal. In these cases, we used standing root biomass, which we assumed was an estimate of belowground NPP. For experiments that determined new soil C in root ingrowth cores (Hoosbeek et al., 2004; Phillips et al., 2012), we used root growth as the proxy. In several longer-term experiments, aboveground biomass was periodically harvested (e.g., Van Kessel, Horwath, Hartwig, Harris, & Lüscher, 2000) or aboveground litter was removed (Cardon et al., 2001; Heath et al., 2005), which minimized the input of aboveground biomass. Because root growth data were not available for these studies, we used standing root biomass as a proxy. For longer-term (1–4 years) experiments without litter removal or biomass harvesting (Olszyk et al., 2003), we used total plant biomass. For all experiments, we only included proxies of C input from the time point closest to the corresponding new soil C measurements. For all experiments <1 year, soil C input proxies were measured at the same time as new soil C stocks.

2.3 | Meta-analysis

We quantified the effect of increased CO_2 on new soil C, soil C input proxies, old C respiration, and old soil C by calculating the natural log of the response ratio (r), a metric commonly used in meta-analyses (Hedges, Gurevitch, & Curtis, 1999; Osenberg et al., 1999):

$$\ln r = \ln(V_{ic}/V_{ac})$$

where V is the value for new soil C, soil C input proxies, old C respiration, or old soil C under increased (ic) or ambient (ac) CO_2 conditions. We performed a mixed-effects meta-analysis in R, using the rma.mv function in the "metafor" package (Viechtbauer, 2010), including "paper" as a random effect (because several papers contributed more than one effect size), and weighting ln$r$ by the inverse of its variance. We estimated missing variances using the average coefficient of variation across the dataset. To ease interpretation, the results from all our analyses were back-transformed and reported as the percentage change under increased CO_2 ($(r - 1) \times 100$).

Several factors have been suggested to affect the response of plant growth and soil C dynamics to CO_2 enrichment: (i) type of vegetation (Ainsworth & Long, 2005), (ii) the CO_2 fumigation technology used (De Graaff, Van Groenigen, Six, Hungate, & van Kessel, 2006), (iii) experiment duration (Norby Warren, Iversen, Medlyn & McMurtrie 2010), (iv) soil texture (Procter, Gill, Fay, Polley, & Jackson, 2015), (v) age of the vegetation (Körner et al., 2005), and (vi) N availability (Van Groenigen et al., 2006). To test whether these factors affected CO_2 responses, we categorized each study based on plant type (that is, woody vs. herb), experimental facility (greenhouse, GH, and growth chamber, GC vs. open-top chamber, OTC, and free air CO_2 enrichment, FACE), and study duration (<1 year vs. 1–4 years). We based our cutoff point on expected abrupt changes in soil C input over time; in the first growing season of an experiment isotopically labeled input mostly consists of root exudates and fine root turnover (Norby, O'neill, Hood, & Luxmoore, 1987), whereas in longer studies, dead coarse root material and aboveground litter will contribute as well (Hobbie, Johnson, Rygiewicz, Tingey, & Olszyk, 2004). One study reported respiration data for more than 1 year. For this study, we time-averaged the short-term and longer-term responses separately and included them as two separate comparisons in our dataset. For each study, we also tabulated the age of vegetation (number of years at the start of the isotopic labeling) and clay content. When studies reported soil texture class but not the exact clay content, we estimated clay content as the mean of the minimum and maximum value of that texture class according to the soil textural triangle (http://en.wikipedia.org/wiki/File:SoilTextureTriangle.jpg). In addition, we categorized studies on soil C stocks and respiration rates according to isotopic labeling method, and we categorized soil C input studies according to the type of proxy that was used (Table 1).

We selected our meta-analytic models using the same approach as Terrer, Vicca, Hungate, Phillips, and Prentice (2016). Briefly, we analyzed the data with all possible models that could be constructed using combinations of the experimental factors described above as main effects, using the "glmulti" package in R. The relative importance of the factors was then calculated as the sum of Akaike weights derived for all the models in which the factor occurred.

We assessed the effect of N availability using studies that included multiple N levels in a full factorial design, comparing CO_2 responses between high vs. low N treatments. The interaction between CO_2 enrichment and soil N availability was calculated according to Lajeunesse (2011):

$$\ln i = \ln r_{+N} - \ln r_{-N}$$

with ln$i$ as the natural log of the interaction term, lnr_{+N} as ln$r$ in the high N treatment, and lnr_{-N} as ln$r$ in the low N treatment.

Models were fitted according to the Knapp and Hartung (2003) method; 95% confidence intervals (CI) of treatment effects were

TABLE 1 Overview of CO_2 enrichment experiments included in our meta-analysis; responses that were reported in each study are indicated by "●"

Reference	System/species	Duration in years[a]	Label[b]	Facility	New C	C input proxy	Old C resp.	Old C
Billes, Rouhier, and Bottner (1993)	*Triticum aestivum*	0.08	C-14	GC	●	● (RB)		
Butterly, Armstrong, Chen, and Tang (2015)	*Triticum aestivum/Pisum sativum*	0.27	C-13	FACE	●	● (RB)		
Cardon et al. (2001)	California grassland	1.8	C_3/C_4	OTC	●	● (RB)	●	●
Carrillo, Dijkstra, Pendall, et al. (2014)	*Bouteloua gracilis*	0.18	C-13	GC			●	
Carrillo, Dijkstra, LeCain, and Pendall (2016)	*Bouteloua gracilis/Pascopyrum smithii*	0.18	C-13	GC	●	● (RB)	●	●
Cheng and Johnson (1998)	*Triticum aestivum*	0.08	C_3/C_4	GC			●	
Cheng et al. (2000)	*Helianthus annuus*	0.15	C_3/C_4	GC	●	● (RB)	●	
Cotrufo and Gorissen (1997)	*Lolium perenne/Agrostis capillaris Festuca ovina*	0.15	C-14	GC	●	● (RB)		
Heath et al. (2005)	*Fagus sylvatica/Quercus robur Carpinus betulus/Betula pendula Abies alba/Pinus sylvestris*	1.3	C_3/C_4	GH	●	● (RB)		●
Hobbie et al. (2004)	*Pseudotsuga mensiezii*	4.0	C-13	OTC	●			●
Hoosbeek et al. (2004)	*Populus alba Populus euramericana Populus nigra*	0.67	C_3/C_4	FACE	●			●
Hungate et al. (1997)	California grassland	1.5	C-13	FACE			●	
Ineson, Cotrufo, Bol, Harkness, and Blum (1996)	*Betula pendula*	0.5	C_3/C_4	FACE	●	● (RB)		
Kuikman, Lekkerkerk, and Van Veen (1991)	*Triticum aestivum*	0.13	C-14	GC	●	● (RB)	●	
Lin, Ehleringer, Rygiewicz, Johnson, and Tingey (1999)	*Pseudotsuga menziesii*	1.3	C-13	OTC			●	
Lukac et al. (2003)	*Poplar plantation*	0.67	C_3/C_4	FACE		● (RG)		
Martens, Heiduk, Pacholski, and Weigel (2009)	*Triticum aestivum*	0.12	C-14	FACE	●	● (RB)		
Nie, Bell, Wallenstein, and Pendall (2015)	*Bouteloua gracilis*	0.08	C-13	GC	●	● (RB)	●	
Nie and Pendall (2016)	*Bouteloua gracilis/Hesperostipa comata*	0.06	C-13	GC			●	
Olszyk et al. (2003)	*Pseudotsuga menziesii*	4.0	C-13	OTC		● (TB)		
Paterson et al. (2008)	*Lolium perenne*	0.18	C-13	GC			●	
Pendall et al. (2003)	Colorado grassland	2.6	C_3/C_4	FACE			●	
Phillips et al. (2012)	*Pinus taeda*	1	C-13[c]	FACE	●	● (RG)		●
Rouhier, Billès, Billès, and Bottner (1996)	*Castanea sativa*	0.02	C-14	GC	●	● (RB)		
Trueman and Gonzalez-Meler (2005)	*Populus deltoides*	4.0	C-13	GH			●	
Van Ginkel, Gorissen, and Van Veen (1997)	*Lolium perenne*	0.12	C-14	GC	●	● (RB)	●	
Van Ginkel, Gorissen, and Polci (2000)	*Lolium perenne*	0.23	C-14	GC	●	● (RB)		
Van Kessel et al. (2000)	*Lolium perenne/Trifolium repens*	4.0	C_3/C_4	FACE	●	● (RB)		●

FACE, free air carbon dioxide enrichment; GC, growth chamber; GH, greenhouse; OTC, open-top chamber; RB, root biomass, TB, total biomass; RG, root growth.

[a]Number of years during which the soil in the study received isotopically labeled C input.

[b]C-14 = isotopic labeling by ^{14}C–CO_2; C-13 = isotopic labeling by ^{13}C–CO_2; C_3/C_4 = isotopic labeling by using a shift in C_3 vs. C_4 vegetation.

[c]This study created a difference in isotopic signature between old soil C and new soil C input by switching soils between ambient and elevated CO_2 treatments.

based on critical values from a *t*-distribution. For all analyses, we inferred an effect of CO_2 if the 95% CI of the mean effect size did not overlap 0. We used a Wald test to determine whether treatment effects were statistically different between study categories.

3 | RESULTS

Averaged across the entire dataset, elevated CO_2 tended to increase new soil C contents (+14.4%, $p = .12$). The effect of elevated CO_2 on new soil C was best predicted by experiment duration and soil texture; the sum of Aikake weights indicates that other predictors were of minor importance (Figure 1). Based on these results, we calculated treatment effects for short- and longer-term experiments, using experiment duration as the sole moderator in our model. Experimentally elevated CO_2 only stimulated new soil C accumulation in short-term experiments (Figure 2a and Table S1). The effect of elevated CO_2 on new C also depended on soil texture; treatment effects on new soil C decreased with clay content (Table S1). We found similar results when we analyzed our data using a model that included both moderators (Fig. S1).

Within the experiments that measured new soil C, elevated CO_2 increased soil C input proxies by 40.7% ($p < .001$), with positive effects both in short- and longer-term experiments (Figure 2b). The effects of elevated CO_2 on soil C input proxies did not depend on experiment duration or any of the other model predictors (Figure 2b and Fig. S2). When we limited our analysis to studies conducted in the field (that is, FACE and OTC studies), we found similar results: the effect of elevated CO_2 on new soil C contents in short-term experiments was significantly higher than in longer-term experiments, but elevated CO_2 increased C input proxies regardless of experimental duration (Table S1).

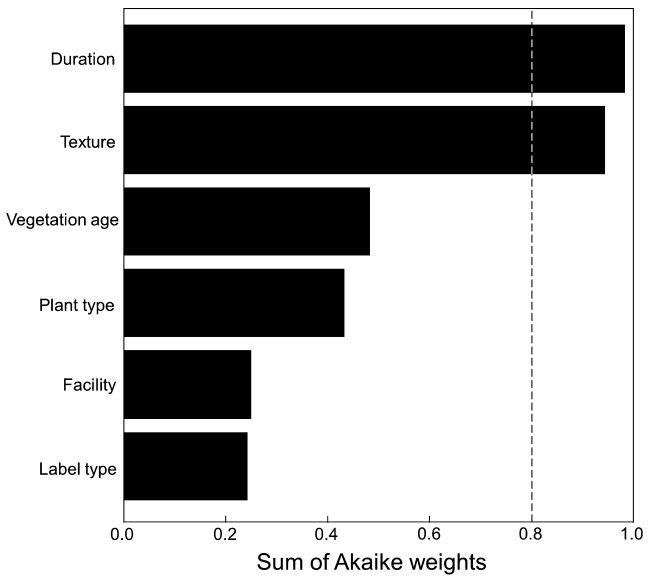

FIGURE 1 Model-averaged importance of the predictors of the CO_2 enrichment effect on new soil C stocks. The importance is based on the sum of Akaike weights derived from model selection using AICc (Akaike's Information Criteria corrected for small samples). Cutoff is set at 0.8 (dashed line) to differentiate important from nonessential predictors

The average effect of elevated CO_2 on soil C input in longer-term studies was strongly affected by the data from one study (Cardon et al., 2001), which reported exceptionally strong positive CO_2 effects (178%–343%, see Data S3). Excluding the results from this study from our analysis lowered CO_2 effects on soil C input proxies for longer-term studies to a similar level as those for short-term studies, whereas CO_2 effects on new soil C stocks remained largely unchanged (Fig. S3). Averaged across the entire dataset, elevated CO_2 did not affect old soil C respiration ($p = .99$) and old soil C stocks ($p = .16$). Treatment effects on old soil C respiration and old soil C stocks were not affected by any of the model predictors (Figure 2c,d, Figs. S4 and S5).

Within studies that included N availability treatments, elevated CO_2 increased the soil C input proxy more strongly at high N levels (Table 2). The effect of elevated CO_2 on old soil C stocks tended to be more positive at high N levels ($p = .11$); we found no $CO_2 \times N$ interactions for the other response variables.

4 | DISCUSSION

Our results show that elevated CO_2 did not affect new soil C contents in longer-term experiments. At the same time, our finding that elevated CO_2 increased soil C input proxies both in short- and longer-term experiments indicates that CO_2 enrichment stimulated soil C input regardless of experiment duration. Increased soil C input with no concomitant increase in new soil C storage can only be explained by increased decomposition rates. Thus, our results strongly suggest that faster decomposition of new C under increased CO_2 negated the higher soil C input rates, thereby limiting the potential for longer-term soil C storage. Experiments included in our dataset show that elevated CO_2 also increases soil C input proxies other than the ones used in our analysis, such as litter production (Gielen et al., 2005), NPP (McCarthy et al., 2010), photosynthetic rate (Heath et al., 2005), and fine root turnover (Lukac, Calfapietra, & Godbold, 2003; Trueman & Gonzalez-Meler, 2005) both in the short term and longer term. Similarly, a recent meta-analysis shows that elevated CO_2 increases fine root production and litter fall regardless of experimental duration (Dieleman et al., 2010). Thus, several lines of evidence suggest continued positive effects of elevated CO_2 on soil C input. This provides further support for our interpretation that the lack of an effect of elevated CO_2 on new soil C accumulation is not due to decreasing treatment effects on soil C input over time, but rather to an increase in decomposition rates under elevated CO_2.

Our finding that new soil C is unresponsive to elevated CO_2—despite increased C input to soil—is inconsistent with the idea that more rapid C turnover through soil is an artifact of the model structure used to infer rates of soil C turnover (Georgiou et al., 2015). Rather, finding that elevated CO_2 increased C input to soil with no

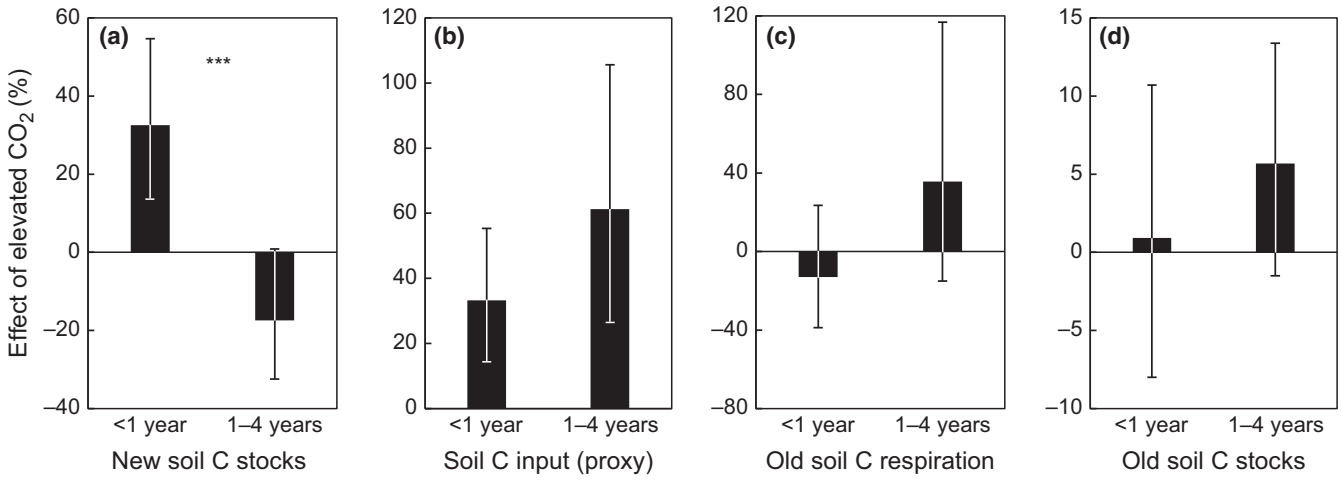

FIGURE 2 Results of a meta-analysis on the response of new soil C stocks, soil C input proxies, old soil C respiration, and old soil C stocks to increased levels of atmospheric CO_2 for short-term (<1 year) and longer-term (1–4 years) studies. (a) Change in new soil C stocks for short-term studies (n = 32) and longer-term studies (n = 24); (b) Change in soil C input proxies for short-term (n = 32) and longer-term studies (n = 24); (c) Change in respiration of old soil C for short-term (n = 21) and longer-term studies (n = 8); (d) Change in old C stocks for short-term studies (n = 10) and longer-term studies (n = 24). Error bars indicate 95% confidence intervals. *** indicates treatment responses that are significantly different between study categories at $p < .001$

TABLE 2 Effect of elevated CO_2 for low and high N addition treatments, and the CO_2 × N interaction term in CO_2 × N factorial experiments for all response variables included in our analysis

	CO_2 effect at low N (%)			CO_2 effect at high N (%)			CO_2 × N interaction (%)			
		95% CI			95% CI			95% CI		
Response variable	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	n
New soil C stocks	−11.7	−31.2	13.3	−2.3	−24.0	25.5	6.7	−12.2	29.8	18
Soil C input (proxy)	43.8	10.2	87.8	60.0	22.2	109.4	13.4	1.2	27.1	18
Old soil C respiration	−5.2	−46.7	68.8	−5.3	−45.8	65.4	−3.0	−48.5	82.9	6
Old soil C stocks	5.5	−4.4	16.3	7.6	−2.4	18.5	2.7	−0.8	6.3	11

effect on the size of the new soil C pool supports the interpretation that elevated CO_2 increases the turnover rate of new soil C (Phillips et al., 2012; Van Groenigen et al., 2014).

Why does increased atmospheric CO_2 stimulate the decomposition of new soil C? Rising levels of atmospheric CO_2 increase the supply of labile C root exudates (Phillips, Finzi, & Bernhardt, 2011) and the release of labile C by mycorrhizae (Cheng et al., 2012), which can stimulate the decomposition of plant litter by saprotrophs (De Graaff, Classen, Castro, & Schadt, 2010; Phillips et al., 2012). This explanation is consistent with direct measurements of higher in situ litter decomposition rates with increased atmospheric CO_2 compared to ambient CO_2 (Carrillo, Dijkstra, LeCain, et al., 2014; Cheng et al., 2012; Cotrufo, De Angelis, & Polle, 2005). It is also consistent with measurements of higher decomposition rates under nongirdled trees compared to girdled trees (Subke et al., 2004). Furthermore, increased CO_2 can improve the efficiency of water use by plants, which reduces soil water loss through transpiration and increases soil water content (Field, Jackson, & Mooney, 1995; Van Groenigen, Osenberg, & Hungate, 2011). This response stimulates decomposition rates in ecosystems where low water availability constrains the activity of soil microbes and their access to substrate (Hungate et al., 1997; Pendall et al., 2003). We note that this latter mechanism will only have a limited impact in experiments where irrigation minimizes the effects of elevated CO_2 on soil moisture contents.

Our analysis suggests that increased turnover of new C could be a general response to atmospheric CO_2 enrichment. Nonetheless, increased CO_2 stimulated new C accumulation in the short term. This positive treatment effects on new soil C in experiments <1 year might reflect an adjustment period, where microbial activity and decomposition rates did not fully respond following a step increase in soil C input rates under elevated CO_2. The change in composition of soil C input over time may have played a role as well. In short-term experiments, plant inputs to soil will consist mostly of root exudates (Norby et al., 1987); the positive effect of CO_2 on new soil C in these experiments likely reflects increased root exudation. Over time, isotopically labeled root litter, mycorrhizal tissue, and leaves contribute to soil C input as well (Hobbie et al., 2004). Indeed, increased CO_2 has been shown to stimulate the decomposition of these types of plant input (Cheng, 1999; Cheng et al., 2012; Phillips et al., 2012).

Our findings of faster decomposition rates with increased CO_2 are corroborated by studies that did not include an isotopic C label. For instance, increased CO_2 has been shown to increase the ability of microbes to decompose soil organic matter (Nie et al., 2013) and to stimulate the activity of enzymes associated with decomposition of both recalcitrant (Carney, Hungate, Drake, & Megonigal, 2007) and labile soil organic matter (Kelley, Fay, Polley, Gill, & Jackson, 2011). However, it should be noted that our analysis only pertains to mineral soils; to the best of our knowledge, no study has reported CO_2 responses of old and new C in organic layers. This is important, because experimentally elevated CO_2 can increase litter fall and stimulate C accumulation in forest floors, thereby forming a minor additional C sink (Drake et al., 2011).

A recent synthesis of data from a much larger set of mostly longer-term CO_2 experiments (n = 53, average experiment duration of 6.8 years) that used a mass balance approach to estimate changes in soil C dynamics found that elevated CO_2 increases the decomposition of both new and old soil C (Van Groenigen et al., 2014). Our new findings confirm those earlier results for the new, but not the old, soil C pool. The lack of a significant treatment effect on old C respiration might be due to low statistical power; the small sample size (n = 8 for experiments 1–4 years) and high variance associated with the respiration of old soil C (Figure 2c, Table S1) limit our ability to detect treatment effects. The large variation in treatment effects may be caused by among-system variation in the recalcitrance and physical protection of the old soil C. Moreover, old soil C stocks are large compared to new soil C stocks, and they are characterized by high spatial variability, making it difficult to detect changes in pool size (Hungate et al., 1995). The impact of spatial variability may be reduced through long-term experiments involving planted communities on homogenized soils. Large differences in isotopic signatures between recently fixed C and old C may improve sensitivity as well (Ogle & Pendall, 2015). Clearly, additional studies are needed to identify the soil properties determining the turnover of old soil C under increased CO_2.

We do not know what caused the negative correlation between clay content and the effect of elevated CO_2 on new soil C stocks. This result seems counterintuitive, as clay minerals are generally expected to promote soil C accumulation (Six, Conant, Paul, & Paustian, 2002). One possible explanation is that the soil disturbance inherent to all experiments in our dataset released previously physically protected C. Experiments that trace soil C input under both ambient and elevated CO_2 conditions involve continuous isotopic labeling of CO_2 (which can be achieved in greenhouses), or replacing vegetation (i.e., by using soil that developed under vegetation with a different photosynthetic pathway than that of the experimental vegetation). As such, all these experiments required a substantial amount of soil disturbance. Undisturbed clay soils contain relatively large amounts of physically protected C (Six et al., 2002). When soil disturbance breaks up soil aggregates, much of this C become available to microbes (Hassink, Bouwman, Zwart, Bloem, & Brussaard, 1993). Thus, disturbed clay soils have relatively large and active microbial communities that might be better adapted to decompose the increased amount of soil C input under elevated CO_2 than soils with low clay contents. Alternatively, clay content may correlate with soil properties that were not considered in this analysis (because they were not always reported) but that may affect decomposition rates (e.g., nutrient availability, soil moisture).

Elevated CO_2 stimulated soil C input proxies more strongly under high than under low N inputs, but this response did not result in additional new soil C storage. These results are consistent with a recent study showing that N additions increase decomposition of new soil C input (Chen et al., 2014). Nonetheless, several studies found that N additions stimulate total soil C storage under elevated CO_2 (e.g., Hungate et al., 2009; Luo, Hui, & Zhang, 2006; Van Groenigen et al., 2006). In combination with our finding that N addition does not stimulate new soil C storage under elevated CO_2, this suggests that N addition stimulates net soil C storage by reducing old soil C decomposition (e.g., Cardon et al., 2001; Cheng & Johnson, 1998). This explanation is consistent with our finding that high N additions tended to increase old C stocks under elevated CO_2. However, because this result is based on a small dataset (n = 11) and is only marginally significant, it requires additional experimental work to be tested more thoroughly.

Two important limitations of our analysis must be noted. First, the experiments in our dataset only lasted 4 years at the most, whereas soil C storage is a process that occurs on decadal timescales. Elevated CO_2 can increase the input of new C into slowly cycling or passive C pools (Iversen, Keller, Garten, & Norby, 2012; Jastrow et al., 2005), a response that could stimulate new soil C storage over time frames longer than the spans of most experiments. As such, we can only speculate about the extent to which our results are representative for responses on longer timescales. However, a recent global synthesis of soil ^{14}C data shows that current soil C models actually overestimate the incorporation of new C in soil with rising CO_2 concentrations (He et al., 2016), suggesting that our finding of increased turnover rates also may apply to longer timescales in real-world ecosystems.

Second, our dataset does not include field experiments in undisturbed natural ecosystems, or systems with a continuous management history. However, our findings are supported by longer-term studies in both continuously managed and natural ecosystems. For instance, Marhan et al. (2010) combined soil ^{13}C data with inverse modeling to show that 5 years of elevated CO_2 increased the decomposition rate of both old and new soil C in cropland by increasing soil moisture contents. Longer-term CO_2 enrichment studies on natural ecosystems often include an isotopic C tracer in the high CO_2 treatment only. Several of these studies found that new C is predominantly allocated to soil C pools with high turnover rates. For instance, Taneva, Pippen, Schlesinger, and Gonzalez-Meler (2006) found in a *Pinus taeda* plantation that after 8 years of elevated atmospheric CO_2, the majority of soil-respired CO_2 was derived from pools with a turnover rate of less than 35 days. Importantly, meta-analyses suggest that on average, increased plant growth under elevated CO_2 does not result in additional soil C storage unless nutrients are also added (e.g., De Graaff et al., 2006; Van

Groenigen et al., 2006). Together, these results strongly suggest that our finding of increased decomposition rates is transferrable to a wide range of ecosystems.

Conventional soil C models assume that decomposition rates (k) are not directly affected by rising CO_2 levels (Friedlingstein et al., 2006; Luo et al., 2016). However, our results (and those of other recent syntheses, e.g., Van Groenigen et al., 2014) indicate that k might increase under elevated CO_2. This inconsistency between models and real-world responses can potentially be avoided when models explicitly represent the relation between microbial dynamics and decomposition rates and the interactions between various C pools. Indeed, microbe-centered models (i.e., models in which decomposition is determined by the size and activity of the microbial biomass, both of which are modeled explicitly) predict less new soil C accumulation following an increase in atmospheric CO_2 than conventional models (Sulman, Phillips, Oishi, Shevliakova, & Pacala, 2014; Wieder, Grandy, Kallenbach, Taylor, & Bonan, 2015; Wutzler & Reichstein, 2013).

This meta-analysis, synthesizing results across 28 studies, suggests that enhanced turnover rates of new soil C with increased atmospheric CO_2 might be common. Therefore, future assessments of terrestrial feedbacks to climate change should consider the effects of increased atmospheric CO_2 on microbial processes such as soil C turnover.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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