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Faster turnover of new soil carbon inputs under increased atmospheric CO₂

Running Head: Soil carbon dynamics under elevated CO₂

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Faster turnover of new soil carbon inputs under increased atmospheric CO₂

Abstract

Rising levels of atmospheric CO₂ 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 CO₂ (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 CO₂ 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 CO₂ 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 CO₂ concentrations may be smaller than previously assumed.

Introduction

Because soils are one of the largest natural sources of the greenhouse gas CO₂ (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 CO₂ 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 CO₂ concentrations (Thornton *et al.*, 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 *et al.*, 1995). Many CO₂ 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 CO₂ (Cardon *et al.*, 2001). A recent meta-analysis used a data-model assimilation approach to show that CO₂ enrichment increases decomposition rates of both new plant inputs and soil organic matter (van Groenigen *et al.*, 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 *et al.*, 2015; van Groenigen *et al.*, 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”; Keith *et al.*, 1986; Balesdent *et al.*, 1987). A similar approach enables us to determine what fraction of total soil CO₂ respiration is derived from decomposition of old C (Rochette *et al.*, 1999), and these results can be combined to assess the net C storage in an ecosystem (Pendall *et al.*, 2005). Results vary from studies that use isotopic labeling to quantify CO₂ 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 *et al.*, 1999) of results from 28 published studies to a) summarize the effect of atmospheric CO₂ enrichment on new and old C stocks in mineral soil, on soil respiration rates and soil C input rates, and to b) explore the factors that shaped the responses to CO₂ enrichment.

Methods

Data Collection

We extracted results for soil C content and CO₂ fluxes from atmospheric CO₂ 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 “CO₂” 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 CO₂ treatments: ambient (between 350–400 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 C₃ and C₄ plants; the abundance of ¹³C relative to ¹²C is less in plant tissue than in atmospheric CO₂ due to isotope discrimination, with C₄ plants discriminating less than C₃ plants (Farquhar *et al.*, 1989). Thus, growing C₃ plants on soil developed under C₄-vegetation (or vice versa) creates a difference in isotopic signature between plants and soil. Second, some experiments grew plants under an atmosphere with CO₂ that had a different composition from atmospheric CO₂ under natural conditions. This was achieved through ¹³C or ¹⁴C labeling of CO₂ 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, i.e. new plant material and old soil C (Keith *et al.*, 1986; Balesdent *et al.*, 1987). Using the same approach, the contribution of old soil C respiration to soil CO₂ efflux was determined as well (Rochette *et al.*, 1999). Because root respiration and CO₂ derived from new C input have a similar isotopic signature, isotopic labeling usually cannot distinguish between the contributions of these two sources to soil CO₂ efflux. As such, we did not quantify CO₂ 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 ¹⁴C-CO₂ or ¹³C-CO₂ 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 CO₂ 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 CO₂ 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). Out 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 7 papers reported old soil C stocks (Table 1).

We extracted final observations on soil C contents (only 1 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 CO₂ 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 S2-5).

Soil C input proxies

For each study we choose 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 *et al.*, 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.

Meta-analysis

We quantified the effect of increased CO₂ 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 *et al.*, 1999; Osenberg *et al.*, 2001):

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

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) CO₂ conditions. We performed a mixed-effects meta-analysis in R, using the `rma.mv` function in the “metafor” package (Viechtbauer *et al.*, 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 CO₂ ($(r - 1) \times 100$).

Several factors have been suggested to affect the response of plant growth and soil C dynamics to CO₂ enrichment: 1) type of vegetation (Ainsworth *et al.*, 2005), 2) the CO₂ fumigation technology used (De Graaff *et al.*, 2006), 3) experiment duration (Norby *et al.*, 2010), 4) soil texture (Procter *et al.*, 2015), 5) age of the vegetation (Körner *et al.*, 2005), and 6) N availability (van Groenigen *et al.*, 2006). To test whether these factors affected CO₂ 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 CO₂ enrichment, FACE), and study duration (< 1 year vs. 1-4 years). We based our cut-off 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 *et al.*, 1987), whereas in longer studies, dead coarse root material and aboveground litter will contribute as well (Hobbie *et al.*, 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 *et al.* (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 CO₂ responses between high vs. low N treatments. The interaction between CO₂ 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, $\ln r_{+N}$ as $\ln r$ in the high N treatment, and $\ln r_{-N}$ 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 based on critical values from a t-distribution. For all analyses, we inferred an effect of CO₂ 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.

Results

Averaged across the entire data set, elevated CO₂ tended to increase new soil C contents (+14.4%, $P = 0.12$). The effect of elevated CO₂ on new soil C was best predicted by experiment duration and soil texture; the sum of Aikake weights indicate that other predictors were of minor importance (Fig. 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 CO₂ only stimulated new soil C accumulation in short-term experiments (Fig. 2a and Table S1). The effect of elevated CO₂ 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 CO₂ increased soil C input proxies by 40.7% ($P < 0.001$), with positive effects both in short- and longer-term experiments (Fig. 2b). The effects of elevated CO₂ on soil C input proxies did not depend on experiment duration or any of the other model predictors (Fig. 2b, 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 CO₂ on new soil C contents in short-term experiments was significantly higher than in longer-term experiments, but elevated CO₂ increased C input proxies regardless of experimental duration (Table S1).

The average effect of elevated CO₂ 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 CO₂ effects (178 - 343%, see table S3). Excluding the results from this study from our analysis lowered CO₂ effects on soil C input proxies for longer-term studies to a similar level as those for short-term studies, whereas CO₂ effects on new soil C stocks remained largely unchanged (Fig. S3). Averaged across the entire data set, elevated CO₂ did not affect old soil C respiration ($P = 0.99$) and old soil C stocks ($P = 0.16$). Treatment effects on old soil C respiration and old soil C stocks were not affected by any of the model predictors (Fig. 2cd, Figs. S4-S5).

Within studies that included N availability treatments, elevated CO₂ increased the soil C input proxy more strongly at high N levels (Table 2). The effect of elevated CO₂ on old soil C stocks tended to be more positive at high N levels ($P = 0.11$); we found no CO₂ × N interactions for the other response variables.

Discussion

Our results show that elevated CO₂ did not affect new soil C contents in longer-term experiments. At the same time, our finding that elevated CO₂ increased soil C input proxies both in short- and longer-term experiments indicate that CO₂ 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 CO₂ 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 CO₂ 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 *et al.*, 2003; Trueman & Gonzalez-Meler, 2005) both in the short- and longer term. Similarly, a recent meta-analysis shows that elevated CO₂ 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 CO₂ on soil C input. This provides further support for our interpretation that the lack of an effect of elevated CO₂ 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 CO₂.

Our finding that new soil C is unresponsive to elevated CO₂ - 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; van Groenigen *et al.*, 2015). Rather, finding that elevated CO₂ increased C input to soil with no effect on the size of the new soil C pool supports the interpretation that elevated CO₂ increases the turnover rate of new soil C (Phillips *et al.*, 2012; van Groenigen *et al.*, 2014).

Why does increased atmospheric CO₂ stimulate the decomposition of new soil C? Rising levels of atmospheric CO₂ increase the supply of labile C root exudates (Phillips *et al.*, 2011) and the release of labile C by mycorrhizae (Cheng *et al.*, 2012), which can stimulate the decomposition of

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plant litter by saprotrophs (Phillips *et al.*, 2012; De Graaff *et al.*, 2010). This explanation is consistent with direct measurements of higher *in situ* litter decomposition rates with increased atmospheric CO₂ compared to ambient CO₂ (Cotrufo *et al.*, 2005; Cheng *et al.*, 2012; Carrillo *et al.*, 2014). It is also consistent with measurements of higher decomposition rates under non-girdled trees compared to girdled trees (Subke *et al.*, 2004). Furthermore, increased CO₂ can improve the efficiency of water use by plants, which reduces soil water loss through transpiration and increases soil water content (Field *et al.*, 1995; van Groenigen *et al.*, 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 CO₂ on soil moisture contents.

Our analysis suggests that increased turnover of new C could be a general response to atmospheric CO₂ enrichment. Nonetheless, increased CO₂ 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 CO₂. 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 CO₂ on new soil C in these experiments likely reflects increased root exudation. Over time, isotopically labelled root litter, mycorrhizal tissue and leaves contribute to soil C input as well (Hobbie *et al.*, 2004). Indeed, increased CO₂ 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 CO₂ are corroborated by studies that did not include an isotopic C label. For instance, increased CO₂ 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 *et al.*, 2007) and labile soil organic matter (Kelley *et al.*, 2011). However, it should be noted that our analysis only pertains to

mineral soils; to the best of our knowledge, no study has reported CO₂ responses of old and new C in organic layers. This is important, because experimentally elevated CO₂ 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 CO₂ 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 CO₂ 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 (Fig. 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 CO₂.

We do not know what caused the negative correlation between clay content and the effect of elevated CO₂ on new soil C stocks. This result seems counter-intuitive, as clay minerals are generally expected to promote soil C accumulation (Six *et al.*, 2002). One possible explanation is that the soil disturbance inherent to all experiments in our data set released previously physically protected C. Experiments that trace soil C input under both ambient and elevated CO₂ conditions involve continuous isotopic labelling of CO₂ (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 becomes available to microbes (Hassink *et al.*, 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 CO₂ than soils with low clay contents. Alternatively, clay content may correlate with soil properties that were not considered in this analysis (because they weren't always reported) but that may affect decomposition rates (e.g. nutrient availability, soil moisture).

Elevated CO₂ 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 CO₂ (e.g. Hungate *et al.*, 2009; Luo *et al.*, 2006, van Groenigen *et al.*, 2006). In combination with our finding that N addition does not stimulate new soil C storage under elevated CO₂, this suggests that N addition stimulates net soil C storage by reducing old soil C decomposition (e.g. Cheng & Johnson, 1998; Cardon *et al.*, 2001). This explanation is consistent with our finding that high N additions tended to increase old C stocks under elevated CO₂. 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 CO₂ can increase the input of new C into slowly cycling or passive C pools (Jastrow *et al.*, 2005; Iversen *et al.*, 2011), 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 time scales. However, a recent global synthesis of soil ¹⁴C data shows that current soil C models actually overestimate the incorporation of new C in soil with rising CO₂ concentrations (He *et al.*, 2016), suggesting that our finding of increased turnover rates also may apply to longer time scales 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 modelling 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 *et al.* (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 suggests 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 (Wieder *et al.*, 2015; Wutzler *et al.*, 2013; Sulman *et al.*, 2014).

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 in the online version of this article:

Fig. S1. Effect of atmospheric CO₂ enrichment on new soil C contents, adjusted for differences in clay content between studies.

Fig. S2. Model-averaged importance of the predictors of the CO₂ fertilization effect on soil C input proxies.

Fig. S3. Effect of atmospheric CO₂ enrichment on new soil C contents and soil C input proxies, excluding the data from Cardon *et al.* (2001).

Fig. S4. Model-averaged importance of the predictors of the CO₂ fertilization effect on old soil C respiration.

Fig. S5. Model-averaged importance of the predictors of the CO₂ fertilization effect on old soil C contents.

Table S1. Summary of the results of the meta-analysis on the response of new old soil C, soil C input proxies, old C respiration and old soil C stocks to atmospheric CO₂ enrichment.

Data S1. Full references to the three studies that were excluded from our meta-analysis.

Data S2. New C stocks and experimental conditions for all studies included in our meta-analysis.

Data S3. Soil C input proxies and experimental conditions for all studies included in our meta-analysis.

Data S4. Respiration of old soil C and experimental conditions for all studies included in our meta-analysis.

Data S4. Old C stocks and experimental conditions for all studies included in our meta-analysis.

Figure captions

Fig. 1 Model-averaged importance of the predictors of the CO₂ 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). Cut-off is set at 0.8 (dashed line) to differentiate important from non-essential predictors.

Fig. 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 CO₂ for short (< 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 $P < 0.001$.

Table 1 Overview of CO₂ 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 ^c	New C	C input proxy ^d	Old C resp.	Old C
Billes <i>et al.</i> , 1993	<i>Triticum aestivum</i>	0.08	C-14	GC	•	• (RB)		
Butterly <i>et al.</i> , 2015	<i>Triticum aestivum</i> / <i>Pisum sativum</i>	0.27	C-13	FACE	•	• (RB)		
Cardon <i>et al.</i> , 2001	California grassland	1.8	C ₃ /C ₄	OTC	•	• (RB)	•	•
Carrillo <i>et al.</i> , 2014	<i>Bouteloua gracilis</i>	0.18	C-13	GC			•	
Carrillo <i>et al.</i> , 2016	<i>Bouteloua gracilis</i> / <i>Pascopyrum smithii</i>	0.18	C-13	GC	•	• (RB)	•	•
Cheng & Johnson, 1998	<i>Triticum aestivum</i>	0.08	C ₃ /C ₄	GC			•	
Cheng <i>et al.</i> , 2000	<i>Helianthus annuus</i>	0.15	C ₃ /C ₄	GC	•	• (RB)	•	
Cotrufo & Gorissen, 1997	<i>Lolium perenne</i> / <i>Agrostis capillaris</i>	0.15	C-14	GC	•	• (RB)		
Heath <i>et al.</i> , 2005	<i>Fagus sylvatica</i> / <i>Quercus rober</i> <i>Carpinus betulus</i> / <i>Betula pendula</i> <i>Abies alba</i> / <i>Pinus sylvestris</i>	1.3	C ₃ /C ₄	GH	•	• (RB)		•
Hobbie <i>et al.</i> , 2004	<i>Pseudotsuga mensiezii</i>	4.0	C-13	OTC	•			•
Hoosbeek <i>et al.</i> , 2004	<i>Populus alba</i> <i>Populus euramericana</i> <i>Populus nigra</i>	0.67	C ₃ /C ₄	FACE	•			•
Hungate <i>et al.</i> , 1997	California grassland	1.5	C-13	FACE			•	
Ineson <i>et al.</i> , 1996	<i>Betula pendula</i>	0.5	C ₃ /C ₄	FACE	•	• (RB)		
Kuikman <i>et al.</i> , 1991	<i>Triticum aestivum</i>	0.13	C-14	GC	•	• (RB)	•	
Lin <i>et al.</i> , 1999	<i>Pseudotsuga mensiezii</i>	1.3	C-13	OTC			•	
Lukac <i>et al.</i> , 2003	Poplar plantation	0.67	C ₃ /C ₄	FACE		• (RG)		
Martens <i>et al.</i> , 2009	<i>Triticum aestivum</i>	0.12	C-14	FACE	•	• (RB)		
Nie <i>et al.</i> , 2015	<i>Bouteloua gracilis</i>	0.08	C-13	GC	•	• (RB)	•	
Nie & Pendall, 2016	<i>Bouteloua gracilis</i> / <i>Hesperostipa comata</i>	0.06	C-13	GC			•	
Olszyk <i>et al.</i> , 2003	<i>Pseudotsuga mensiezii</i>	4.0	C-13	OTC		• (TB)		
Paterson <i>et al.</i> , 2008	<i>Lolium perenne</i>	0.18	C-13	GC			•	
Pendall <i>et al.</i> , 2003	Colorado grassland	2.6	C ₃ /C ₄	FACE			•	
Phillips <i>et al.</i> , 2012	<i>Pinus taeda</i>	1	C-13 ^e	FACE	•	• (RG)		•
Rouhier <i>et al.</i> , 1996	<i>Castanea sativa</i>	0.02	C-14	GC	•	• (RB)		
Trueman & Gonzalez-Meler, 2005	<i>Populus deltoids</i>	4.0	C-13	GH			•	
Van Ginkel <i>et al.</i> , 1997	<i>Lolium perenne</i>	0.12	C-14	GC	•	• (RB)	•	
Van Ginkel <i>et al.</i> , 2000	<i>Lolium perenne</i>	0.23	C-14	GC	•	• (RB)		
Van Kessel <i>et al.</i> , 2000	<i>Lolium perenne</i> / <i>Trifolium repens</i>	4.0	C ₃ /C ₄	FACE	•	• (RB)		•

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

^b C-14 = isotopic labelling by ^{14}C -CO₂; C-13 = isotopic labelling by ^{13}C -CO₂; C₃/C₄ = isotopic labelling by using a shift in C₃ vs. C₄ vegetation.

^c FACE = Free Air Carbon dioxide Enrichment; GC= Growth Chamber; GH = Greenhouse; OTC=Open Top Chamber.

^d RB= root biomass, TB= total biomass, RG = root growth.

^e This study created a difference in isotopic signature between old soil C and new soil C input by switching soils between ambient and elevated CO₂ treatments.

Table 2 Effect of elevated CO₂ for low and high N addition treatments, and the CO₂ × N interaction term in CO₂ × N factorial experiments for all response variables included in our analysis.

Response variable	CO ₂ effect at low N (%)			CO ₂ effect at high N (%)			CO ₂ × N interaction (%)			n
	95% CI			95% CI			95% CI			
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	
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



