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.

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The responses of terrestrial ecosystems to increasing CO$_2$ concentrations in the atmosphere are expected to be strongly affected by nitrogen (N) availability, due to its limiting effect on

10   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,

15   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. Data on the development of NPP stimulation under long-term free air CO$_2$ enrichment (FACE) experiments indicate that

20   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.

25   In their recent meta-analysis, Liang et al. (2016) aimed at this and concluded that increased biological N$_2$ fixation (BNF) together with decreased 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 dataset towards experiments with dominance of symbiotic BNF, questioning the generality of the found increased in BNF in all terrestrial

30   ecosystems. Second, one of the most crucial processes for N availability in terrestrial

ecosystems has not been considered by Liang et al.: the actual soil N mineralization measured as gross rates.

Biological N_2 fixation can occur in most terrestrial ecosystems, highest rates often 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 extend, 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 derived from a data set, having an overrepresentation of ecosystems dominated by plants with symbiotic N_2 fixation relative to most ecosystems. Alternatively, when considering FACE and 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 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 was investigated by Feng et al. (2015) or Liang et al. (2016) was dominated by plants with symbiotic N_2 fixation. Therefore, enhanced BNF cannot explain why no PNL has 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 of or alleviate a PNL in the majority of terrestrial ecosystems? Liang et al. (2016) rightly 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 in soils (Davidson et al., 1992) and, hence, 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 overall, across all available data, the gross N

mineralization was not affected by elevated CO_2, the rates were significantly increased in N limited ecosystems (Rütting and Andresen, 2015). The importance of that finding lies in the fact that only the 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 enhanced supply of plant available N, which can alleviate the PNL or prevent its development under eCO_2.

Certainly, BNF also occurs in ecosystems not dominated by plants with symbiotic N_2 fixation. A question is, if this non-symbiotic BNF is large enough to sustain increased N demand under elevated CO_2. To provide some answer to this question, I will discuss as a case, data from the spruce forest Höglwald, one of the most in-detail studied ecosystems in terms of N cycling (Butterbach-Bahl and Gundersen, 2011), under current conditions together with likely responses to an elevated CO_2 level (Table 1), as already brought forward in my comment to the Liang et al. paper (Rütting, 2016). The current annual plant N uptake of the Höglwald forest is 100 kg N ha^{-1} yr^{-1}, which is expected to increase by 8 % or 8 kg N ha^{-1} yr^{-1} under eCO_2 (based on the average response in Feng et al., 2015). If we assume a reduction of N leaching by 42 % (as found by Liang et al., 2016) and an increase in gaseous N losses by 19 % (Van Groenigen et al., 2011), an additional amount of 1.5 kg N ha^{-1} yr^{-1} is needed to balance the enhanced plant N demand. If BNF should provide this, an increase by 75 % is needed, assuming the current day rate of 2 kg N ha^{-1} yr^{-1} (Table 1). This increase is well above the average increase in non-symbiotic plant communities (Fig. 1) and outside the 95 % confidence interval reported by Liang et al. (2016) (average = 14 %; range -9 % to 41 %). Therefore, it is unlikely that BNF can prevent the development of a PNL. On the other hand, a stimulation by as little as 0.3 % of gross N mineralization (currently 550 kg N ha^{-1} yr^{-1}) can satisfy the enhanced plant N demand (Table 1) and prevent the development of a PNL. Such a small stimulation is much smaller than the average value we found for N limited ecosystem (+14 %) and the (non-significant) values for all ecosystems (+6 %) (Rütting and Andresen, 2015). Unresolved is for how long an increase in N mineralization can satisfy the increased N demand under elevated CO_2. Even though this mechanism no N loss from the ecosystem, the redistribution of N from soil to vegetation could in the long-term diminish the pool of N in mineralizable organic matter, 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 an 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 prevent the development of a PNL under elevated CO_2. However, due to the limited spatial extend of plant communities dominated by symbiotic N_2 fixation, the stimulation in BNF suggested by Liang et al. (2016) is a special case only, which is actually in agreement with the conceptual model by Rütting and Andresen (2015). However, in the majority of terrestrial ecosystems, with limited or no BNF, the eCO_2 enhanced carbon inputs to the soil stimulates in a priming-like mechanism the gross N mineralization rate (Dijkstra et al., 2013; Rütting and Andresen, 2015), which can explain the absent of the development of a PNL in N limited ecosystems (Fig. 2). Further studies are needed to determine if this stimulation will be maintained in the long-term.

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Table 1: Exemplary data on the nitrogen fluxes (kg N ha^{-1} yr^{-1}) from the spruce forest Höglwald (Butterbach-Bahl and Gundersen, 2011) with no symbiotic N_2 fixation under current conditions (aCO_2) and estimated fluxes under elevated CO_2 (eCO_2), based on expected changes.

	aCO_2 [a]	eCO_2	Δ	Change
Plant N uptake	100	108	8	8% [b]
N leaching	20	11.6	-8.4	-42% [c]
N_{gas} emission	10	11.9	1.9	19% [d]
Alternative pathways for balancing N budget				
Biol. N_2 fixation	2	3.5	1.5	75%
Gross N mineralization	550	551.5		0.3%

5 [a] Butterbach-Bahl and Gundersen (2011)

[b] Feng et al. (2015)

[c] Liang et al. (2016)

[d] van Groenigen et al. (2011), based on data of nitrous oxide emission

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 = Free Air CO_2 Enrichment, OTC = Open Top Chambers; N_2 fixing = plant communities dominated by plants with symbiotic N_2 fixation; Non = plant communities not dominated by symbiotic N_2 fixation. Number in parenthesis is the number of data points.
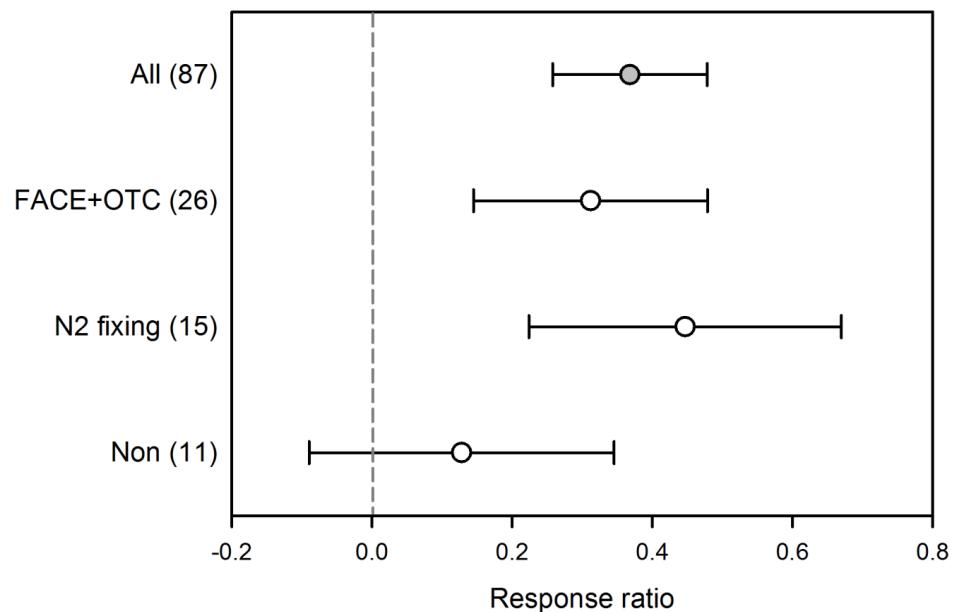
Figure 2: Conceptual model of the proposed mechanism preventing the development of or alleviating progressive nitrogen (N) limitation under elevated CO_2 (modified from Luo et al., 2004). Increased carbon inputs to soil stimulate in a priming like mechanism gross N mineralization (+), which keeps plant available N at high enough levels to sustain enhanced net primary productivity (NPP).