

## OPINION

# Toward improved model structures for analyzing priming: potential pitfalls of using bulk turnover time

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## Abstract

Many studies have shown that elevated atmospheric CO<sub>2</sub> concentrations result in increased plant carbon inputs to soil that can accelerate the decomposition of native soil organic matter, an effect known as priming. Consequently, it is important to understand and quantify the priming effect for future predictions of carbon–climate feedbacks. There are potential pitfalls, however, when representing this complex system with a simple, first-order model. Here, we show that a multi-pool soil carbon model can match the change in bulk turnover time calculated from overall respiration and carbon stocks (a one-pool approach) at elevated CO<sub>2</sub>, without a change in decomposition rate constants of individual pools (i.e., without priming). Therefore, the priming effect cannot be quantified using a one-pool model alone, and even a two-pool model may be inadequate, depending on the effect size as well as the distribution of soil organic carbon and turnover times. In addition to standard measurements of carbon stocks and CO<sub>2</sub> fluxes, we argue that quantifying the fate of new plant inputs requires isotopic tracers and microbial measurements. Our results offer insights into modeling and interpreting priming from observations.

**Keywords:** carbon cycle dynamics, climate change, elevated CO<sub>2</sub>, microbial biomass, priming effect, soil carbon modeling, soil carbon storage

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## Introduction

Soils are a major reservoir of carbon, containing more than double the carbon currently in the atmosphere. As atmospheric CO<sub>2</sub> levels increase, plant productivity generally increases (Ainsworth & Long, 2005). However, increased carbon inputs to soils do not necessarily result in more soil carbon storage. An increase in plant inputs to soil may enhance microbial activity, thereby accelerating the decomposition rate of native soil organic matter (SOM) and limiting carbon storage. This ‘priming effect’ has been observed in field and laboratory studies of increased carbon inputs to soils (Carney *et al.*, 2007; Paterson *et al.*, 2008; Cheng *et al.*, 2014). Although the underlying mechanism is not well understood, this process could have a significant effect on global carbon cycle responses to climate change and rising CO<sub>2</sub>. Direct observations are difficult, so it is uncertain how widespread or large this effect is. It is therefore important to develop accurate detection and quantification of priming, and to represent this process

in Earth system models (ESMs) for better prediction of carbon–climate feedbacks.

Here, we provide a quantitative examination and cautionary note on analytical approaches that use bulk soil turnover time (such as one based on a one-pool model) to infer a change in decomposition rate constants (Torbert *et al.*, 2004; Prior *et al.*, 2008; Foereid *et al.*, 2014; van Groenigen *et al.*, 2014). Such methods have been used to infer priming in response to increased soil carbon inputs. We show, numerically and conceptually, why a one-pool SOM model alone is unable to infer an increase in SOM decomposition rates given observations of respiration and carbon stocks over time, and that other simple linear models (e.g., a two-pool model) may also have limited power of detection. We also discuss the minimal required model structure to support conclusions on priming and process-based representation of this potentially important carbon feedback in ESMs.

## One-pool model of a multi-pool system

Soils have the property that the mean age of SOM is much older than the mean age of heterotrophic respiration, implying that a fraction of the carbon entering

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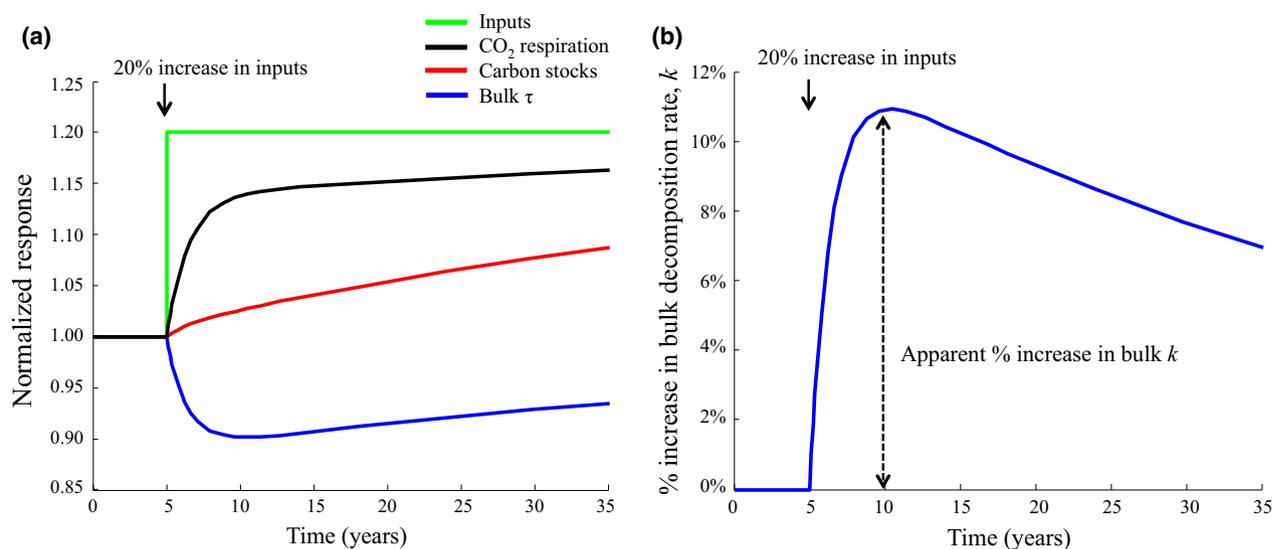
soils is respired on the order of weeks to months, while some persists for decades to centuries or longer. Soil carbon models have traditionally approximated this behavior by considering decomposition as a combination of two or more exponential decay terms with a broad range of time constants ('multi-pool models'). Three-pool models typically do a good job of characterizing carbon cycling in many different soils (Parton *et al.*, 1987; Torn *et al.*, 2009). In contrast, treating decomposition with a single exponential decay rate ('single-pool models') gives qualitatively different behavior that poorly represents the dynamics of SOM (Parton *et al.*, 1987).

As soil carbon is not one homogeneous SOM pool, the qualitative behavior of bulk turnover time (i.e., the turnover time estimated from treating the soil as one pool) may mistakenly be interpreted as priming, even without changes to intrinsic decomposition rates ( $k_i$ ; or other proposed mechanisms for priming). To demonstrate this, we use a traditional two-pool model (for simplicity), with fast ( $\tau_1 = 1/k_1 = 1.5$  years)- and slow ( $\tau_2 = 1/k_2 = 50$  years)-cycling pools, to show that an increase in the overall (bulk) decomposition rate constant ( $k$ ) will be inferred despite constant decomposition rate constants ( $k_1$  and  $k_2$ ) of individual pools (Fig. 1). We calculate bulk turnover time as soil carbon stocks over respiration; however, similar results would be predicted from a one-pool model where bulk turnover time is estimated by parameter fitting to observed

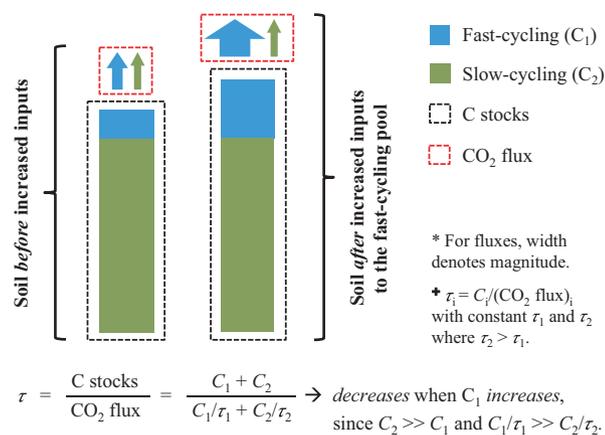
soil carbon stocks over time constrained by plant growth (carbon inputs) and microbial respiration (carbon outputs). We perturb the soil from steady state with a 20% step increase in carbon inputs, matching the average effect of elevated  $\text{CO}_2$  in van Groenigen *et al.* (2014) as an example.

The result is that total respiration responds more quickly than total carbon stocks, as the soil now has a larger proportion of fast- vs. slow-cycling carbon pools because of the new inputs (Fig. 1a). As a result, a faster bulk decomposition rate is calculated when the (fast and slow) carbon pools are aggregated into a one-pool model (Fig. 1b). However, this increase in decomposition does not result from a change in individual pool decomposition rates,  $k_i$ , but rather from having more carbon in the fast-cycling pool; the increase is an artifact of treating a multi-pool system as a one-pool system and persists for decades to centuries. This effect on bulk  $k$  (and  $\tau$ ) in response to elevated  $\text{CO}_2$  ('false priming') is also evident in simulations of five ESMs participating in the CMIP5 experiment, despite the fact that these models do not include mechanisms that could produce priming (Koven *et al.*, 2015).

The conceptual diagram in Fig. 2 illustrates how an aggregated one-pool model – applied to a system that has more than one carbon pool – can infer a decrease in the bulk turnover time (increase in  $k$ ) as a consequence of the inappropriate model structure. We start with a two-pool model, as the simplest example of multiple



**Fig. 1** Results from aggregating a two-pool SOM model with fixed pool turnover times ( $\tau_1$  and  $\tau_2$ ) in response to a 20% increase in carbon inputs. (a) Normalized bulk turnover time ( $\tau$ ), total soil carbon stocks, and  $\text{CO}_2$  respiration from a two-pool model ( $\tau_1 = 1.5$  years and  $\tau_2 = 50$  years) in response to a 20% step increase (at year 5) in soil carbon inputs. Carbon use efficiencies of 0.30 and 0.45 (respired fractions of 0.70 and 0.55) were used for the fast and slow carbon pools, respectively, where a fraction of the carbon uptake from each pool is transferred between soil carbon pools, while the remainder is respired. (b) Response of the bulk decomposition rate constant ( $k = 1/\tau$ ) as a percent increase after the disturbance.



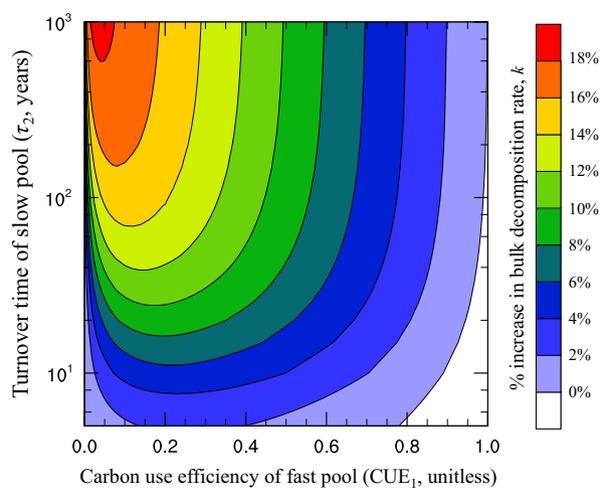
**Fig. 2** Conceptual diagram illustrating how aggregating a system with two SOM pools into a one-pool SOM model can exhibit a false priming response. This appears as a decrease in the bulk turnover time ( $\tau$ ) without a change in the individual turnover times of the fast ( $C_1$ )- and slow ( $C_2$ )-cycling pools ( $\tau_1$  and  $\tau_2$ , respectively). The bulk turnover time (one-pool model) of an aggregated multi-pool system is defined as the total concentration of carbon stocks divided by the total  $\text{CO}_2$  flux respired as output. Turnover time is the reciprocal of the decomposition rate constant ( $k$ ). (Left) Two SOM pools before an increase in carbon inputs. (Right) Response of the two SOM pools to an increase in carbon inputs into the fast-cycling pool. In this case, the bulk turnover time  $\tau$  decreases ( $k$  increases) with time. Note, for simplicity of illustration, carbon use efficiencies equal to zero (respired fraction equal to one) are used in this figure.

carbon pools, and aggregate the outputs and carbon stocks into the structure of a one-pool model to calculate the change in bulk turnover time.

For simplicity, we use a two-pool model to show the weakness of aggregating a system with multiple underlying carbon pools into a one-pool model, but even a model with two or more pools may lead to errors in assessing the effects of  $\text{CO}_2$  fertilization or inferring SOM priming. Depending on the model parameters, a two-pool model can result in a wide range of false priming (reduction in bulk turnover time) responses to increased inputs, as shown in our sensitivity analysis (Fig. 3).

### Bias in quantifying priming with a one-pool model

A single-pool model can be used to detect the presence of priming only when a sufficiently large change in respiration is observed, that is, when more carbon is respired than (a) is added or (b) the bias that results from aggregating a multi-pool system. For example, if inputs increased by 20% and outputs by 25%, the additional 5% increase is clearly from faster decomposition rates of existing carbon stocks. If outputs increased by <20%, however, it is possible that the carbon use efficiency (CUE; defined as the fraction of carbon



**Fig. 3** Sensitivity analysis depicting the potential magnitude of false priming inferred from aggregating two SOM pools with a range of parameter values into a one-pool model. Contour plot of the percent increase in overall  $k$  [taken 5 years after a 20% increase in inputs to approximate the observational meta-analysis of van Groenigen *et al.* (2014), as an example] for a range of carbon use efficiencies of the fast pool ( $\text{CUE}_1$ ) and turnover times of the slow pool ( $\tau_2$ ). The turnover time of the fast pool ( $\tau_1 = 1$  year) and carbon use efficiency of the slow pool ( $\text{CUE}_2 = 0$ ; i.e., all carbon used for respiration) were held constant to explore the effect of  $\text{CUE}_1$  and  $\tau_2$  only.

uptake from each pool that is allocated to microbial growth and transferred to another soil carbon pool, i.e., not respired) and shift in pool sizes of the underlying multi-pool system caused the observed change in bulk decomposition rate (Figs 1–3).

To determine the likely range of bias due to analyzing observations with a one-pool model, we performed a sensitivity analysis using a range of carbon use efficiencies and pool-specific decomposition rate constants (Fig. 3). We again aggregated a two-pool model into a one-pool model and examined the false priming response that resulted from different parameterizations. Because the typical values of the model parameters can vary within actual soil and between models, we present the potential magnitude of false priming for a range of carbon use efficiencies of the fast pool ( $\text{CUE}_1$ ) and turnover times of the slow pool ( $\tau_2$ ).

We infer from Fig. 3 that only respiration above the ~9–16% increase in  $k$  obtained by aggregating two SOM pools into a one-pool model can be attributed to priming, depending on the range of representative system parameters. This false priming estimate is corroborated by the ~7–14% reduction in overall turnover time observed in the CMIP5 models in response to a 20% increase in NPP (Koven *et al.*, 2015). Consequently, the magnitude of priming that can be concluded from a one-pool model alone is roughly equal to the difference

between the inferred change in  $k$  and that expected from simply treating a multi-pool system as a single pool – i.e., much smaller than estimated in most of the studies cited above. In cases where the reported response of bulk  $k$  is within the range of the response (bias) expected from using the typical range of Century model (Parton *et al.*, 1987) parameters (Fig. 3), an increase in intrinsic decomposition rates (priming) cannot be concluded from an analysis or meta-analysis that relies on a one-pool model.

### Toward models and observations to quantify and predict priming

The mechanisms hypothesized to cause SOM priming (e.g., increased microbial production of extracellular enzymes, enhanced mycorrhizal activity, changes in microbial community structure) are absent from conventional pool-based models (Blagodatsky *et al.*, 2010; Kuzyakov, 2010). It is therefore possible that the typically rapid microbial turnover of increased exudation or fine-root necromass could explain the increase in respiration observed in litter addition and CO<sub>2</sub> enrichment experiments that have not traced sources of respiration, for instance, without there being a change in the original SOM pool dynamics. For example, such an increase in respiration without a change in decomposition rate constants has been observed across a tropical montane forest (Giardina *et al.*, 2014). Unless the increase in respiration is significantly larger than the sum of increased inputs and results in an overall decrease of soil carbon, or unless observations, such as isotopic tracers, are available that trace the fate of inputs and the source of respiration, inferences of enhanced degradation of existing SOM will remain highly uncertain. Analyzing observations with a model structure that includes the hypothesized mechanisms of priming (e.g., microbial and enzymatic activity) is also an important next step.

### Conclusions

Soil carbon comprises a range of organic matter pools, and therefore, using a simple, first-order model to infer complex carbon dynamics may lead to erroneous conclusions. Using a multi-pool soil carbon model with an imposed increase in carbon inputs, we have shown that the behavior of bulk turnover time (i.e., the turnover time estimated from aggregating multiple pools into a single pool) may mistakenly be interpreted as priming, despite constant intrinsic decomposition rates of individual SOM pools. Thus, we conclude that the priming effect cannot be quantified using measurements of bulk carbon stocks and CO<sub>2</sub> flux alone, but requires knowledge of the fate of new plant inputs.

To distinguish whether CO<sub>2</sub> respiration originates from new carbon inputs or older native soil, studies using natural abundance radiocarbon or <sup>13</sup>C- or <sup>14</sup>C-labeled inputs provide useful results (Kuzyakov *et al.*, 2000; Fontaine *et al.*, 2007; Paterson & Sim, 2013; Hopkins *et al.*, 2014). As microbes are an active driver of carbon and nitrogen turnover in soil, microbial biomass measurements can also provide a constraint on changes to carbon dynamics (Blagodatskaya & Kuzyakov, 2008; Blagodatsky *et al.*, 2010). These data should be used to inform estimates of priming, whether analyzed as changes in decomposition rate constants in multi-pool models or as microbial activity in microbe-enabled models (Blagodatsky *et al.*, 2010; Riley *et al.*, 2014; Wang *et al.*, 2014; Tang & Riley, 2015). Such information can then be used to parameterize this priming effect in SOM models (Guenet *et al.*, 2013; Wieder *et al.*, 2013; Sulman *et al.*, 2014) that can be incorporated into ESMs.

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### References

- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytologist*, **165**, 351–372.
- Blagodatskaya EV, Kuzyakov Y (2008) Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. *Biology and Fertility of Soils*, **45**, 115–131.
- Blagodatsky S, Blagodatskaya EV, Yuyukina T, Kuzyakov Y (2010) Model of apparent and real priming effects: linking microbial activity with soil organic matter decomposition. *Soil Biology and Biochemistry*, **42**, 1275–1283.
- Carney KM, Hungate BA, Drake BG, Megonigal JP (2007) Altered soil microbial community at elevated CO<sub>2</sub> leads to loss of soil carbon. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 4990–4995.
- Cheng W, Parton WJ, Gonzalez-Meler MA *et al.* (2014) Synthesis and modeling perspectives of rhizosphere priming. *New Phytologist*, **201**, 31–44.
- Foereid B, Ward DS, Mahowald N, Paterson E, Lehmann J (2014) The sensitivity of carbon turnover in the Community Land Model to modified assumptions about soil processes. *Earth System Dynamics*, **5**, 211–221.
- Fontaine S, Barot S, Barré P, Bdioui N, Mary B, Rumpel C (2007) Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature*, **450**, 277–281.
- Giardina CP, Litton CM, Crow SE, Asner GP (2014) Warming-related increases in soil CO<sub>2</sub> efflux are explained by increased below-ground carbon flux. *Nature Climate Change*, **4**, 822–827.
- van Groenigen KJ, Qi X, Osenberg CW, Luo Y, Hungate BA (2014) Faster decomposition under increased atmospheric CO<sub>2</sub> limits soil carbon storage. *Science*, **344**, 508–509.
- Guenet B, Moyano FE, Vuichard N, Kirk GJD, Bellamy PH, Zaehle S, Ciais P (2013) Can we model observed soil carbon changes from a dense inventory? A case study

- over England and Wales using three versions of the ORCHIDEE ecosystem model (AR5, AR5-PRIM and O-CN). *Geoscientific Model Development*, **6**, 2153–2163.
- Hopkins FM, Filley TR, Gleixner G, Lange M, Top SM, Trumbore SE (2014) Increased belowground carbon inputs and warming promote loss of soil organic carbon through complementary microbial responses. *Soil Biology and Biochemistry*, **76**, 57–69.
- Koven CD, Chambers JQ, Georgiou K *et al.* (2015) Controls on terrestrial carbon feedbacks by productivity vs. turnover in the CMIP5 Earth System Models. *Biogeosciences Discussions*, **12**, 5757–5801.
- Kuzyakov Y (2010) Priming effects: interactions between living and dead organic matter. *Soil Biology and Biochemistry*, **42**, 1363–1371.
- Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. *Soil Biology and Biochemistry*, **32**, 1485–1498.
- Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal*, **51**, 1173–1179.
- Paterson E, Sim A (2013) Soil-specific response functions of organic matter mineralization to the availability of labile carbon. *Global Change Biology*, **19**, 1562–1571.
- Paterson E, Thornton B, Midwood AJ, Osborne SM, Sim A, Millard P (2008) Atmospheric CO<sub>2</sub> enrichment and nutrient additions to planted soil increase mineralisation of soil organic matter, but do not alter microbial utilisation of plant- and soil C-sources. *Soil Biology and Biochemistry*, **40**, 2434–2440.
- Prior SA, Torbert HA, Runion GB, Rogers HH, Kimball BA (2008) Free-air CO<sub>2</sub> enrichment of sorghum: soil carbon and nitrogen dynamics. *Journal of Environmental Quality*, **37**, 753–758.
- Riley WJ, Maggi FM, Kleber M, Torn MS, Tang JY, Dwivedi D, Guerry N (2014) Long residence times of rapidly decomposable soil organic matter: application of a multi-phase, multi-component, and vertically resolved model (BAMS1) to soil carbon dynamics. *Geoscientific Model Development*, **7**, 1333–1355.
- Sulman BN, Phillips RP, Oishi AC, Shevliakova E, Pacala SW (2014) Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO<sub>2</sub>. *Nature Climate Change*, **4**, 1099–1102.
- Tang J, Riley WJ (2015) Weaker soil carbon-climate feedbacks resulting from microbial and abiotic interactions. *Nature Climate Change*, **5**, 56–60.
- Torbert HA, Prior SA, Runion GB, Davis MA, Pritchard SG, Rogers HH (2004) Nitrogen and carbon cycling in a model longleaf pine community as affected by elevated atmospheric CO<sub>2</sub>. *Environmental Management*, **33**, 132–138.
- Torn MS, Swanston CW, Castanha C, Trumbore SE (2009) Storage and Turnover of Organic Matter in Soil. In: *Biophysico-Chemical Processes Involving Natural Nonliving Organic Matter in Environmental Systems* (eds Senesi N, Xing B, Huang PM), pp. 219–272. John Wiley & Sons Inc, Hoboken, NJ, USA.
- Wang G, Mayes MA, Gu L, Schadt W (2014) Representation of dormant and active microbial dynamics for ecosystem modeling. *PLoS ONE*, **9**, e89252.
- Wieder WR, Bonan GB, Allison SD (2013) Global soil carbon projections are improved by modelling microbial processes. *Nature Climate Change*, **3**, 909–912.