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Nitrogen mineralization, not N_2 fixation, alleviates progressive nitrogen limitation – Comment on "Processes regulating progressive nitrogen limitation under elevated carbon dioxide: a meta-analysis" by Liang et al. (2016)

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The responses of terrestrial ecosystems to increasing carbon dioxide (CO_2) concentrations in the atmosphere are expected to be strongly affected by nitrogen (N) availability due to its limiting effect on ecosystem productivity (Hungate et al., 2003; Wang and Houlton, 2009). A popular hypothesis is the progressive N limitation (PNL), which assumes that an enhanced net primary productivity (NPP) due to elevated CO_2 leads to storage of not only carbon, but also N in long-lived ecosystems pools such as woody biomass or soil organic matter (Luo et al., 2004). This storing of N is hypothesized to decrease the N availability for plant N uptake, posing a negative feedback to enhanced NPP. This negative feedback is expected to become progressively more pronounced through time. However, in the original formulation of the PNL hypothesis, soil processes are largely ignored, though they are mentioned as potential mechanisms that can delay or prevent the development of a PNL (Luo et al., 2004). Data on the development of NPP stimulation under long-term free air CO_2 enrichment (FACE) experiments indicate that most ecosystems have not developed a PNL on decadal scale (Feng et al., 2015), although some experiments did show a clear decreased NPP stimulation due to PNL. Understanding why a PNL is often not (yet) present in most long-term FACE experiments requires a comprehensive assessment of processes that might alleviate, prevent or delay the development of a PNL.

In their recent meta-analysis, Liang et al. (2016) aimed at this and concluded that increased biological N_2 fixation (BNF), together with decreased nitrate (NO_3^-) leaching, "may potentially alleviate PNL under elevated CO_2 conditions". However, this conclusion is misleading due to at least two facts. First, there is a bias in the data set towards experiments with dominance of symbiotic BNF, questioning the generality of the found increase in BNF in all terrestrial ecosystems. Second, one of the most crucial processes for N availability in terrestrial ecosystems has not been considered by Liang et al. (2016): the actual soil N mineralization measured as gross rates.

Biological N_2 fixation can occur in most terrestrial ecosystems. The highest rates of BNF occur in ecosystems dominated by symbiotic N_2 fixation, such as legumes (Evans and Barber, 1977; Cleveland et al., 1999). However, these ecosystems are limited in areal extent, for instance legumes cover only about 10 % of the agricultural land globally (Smil, 1999). Moreover, in natural ecosystems symbiotic N_2 fixation might be downregulated (Batterman et al., 2013). In their meta-analysis, Liang et al. (2016) found that BNF increased on average by 44 % under elevated CO_2. However, this increase was derived from a data set with an overrepresentation of ecosystems dominated by plants with symbiotic N_2 fixation relative to most ecosystems. Considering FACE and open-top chamber (OTC) studies only, 15 of the 26 data points originated from experiments dominated by symbiotic N_2 fixation. In those, the BNF was significantly increased under elevated CO_2, by 56.3 % on average (95 % confidence interval: +25.1 to +95.4 %; Fig. 1). In contrast, ecosystems not dominated by symbiotic N_2 fixation showed no significant increase in the BNF (mean: +13.6 %; 95 % confidence interval: −8.6 to +41.3 %). This contrast becomes even more clear if rice paddies were excluded from non-N_2

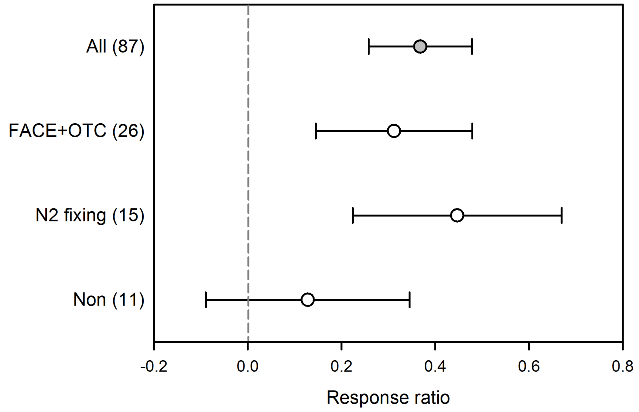

Figure 1. Response ratio of biological N_2 fixation to elevated CO_2 (mean ± 95 % confidence interval). Data from Liang et al. (2016), separated into different groups: FACE is free air CO_2 enrichment, OTC is open-top chambers, N_2 fixing is plant communities dominated by plants with symbiotic N_2 fixation, Non are plant communities not dominated by symbiotic N_2 fixation. The number in parenthesis is the number of data points.

fixing ecosystems (mean: +4.1 %; 95 % confidence interval: −20.2 to +35.7 %), as these paddies have substantial biological crusts with N_2 fixating cyanobacteria (Hoque et al., 2001).

None of the long-term FACE experiments, for which biomass responses to elevated CO_2 were investigated by Feng et al. (2015) or Liang et al. (2016), were dominated by plants with symbiotic N_2 fixation. Therefore, enhanced BNF cannot explain why PNL has not developed after decade-long exposure to elevated CO_2 in the majority of these FACE experiments. The mechanism and conclusion presented by Liang et al. (2016; Fig. 5) represents a special case, limited to ecosystems dominated by plants with symbiotic N_2 fixation.

What mechanism can then potentially prevent the development or alleviation of a PNL in the majority of terrestrial ecosystems? An increase in the N use efficiency (NUE) of plants could prevent the development of a PNL, which has indeed been observed in grassland species (Lee et al., 2011). However, out of four forest FACE experiments, NUE was only increased in a poplar plantation under elevated CO_2, while NUE was unchanged in the remaining three experiments (Finzi et al., 2007). Therefore, it is unclear if this mechanism is widespread in alleviating PNL. Liang et al. (2016) identified N mineralization, the transfer of organically bound N to mineral N, as a major source for plant-available N. However, they failed to recognize that net N mineralization, which was the measure they looked at, does not represent the actual N mineralization dynamics in soils (Davidson et al., 1992), hence is not the supply capacity for plant-available N. The actual soil N mineralization is measurable as the gross N mineralization rate (Davidson et al., 1992). We recently reviewed how gross N transformations are altered in ecosystems exposed to elevated CO_2 (Rütting and Andresen, 2015). Although we found that across all available data, the gross N mineralization was not affected by elevated CO_2, rates were significantly increased in N-limited ecosystems (Rütting and Andresen, 2015). The importance of that finding lies in the fact that only N-limited ecosystems are expected to be at risk of developing a PNL (Hu et al., 2006). In fact, ecosystems dominated by plants with symbiotic N_2 fixation are not N limited and not prone to develop a PNL (Hu et al., 2006). Therefore, in N-limited ecosystems (prone to PNL), the observed increased gross N mineralization directly provides an enhanced supply of plant-available N, which can alleviate the PNL or prevent its development under elevated CO_2.

A question is which of the different processes can provide a large enough quantity of N to sustain the increased N demand under elevated CO_2. Based on literature data, it is possible to quantify additional N supply by the different processes, N_2 fixation, N mineralization and NO_3^- leaching, under elevated CO_2. Annual N_2 fixation rates in natural ecosystems, not dominated by symbiotic N_2 fixing plants, are in the range 1.5–25 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ (Cleveland et al., 1999). Assuming an increase of 14 % under elevated CO_2 (as calculated for non-N_2 fixing plant communities, Fig. 1), an additional amount of 0.2–3.5 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ is provided. Annual NO_3^- leaching losses from temperate watershed are on average 0.3 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ (range 0.02–2.3 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$; Brookshire et al., 2012). Liang et al. (2016) reported a decrease in NO_3^- leaching by 42 % under elevated CO_2. However, when considering N-limited ecosystems in their data set ($N = 4$), NO_3^- leaching decreased on average by 21 %. Therefore, reduced NO_3^- leaching under elevated CO_2 is in the range of 0.004 to 0.48 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ in N-limited temperate ecosystems. That means that the two processes identified by Liang et al. (2016) combined lead to an increase in N availability of at most 4 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$. Only few studies have reported annual gross N mineralization rates, which range between 120 and 450 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ for temperate grasslands (Jamieson et al., 1999; Wang et al., 2016) and 800–1000 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ in a Norway spruce forest (Rosenkranz et al., 2010). Assuming a 14 % increase in this rate under elevated CO_2 (as found for N-limited ecosystems by Rütting and Andresen, 2015), an additional amount of plant-available N of 17 to 140 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ will be produced annually. In other words, a small change in a large flux (i.e. gross N mineralization) might be more important than a large change in a small flux (i.e. N_2 fixation and NO_3^- leaching) to alleviate a PNL.

The question of for how long an increase in gross N mineralization can satisfy the increased N demand under elevated CO_2 is unresolved. By this mechanism no N loss from the ecosystem occurs, but the redistribution of N from soil to vegetation could diminish the pool of N in mineralizable

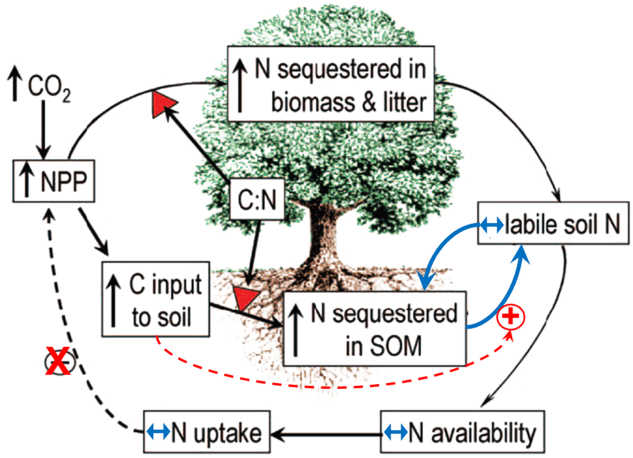

Figure 2. Conceptual model of the proposed mechanism for preventing a progressive nitrogen (N) limitation under elevated CO_2 (modified from Luo et al., 2004; used with permission). Increased carbon (C) inputs to soil stimulate gross N mineralization (blue arrows) in a priming like mechanism (red dashed line), which keeps a sufficient amount of plant-available N (labile soil N) to satisfy the enhanced plant N demand (uptake), thereby preventing the negative feedback on net primary productivity (NPP).

organic matter in the long-term, despite recycling via litter production. A recent multi-model study found that in several models the "mining" for N via enhanced mineralization was limited due to changes in soil organic matter quality, and might only temporarily alleviate a PNL (Zaehle et al., 2014). On the other hand, a second study using the same set of models found increased N mineralization rates due to larger soil organic matter N, which decreased N limitation (Walker et al., 2015). Experimental testing of the alternative model predictions is needed, which requires access to long-term experiments with elevated CO_2.

In conclusion, several processes can contribute to preventing the development of a PNL under elevated CO_2. However, due to the limited spatial extent of plant communities dominated by symbiotic N_2 fixation, the stimulation in BNF suggested by Liang et al. (2016) is a special case only and is in agreement with the conceptual model by Rütting and Andresen (2015). In the majority of terrestrial ecosystems, with limited or no BNF, enhanced carbon inputs to the soil under elevated CO_2 stimulate the gross N mineralization rate (Dijkstra et al., 2013; Rütting and Andresen, 2015) in a priming-like mechanism, which can explain the absence of the development of a PNL in N-limited ecosystems (Fig. 2). Further studies are needed to determine whether this stimulation will be maintained in the long term.

1 Data availability

This article reanalyses data from Liang et al. (2016), which are freely available as a supplement to that article (http://www.biogeosciences.net/13/2689/2016/bg-13-2689-2016-supplement.zip).

Competing interests. The authors declare that they have no conflict of interest.

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