Faster Decomposition Under Increased Atmospheric CO_2 Limits Soil Carbon Storage

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Soils contain the largest pool of terrestrial organic carbon (C) and are a major source of atmospheric carbon dioxide (CO_2). Thus, they may play a key role in modulating climate change. Rising atmospheric CO_2 is expected to stimulate plant growth and soil C input but may also alter microbial decomposition. The combined effect of these responses on long-term C storage is unclear. Combining meta-analysis with data assimilation, we show that atmospheric CO_2 enrichment stimulates both the input (+19.8%) and the turnover of C in soil (+16.5%). The increase in soil C turnover with rising CO_2 leads to lower equilibrium soil C stocks than expected from the rise in soil C input alone, indicating that it is a general mechanism limiting C accumulation in soil.

Carbon exchange between land and the atmosphere is a major focus of Earth system models, because the C cycle is sensitive to environmental change and because alterations of the C cycle affect our climate. Earth system models project that rising atmospheric CO_2 will promote C uptake by the terrestrial biosphere (*1*). The resulting increase in C stocks in plant biomass and soil organic matter (*2*) would slow the rise in atmospheric CO_2 concentrations and may help to slow climate change. Data support part of these model predictions: Experimentally increased CO_2 concentrations usually stimulate photosynthesis and plant growth (*3*). However, the response of soil C stocks is less well understood, because changes in soil C content are difficult to detect (*4*, *5*). Thus, global models projecting future C dynamics of the biosphere have strong empirical support for the effects of CO_2 on plant growth (*3*) but limited empirical support for assumed effects on soil C accumulation.

Soil C stocks are determined by the balance between plant growth and the subsequent input of plant detritus to soil and C losses through microbial decomposition. Earth system models typically treat decomposition as a function of temperature and water content (*1*) and do not include direct effects of increased CO_2, which are generally assumed to be small (*6*). These models commonly describe soil C dynamics with first-order kinetics (*7*), such that C loss from soil increases proportionally with the size of the soil C pool (*8*) (Eq. 1). Thus, if increased CO_2 enhances C input to soil, these models project that decomposition will also increase. Consistent with these expectations, CO_2 enrichment is frequently found to increase CO_2 efflux from soil (*9*). However, in some cases this increase was greater than the first-order expectation (*10*, *11*), suggesting that increased CO_2 may stimulate decomposition beyond what is expected from increased substrate availability alone. It is not known whether this disproportionate response to increased atmospheric CO_2 is general across ecosystems.

Disentangling C input to and loss from soil is possible in short-term laboratory experiments using isotopic tracers (*10*) and can be inferred from mass balance calculations (*12*). However, synthetic approaches disentangling C inputs and losses across broad data sets from the field have not been developed. Here, we use an approach that combines measurements of plant production, microbial respiration, and soil C stocks to estimate CO_2 effects on soil C turnover, thereby providing insight into the mechanisms determining long-term soil C storage (*13*). We derived effect sizes from a one-pool biogeochemical model of soil C cycling (*8*), the same form used by several global C cycling models (*1*, *2*)

$$C_t = C_0[\exp(-kt)] + I/k[1 - \exp(-kt)] \quad (1)$$

where C_t is the soil C content (g C m^{-2}) at time t (year); C_0 is the soil C content at the start of a CO_2 enrichment experiment (g C m^{-2}); k is the decomposition rate constant ($year^{-1}$, the rate at which C leaves the soil system); and I is the annual input of C to soil (g C m^{-2} $year^{-1}$). The model was constrained by multiple independent data streams from 53 CO_2 enrichment experiments (see table S1 and databases S1 to S4). We then used meta-analysis to synthesize the results (*13*).

Using this approach, the data indicate that CO_2 enrichment increased soil C input (I in Eq. 1) by 19.8% (Fig. 1A), with lower responses in cropland (10.9%) compared with grassland (20.1%) and forest (23.3%) (table S2). These estimates are consistent with past syntheses of the responses of plant production to experimental CO_2 enrichment (*3*).

If the decomposition rate constant k of soil C in Eq. 1 were unaffected by CO_2 enrichment, then microbial decomposition would change proportionally with the size of the soil C pool. That is, C loss from decomposition would increase with CO_2 enrichment because the pool of soil C increased, not because the rate of decomposition (i.e., k) increased. However, our meta-analysis showed that CO_2 enrichment significantly increased k by 16.5% (Fig. 1A). The average effect

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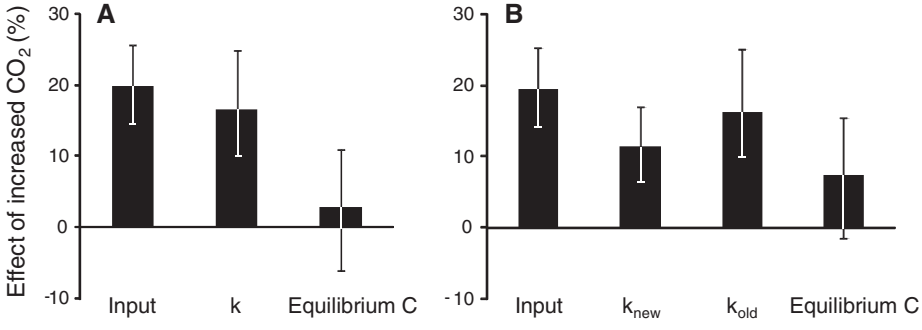

Fig. 1. Results of a meta-analysis on the response of soil C dynamics to increased levels of atmospheric CO_2. (**A**) The effect of increased CO_2 on soil C input (input), soil C turnover (k), and projected equilibrium soil C, based on a one-pool soil C model (Eq. 1). (**B**) The effect of increased CO_2 on soil C input, new soil C turnover (k_{new}), old soil C turnover (k_{old}), and projected equilibrium soil C, based on a two-pool soil C model (Eq. 2). Results are based on 53 experimental comparisons. Effect sizes were weighted by replication, adjusted by the number of comparisons per experimental site. All error bars represent 95% confidence intervals.

of increased CO_2 was similar in grasslands, forests, and croplands, although the effect in the latter category was not significant (see table S2). Correspondingly, increased atmospheric CO_2 significantly reduced soil residence time ($1/k$, the average time that a C atom spends in the soil) by 2.4 years (95% confidence interval, 1.5 to 3.8 years) (see table S3).

Why does increased atmospheric CO_2 stimulate the turnover of soil C? Larger soil C input rates under increased CO_2 cause an enhanced supply of easily metabolized substrates (*10*), which can stimulate the decomposition of native soil organic matter, mobilizing C reserves assumed to be protected from microbial attack (*14*). This process, commonly called "priming" (*15*), has previously been described as short-term and idiosyncratic (*16*). However, recent studies indicate that it is a widespread and persistent phenomenon (*17*, *18*). Our results now suggest that it is also a general and prolonged response to increased atmospheric CO_2.

Furthermore, atmospheric CO_2 enrichment can increase soil water content (*19*), due to improved efficiency of water use by plants, which reduces soil water loss through transpiration (*20*). Because low water availability limits the physiological performance of soil microbes and their access to substrate, a CO_2-induced increase in soil water content may increase decomposition rates in arid and semiarid ecosystems (*21*).

Our results are based on a one-pool soil C model, but two- or three-pool soil C models that distinguish labile and recalcitrant C pools may describe changes in soil C stocks over time more accurately (*22*); however, parameters in a conventional multipool soil C model could not be estimated with the available data (*13*). Thus, we took a slightly different approach and applied a model that distinguished the k of soil C initially present at each experimental site (k_{old}) from the k of soil C added after CO_2 enrichment started (k_{new}).

$$C_t = C_0[\exp(-k_{old} \times t)] + I/k_{new}[1 - \exp(-k_{new} \times t)] \quad (2)$$

Based on this approach, we found that CO_2 enrichment increased both k_{old} and k_{new} (Fig. 1B and table S4) to similar degrees. These findings corroborate recent studies suggesting that increased CO_2 stimulates the decomposition of old soil C (*10*, *11*) as well as new soil C pools (*23*).

Given enough time, soil C stocks will eventually reach equilibrium of I/k (Eq. 1) or I/k_{new} (Eq. 2), where soil C input through plant growth is balanced by soil C loss through decomposition. If increased CO_2 alters only I and not k, an assumption made in early Earth system models (*1*), predicted equilibrium soil C contents for the experiments in our database would increase to the same degree as soil C input rates, that is, by 19.8%. However, when we take into account the effect of CO_2 on k, increased CO_2 does not significantly affect the predicted equilibrium soil C contents (Fig. 1, A and B). In other words, the observed increase in k largely negates the predicted soil C accumulation due to increased atmospheric CO_2. Although increased CO_2 stimulates plant growth and C input to soil, the microbial response counteracts this response, thereby reducing the net effect of rising CO_2 levels on soil C stocks.

The effect of increased CO_2 on I/k and I/k_{new} (which represent projected long-term responses) are quantitatively similar to the effect of increased CO_2 on soil C contents found in several recent meta-analyses focusing on short-term responses (*24*, *25*). This suggests that studies that are focused on processes (and thus allow estimation of I and k) and those focused on soil C storage provide complementary answers. Importantly, our approach allows the separation of inputs and losses and thus explains the apparent mismatch between the stimulation of plant growth and the limited response of soil C (*25*, *26*).

Current Earth system models include only some of the possible processes underlying the response of k to increased atmospheric CO_2. In most models, atmospheric CO_2 enrichment could influence decomposition by altering soil moisture (*1*). Furthermore, some Earth system models partition plant litter into multiple pools with different decomposition rates. Increased CO_2 could drive changes in k due to shifts in vegetation composition, because the ratio of these pools differs between vegetation types (*1*). However, because of their relative short duration, experiments in our data set did not allow for the large shifts in vegetation composition that affect soil C dynamics in these models (*27*). Therefore, this mechanism does not explain our findings. Alternatively, Earth system models that include a nitrogen (N) cycle can simulate changes in C to N ratio and decomposability of litter (*28*). However, because atmospheric CO_2 enrichment generally has little effect on litter quality (*6*), this mechanism probably plays a limited role in explaining the response of k. The priming effect itself is not explicitly represented in any Earth system model. Including priming in ecosystem models captures increased decomposition rates with increased atmospheric CO_2 (*29*), a result consistent with our findings. Future Earth system models might improve by incorporating the priming effect in their land surface mode as well.

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Supplementary Materials

www.sciencemag.org/content/344/6183/508/suppl/DC1
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