

OPINION

Application of a two-pool model to soil carbon dynamics under elevated CO₂

KEES JAN VAN GROENIGEN¹, JIANYANG XIA^{2,3}, CRAIG W. OSENBERG⁴, YIQI LUO^{2,5} and BRUCE A. HUNGATE^{1,6}

¹Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, USA, ²Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019-0245, USA, ³Tiantong National Forest Ecosystem Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China, ⁴Odum School of Ecology, University of Georgia, Athens, GA 30602, USA, ⁵Center for Earth System Sciences, Tsinghua University, Beijing 100084, China, ⁶Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA

Abstract

Elevated atmospheric CO₂ concentrations increase plant productivity and affect soil microbial communities, with possible consequences for the turnover rate of soil carbon (C) pools and feedbacks to the atmosphere. In a previous analysis (Van Groenigen *et al.*, 2014), we used experimental data to inform a one-pool model and showed that elevated CO₂ increases the decomposition rate of soil organic C, negating the storage potential of soil. However, a two-pool soil model can potentially explain patterns of soil C dynamics without invoking effects of CO₂ on decomposition rates. To address this issue, we refit our data to a two-pool soil C model. We found that CO₂ enrichment increases decomposition rates of both fast and slow C pools. In addition, elevated CO₂ decreased the carbon use efficiency of soil microbes (CUE), thereby further reducing soil C storage. These findings are consistent with numerous empirical studies and corroborate the results from our previous analysis. To facilitate understanding of C dynamics, we suggest that empirical and theoretical studies incorporate multiple soil C pools with potentially variable decomposition rates.

Keywords: carbon cycle, data assimilation, data-model fusion, priming, soil carbon model

Received 14 April 2015 and accepted 7 July 2015

Introduction

Soils contain about twice as much C as the atmosphere and three times as much C as live vegetation, and soil respiration forms a principle component of the global C cycle (Cias *et al.*, 2013). The soil C pool may therefore play a key role in modulating climate change, but its response to future atmospheric conditions is uncertain. We previously synthesized data on soil C contents, soil respiration, and soil C inputs from CO₂ enrichment experiments to determine whether the decomposition rate (*k*) of soil organic C changed under elevated atmospheric CO₂ (Van Groenigen *et al.*, 2014). We offered two possible explanations for the observed increase in decomposition: priming (i.e., increased decomposition of soil organic matter due to increased soil C inputs), or a CO₂-induced increase in soil water content which in turn stimulated microbial activity. Georgiou *et al.* (2015) offer another possible explanation: the increase in *k* may have been an artifact resulting from fitting a one-pool model to data from a multi-pool system. In this alternative explanation, actual decomposition rates

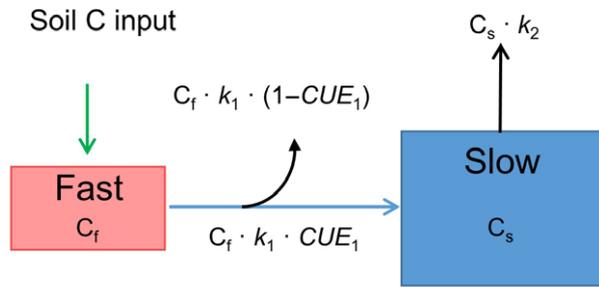
may not have changed; rather the size of the labile (hereafter, 'fast') C pool may have increased relative to that of the recalcitrant (i.e., 'slow') pool, giving the impression of a change in *k*. To determine whether this mechanism could explain our results, we here estimate parameters in a two-pool model using data from our original meta-analysis.

Application of a two-pool soil C model

For our new analysis, we used a two-pool model which was introduced by Andr n & K tterer (1997) (Fig. 1). It is the same model that was used by Georgiou *et al.* (2015) to illustrate the theoretical possibility of the artifact described above. Unlike the models used in Van Groenigen *et al.* (2014), this model includes pools with different turnover rates and it allows for C transfer from the fast pool to the slow pool; these properties are essential for the alternative hypothesis proposed by Georgiou *et al.* (2015).

To estimate model parameters, we followed the data assimilation approach outlined by Van Groenigen *et al.* (2014). Briefly, the two-pool model was fitted to the observed soil C data for both the ambient and the

Correspondence: Kees Jan van Groenigen, tel. +1 928 523 5897, e-mail: cjvangroenigen@nau.edu



C_f : amount of soil organic C in fast pool
 C_s : amount of soil organic C in slow pool
 k_1 : decomposition rate of fast pool
 k_2 : decomposition rate of slow pool
 CUE_1 : carbon use efficiency of fast pool

Fig. 1 Schematic representation of the two-pool soil C model used in our analysis. This model was adopted from Andrén & Kätterer (1997).

increased CO₂ treatments for each experimental site in our dataset. We constructed a joint probability density function (PDF) for the model parameters using probabilistic inversion (Xu *et al.*, 2006). Samples were taken from the joint PDF using a Markov chain Monte Carlo technique and were then used to construct marginal distributions for model parameters. We calculated a cost function J expressing the difference between modeled and observed soil C data (Luo *et al.*, 2003):

$$J = \sum_{i=1}^n (C_m(t_i) - C_o(t_i))^2 \quad (1)$$

where n is the total number of sampling dates, each of which occurred t_i years after the start of CO₂ enrichment, and C_m and C_o are the modeled and observed soil C pool at time t_i , respectively. The cost function was minimized with a Metropolis-Hastings algorithm, combined with a convergence test.

The prior distributions of model parameters I , k_1 and k_2 , and CUE_1 were chosen to be uniform between a lower and upper limit (Table 1). These limits represent constraints based upon prior knowledge about the approximate ranges of soil C input (Raich & Schlesinger, 1992), decomposition rates of fast and slow soil C pools (Trumbore, 2000; Six & Jastrow, 2002; Manzoni *et al.*, 2012a), and carbon use efficiency of soil microbes (Andrén & Kätterer, 1997; Manzoni *et al.*, 2012a,b). The application of a two-pool model requires data on the initial distribution of soil C among the pools, information that was not available for any of the studies in our dataset (Van Groenigen *et al.*, 2014). We solved this issue by introducing an additional model parameter in our analysis: f , the fraction of the initial soil C stock presents in the fast soil C pool (Table 1).

Table 1 Prior distributions of parameters (and associated units) of the two-pool model used in our data assimilation. For each parameter, the prior distribution was uniform between the upper and lower limit

Parameter	Description	Lower limit	Upper limit	Unit
I	Soil C input	50	650	$\text{g C m}^{-2} \text{ yr}^{-1}$
k_1	Decomposition rate of fast pool	0.1	0.9	yr^{-1}
k_2	Decomposition rate of slow pool	0.001	0.1	yr^{-1}
CUE_1	Carbon use efficiency of fast pool	0.1	0.8	–
f	Fraction of initial C stock in fast pool	0.001	0.1	–

The lower and upper limits of the prior distribution of f were based on the partitioning of soil C between labile and recalcitrant pools used in conceptual models (Andrén & Kätterer, 1997; Trumbore, 1997). We assumed that within each experiment, f was the same for ambient and elevated CO₂ treatments. We further constrained model parameters by observations on soil or microbial respiration and plant growth, see Van Groenigen *et al.* (2014) for details. All analyses were performed in MATLAB R2012b (Mathworks, Natick, MA, USA).

The model parameters were estimated as the mean of the sampling distribution generated by the Metropolis-Hastings algorithm. We then used meta-analysis to summarize the CO₂ effects on model parameters across our dataset (e.g., Osenberg *et al.*, 1999), using the natural log of the response ratio as the effect size (Hedges *et al.*, 1999). METAWIN 2.1 was used to generate mean effect sizes and 95% bootstrapped CIs (4999 iterations) (Rosenberg *et al.*, 2000). Effect sizes were weighted by replication (to give more weight to better estimates), adjusted by the number of comparisons per experimental site (to downweight studies with multiple effect sizes and thus avoid pseudoreplication: Van Groenigen *et al.*, 2014). Treatment effects were considered significant if the 95% CI of the effect size did not overlap with 0.

Applying our two-pool approach to the 53 studies in our original dataset, we found that elevated CO₂ increased the decomposition rates of both the fast and slow C pools (Fig. 2). Elevated CO₂ increased the decomposition of slow C, the dominant C pool, to almost the same extent as it did the single decomposition rate, k , in the one-pool model (Van Groenigen *et al.*, 2014). In addition, CUE_1 decreased under elevated CO₂,

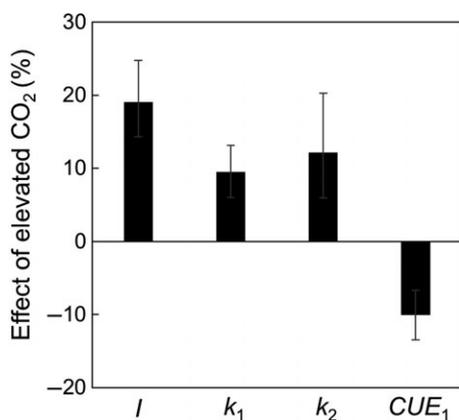


Fig. 2 Results of a data assimilation analysis of our soil C dataset using a two-pool soil C model. The effect of increased CO₂ on soil C input (I), decomposition rate of the fast soil C pool (k_1), decomposition rate of the slow soil C pool (k_2), and carbon use efficiency of the fast soil C pool (CUE_1), based on a two-pool soil C model (Fig. 1). Averaged across our dataset, I equaled $283 \pm 78 \text{ g C m}^{-2} \text{ yr}^{-1}$, k_1 equaled $0.51 \pm 0.21 \text{ yr}^{-1}$, k_2 equaled $0.06 \pm 0.02 \text{ yr}^{-1}$, and CUE_1 equaled 0.43 ± 0.18 under ambient CO₂ conditions (average \pm standard deviation of posterior distribution). Results are based on 53 experimental comparisons. All error bars represent 95% confidence intervals.

a response that further limits soil C storage (because low CUE_1 values cause more C to be respired during transfer from the fast to the slow pool). Averaged across all experiments in our dataset, f (the initial allocation of C to the fast pool) equaled 0.05 (results not shown).

In general, simple models fit to complex dynamics can yield parameters that are inconsistent with the inferred mechanistic controls (e.g., Ågren, 2000; Davidson & Janssens, 2006). Thus, in theory, our previous finding that elevated CO₂ induced an increase in the decomposition rate k (Van Groenigen *et al.*, 2014) could have been an artifact of applying a one-pool model to a two-(or multi-) pool system (Georgiou *et al.*, 2015). However, further analysis (Fig. 2) suggests this was not the case: decomposition rates in a two-pool model also increased with elevated CO₂. The fact that our one-pool and two-pool analyses yield similar results further suggests that adding more pools with even faster decomposition rates (representing labile material such as fine-root necromass and root exudates) would not greatly affect the outcome either. The significant drop in CUE_1 values under elevated CO₂ could possibly be an indication of increased C expense for N priming, but may also indicate C overflow respiration due to increased C availability to soil microbes (Craine *et al.*, 2007; Manzoni *et al.*, 2012a).

Georgiou *et al.* (2015) described the possible bias in applying a one-pool model by estimating k by dividing

soil respiration by the size of the soil C stock. However, our data assimilation method used a fundamentally different approach (Luo *et al.*, 2011); we directly estimated k from the change in soil C contents over time and constrained these estimates based on the observed responses of plant growth and microbial respiration. The two approaches yield different results; for example, simply dividing respiration rates by soil C stocks yield an *apparent* average CO₂ effect on k of +21% for the studies in our dataset, larger than that reported by Van Groenigen *et al.* (2014). This suggests that much of the artifact arises from the estimation methods, and not necessarily, from the application of a one-pool model.

Consistent with our results, numerous empirical studies indicate that decomposition rates are not fixed. For example, meta-analyses show that despite increased soil C input under elevated CO₂, sites with low N availability accumulate little or no soil C (Hungate *et al.*, 2009), a result that strongly suggests an increase in decomposition rates. A large body of scientific evidence also shows an increase in soil organic matter decomposition following the addition of organic substrate (Kuzyakov, 2010). Collectively, these data provide strong support for the interpretation that increased CO₂ leads to an increase in decomposition rates. Trying to fit models with fixed decomposition rates to these results may therefore lead to incorrect conclusions, just as fitting oversimplified models may yield erroneous inferences.

What microbial response caused the increase in decomposition rates under elevated CO₂? Recent studies suggest that multiple mechanisms might be responsible. For instance, elevated CO₂ has been shown to increase the activity of enzymes associated with decomposition of recalcitrant soil organic matter (Carney *et al.*, 2007; Phillips *et al.*, 2011) and to increase decomposition of soil organic matter by stimulating the growth of mycorrhizae (Cheng *et al.*, 2012). Our two-pool analysis does not explicitly represent these or other microbial responses; rather, it assesses the resulting effect of such responses on decomposition rates (i.e., k_1 and k_2). As such, our approach provides no new insights in microbial mechanisms involved in decomposition processes. It builds upon the approach in which time series of soil C data are used to estimate how k -values vary with environmental conditions (e.g., Andr n & K tterer, 1997; Luo *et al.*, 2001, 2003). We fully agree with Georgiou *et al.* (2015) that models explicitly representing the relation between microbial dynamics and decomposition rates may increase predictive power. Such models may also provide mechanistic insight in the role of microbes in mediating the effect of CO₂ on decomposition rates (e.g., Sulman *et al.*, 2014; Tang & Riley, 2014; Wieder *et al.*, 2015).

Indeed, earth system models will best capture the response of decomposition to elevated CO₂, if the mechanisms that alter decomposition rates are known and incorporated into the models.

Conclusion

Our analyses suggest that decomposition rates of soil organic matter change after a step increase in atmospheric CO₂, for both a one-pool model (Van Groenigen *et al.*, 2014) and a two-pool model (Fig. 2). Both types of models are used in earth system models to simulate soil C changes with climate change (Friedlingstein *et al.*, 2006), but these models assume that decomposition rates (*k*'s) are invariant and do not change with CO₂. This could lead to serious problems with predictions about long-term soil C storage; constant *k*'s mean that increased inputs to soil will lead to proportionate increases in soil C, whereas increases in *k* will reduce the C storage potential of soils and thus the ability of soil to buffer the Earth from releases of CO₂ into the atmosphere.

What can be done to improve predictions of soil C dynamics under elevated CO₂? We suggest that data assimilation efforts on soil C dynamics make use of multi-pool models with flexible decomposition rates. We also support the suggestion of Georgiou *et al.* (2015) to inform models with the use of isotopic data, and we agree that models that explicitly represent microbial dynamics may yield important insights. Several of these models include equations that can capture priming effects (e.g., Wutzler & Reichstein, 2013). However, as the models become more complicated, they must also be better constrained by empirical data. For instance, future experiments should include measurements that can be used to estimate CUE (e.g., microbial specific respiration) and the decomposition rates of labile vs. recalcitrant organic matter pools (e.g., activity of enzymes associated with the decomposition of labile or recalcitrant pools). That said, many long-term CO₂ enrichment experiments have already finished and can no longer contribute data. As such, estimation methods (like ours) will be needed that can deal with the limited data streams. Incorporating diverse types of data and approaches will be essential for progress. This integration of models of different complexity with data of different dimensionality poses a significant challenge for the global change research community.

Acknowledgements

This work was supported by the U.S. Department of Energy, Office of Science, Biological and Environmental Research

Program, under Award Number DE-SC-0010632. Jianyang Xia and Yiqi Luo received financial support from the U.S. Department of Energy, Terrestrial Ecosystem Sciences grant DE-SC-0008270. Many thanks to Natasja van Gestel for a productive discussion on model structures and the data assimilation procedure. Finally, we wish to thank Will Wieder for valuable comments on our manuscript.

References

- Ågren GI (2000) Temperature dependence of old soil organic matter. *Ambio*, **29**, 55.
- Andr n O, K tterer T (1997) ICBM: the introductory carbon balance model for exploration of soil carbon balances. *Ecological Applications*, **7**, 1226–1336.
- Carney KM, Hungate BA, Drake BG, Megonigal JP (2007) Altered soil microbial community at elevated CO₂ leads to loss of soil carbon. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 4990–4995.
- Cheng L, Booker FL, Tu C *et al.* (2012) Arbuscular mycorrhizal fungi increase organic carbon decomposition under elevated CO₂. *Science*, **337**, 1084–1087.
- Cias P, Sabine C, Bala G *et al.* (2013) Carbon and other biogeochemical cycles. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Stocker TF, Qin D, Plattner GK, *et al.*), pp. 465–570. Cambridge University Press, Cambridge.
- Craine JM, Morrow C, Fierer N (2007) Microbial nitrogen limitation increases decomposition. *Ecology*, **88**, 2105–2113.
- Davidson EA, Janssens IA (2006) Climate change. *Nature*, **440**, 165–173.
- Friedlingstein P, Cox P, Betts R *et al.* (2006) Climate-carbon cycle feedback analysis: results from the C⁴MIP model intercomparison. *Journal of Climate*, **19**, 3337–3353.
- Georgiou K, Koven CD, Riley WJ, Torn MS (2015) Pitfalls in estimating priming using bulk turnover time. *Global Change Biology* (this issue).
- Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**, 1150–1156.
- Hungate BA, van Groenigen KJ, Six J *et al.* (2009) Assessing the effect of elevated CO₂ on soil carbon: a comparison of four meta-analyses. *Global Change Biology*, **15**, 2020–2034.
- Kuzyakov Y (2010) Priming effects: interactions between living and dead organic matter. *Soil Biology and Biochemistry*, **42**, 1363–1371.
- Luo Y, Wu L, Andrews JA, White L, Matamala R, Schafer KVR, Schlesinger WH (2001) Elevated CO₂ differentiates ecosystem carbon processes: Deconvolution analysis of Duke Forest FACE data. *Ecological Monographs*, **71**, 357–376.
- Luo Y, White LW, Canadell JG *et al.* (2003) Sustainability of terrestrial carbon sequestration: A case study in Duke Forest with inversion approach. *Global Biogeochemical Cycles*, **17**, GB1012.
- Luo Y, Ogle K, Tucker C *et al.* (2011) Ecological forecasting and data assimilation in a data-rich era. *Ecological Applications*, **21**, 1429–1442.
- Manzoni S, Taylor P, Richter A, Porporato A, Ågren GI (2012a) Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytologist*, **196**, 79–91.
- Manzoni S, Pi neiro G, Jackson RB, Jobb gy EG, Kim JH, Porporato A (2012b) Analytical models of soil and litter decomposition: Solutions for mass loss and time-dependent decay rates. *Soil Biology and Biochemistry*, **50**, 66–76.
- Osenberg CW, Sarnelle O, Cooper SD, Holt RD (1999) Resolving ecological questions through meta-analysis: goals, metrics and models. *Ecology*, **80**, 1105–1117.
- Phillips RP, Finzi AC, Bernhardt ES (2011) Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO₂ fertilization. *Ecology Letters*, **14**, 187–194.
- Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus*, **44**, 81–99.
- Rosenberg MS, Adams DC, Gurevitch J (2000) *METAWIN, Statistical Software for Meta-Analysis, Version 2*. Sinauer, Sunderland, MA.
- Six J, Jastrow JD (2002) Organic matter turnover. In: *Encyclopaedia of Soil Science* (ed. Lal R), pp. 936–942. Marcel Dekker, New York, NY.
- Sulman BN, Phillips RP, Oishi CA, Shevliakova E, Pacala SW (2014) Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO₂. *Nature Climate Change*, **4**, 1099–1102.
- Tang J, Riley WJ (2014) Weaker soil carbon–climate feedbacks resulting from microbial and abiotic interactions. *Nature Climate Change*, **5**, 56–60.

- Trumbore SE (1997) Potential responses of soil organic carbon to global environmental change. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 8284–8291.
- Trumbore SE (2000) Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications*, **10**, 399–411.
- Van Groenigen KJ, Qi X, Osenberg CW, Luo Y, Hungate BA (2014) Faster decomposition under elevated CO₂ limits soil carbon storage. *Science*, **344**, 508–509.
- Wieder WR, Grandy AS, Kallenbach CM, Taylor PG, Bonan GB (2015) Representing life in the Earth system with soil microbial functional traits in the MIMICS model. *Geoscientific Model Development Discussions*, **8**, 2011–2052.
- Wutzler T, Reichstein M (2013) Priming and substrate quality interactions in soil organic matter models. *Biogeosciences*, **10**, 2089–2103.
- Xu T, White L, Hui D, Luo Y (2006) Probabilistic inversion of a terrestrial ecosystem model: Analysis of uncertainty in parameter estimation and model prediction. *Global Biogeochemical Cycles*, **20**, GB2007.