

and thus can only enhance the likelihood of failure by altering some physical property of, or near, the triggered fault⁸. Our hypotheses and theoretical calculations²⁴ suggest that such alteration requires large deformations of the order of the dynamic thresholds estimated here. Although our observations indicate that transient dynamic deformations trigger earthquakes, the mechanism(s) by which they do so remain unknown^{11,13,25–28}. Evidence presented here for a possible triggering threshold and for significant time delays (in some cases) between the shaking and seismicity rate increases provide insights for elucidating the triggering mechanism. □

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Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂

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The current rise in atmospheric CO₂ concentration is thought to be mitigated in part by carbon sequestration within forest ecosystems^{1,2}, where carbon can be stored in vegetation or soils. The storage of carbon in soils is determined by the fraction that is sequestered in persistent organic materials, such as humus. In experimental forest plots of loblolly pine (*Pinus taeda*) exposed to high CO₂ concentrations^{3,4}, nearly half of the carbon uptake is allocated to short-lived tissues, largely foliage. These tissues fall to the ground and decompose, normally contributing only a small portion of their carbon content to refractory soil humic materials⁵. Such findings call into question the role of soils as long-term carbon sinks, and show the need for a better understanding of carbon cycling in forest soils. Here we report a significant accumulation of carbon in the litter layer of experimental forest plots after three years of growth at increased CO₂ concentrations (565 μl l⁻¹). But fast turnover times of organic carbon in the litter layer (of about three years) appear to constrain the potential size of this carbon sink. Given the observation that carbon accumulation in the deeper mineral soil layers was absent, we suggest that significant, long-term net carbon sequestration in forest soils is unlikely.

The FACE (free air CO₂ enrichment) experiment in the Duke Forest (Orange County, North Carolina, USA) is composed of six plots 30-m in diameter^{3,4}. Three experimental plots are fumigated with CO₂ to maintain the atmospheric CO₂ concentration 200 μl l⁻¹ above ambient. Three control plots are fumigated with ambient air only (365 μl l⁻¹). The experiment began on 27 August 1996 and is continuous (24 h d⁻¹; 365 d yr⁻¹) except in extreme weather⁴. During the first two years of the experiment, net primary production increased by 25% in the fumigated plots³.

The forest is derived from three-year-old pine seedlings that were planted in 1983 in a 2.4 × 2.4 m spacing. In 1996, the forest was approximately 14 m tall, with a closed canopy and pine accounting for 98% of the basal area. The 32-ha site contains an elevation gradient of 15 m between the highest and lowest points, but topographic relief is ≤1° throughout. Soils are of the Enon Series, a low-fertility Ultic Alfisol, which is typical of many upland areas of the southeastern United States. The soil is derived from igneous rock, yielding a relatively acidic (pH = 5.75), well-developed soil profile with mixed clay mineralogy. Boreholes show up to 1 m of topsoil, underlain by 5 m of saprolite, with highly fractured granodiorite to diorite bedrock at greater depth. The static water table is at 6 m, but the site is poorly drained from late autumn until early spring, leading to saturated surface soils. The mean annual temperature is 15.5 °C and mean annual precipitation is 1,140 mm.

The CO₂ used for fumigation is derived from natural gas and strongly depleted in ¹³C: δ¹³C = -43.0 ± 0.6 (mean ± s.e.; in ‰) versus the Pee Dee Belemnite standard, PDB. Using this CO₂ to increase the atmospheric concentration by 200 μl l⁻¹ changes the δ¹³C of atmospheric CO₂ in the FACE plots from -8‰ to -20‰. As a result of the photosynthetic fractionation, needles grown under increased CO₂ have a δ¹³C value of -39.3‰ (ref. 6), and the δ¹³C

value of new roots less than 2 mm in diameter ranges from -38.5‰ to -39‰ (R. Matamala, unpublished results). We follow the incorporation of this isotopic signal into soil organic components as an index of their dynamics.

During construction of the experiment, pretreatment soil samples were collected and archived from 16 excavations surrounding each plot. In early October 1999, after three growing seasons of fumigation, twelve soil cores 4.76 cm in diameter were collected from stratified, random positions within each plot. Each sample consisted of the undecomposed plant materials on the soil surface (that is, the forest floor) and soil layers extending from 0 to 15 cm and from 15 to 30 cm depths, which collectively include nearly all of the root biomass⁷. The leaves fall in late October, so this sampling time corresponded to the annual minimum in forest-floor mass. The volume and mass of stones were determined for each sample and subtracted from the sample mass to estimate soil bulk density (g cm⁻³). All samples were dried at 48 °C for 5 days, and mineral soils were sieved (<2 mm) to remove coarse roots and stones.

The organic material in 30-g subsamples of the mineral soil was separated into coarse particulate organic matter (POM; >0.5 mm), fine POM (53 μm–0.5 mm), and mineral-associated (<53 μm) fractions^{8,9}. During decomposition, fresh plant litter is transformed sequentially into these fractions, which have increasing stability and potential to account for long-term carbon sequestration in soils¹⁰. The fraction <53 μm, including dissolved organic matter, was obtained following centrifugation (2,000 r.p.m. for 10 min). Samples of each fraction and bulk samples of the soil and forest floor were analysed for %C, %N, and δ¹³C using a SIRA Series II isotope ratio mass spectrometer (Micromass, Manchester, UK), operated in automatic trapping mode after Dumas combustion of samples in a C and N analyser (NA1500 Series 1, Carlo Erba Instrumentazione, Milan, Italy). The reference CO₂, calibrated against the PDB standard, was obtained from Oztech (Dallas, Texas). Data are expressed as δ¹³C after correction for the isotope contribution of the O₂ used in sample combustion.

The mean of samples within each plot is considered to be the experimental unit for statistical analyses, giving a sample size of three each for the experimental and control plots. There were no

significant differences in the mass of the forest floor between control and experimental plots at the beginning of the experiment¹¹. In pretreatment samples of soil from 0–15 cm depth, %C was 1.432% in control plots and 1.542% in fumigated plots, but these mean values were also not significantly different ($F = 0.388$, $P = 0.567$, $n = 3$ in one-way analysis of variance, ANOVA). In subsequent evaluations of differences in forest floor and mineral soil parameters between control and fumigated plots, we used a one-way ANOVA, incorporating a covariate to account for initial conditions.

At the end of three years of CO₂ fumigation, significant differences were seen between control and fumigated plots for total mass and the carbon and nitrogen content of the forest floor, %C in the mineral soil at 0–15 cm depth, and ¹³C in the forest floor and in bulk and size-fractionated carbon in the mineral soil from 0–15 cm depth (Table 1). No significant differences were seen in soils below 15 cm depth. Differences in the forest floor derive solely from an increase in its mass in CO₂-fumigated plots, because %C and %N were not altered by the experiment. Greater %C, without a concomitant change in %N, contributed to a greater pool of carbon in the mineral soil of fumigated plots, but this difference in C mass was not statistically significant. A two-way ANOVA, with time (1996 versus 1999) and treatment (365 and 565 μl l⁻¹ CO₂) as main effects, indicates no significant effect of time ($P = 0.70$) or treatment ($P = 0.085$) on %C in the 0–15 cm soil depth of control or fumigated plots nor any interaction between time and treatment ($P = 0.41$). This result indicates that the difference in %C in the 0–15 cm soil layer is related to initial plot differences and not to the experimental treatment.

In non-steady-state conditions, the mean residence time (MRT) of carbon pools can be estimated from: $C_t = C_0 e^{-kt} + (I/k)(1 - e^{-kt})$ solved by iteration for k , where C_t is the carbon stock after three years of fumigation, C_0 is the pre-fumigation stock, t is the duration of the experiment, I is the annual C input from litterfall and root turnover, and k is the decomposition constant¹². For the control and fumigated plots, the MRT values (=1/ k) for C in the forest floor were 2.50 and 2.86 yr, respectively.

Differences in δ¹³C result for the entry of new plant debris

Table 1 Forest floor and soil parameters (mean ± s.e.) after three years of CO₂ fumigation

Forest floor									
	Mass (g m ⁻²)	%C	%N	C:N	Total C (g m ⁻²)	Total N (g m ⁻²)	δ ¹³ C		
Control plots	1,833.5 (206.5)	38.24 (0.61)	0.90 (0.02)	42.71 (1.06)	700.98 (87.23)	16.55 (2.24)	-28.90 (0.27)		
Fumigated plots	2,359.6 (32.4)	37.68 (0.41)	0.88 (0.02)	43.36 (0.74)	883.92 (24.30)	20.57 (0.75)	-34.15 (0.71)		
<i>P</i>	0.008	0.484	0.471	0.637	0.014	0.009	0.002		
Mineral soil 0–15 cm depth									
	%C	%N	C:N	Total C (g m ⁻²)	Total N (g m ⁻²)	δ ¹³ C (‰)			
						Bulk soil	Coarse POM	Fine POM	<53 μm fraction
Control plots	1.31 (0.07)	0.07 (0.01)	18.09 (0.91)	1,901.43 (51.63)	105.8 (8.5)	-26.244 (0.182)	-26.819 (0.272)	-27.144 (0.120)	-25.831 (0.199)
Fumigated plots	1.59 (0.07)	0.08 (0.01)	18.98 (1.18)	2,207.65 (136.33)	118.6 (13.6)	-28.054 (0.195)	-29.746 (0.106)	-28.479 (0.078)	-27.214 (0.127)
<i>P</i>	0.037	0.839	0.581	0.180	0.570	0.002	0.001	0.001	0.004
Mineral soil 15–30 cm depth									
	%C	%N	C:N	Total C (g m ⁻²)	Total N (g m ⁻²)	δ ¹³ C (‰)			
						Bulk soil	Coarse POM	Fine POM	<53 μm fraction
Control plots	0.484 (0.054)	0.030 (0.003)	16.1 (0.47)	657.1 (61.3)	40.8 (3.9)	-24.199 (0.457)	-24.334 (0.381)	-26.110 (0.261)	-24.096 (0.507)
Fumigated plots	0.539 (0.057)	0.033 (0.004)	16.2 (0.52)	747.4 (46.4)	46.2 (1.7)	-24.955 (0.554)	-25.451 (0.156)	-26.840 (0.268)	-24.515 (0.585)
<i>P</i>	0.606	0.356	0.946	0.263	0.286	0.352	0.053	0.123	0.617

The *P* value is derived from one-way ANOVA used to test for treatment effects, with a covariate included in the model to account for initial site differences in forest floor mass and %C and %N of the mineral soil layers. One collection of forest floor mass and one measurement of %C in the mineral soil at 0–15 cm depth were deleted from the analysis following a test for outliers³⁰. POM, particulate organic matter.

into forest floor materials and into coarse POM of the mineral soil. In the fumigated plots, more than 50% of the organic carbon in the forest floor is derived from plant tissues grown since the beginning of the experiment. The change in $\delta^{13}\text{C}$ in forest floor carbon can be used to provide an alternative estimate of its MRT in the fumigated plots. We assume an exponential decline in $\delta^{13}\text{C}$ in plant litter after the onset of fumigation, and derive k by iteration using the formula: $1 - f = e^{-kt}$, where f is the fraction of organic matter replaced by new carbon with depleted $\delta^{13}\text{C}$ (that is, $f = (\delta^{13}\text{C}_{\text{increased}} - \delta^{13}\text{C}_{\text{ambient}}) / (\delta^{13}\text{C}_{\text{new}} - \delta^{13}\text{C}_{\text{ambient}})$) (ref. 13). Assuming that $\delta^{13}\text{C}$ of fresh litter (C_{new}) in the fumigated plots is -37.5‰ (ref. 14), the MRT for carbon in the forest floor is 3.23 yr ($k = 0.31$)—in good agreement with the literature¹⁵ and with the estimate derived above ($k = 0.35$).

Changes in $\delta^{13}\text{C}$ in bulk soil organic matter at 0–15 cm depth yield an estimated 20-year mean residence time for this pool. The greatest change in $\delta^{13}\text{C}$ is seen in coarse POM and the least in the mineral-associated fraction, consistent with the increasing stability of carbon in finer fractions of soil organic matter^{8–10}. A small change in $\delta^{13}\text{C}$ in the coarse POM at 15–30 cm depth indicates inputs of fresh plant debris at that depth, but the absence of change in $\delta^{13}\text{C}$ in the mineral-associated fraction suggests that there has been little production or downward movement of dissolved organic carbon compounds, such as fulvic acids, during the three-year period.

Growth of this forest under increased CO_2 has increased the production of dead plant debris, which is delivered to the forest floor and to the mineral soil through plant litterfall^{3,14}, leaching of above-ground plant components by rain¹⁶, and root turnover⁷. The cumulative change in these inputs, owing to growth at high CO_2 , is about 166 g C m^{-2} for the three growing seasons of CO_2 fumigation (Table 2). This higher input of organic materials can—within experimental error (Table 1)—account for the greater mass of carbon held in the forest floor of CO_2 -fumigated plots at the end of the third growing season (183 g C m^{-2}). Additional carbon may derive from root exudations of low-molecular-weight carbon compounds (for example, see ref. 17), which are reported to increase when plants are grown at high CO_2 (refs 18, 19). The non-significant change in the mass of organic carbon in the mineral soil is similar to the results of several CO_2 -fumigation experiments in grasslands, which demonstrate substantial turnover of soil carbon pools with little or no net accumulation in the profile^{20,21}. These results are in contrast to recent predictions of a large potential sink for C in soils^{22,23}.

Although soil carbon accumulates rapidly during the initial growth of pine plantations in the southeastern United States²⁴, wood growth is normally the largest sink for carbon in these forests^{24,25}. In the Duke forest experiment, trees in the control plots sequestered about $430 \text{ g C m}^{-2} \text{ yr}^{-1}$ (ref. 3) during their first 16 years of growth, and the forest floor has accumulated at about $44 \text{ g C m}^{-2} \text{ yr}^{-1}$, similar to rates measured in 15-year old plantations in Virginia²⁵. Such reforested lands in the eastern United States sequester 0.07 to $0.17 \text{ Pg C yr}^{-1}$ (refs 26, 27)—about 10% of the US

fossil-fuel emissions, currently estimated at 1.4 Pg C yr^{-1} (ref. 28). Of the total estimated US sink of $0.15\text{--}0.35 \text{ Pg C yr}^{-1}$ in vegetation and soils², Schimel *et al.*²⁸ suggest that only $0.08 \text{ Pg C yr}^{-1}$, or less than $20 \text{ g C m}^{-2} \text{ yr}^{-1}$, has occurred in forests as a result of CO_2 fertilization of plant growth during the past century—changes in land use account for a larger fraction²⁹.

In response to the step-function increase of $200 \mu\text{l l}^{-1}$ in atmospheric CO_2 , this southern pine forest shows an incremental sink for C (183 g C m^{-2}) in the forest floor at the end of three years of fumigation (Table 2). The decomposition constant (k) estimated for the fumigated plots indicates that at equilibrium (C_∞), the forest floor under increased CO_2 will contain $1,103 \text{ g C m}^{-2}$ ($C_\infty = I/k$ and $k = 0.31$). Thus, 80% of the equilibrium forest-floor mass, and 46% of the incremental sequestration due to CO_2 fertilization, has already accumulated. We expect that the incremental sequestration due to growth at high CO_2 will be substantially less than $60 \text{ g C m}^{-2} \text{ yr}^{-1}$ in future years. In the absence of significant changes in the carbon content of the mineral soil, these data suggest only a limited potential for long-term soil carbon sequestration in this forest in response to rising CO_2 in Earth's atmosphere. The larger sink for carbon in vegetation, compared to soils, differs from the results of recent models of the response of the biosphere to climate change and rising CO_2 (ref. 23). □

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Table 2 Estimated inputs of organic matter to soils

	Control plots	Fumigated plots
Inputs		
Litterfall ¹⁴	744	883
Throughfall ¹⁶	24	31
Root turnover ⁷	37	57
Total inputs	805	971
Pools		
Forest floor	701	884
Soil 0–15 cm depth	1,901	2,208
Soil 15–30 cm depth	657	747
Total C pool	3,259	3,839

Inputs were measured from 1 January 1997 to 30 September 1999 (1,003 d, 2.75 yr), and soil carbon pools were measured in early October 1999 (compare Table 1).

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Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere

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Northern mid-latitude forests are a large terrestrial carbon sink^{1–4}. Ignoring nutrient limitations, large increases in carbon sequestration from carbon dioxide (CO₂) fertilization are expected in these forests⁵. Yet, forests are usually relegated to sites of moderate to poor fertility, where tree growth is often limited by nutrient supply, in particular nitrogen^{6,7}. Here we present evidence that estimates of increases in carbon sequestration of forests, which is expected to partially compensate for increasing CO₂ in the atmosphere, are unduly optimistic⁸. In two forest experiments on maturing pines exposed to elevated atmospheric CO₂, the CO₂-induced biomass carbon increment without added nutrients was undetectable at a nutritionally poor site, and the stimulation at a nutritionally moderate site was transient, stabilizing at a marginal gain after three years. However, a large synergistic gain from higher CO₂ and nutrients was detected with nutrients added. This gain was even larger at the poor site (threefold higher than the expected additive effect) than at the moderate site (twofold higher). Thus, fertility can restrain the response of wood carbon sequestration to increased atmospheric CO₂. Assessment of future carbon sequestration should consider the limitations imposed by soil fertility, as well as interactions with nitrogen deposition.

By burning fossil fuel and forests, and converting land to intensive agriculture use, humans have elevated the atmospheric concentration of CO₂ (ref. 3) and the deposition of atmospheric nitrogen (N)^{9,10}. Growth of many tree species is enhanced with provisions of both CO₂ and N in the suboptimal range¹¹, making it difficult to assess the effect of increased availability of either one when the supply of both increases concurrently¹⁰. Experiments indicate decreased nutrient availability¹², owing to increased carbon (C)/N ratios in elevated CO₂-grown foliage and litter¹³, but increased nutrient uptake with elevated CO₂-induced growth enhancement of fine roots¹⁴. Because most forests occur on low-nutrient soils, the uncertain effects of elevated CO₂ on nutrient supply hinders our ability to estimate forest C sequestration for future global C budgets.

If tree nutrient uptake does not increase in proportion to the growth response to elevated CO₂, then maturing pine trees should show less elevated CO₂-induced growth enhancements on low-fertility sites than on moderate sites, and thus should respond more to elevated CO₂ under improved nutrition. To evaluate these predictions, we used two field experiments with related loblolly pine (*Pinus taeda* L.) genotypes: the longest running forest-based free-air CO₂ enrichment (FACE) experiment conducted on a moderately fertile site; and a whole-tree chamber CO₂ enrichment experiment on an infertile site. The large difference in fertility of the two sites is indicated by a much greater increase in growth at the infertile site (130%) than at the moderate site (15%) when added nutrients augmented the sites to the same optimal fertility⁷. Additional site and soil characteristics that reflect fertility are provided in Methods.

The FACE prototype (FACE_p) was built in 1993 in a 10-year-old, 8.5-m tall loblolly pine plantation in the lower Piedmont plateau, growing on moderately low fertility, acidic clay-loam, at the Duke Forest of Duke University, North Carolina (35° 58' N, 79° 08' W; elevation 130 m). Currently the pines are about 15-m tall, and comprise 98% of the basal area¹⁵. FACE_p has enriched (550 p.p.m.v. CO₂) a 30-m diameter circular patch in the forest since 1994, during daylight hours of the growing season¹⁶. Before CO₂ enrichment in FACE_p commenced, growth (that is, the amount of C sequestered in woody biomass increment) was similar in FACE_p and an adjacent,

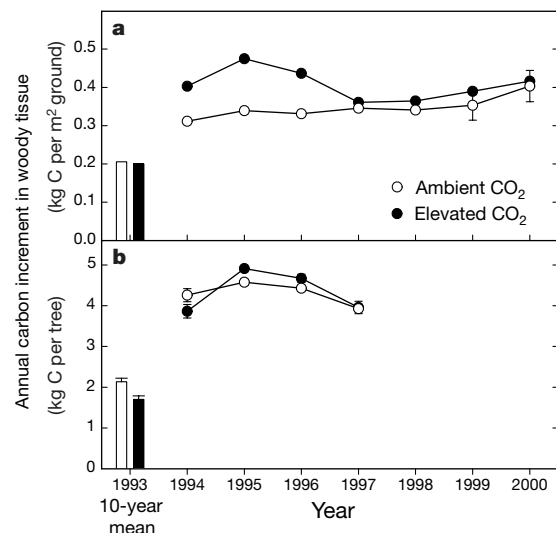


Figure 1 A comparison of annual carbon increment under elevated atmospheric CO₂ concentration (initiated in 1994) and ambient concentration without nutrient addition. **a**, Plot-level comparison between the free-air CO₂ enrichment prototype (FACE_p) and a nearby untreated, ambient CO₂ plot (in the past 2 yr, the number of untreated plots was increased to five). **b**, Individual tree comparison between trees in FACE_p and trees selected at random from the entire stand. Data for 1993 are shown as means for the first 10 yr of the stand's life.