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RAPID COMMUNICATION

Elevated atmospheric carbon dioxide increases soil carbon

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Abstract

The general lack of significant changes in mineral soil C stocks during CO_2-enrichment experiments has cast doubt on predictions that increased soil C can partially offset rising atmospheric CO_2 concentrations. Here, we show, through meta-analysis techniques, that these experiments collectively exhibited a 5.6% increase in soil C over 2–9 years, at a median rate of 19 g C m^{-2} yr^{-1}. We also measured C accrual in deciduous forest and grassland soils, at rates exceeding 40 g C m^{-2} yr^{-1} for 5–8 years, because both systems responded to CO_2 enrichment with large increases in root production. Even though native C stocks were relatively large, over half of the accrued C at both sites was incorporated into microaggregates, which protect C and increase its longevity. Our data, in combination with the meta-analysis, demonstrate the potential for mineral soils in diverse temperate ecosystems to store additional C in response to CO_2 enrichment.

Keywords: carbon sequestration, ^{13}C stable isotope, FACE experiment, meta-analysis, microaggregates, open-top chamber, roots, soil organic matter, sweetgum forest, tallgrass prairie grassland

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Introduction

Most field-scale CO_2-enrichment studies have failed to detect significant changes in soil C against the relatively large, spatially heterogeneous pool of existing soil organic matter (SOM), leading to the general conclusion that the potential for increased soil C is limited (Hungate *et al.*, 1997; Gill *et al.*, 2002; Hagedorn *et al.*, 2003; Lichter *et al.*, 2005). Yet, it is currently unclear whether the lack of change in these studies is a general response or a function of (1) the low statistical power of most experiments and/or (2) the magnitude of CO_2-stimulated C inputs relative to the duration of the experiments (Hungate *et al.*, 1996; Filion *et al.*, 2000; Smith, 2004). A further concern is that if CO_2-stimulated increases in soil organic C do occur, they will be allocated to rapidly cycling, labile pools with little, if any, long-term stabilization (Hungate *et al.*, 1997; Lichter *et al.*, 2005).

One of the few elevated-CO_2 experiments to report a significant increase in soil C is our study of native grassland in Kansas (Jastrow *et al.*, 2000; Williams *et al.*, 2000, 2004). Here, we present corroborating results from a study in temperate deciduous forest, along with additional data from the grassland experiment, to show that similar mechanisms are responsible for the increase and affect the potential longevity of accrued C at both sites, even though they differ in climate, vegetation, and soil properties. We also discuss factors that enabled detection of C accrual despite high background C concentrations and low treatment replication. Lastly, we present a meta-analysis of published data from a wide range of ecosystems to support the generality of our experimental results.

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Materials and methods

Site description and sampling

The deciduous forest free-air CO_2 enrichment (FACE) experiment was constructed in a 10-year-old sweetgum (*Liquidambar styraciflua* L.) plantation in Oak Ridge, TN (Norby *et al.*, 2001). When the experiment began in

April 1998, the average tree height was about 12 m. The site is located on Wolftever silty clay loam (fine, mixed, semiactive, thermic Aquic Hapludult). The ongoing experiment consists of two 25 m diameter plots exposed to elevated CO_2 at 542 μmol mol^{-1} (5-year daytime average) during the growing season (April–November) and three ambient-CO_2 plots (CO_2 concentrations averaged 384–398 μmol mol^{-1}).

The 8-year grassland experiment used open-top chambers placed on native prairie in Manhattan, KS (Owensby *et al*., 1993). The site, which is representative of mixed C4/C3 grasslands in the eastern Great Plains and Corn Belt regions, was located on a 5% slope and was dominated by warm-season C4 grasses, with C3 species contributing only about 15% to aboveground biomass (Owensby *et al*., 1999). Although bare patches occurred between plant stems and crowns, virtually all surface soil was heavily occupied by roots and rhizomes. The soil series was Tully silty clay loam (fine, mixed, superactive, mesic, Pachic Argiustoll). Experimental treatments were (1) ambient CO_2, no chamber; (2) ambient CO_2, with chamber, and (3) elevated CO_2, with chamber. Treatments, which began in May 1989, were replicated three times on 4.5 m diameter plots. Elevated-CO_2 concentrations were maintained at twice ambient on the basis of real-time measurements. Measured CO_2 concentrations in the elevated treatment averaged 709 μmol mol^{-1} during the day and 811 μmolmol^{-1} at night.

At both sites, soil was sampled with a 4.8 cm diameter corer after removal of surface litter. Cores were divided into depth increments of 0–5, 5–15 and 15–30 cm and pooled within plots. The forest site was sampled randomly in October 1997 (pretreatment; 6 cores per plot to 30 cm), November 2000 (12 cores per plot to 15 cm) and October 2002 (18 cores per plot to 30 cm). The prairie experiment was sampled at its conclusion in early November 1996 (4 cores to 30 cm and 2 additional cores to 5 cm per plot) by using the stratified random design described in Jastrow *et al*. (2000). In this design, the cores were randomly placed on or near the crowns of the dominant C4 species, but roots of C3 species were intermixed with C4 roots and were not excluded.

Analytical procedures

After removal of roots and rhizomes, soil was passed through a 4 mm sieve and dried at 65–70 °C. Subsamples were gently crushed to pass through a 2 mm sieve, and remaining litter and root pieces longer than 3–4 mm were removed. Another subsample of 4 mm sieved soil was separated into stable microaggregates (53–250 μm in diameter) and nonmicroaggregated soil by using a microaggregate isolator (Six *et al*., 2000). Briefly, samples were immersed in deionized water over a 250 μm sieve and shaken with 50 glass beads at 180 strokes min^{-1} on a reciprocating shaker. Continuous water flow flushed microaggegates and other soil components <250 μm through the device and onto a 53 μm sieve. Material retained on the 53 μm sieve was wet-sieved (50 up-down strokes in 2 min). Nonaggregated fine (53–250 μm) particulate organic matter (POM) was separated from microaggregates by flotation in sodium polytungstate solution (2.0 g cm^{-3}). Both the nonaggregated POM and stable microaggregates were washed with deionized water, and the POM was combined with the other nonmicroaggregated soil. Whole soil and fractions were dried at 65 °C, ground, and analyzed for C and N by dry combustion with a Carlo Erba NC2500 elemental analyzer (Thermo Electron, Waltham, MA, USA). Soil at both sites was free of carbonates.

Stable C isotope ratios in soil from the forest site were determined by using a Carlo Erba EA1108 elemental analyzer interfaced with a isotope ratio mass spectrometer (Thermo Electron, Waltham, MA, USA) operating in continuous-flow mode. Results were expressed in standard $\delta^{13}C$ notation and reported relative to the international Vienna Pee Dee Belemnite standard. Overall precision (machine plus sample preparation error) was 0.1‰. The fraction (f) of soil C derived from ^{13}C-depleted CO_2 fixed by plants in elevated-CO_2 plots was calculated as $f = (\delta_t - \delta_i)/(\delta_o - \delta_i)$ where δ_t is the $\delta^{13}C$ of soil after 3 years (2000) or 5 years (2002) of treatment; δ_i is the $\delta^{13}C$ of inputs produced under elevated CO_2; and δ_o is the $\delta^{13}C$ of pretreatment (1997) soil. The value of δ_i (−37.5‰) was estimated from roots collected from ingrowth cores (Matamala *et al*., 2003).

Data analyses and meta-analysis

For the forest study, data were analyzed by repeated measures analysis of variance (ANOVA). Calculation of C accrual attributed to CO_2 enrichment was adjusted for initial conditions (accrual = [2002 elevated − 1997 elevated] − [2002 ambient − 1997 ambient]). For the prairie study, data were analyzed by ANOVA with orthogonal treatment contrasts in a randomized complete-block design. Experimental blocks were positioned at different elevations along the slope, and orthogonal contrasts were used to test two preplanned, independent null hypotheses about the CO_2 treatments: (1) no difference between ambient controls (ambient, with chamber = ambient, no chamber) and (2) no difference between elevated-CO_2 treatment and the ambient controls. Given constraints on replication and the consequent low statistical power of the experiments (Hungate *et al*., 1996; Filion *et al*., 2000), a probability level of 0.10 was chosen as the criterion for statistical significance. All reported errors are standard errors.

The metadata (see supplementary Table S1) were analyzed by using MetaWin 2.0 software (Rosenberg *et al.*, 2000), with the effect size for each observation calculated as the natural log of the response ratio. The mean effect size is the weighted mean of individual effect sizes, with the reciprocal of the standard deviation as the weighting factor. Data were obtained from published sources identified by searching the Web of Science® (http://thomsonscientific.com/products/wos/). When data were presented graphically, values were obtained directly from authors or estimated by digitizing an image of the figure. Data reported as concentrations were converted to stocks by using published bulk densities for the site; in a few cases bulk densities were unavailable and values were estimated.

Our primary criteria for inclusion in the meta-analysis were (1) study duration was at least two growing seasons and (2) CO_2 enrichment used FACE (or similar) technology, open-top chambers, or other outdoor fumigation apparatus. We excluded data from (1) natural CO_2 springs, because of their inherent variability and lack of control; (2) studies conducted in greenhouses or controlled environment chambers; and (3) studies where plants were grown in containers with surface areas $<1\,m^2$ or depths $<1\,m$. Most studies were conducted on existing soils, *in situ*, but constructed soils were included if the studies met our large container criteria. However, constructed soils were excluded if (1) the soil was diluted with sand or similar materials or (2) the soil was imported from outside the region (usually to provide SOM with a contrasting C isotope signature). We also excluded one study with treatment differences corresponding to accrual $>800\,g\,C\,m^{-2}\,yr^{-1}$.

We required that plots were the unit of replication (not samples within a plot) and that treatments were replicated at least twice, eliminating studies that aggregated data over a range of CO_2 concentrations. The analysis was also limited to studies that reported means, standard deviations or standard errors, and number of replicates (or for which these parameters could be obtained from the investigators). This criterion eliminated two otherwise eligible studies that would have contributed six data points to the analysis.

When results from the same experiment were reported over time, we used data from only the latest sampling date because meta-analysis assumes that studies are independent (Gurevitch & Hedges, 1999). However, we adjusted the data for reported variations in initial C stocks by normalizing to the overall average of pretreatment C stocks; when pretreatment differences were not reported, they were assumed to be negligible. When different vegetation, soil types or elevated-CO_2 concentrations were investigated at the same facility, these studies were considered independent and were included in the analysis as separate observations. Similarly, when studies incorporated additional manipulations, the results were included as separate observations if independent ambient-CO_2 controls were available with the same additional manipulations as elevated-CO_2 plots.

Results and discussion

Organic C in the surface 5 cm of the forest soil increased linearly during 5 years of exposure to elevated CO_2,

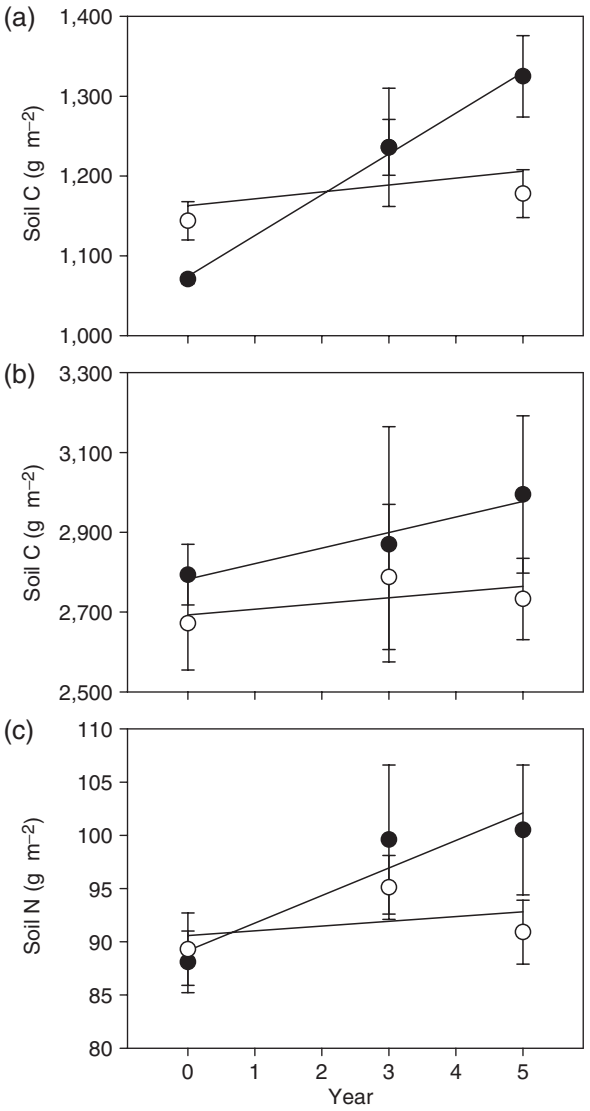

Fig. 1 Mean forest soil C and N stocks (± SE) in elevated (solid symbols) and ambient (open symbols) CO_2 treatments over time. (a) Carbon at 0–5 cm; treatment × time interaction in repeated-measures analysis of variance indicated differing effects of CO_2 treatments over time ($P = 0.032$). (b) Carbon at 0–15 cm (treatment × time $P = 0.48$). (c) Nitrogen at 0–5 cm (treatment × time $P = 0.081$).

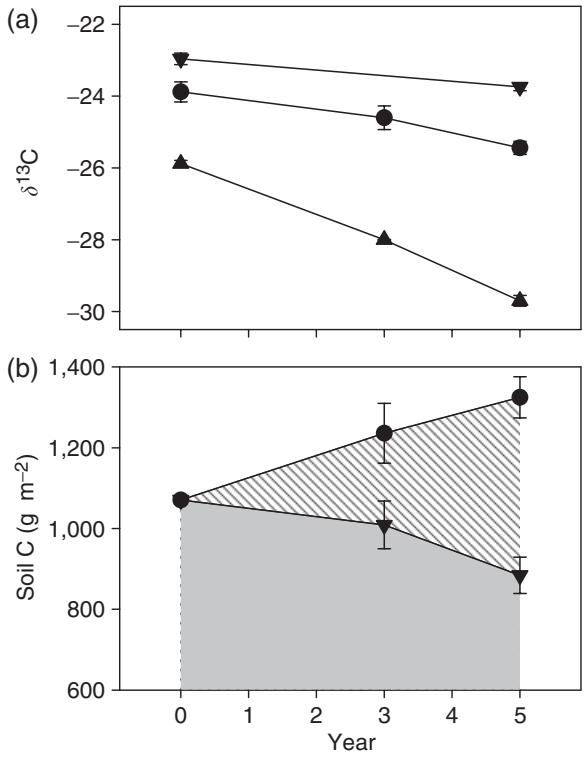

Fig. 2 Incorporation of free-air CO_2 enrichment (FACE)-derived C into forest soil over time. (a) Changes in the stable isotopic composition of whole soil C (means ± SE) from the elevated-CO_2 treatment at 0–5 cm (▲), 5–15 cm (●), and 15–30 cm (▼). (b) Loss of pretreatment C (▼; shaded area) and accrual of FACE-derived C (● ; hatched area) at 0–5 cm under elevated CO_2 (means ± SE) calculated from the mass balance of stable C isotopes.

Table 1 Mean (± SE) whole soil C and N stocks and accrual by depth in prairie soil after 8 years of CO_2 treatment

Depth and treatment	Organic C ($g\,m^{-2}$)	Total N ($g\,m^{-2}$)
0–5 cm		
Elevated CO_2	2494 ± 132	202 ± 9
Ambient CO_2	2368 ± 61	197 ± 4
Accrual	126 ± 32	5 ± 3
(Probability > *F*)	(0.0162)	(0.1180)
0–15 cm		
Elevated CO_2	6153 ± 268	505 ± 19
Ambient CO_2	5884 ± 164	494 ± 11
Accrual	269 ± 77	11 ± 5
(Probability > *F*)	(0.0249)	(0.1145)
0–30 cm		
Elevated CO_2	10370 ± 436	865 ± 34
Ambient CO_2	9900 ± 282	837 ± 21
Accrual	470 ± 150	27 ± 10
(Probability > *F*)	(0.0352)	(0.0580)

Values for chambered and unchambered ambient controls did not differ ($P > 0.14$) and are combined ($n = 6$); for elevated CO_2, $n = 3$. Standard errors and probability > F for accrual values determined after adjusting for topographic effects on soil C and N (see supplementary Table S2). Below 30 cm, no significant response to CO_2 treatment was found in an independent set of random samples taken to 90 cm (data not shown).

while C in the ambient plots remained relatively constant (Fig. 1a). No significant changes in soil C were found at deeper depths for either elevated or ambient CO_2. Consistent with vegetative effects on soil formation (Jenny, 1941), increases in soil C storage, particularly in forests, are more likely to occur near the surface, where inputs from roots and aboveground litter are greatest. If we had sampled to 15 cm in one increment, the C accrued in the surface 5 cm would have been diluted with the unchanged C pool at 5–15 cm, and we would not have detected a significant change (Fig. 1b). This finding raises the possibility that actual changes in soil C have been masked in some CO_2 enrichment studies because the surface 10–20 cm was sampled in one increment.

Because the CO_2 source used at the forest site was depleted in ^{13}C ($\delta^{13}C = -55‰$), the $\delta^{13}C$ of CO_2 in the elevated treatment was altered, which decreased the ^{13}C signature of the vegetation (Matamala *et al.*, 2003). We used the subsequent decrease in the $\delta^{13}C$ of SOM (Fig. 2a) to determine that 441 ± 5 $g\,m^{-2}$ of FACE-derived C was present in the surface 5 cm after 5 years. This amount was sufficient to account for both the observed 5-year accrual of 220 $g\,C\,m^{-2}$ and replacement of 221 $g\,m^{-2}$ of pretreatment C (Fig. 2b). With no changes in C stocks below 5 cm, decreases in $\delta^{13}C$ (Fig. 2a) accounted for the replacement of pretreatment C with 196 ± 49 and 99 ± 30 $g\,m^{-2}$ of FACE-derived C at 5–15 and 15–30 cm, respectively. These amounts are consistent with a profile of declining C inputs with increasing soil depth.

In contrast to the forest, soil C at the prairie site increased significantly throughout the surface 30 cm with CO_2 enrichment (Table 1), reflecting the typically higher root densities and greater C inputs at depth in prairie. Because the prairie site was on a slope, experimental blocks were positioned at different elevations. This design was essential for distinguishing the effect of CO_2 treatment on soil C from the influence of topography, another well-known soil forming factor (see supplementary Table S2).

The detection of soil C accrual depends not only on sampling issues and variability, but also on the rate of inputs to SOM. Smith (2004) demonstrated that the time required for a change in soil C to become measurable declines as a function of the percentage stimulation in C inputs. In both the forest and prairie experiments, the

vegetation responded to CO_2 enrichment by substantially increasing belowground C allocation. Elevated CO_2 stimulated net primary production in the forest by an average of 24%, but 76% of this response was allocated to fine roots after the first 2 years. From the third year on, the peak standing crops of fine roots in the surface 15 cm increased by an average of 140% under elevated CO_2, while leaf litter increased by only 8% (Norby *et al*., 2004). Because of the rapid turnover of sweetgum fine roots (Matamala *et al*., 2003; Norby *et al*., 2004), CO_2 stimulation of root production quickly delivered a large increase of inputs to SOM, particularly within the surface 5 cm (where root density was about three times that at 5–15 cm for both elevated and ambient CO_2; data not shown). Below 5 cm, the CO_2 response was apparently insufficient to discernibly increase soil C within 5 years. In the prairie, CO_2 enrichment stimulated root production by an average of 41%, compared with a 17% increase in aboveground production (Owensby *et al*., 1999; Jastrow *et al*., 2000). Although belowground standing crops were two to four times greater in the prairie than in the forest, sweetgum roots turn over three to four times faster than prairie grass roots (Hayes & Seastedt, 1987; Matamala *et al*., 2003). Hence, CO_2 enhancement of belowground inputs was of similar magnitude in both forest and prairie surface soils and greater than in many other experiments with lower belowground productivity and/or smaller relative responses (e.g. Hungate *et al*., 1997; Leavitt *et al*., 2001; Gill *et al*., 2002; Pendall *et al*., 2004; Lichter *et al*., 2005).

The annual rate of soil C accrual was similar for both experiments, even though differences in ecosystem rooting strategies caused C to be accumulated at different depths. Atmospheric CO_2 enrichment increased C stocks in the forest soil at an average rate of $44 \pm 9\,g\,C\,m^{-2}\,yr^{-1}$. In the prairie, the incremental increase in C stocks corresponded to an average accrual rate of $59 \pm 19\,g\,C\,m^{-2}\,yr^{-1}$. In an independent sampling of the prairie experiment, Williams *et al*. (2004) found a similar rate of accrual within the surface 15 cm. Soil C accrual at both sites was comparable with the $52\,g\,C\,m^{-2}\,yr^{-1}$ accrued in the litter layer of a pine forest FACE experiment, where CO_2 enrichment stimulated foliage production more than root production (Lichter *et al*., 2005). However, unlike C accumulated in surface litter, which is stabilized only by its biochemical resistance to decomposition, C accrued in mineral soil can also be stabilized by physical protection and chemical associations with soil minerals, potentially increasing the residence times of more labile constituents (Christensen, 1996).

In both experiments, a portion of the accumulated C was associated with soil minerals in stable aggregates.

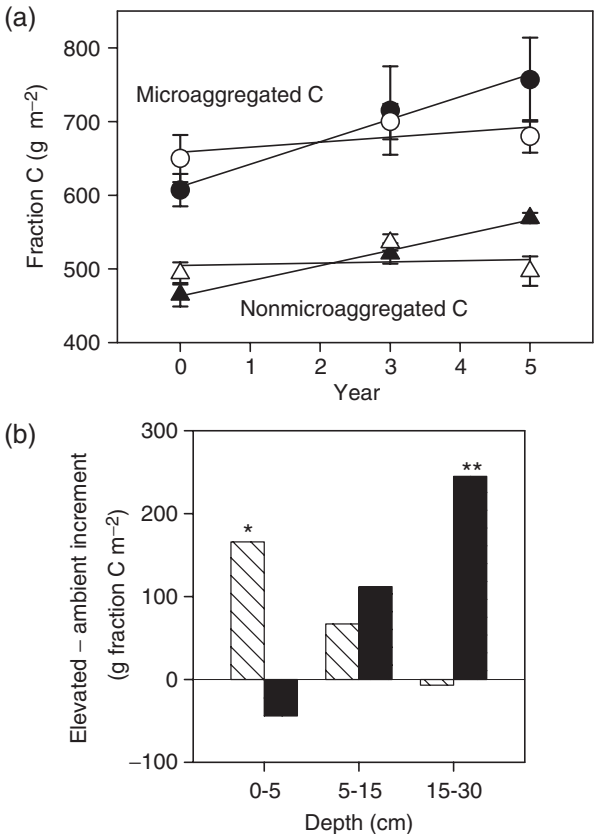

Fig. 3 Distribution of C stocks between microaggregated and nonmicroaggregated soil. (a) Changes in fraction C (means ± SE) over time for forest soil in elevated (solid symbols) and ambient (open symbols) CO_2 treatments at 0–5 cm; treatment × time interaction in repeated-measures analysis of variance indicated differing effects of elevated- and ambient-CO_2 treatments over time (microaggregated $P = 0.038$; nonmicroaggregated $P = 0.078$). (b) Allocation of C stocks accrued in prairie soil under elevated CO_2 between microaggregated (solid bar) and nonmicroaggregated (hatched bar) fractions by depth (* $P \leq 0.10$; ** $P < 0.05$).

In the forest, the proportion of whole-soil C found in microaggregated soil averaged 58% in both elevated-CO_2 and ambient plots and was unchanged over time (Fig. 3a). This suggests that additional inputs derived from CO_2 enrichment were processed and protected in much the same manner as in ambient soil, with little apparent saturation of this protection mechanism, even after 5 years. The formation of microaggregates is a key factor in physically protecting particulate SOM from rapid decomposition and helps to create conditions wherein microbial residues and breakdown products can be stabilized in organomineral complexes (Golchin *et al*., 1994; Christensen, 1996; Six *et al*., 2002).

Even though the prairie soil had larger C stocks, 55% of the accrued C was also incorporated into microag-

gregates, but the extent of protection varied with depth (Fig. 3b). In the surface 5 cm, where native SOM was greatest, the capacity of microaggregates to protect additional C appeared saturated, and C accumulated in less protected nonmicroaggregated pools – mostly as POM, as seen in other studies (Haile-Mariam *et al.*, 2000; Gill *et al.*, 2002; Hagedorn *et al.*, 2003; Lichter *et al.*, 2005). Below 5 cm, however, most of the accrued C was incorporated into microaggregates. Long-term laboratory incubations of soil from the prairie experiment confirmed the protection afforded by microaggregates in deeper soil; Williams *et al.* (2004) found that 55% of the CO_2-stimulated increase in soil C at 0–5 cm was mineralized compared with only 16% at 5–15 cm. Thus, the potential for some accrued C to be stabilized in longer-lived pools is greater in the forest soil and at depth in the prairie soil, because more of this C has entered microaggregate protected pools.

Soil C accrual was accompanied by significant increases in soil N (Fig. 1c, Table 1) at average rates of $2.2 \pm 0.6\,g\,N\,m^{-2}\,yr^{-1}$ in the forest and $3.4 \pm 1.3\,g\,N\,m^{-2}\,yr^{-1}$ in the prairie. Thus, in addition to enhancing C inputs to soil through increased primary production, elevated CO_2 apparently also caused some combination of reduced N losses, stimulated N fixation, and redistribution of subsurface N via greater root exploration at depth. These results challenge the hypothesis that N cycling feedbacks will constrain ecosystem C accumulation (Zak *et al.*, 1993; Luo *et al.*, 2004). Rather, in these ecosystems the N cycle appears sufficiently flexible – at least for the duration of these experiments – to support soil C accrual in response to CO_2 enrichment.

Even though most field experiments have been unable to individually discern a response to CO_2 enrichment, meta-analysis provides a quantitative, statistical means for evaluating the integrated, collective results of these studies. Meta-analysis of 35 independent experimental observations (Fig. 4) indicated that CO_2 enrichment increased soil C by 5.6% (95% CI = 2.8–8.4%), supporting the generality of the accrual measured in the forest and prairie experiments. This response corresponded to a median annual accrual rate of $19\,g\,C\,m^{-2}\,yr^{-1}$ with an interquartile range of 2–$54\,g\,C\,m^{-2}\,yr^{-1}$. Given the large stimulation of belowground inputs and unsaturated protection mechanisms in our forest and prairie soils, it is not surprising that our measured rates are somewhat greater than the median rate for the metadata.

Real-world responses to CO_2 fertilization will not be independent of other changing environmental forcing factors (e.g. temperature, moisture, ozone, and N deposition), but a better understanding of the full range of single factor responses is still needed to improve modelling efforts to predict multifactor responses (Norby & Luo, 2004). Our findings clearly demonstrate that mineral soil C, including microaggregate protected pools, can increase measurably in response to a step-function increase in atmospheric CO_2 concentrations. The results confirm model predictions that experimental measurement of soil C accrual over relatively short time periods requires a large stimulation of inputs (Smith, 2004) and also demonstrate that sampling methods can mask even relatively large and rapid changes. Our data also indicate that the C storage capacities of mineral soils – even those with large organic matter stocks – are not necessarily saturated at present and may be capable of serving as C sinks if inputs increase as a result of passive CO_2 fertilization or active management efforts to sequester C. Further, some of this C may enter into longer-lived pools. The meta-analysis, which included some multifactor studies and data collected over a wide range of climatic conditions, suggests that soil C accrual, albeit of a smaller magnitude than our

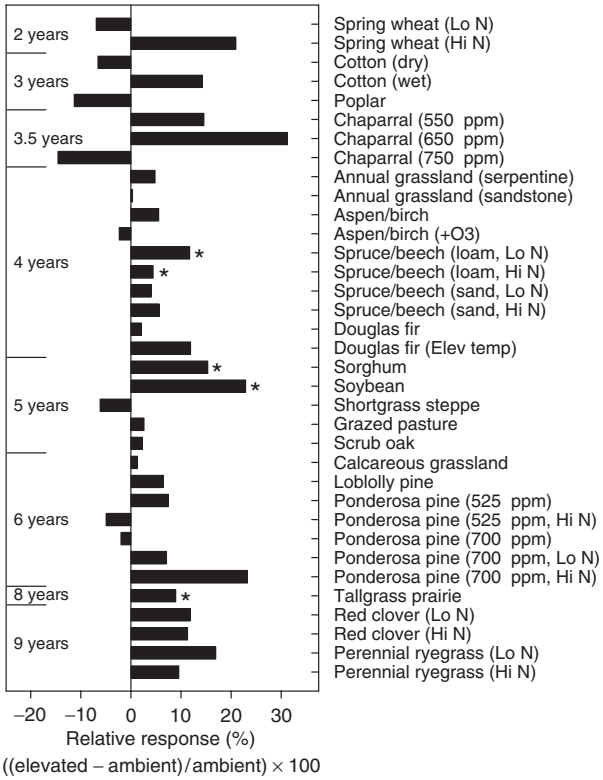

Fig. 4 Response of soil C stocks in elevated-CO_2 treatments relative to ambient controls for published free-air CO_2 enrichment and outdoor chamber studies $\geq$ 2 years in duration. Responses were adjusted for pretreatment variations in C stocks, where available. Soil depths ranged from 5 to 20 cm. Asterisks identify studies reporting a significant CO_2 effect ($P < 0.10$). See supplementary Table S1 for sources and study information.

experimental results, is likely to be a general response to CO_2 enrichment. While such a response would not begin to offset anthropogenic CO_2 emissions, it is not insignificant. If mineral soil C in the surface 20 cm of the world's temperate forests, temperate grasslands, shrublands, and croplands (234 Pg C over 4350×10^6 ha according to Jobbágy & Jackson, 2000) were to increase by 5.6% or at a rate of 19 g C m^{-2} yr^{-1}, then 8–13 Pg of C might be accumulated within a 10-year period.

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Supplementary Material

The following supplementary material is available (on request) for this article online: http://www.blackwell-publishing.com/products/journals/suppmat/GCB/GCB1077/GCB1077sm.

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