



News and Views

A call to investigate drivers of soil organic matter retention vs. mineralization in a high CO₂ world

Sharon A. Billings^{a,*}, John Lichter^b, Susan E. Ziegler^c, Bruce A. Hungate^d, Daniel de B. Richter^e

^a Department of Ecology and Evolutionary Biology and Kansas Biological Survey, University of Kansas, 2101 Constant Ave., Lawrence, KS 66047, USA

^b Biology Department and Environmental Studies Program, Bowdoin College, Brunswick, ME 04011, USA

^c Department of Earth Science, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1B 3X5

^d Department of Biological Sciences and Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011, USA

^e Nicholas School of the Environment, Duke University, Durham, NC 27708, USA

ARTICLE INFO

Article history:

Received 16 July 2009

Received in revised form

5 January 2010

Accepted 11 January 2010

Available online 21 January 2010

Keywords:

Soil organic matter

Soil organic carbon

Soil organic nitrogen

Elevated CO₂

Organic matter structure

Microbial stoichiometry

Priming effect

ABSTRACT

Understanding how elevated atmospheric CO₂ alters the formation and decomposition of soil organic carbon (SOC) is important but challenging. If elevated CO₂ induces even small changes in rates of formation or decay of SOC, there could be substantial feedbacks on the atmosphere's concentration of CO₂. However, the long turnover times of many SOC pools – decades to centuries – make the detection of changes in the soil's pool size difficult. Long-term CO₂ enrichment experiments have offered unprecedented opportunities to explore these issues in intact ecosystems for more than a decade. Increased NPP with elevated CO₂ has prompted the hypothesis that SOC may increase at the same time that increased vegetation nitrogen (N) uptake and accumulation indicates probable declines in SON. Varying investigators thus have hypothesized that SOC will increase and SON will decline to explain increased NPP with elevated CO₂; researchers also invoke biogeochemical theory and stoichiometric constraints to argue for strong limitations on the co-occurrence of these phenomena. We call for researchers to investigate two broad research questions to elucidate the drivers of these processes. First, we ask how elevated CO₂ influences compound structure and stoichiometry of that proportion of NPP retained by soil profiles for relatively long time periods. We also call for investigations of the mechanisms underlying the decomposition of mineralizable organic matter with elevated CO₂. Specifically, we need to understand how elevated CO₂ influences microbial priming (driven by enhanced microbial energy needs associated with increases in biomass or activity) and microbial mining of N (driven by enhanced microbial N demand associated with greater vegetative N uptake), two processes that necessarily will be constrained by the stoichiometry of both substrates and microbial demands. Applying technologies such as nuclear magnetic resonance and the detection of biomarkers that reveal organic matter structure and origins, and studying microbial stoichiometric constraints, will dramatically improve our ability to predict future patterns of ecosystem C and N cycling.

© 2010 Elsevier Ltd. All rights reserved.

1. Essay text

Worldwide, soils contain between 2000 and 2400 Pg of C in the top 2 m (Jobbágy and Jackson, 2000). If elevated CO₂ causes even a small change in the rate of formation or decay of such a large pool, this will have a substantial feedback on atmospheric CO₂. However, the long turnover times of many soil organic C (SOC) pools – decades to centuries – make the detection of changes in the soil's pool size difficult. In an attempt to address this issue, many CO₂

enrichment experiments have been conducted over relatively long time frames, but consistent responses of SOC pool sizes to elevated CO₂ have not been observed. In this essay, we briefly discuss the processes governing the responses of SOC pools to elevated CO₂ and contributing to observed inconsistencies in SOC responses, and specify research needs for accurately characterizing soil – and thus ecosystem – C and nitrogen (N) cycling in the future.

Exposing ecosystems to elevated CO₂ frequently induces two responses important for C and N cycling; one results in soil organic matter (SOM) additions, the other in SOM depletion. First, elevated CO₂ increases net primary productivity (NPP) and organic inputs to the soil (Norby et al., 2005; DeLucia et al., 2005; Palmroth et al., 2006; Schlesinger et al., 2006; Pritchard et al., 2008). This has prompted investigators to hypothesize that SOC will increase with

* Corresponding author. Tel.: +1 785 864 1560; fax: +1 785 864 1534.

E-mail addresses: sharonb@ku.edu (S.A. Billings), jlichter@bowdoin.edu (J. Lichter), sziegler@mun.ca (S.E. Ziegler), bruce.hungate@nau.edu (B.A. Hungate), richter@duke.edu (D.deB. Richter).

elevated CO₂ as well. Many studies have explored this issue, in a diverse array of ecosystems. Estimates of the response of SOC pool size to elevated CO₂ reveal remarkably mixed results (Lichter et al., 2005, 2008, van Groenigen et al., 2006), including declines (Langley et al., 2009) and increases in some pools of SOC with elevated CO₂ (Loya et al., 2003; Jastrow et al., 2005; Hoosbeek et al., 2006).

Second, in addition to increased inputs of organic matter to soil, the enhanced NPP often observed with elevated CO₂ also results in greater nitrogen (N) stored in live vegetation and litterfall (Hungate et al., 2006; Finzi et al., 2007). The enhanced vegetation accrual of N is most simply explained by reduced soil organic N (SON) in these soils relative to control plots (Gill et al., 2006). Increased biological N fixation, whether symbiotic or asymbiotic, could also contribute to the N in circulation (Lüscher et al., 2000; Hartwig et al., 2000), but is challenging to quantify, not consistently observed with elevated CO₂ (Hofmockel and Schlesinger, 2007), and likely too small to explain observed increases in vegetation N with elevated CO₂ in several ecosystems. An increased C:N ratio of vegetation could allow sustained NPP stimulation with no additional N. Nitrogen concentration of vegetation typically declines with elevated CO₂ (Reich et al., 2006), but a number of long-term CO₂ experiments with sustained biomass responses also report increased vegetation N pools. Thus, investigators have hypothesized that a compensatory decline in the SON pool is likely to occur where elevated CO₂ consistently increases NPP; this process would redistribute N from organic matter pools with relatively low C:N (SOM) to pools exhibiting higher C:N (vegetation) (Luo et al., 2004). Though changing SOC pool sizes with elevated CO₂ have been quantified and compared to NPP increases in the literature, explorations of SON depletion with elevated CO₂ that explicitly relate changes in SON pool sizes over time to vegetation N enhancement in a quantifiable manner are rare.

Here, we highlight two broad research questions focusing on SOM retained by soil profiles, vs. that which is mineralized and the heterotrophic microorganisms responsible for its decomposition. Addressing these questions will be critical for our attempts to predict future ecosystem C and N cycling. The first question focuses on the organic material entering and *remaining within* soil profiles with elevated CO₂. We need to understand the factors governing the proportion of NPP that is retained by a soil profile for relatively long time periods (decades to centuries). *What is it about the organic matter retained within a soil profile that governs its relative lack of reactivity, and how will those features change with elevated CO₂?*

Though we have significant knowledge of key differences between labile and relatively recalcitrant compounds (Balesdent, 1987; Allison, 2006; Billings, 2006), much remains to be learned about the drivers of low organic matter reactivity that can influence SOM retention within a profile. For example, our understanding of the transformational processes within soils that govern compound architecture and stoichiometry, and how these characteristics change over time with elevated CO₂, is lacking. The use of biomarkers that reveal organic matter origins (Hedges et al., 1994; Feng et al., 2008; Simpson et al., 2008) and technologies such as nuclear magnetic resonance (Hockaday et al., 2009; Ono et al., 2009) hold great promise for furthering our understanding of compounds and decomposition byproducts most likely “left behind” by microbial communities, and how elevated CO₂ influences compound structure. These insights will be critical for predicting the proportion of enhanced NPP associated with elevated CO₂ likely to remain in soil profiles for relatively long time periods.

The second question focuses on the organic material *lost* from soil profiles due to microbial mineralization. We need a much better understanding of the drivers of substrate decomposition with elevated CO₂. The lack of a consistent increase in mineral SOC content with elevated CO₂, in spite of increased inputs, implies an alteration in the heterotrophic activity responsible for C mineralization. Indeed,

the enzymatic activity of heterotrophic soil microbial communities can change with elevated CO₂ (Finzi et al., 2006; Carney et al., 2007; Billings and Ziegler, 2008), and studies of soil microbial biomarkers imply that the activity of organisms adept at processing relatively recalcitrant pools of SOM may increase with elevated CO₂ (Carney et al., 2007; Billings and Ziegler, 2008), with corresponding changes in the C:N ratio of material being mineralized (Billings and Ziegler, 2005). These changes in heterotrophic, microbial metabolism likely will alter substrate-use efficiency (del Giorgio and Cole, 1998), a key driver of the fate of SOM. Thus, our second question asks: *How does elevated CO₂ influence the drivers of microbial breakdown of mineralizable substrates?*

One mechanism that can alter decomposition of mineralizable SOC with elevated CO₂ is the priming effect (Langley et al., 2009), whereby enhancement of organic matter inputs promotes greater activity of soil microbial communities in accessing both recently added SOC and older material for energy to support increased activity and/or biomass (Kuzyakov et al., 2000; Fontaine et al., 2007; Paterson, 2009). Sustained over time, this effect would result in losses of mineral SOC (Fig. 1). Depending on the magnitude of those losses relative to additional inputs with elevated CO₂, net SOC losses are feasible as has been observed in some CO₂ enrichment experiments (Langley et al., 2009). This mechanism is consistent with biomarker studies suggesting that elevated CO₂ induces heterotrophic microbial communities to access relatively slow-turnover pools of SOC (Carney et al., 2007; Billings and Ziegler, 2005, 2008). Increasing our understanding of microbial priming, hinted at in many elevated CO₂ studies (van Kessel et al., 2000; Martín-Oldmedo et al., 2002; Trueman and Gonzalez-Meler, 2005; Xie et al., 2005; Carney et al., 2007; Paterson et al., 2008; Hoosbeek and Scarascia-Mugnozza, 2009, Langley et al., 2009), is critical for predicting future SOC stocks and dynamics.

Another mechanism likely driving enhanced decomposition with elevated CO₂ is increased microbial N limitation, which could occur with no increase in microbial biomass. As vegetation removes increasing quantities of mineral N from soils to support enhanced NPP with elevated CO₂, extant microbial communities must “mine” the soil of mineralizable SOM to a greater degree to satisfy their N demand. This enhanced rate of SOM turnover would be associated with increased rates of SOC oxidation and release of CO₂ (Fig. 1, Kuzyakov et al., 2000). Such a scenario requires that gross rates of N mineralization increase, an effect only sometimes observed with elevated CO₂ (Zak et al., 2003; Jin and Evans, 2007). The increase in N mineralization required to explain increased plant N acquisition with elevated CO₂ is of a similar magnitude as background variation in N cycling rates (Reich et al., 2006), challenging our attempts to assess these processes. Moreover, the destructive soil sampling required for mineralization assays limits the temporal resolution of available data sets, and changes in gross N mineralization within distinct pools of SON with elevated CO₂ may be obscured when we assess N cycling parameters on bulk soil samples. Thus, further measurements of gross N fluxes with elevated CO₂ at much greater temporal and spatial resolution will be one key contribution to our understanding of microbial N limitations.

These motivators of heterotrophic microbial activity – seeking energy to support the biomass enhancements fueled by added SOC inputs and seeking N (and other nutrients) to relieve the nutrient limitations imposed by greater vegetative uptake – are not mutually exclusive, and cannot be effectively considered in isolation from each other. However, recognizing that increased substrate availability and N limitation may have varying effects on different microbial populations is important for understanding how SOM turnover times may be influenced by elevated CO₂. For example, if the active microbial populations within a soil profile have varying stoichiometric constraints (Sinsabaugh et al., 2008), they will likely exhibit varying degrees of C- vs. N limitation if C and N availability increase

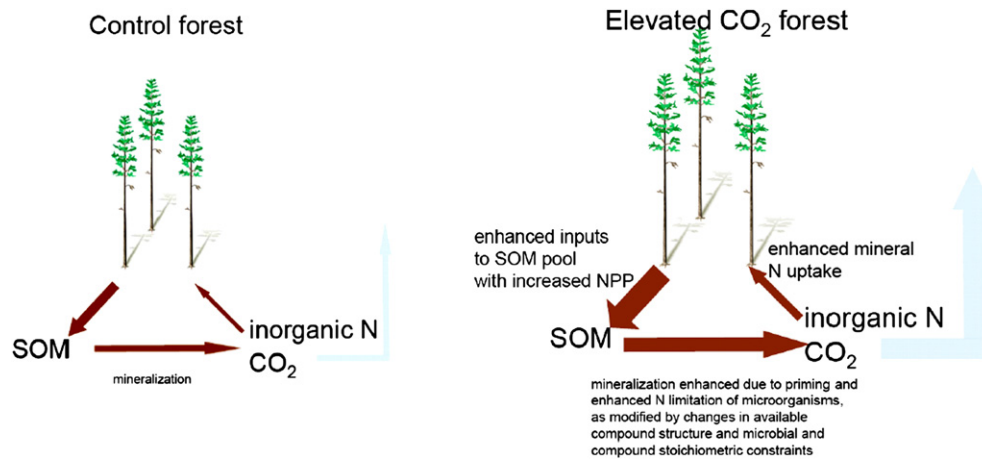


Fig. 1. Depiction of forest organic matter pools and fluxes that are critical determinants of soil organic matter (SOM) content. Thickness of arrows approximates relative magnitudes of processes; faded arrows represent gaseous diffusion of CO₂ into the atmosphere. SOM, derived from vegetation detritus and root exudates, is comprised of a complex suite of compounds exhibiting varying degrees of reactivity and turnover times. Elevated CO₂ induces increased forest net primary productivity (NPP), with associated enhancement of organic inputs to SOM pools. An increase in SOM pool size may not be detected, however, if mineralization is enhanced. This could occur via microbial priming due to greater microbial energy needs associated with greater microbial biomass or activity levels, or microbial “mining” of nitrogen (N) if microbial N limitation increases due to greater vegetation N uptake. Both mechanisms – priming and greater N limitations of heterotrophic microorganisms – result in enhanced turnover of SOM, mitigating gains in SOM pool size with elevated CO₂. Conversely, additional inputs of organic material to soil with elevated CO₂ likely confound our abilities to detect the declines in soil organic N that must occur to satisfy additional vegetation demand. These processes are governed by the structure and stoichiometry of organic compounds in the soil, as well as the stoichiometric constraints of microorganisms accessing that material.

and decrease, respectively, with elevated CO₂. These responses, in turn, will likely govern patterns of decomposition of organic compounds significantly altered from those observed with lower [CO₂]. We do not know the extent to which microbial populations can shift their stoichiometry to adapt to lower N availability, or if they can adapt their enzyme production for the breakdown of the structurally complex but N-rich compounds (Allison, 2006) often “left behind” and thus retained as passive SOM. Those organisms adept at accessing relatively recalcitrant but N-rich compounds would benefit under increasingly limited N conditions, consistent with studies showing an increase in the activity levels of such organisms with elevated CO₂ (Billings and Ziegler, 2005, 2008; Carney et al., 2007). Work to increase our understanding of the adaptive stoichiometry of microbial populations, and of the relative abundance of organic compounds’ stoichiometries, is therefore critical for predicting SOM processing in a high CO₂ world.

The observed variation in responses to elevated CO₂ of multiple pools of mineral SOC and N dynamics across elevated CO₂ research sites certainly reflects ecosystem variation in soil type, vegetation, land use history, and climate, as well as the challenges of detecting relatively small changes in large and heterogeneous pools of SOM. However, our ability to detect patterns in the responses of SOM pool size to elevated CO₂ is also challenged by the simultaneous and counteracting forces of enhanced inputs to soil profiles and enhanced nutrient and energy needs of heterotrophic microbial communities – processes that have prompted hypotheses of increasing SOC and decreasing SON pools. We suggest that addressing the two broad research topics outlined here – the characteristics of SOM compounds retained by soil profiles and altered energy and nutrient drivers of the decomposition of SOM mineralized within soil profiles with elevated CO₂ – will greatly enhance our abilities to predict ecosystem C and N cycling in a high CO₂ world. We call for studies exploring the architectural complexity and stoichiometry of organic compounds produced with elevated CO₂ to help us predict the reactivity of these compounds, and the stoichiometry and substrate-use efficiency of active groups of soil microorganisms metabolizing these substrates under elevated CO₂ to help us predict their turnover times. This work needs to be conducted in multiple ecosystems, over experimental time frames of years and decades (Richter et al., 2007) to encompass

the many different microbial communities that dictate the fate of SOM across ecosystem time (Ohtonen et al., 1999; Pennanen et al., 1999; Merila et al., 2002). Through these investigations, we can make great strides in our abilities to predict future fluxes and stocks of ecosystem C and N, and in turn how biogeochemical cycling of these resources are likely to influence the atmosphere and Earth’s climate.

Acknowledgements

The authors have benefited from grants provided by the National Science Foundation and the Office of Science (BER) at the US Department of Energy. Two anonymous reviewers provided thoughtful commentaries that greatly improved this essay.

References

- Allison, S.D., 2006. Brown ground: a soil carbon analogue for the green world hypothesis? *The American Naturalist* 167, 619–627.
- Balesdent, J., 1987. The turnover of soil organic fractions estimated by radiocarbon dating. *Science of the Total Environment* 62, 405–408.
- Billings, S.A., 2006. Soil organic matter dynamics and land use change at a grassland/forest ecotone. *Soil Biology and Biochemistry* 38, 2934–2943.
- Billings, S.A., Ziegler, S.E., 2005. Linking microbial activity and soil organic matter transformations in forest soils under elevated CO₂. *Global Change Biology* 11, 203–212.
- Billings, S.A., Ziegler, S.E., 2008. Altered patterns of soil carbon substrate usage and heterotrophic respiration in a pine forest with elevated CO₂ and N fertilization. *Global Change Biology* 14, 1025–1036.
- Carney, K.M., Hungate, B.A., Drake, B.G., Megonigal, J.P., 2007. Altered soil microbial community at elevated CO₂ leads to loss of soil carbon. *Proceedings of the National Academy of Sciences* 104, 4990–4995.
- del Giorgio, P.A., Cole, J.J., 1998. Bacterial growth efficiency in natural aquatic systems. *Annual Review of Ecology and Systematics* 29, 503–541.
- DeLucia, E.H., Moore, D.J., Norby, R.J., 2005. Contrasting responses of forest ecosystems to rising atmospheric CO₂: implications for the global C cycle. *Global Biogeochemical Cycles* 19, GB3006.
- Feng, X.J., Simpson, A.J., Wilson, K.P., Williams, D.D., Simpson, M.J., 2008. Increased cuticular carbon sequestration and lignin oxidation in response to soil warming. *Nature Geoscience* 1, 836–839.
- Finzi, A.C., Sinsabaugh, R.L., Long, T.M., Osgood, M.P., 2006. Microbial community response to atmospheric carbon dioxide enrichment in a warm-temperate forest. *Ecosystems* 9, 215–226.
- Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., Ceulemans, R., 2007. Increases in nitrogen uptake rather than nitrogen-use

- efficiency support higher rates of temperate forest productivity under elevated CO₂. Proceedings of the National Academy of Sciences of the United States of America 104, 14014–14019.
- Fontaine, S., Barot, S., Barre, P., Bdioui, N., Mary, B., Rumpel, C., 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature* 450, 277–280.
- Gill, R.A., Anderson, L.J., Polley, H.W., Johnson, H.B., Jackson, R.B., 2006. Potential nitrogen constraints of soil carbon sequestration under low and elevated atmospheric CO₂. *Ecology* 87, 41–52.
- Hartwig, U.A., Luscher, A., Daepf, M., Blum, H., Soussana, J.F., Nosberger, J., 2000. Due to symbiotic N-2 fixation, five years of elevated atmospheric pCO₂ had no effect on the N concentration of plant litter in fertile, mixed grassland. *Plant and Soil* 224, 43–50.
- Hedges, J.I., Cowie, G.L., Richey, J.E., Quay, P.D., Benner, R., Strom, M., Forsberg, B.R., 1994. Origins and processing of organic-matter in the Amazon River as indicated by carbohydrates and amino-acids. *Limnology and Oceanography* 39, 743–761.
- Hockaday, W.C., Masiello, C.A., Randerson, J.R., Smernik, R.J., Baldock, J.A., Chadwick, O.A., Harden, J.W., 2009. Measurement of soil carbon oxidation state and oxidative ratio by C-13 nuclear magnetic resonance. *Journal of Geophysical Research-Biogeosciences* 114 Article Number: G02014.
- Hofmockel, K.S., Schlesinger, W.H., 2007. Carbon dioxide effects on heterotrophic dinitrogen fixation in a temperate pine forest. *Soil Science Society of America Journal* 71, 140–144.
- Hoosbeek, M.R., Yongtao, L., Scarascia-Mugnozza, G.E., 2006. Free atmospheric CO₂ enrichment (FACE) increased labile and total carbon in the mineral soil of a short rotation poplar plantation. *Plant and Soil* 281, 247–254.
- Hoosbeek, M.R., Scarascia-Mugnozza, G.E., 2009. Increase litter build up and soil organic matter stabilization in a poplar plantation after 6 years of atmospheric CO₂ enrichment (FACE): final results of POP-EuroFACE compared to other forest FACE experiments. *Ecosystems* 12, 220–239.
- Hungate, B.A., Johnson, D.W., Dijkstra, P., Hymus, G., Stiling, P., Megonigal, P., Pagel, A.L., Moan, J.L., Day, F., Li, J., Hinkle, C.R., Drake, B.G., 2006. Nitrogen cycling during seven years of atmospheric CO₂ enrichment in a scrub oak woodland. *Ecology* 87, 26–40.
- Jastrow, J.D., Miller, R.M., Matamala, R., Norby, R.J., Boutton, T.W., Rice, C.W., Owensby, C.E., 2005. Elevated atmospheric carbon dioxide increases soil carbon. *Global Change Biology* 11, 2057–2064.
- Jin, V., Evans, R.D., 2007. Elevated CO₂ affects microbial carbon substrate use and N cycling in Mojave Desert soils. *Global Change Biology* 13, 1–12.
- Jobbágy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* 10, 423–436.
- van Kessel, C., Nitschelm, J., Horwath, W.R., Harris, D., Walley, F., Luscher, A., Hartwig, U., 2000. Carbon-13 input and turnover in a pasture soil exposed to long-term elevated atmospheric CO₂. *Global Change Biology* 6, 123–135.
- Kuzuyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. *Soil Biology and Biochemistry* 32, 1485–1498.
- Langley, J.A., McKinley, D.C., Wolf, A.A., Hungate, B.A., Drake, B.G., Megonigal, J.P., 2009. Priming depletes soil carbon and releases nitrogen in a scrub-oak ecosystem exposed to elevated CO₂. *Soil Biology and Biochemistry* 41, 54–60.
- Lichter, J., Barron, S.H., Bevacqua, C.E., Finzi, A.C., Irving, K.F., Stemmler, E.A., Schlesinger, W.H., 2005. Soil carbon sequestration and turnover in a pine forest after six years of atmospheric CO₂ enrichment. *Ecology* 86, 1835–1847.
- Lichter, J., Billings, S.A., Ziegler, S.E., Gaiandh, D., Ryals, R., Finzi, A.C., Jackson, R.B., Stemmler, E.A., Schlesinger, W.H., 2008. Soil carbon sequestration in a pine forest after nine years of atmospheric CO₂ enrichment. *Global Change Biology* 14, 2910–2922.
- Loya, W.M., Pregitzer, K.S., Karberg, N.J., King, J.S., Giardina, C.P., 2003. Reduction of soil carbon formation by tropospheric ozone under increased carbon dioxide levels. *Nature* 425, 705–707.
- Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, R., Zak, D.R., Field, C.B., 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* 54, 731–739.
- Lüscher, A., Hartwig, U.A., Suter, D., Nosberger, J., 2000. Direct evidence that symbiotic N-2 fixation in fertile grassland is an important trait for a strong response of plants to elevated atmospheric CO₂. *Global Change Biology* 6, 655–662.
- Martín-Olmedo, P.D., Rees, R.M., Grace, J., 2002. The influence of plants grown under elevated CO₂ and N fertilization on soil nitrogen dynamics. *Global Change Biology* 8, 643–657.
- Merila, P., Strommer, R., Fritze, H., 2002. Soil microbial activity and community structure along a primary succession transect on the land-uplift coast in western Finland. *Soil Biology and Biochemistry* 34, 1647–1654.
- Norby, R.J., Delucia, E. H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., de Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarascia-Mugnozza, G.E., Schlesinger, W.H., Oren, R., 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. Proceedings of the National Academy of Sciences of the United States of America 102, 18052–18056.
- Ohtonen, R., Fritze, H., Pennanen, T., Jumpponen, A., Trappe, J., 1999. Ecosystem properties and microbial community changes in primary succession on a glacier forefront. *Oecologia* 119, 239–246.
- Ono, K., Hirai, K., Morita, S., Ohse, K., Hiradate, S., 2009. Organic carbon accumulation processes on a forest floor during an early humification stage in a temperate deciduous forest in Japan: evaluations of chemical compositional changes by C-13 NMR and their decomposition rates from litterbag experiments. *Geoderma* 151, 351–356.
- Palmroth, S., Oren, R., McCarthy, H.R., Johnsen, K.H., Finzi, A.C., Butnor, J.R., Ryan, M.G., Schlesinger, W.H., 2006. Aboveground sink strength in forests controls the allocation of carbon below ground and its [CO₂]-induced enhancement. Proceedings of the National Academy of Sciences of the United States of America 103, 19362–19367.
- Paterson, E., 2009. Comments on the regulatory gate hypothesis and implications for C-cycling in soil. *Soil Biology and Biochemistry* 41, 1352–1354.
- Paterson, E., Thornton, B., Midwood, A.J., Osborne, S.M., Sim, A., Millard, P., 2008. Atmospheric CO₂ enrichment and nutrient additions to planted soil increase mineralization of soil organic matter, but do not alter microbial utilization of plant- and soil C-sources. *Soil Biology and Biochemistry* 40, 2434–2440.
- Pennanen, T., Liski, J., Baath, E., Kitunen, V., Uotila, J., Westman, C.J., Fritze, H., 1999. Structure of the microbial communities in coniferous forest soils in relation to site fertility and stand development stage. *Microbial Ecology* 38, 168–179.
- Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., Finzi, A.C., Jackson, R.B., Matamala, R., Rogers, H.H., Oren, R., 2008. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO₂-enrichment: a six-year-minirhizotron study. *Global Change Biology* 14, 588–602.
- Reich, P.B., Hungate, B.A., Luo, Y., 2006. Carbon–nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology and Systematics* 37, 611–636.
- Richter, D.D., Hofmockel, M., Callahan, M.A., Powlson, D.S., Smith, P., 2007. Long-term soil experiments: keys to managing earth's rapidly changing ecosystems. *Soil Science of America Journal* 71, 266–279.
- Schlesinger, W.H., Bernhardt, E.S., DeLucia, E.H., Ellsworth, D.S., Finzi, A.C., Hendrey, G.R., Hofmockel, K.S., Lichter, J., Matamala, R., Moore, D., Oren, R., Phippen, J.S., Thomas, R.B., 2006. The Duke Forest FACE experiment: CO₂ enrichment of a loblolly pine forest. In: Nösberger, J., Long, S.P., Norby, R.J., Stitt, M., Hendrey, G.R., Blum, H. (Eds.), *Managed Ecosystems and CO₂ Case Studies, Processes, and Perspectives*. Ecological Studies, vol. 187, pp. 197–212.
- Simpson, M.J., Otto, A., Feng, X., 2008. Comparison of solid-state carbon-13 nuclear magnetic resonance and organic matter biomarkers for assessing soil organic matter degradation. *Soil Science Society of America Journal* 72, 268–276.
- Sinsabaugh, R.L., Lauber, C.L., Weintraub, M.N., Ahmed, B., Allison, S.D., Crenshaw, C., Contosta, A.R., Cusack, D., Frey, S., Gallo, M.E., Gartner, T.B., Hobbie, S.E., Holland, K., Keeler, B.L., Powers, J.S., Stursova, M., Takacs-Vesbach, C., Waldrop, M.P., Wallenstein, M.D., Zak, D.R., Zeglin, L.H., 2008. Stoichiometry of soil enzyme activity at global scale. *Ecology Letters* 11, 1252–1264.
- Trueman, R.J., Gonzalez-Meler, M.A., 2005. Accelerated belowground C cycling in a managed agriforest ecosystem exposed to elevated carbon dioxide concentrations. *Global Change Biology* 11, 1258–1271.
- Xie, Z., Cadisch, G., Edwards, G., Baggs, E.M., Baggs, H., 2005. Carbon dynamics in a temperate grassland soil after 9 years exposure to elevated CO₂ (Swiss FACE). *Soil Biology and Biochemistry* 37, 1387–1395.
- van Groenigen, K.J., Six, J., Hungate, B.A., de graaf, M.A., van Breemen, N., van Kessel, C., 2006. Element interactions limit soil carbon storage. Proceedings of the National Academy of Sciences of the United States of America 103, 6571–6574.
- Zak, D.R., Holmes, W.E., Finzi, A.C., Norby, R.J., Schlesinger, W.H., 2003. Soil nitrogen cycling under elevated CO₂: a synthesis of forest FACE experiments. *Ecological Applications* 13, 1508–1514.