REVIEW ARTICLE

Nitrogen cycle responses to elevated CO_2 depend on ecosystem nutrient status

Tobias Rütting · Louise C. Andresen

Abstract Nitrogen (N) limitation of terrestrial ecosystems is a crucial factor for predicting how these ecosystems respond and feedback to climate change. Nitrogen availability for plants in terrestrial ecosystems depends on the internal soil N cycle and inputs to the ecosystem via biological N_2 fixation. We reviewed the effect of elevated atmospheric CO_2 concentrations (eCO_2) on gross soil N transformations to advance our understanding of ecosystem responses to eCO_2. Overall, neither gross mineralization nor gross nitrification was altered by eCO_2. However, emerging from ecosystem specific analysis, we propose a new conceptual model for eCO_2 effects on gross mineralization based on ecosystem nutrient status: gross mineralization is only stimulated in N limited ecosystems, but unaffected in phosphorus limited ecosystems. Moreover, the ratio of ammonium oxidation to immobilization is decreased under eCO_2, indicating a tighter N cycle with reduced ecosystem N losses. This

new conceptual model on N cycle responses to eCO_2 should be tested in the future in independent experiments and it provides a new concept for refining mechanistic models of ecosystem responses to climate change.

Keywords Elevated CO_2 · Climate change · Nitrogen cycle · Gross rates · Nutrient limitation · Progressive nitrogen limitation · Phosphorus limitation

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N limitation of terrestrial ecosystem responses to eCO_2

Rising atmospheric carbon dioxide (CO_2) concentration leads to an increase in the net flux of carbon (C) from the atmosphere into plants, i.e. increased net primary productivity (NPP) (Ainsworth and Long 2005; Luo et al. 2006). By negative feedback this slows climate change by sequestering C at a rate corresponding to about one fourth of anthropogenic CO_2 emissions (Le Quéré et al. 2013). Enhanced NPP of terrestrial ecosystems also results in an enhanced C input into the soil via rhizodeposition and litter (above- and belowground), which was predicted to lead to an increase in the soil organic matter (SOM) content and thus sequestration of C (Drigo et al. 2008). Potentially, the additional sequestration of C in SOM will also cause a simultaneous increase in nitrogen

(N) sequestration (Luo et al. 2004), the nutrient limiting productivity of most terrestrial ecosystems (LeBauer and Treseder 2008). This sequestration of N in SOM may also reduce N availability for plant uptake, leading to a progressive N limitation (PNL) of the enhanced plant productivity under rising CO_2 (Luo et al. 2004). Consequently, the future responses of terrestrial ecosystems to elevated CO_2 (eCO_2) and C sequestration are expected to be controlled by N availability (Hungate et al. 2003; Reich et al. 2006). Reduced C sequestration caused by PNL would feedback to enhance global warming, as indicated by recent global climate modelling studies considering C–N interactions in the terrestrial biosphere (Friedlingstein and Prentice 2010; Zaehle and Dalmonech 2011). However, a recent meta-analysis showed that generally the soil C content is unaffected by eCO_2, despite higher C inputs (van Groenigen et al. 2014). This finding challenges the prediction of PNL in terrestrial ecosystems. Thus, an urgent climate change research question remains: How is plant N availability affected by eCO_2?

Potential mechanisms avoiding PNL

In natural terrestrial ecosystems which are not fertilized with N, the availability of N for plant uptake is largely dependent on the soil's N cycle, particularly N mineralization and biological N_2 fixation (BNF). Stimulation of these N cycle processes by eCO_2 can sustain plant N availability and C sequestration in natural ecosystems (Barnard et al. 2006; De Graaff et al. 2006; Hartwig and Sadowsky 2006; Müller et al. 2009; Rütting et al. 2010). The likelihood of PNL is expected to be small in ecosystems with high external N inputs, where N supply meets N demand (Hu et al. 2006; Luo et al. 2004). However, the impact of eCO_2 on the complex network soil N cycle processes and potential feedbacks on plant N availability is still poorly understood (Hungate et al. 2009). While BNF provides a means to avoid PNL it is limited to ecosystems with an abundance of N_2-fixing taxa. Increased gross (or actual) N mineralization can, however, lead to enhanced N supply to plants in any natural ecosystem. Enhanced C inputs via rhizodeposition under eCO_2 (De Graaff et al. 2007; Phillips et al. 2011; van Groenigen et al. 2014) may lead to a

stimulation of microbial SOM decomposition ('priming'), which in turn may enhance gross N mineralization (Dijkstra et al. 2008; Rütting et al. 2010). However, Dijkstra et al. (2013) suggested that the stimulation of gross mineralization may be restricted to N limited ecosystems. Earlier reviews showed that in general neither gross N mineralization nor gross nitrification were affected by eCO_2 (Barnard et al. 2005; De Graaff et al. 2006; Reich et al. 2006; Zak et al. 2003). However, these conclusions were influenced by two facts: first, the number of considered studies was in general low (3–14 data points) and second, large variations in the response of gross N transformations to eCO_2 were observed. While some studies found an increase in gross N transformation rates under eCO_2, others reported a decrease, making generalization challenging (Reich et al. 2006). Moreover, no mechanistic explanation for the observed variation has currently been presented. Over the last decade further investigations on the effect of eCO_2 on gross N transformations have been conducted. It is timely to review the expended literature with the specific aim of examining the observed variation in gross N transformation responses to eCO_2.

Data set and analysis

This paper synthetizes the findings of 19 studies that have reported on eCO_2 effects on gross N transformations (Table 1), conducted in either open top chamber (OTC) or free-air CO_2 enrichment (FACE) facilities. Mesocosm studies were not included, as these represent highly disturbed systems. The studies were separated by ecosystem type: grasslands, forests, deserts or those dominated by N_2 fixing plant species (at the time of investigation). In these studies, gross N transformations were investigated by using ^{15}N enrichment techniques. Multiple data points for a particular facility (e.g. different soil depth, co-treatments or dates) were considered as independent. The gross N transformation rates were taken from tables or extracted from published figures using WebPlotDigitizer 3.3 (www.arohatgi.info/WebPlotDigitizer). This resulted in a total of 107 gross mineralization, 86 gross NH_4^+ consumption and 46 gross nitrification rates in the database. For each of the three N processes, response ratios (*RR*) were calculated as the natural logarithm of the ratio between gross rate under eCO_2 (R_e) and ambient conditions (R_a):

Table 1 Overview over studies investigating gross nitrogen transformations in experiment with elevated CO_2 in open top chamber (OTC) or free air CO_2 enrichment (FACE) studies, covering different ecosystems

Site name	Design	Ecosystem	Limitation[a]	Reference
NDFF	FACE	Desert	N	Jin and Evans (2007)
Aspen	FACE	Forest	N	Holmes et al. (2003, 2006)
Duke	FACE	Forest	N/NP[b]	Finzi and Schlesinger (2003); Phillips et al. (2011)
Oak Ridge	FACE	Forest	N	Iversen et al. (2011); Sinsabaugh et al. (2003)
Florida	OTC	Forest	–	McKinley et al. (2009)
Michigan	OTC	Forest	–	Mikan et al. (2000)
BioCON	FACE	Grassland	N/NP[b]	West et al. (2006)
CLIMAITE	FACE	Grassland	NP	Björsne et al. (2014); Larsen et al. (2011)
GiFACE	FACE	Grassland	N	Müller et al. (2009)
JRGCE	FACE	Grassland	P	Niboyet et al. (2011)
NZ FACE	FACE	Grassland	N	Rütting et al. (2010)
SwissFACE	FACE	Grassland	N	Richter et al. (2003)
SwissFACE	FACE	N_2 fix	P	Richter et al. (2003)
California	OTC	Grassland	–	Williams et al. (2001)
JRGCE	OTC	Grassland	–	Hungate et al. (1997a)
MECCA	OTC	Grassland	–	Hungate et al. (1997b)
Florida	OTC	N_2 fix	–	Hungate et al. (1999)

For FACE studies the nutrient limiting plant growth is indicated, based on original literature

[a] Only for FACE studies, used for analysing effects of nutrient limitation on nitrogen transformations

[b] Ecosystem generally nitrogen limited, but experimental plots receiving nitrogen fertilization are classified as NP limited

$$RR = \ln\left(\frac{R_e}{R_a}\right) \qquad (1)$$

Thereby, a value of zero indicates no difference between eCO_2 and ambient CO_2, while significant effects ($p < 0.05$) are indicated if the 95 % confidence interval (CI) does not overlap with zero. Outliers were identified using Grubbs test (Sokal and Rohlf 2012).

To investigate the relationship between the RR for NH_4^+ consumption and the RR for mineralization a bivariate line fitting (Warton et al. 2006) was conducted using the standardized major axis in the SMATR software (Falster et al. 2003). Lines were separately fitted for each of the four ecosystems, which further allowed the investigation of ecosystem differences by comparing fitted slopes (Warton et al. 2006). A slope significantly larger than unity indicates stronger stimulation of NH_4^+ consumption, while a slope smaller unity indicates that gross mineralization is stronger stimulated by eCO_2 than NH_4^+ consumption.

Contrasting effects of eCO_2 on N cycling in different ecosystems

Averaged across all data points neither gross mineralization nor NH_4^+ consumption nor nitrification were affected by eCO_2 (Fig. 1), which agrees with earlier review studies (Barnard et al. 2005; De Graaff et al. 2006). However, responses varied with experimental method of eCO_2. Gross mineralization was reduced in OTC studies, but unaffected in FACE studies (Fig. 1a). On the other hand, gross nitrification tended to decrease in FACE studies ($p < 0.09$) but not in OTC studies. However, the low number of data point for gross nitrification make results less certain. Given these potential differences between experimental exposure methods, the fact that FACE represents the ecologically most relevant experimental approach to investigate ecosystem responses to rising CO_2 (Hendrey and Miglietta 2006), and because FACE studies provided the most data points, the remainder of the review will focuses solely on FACE studies.
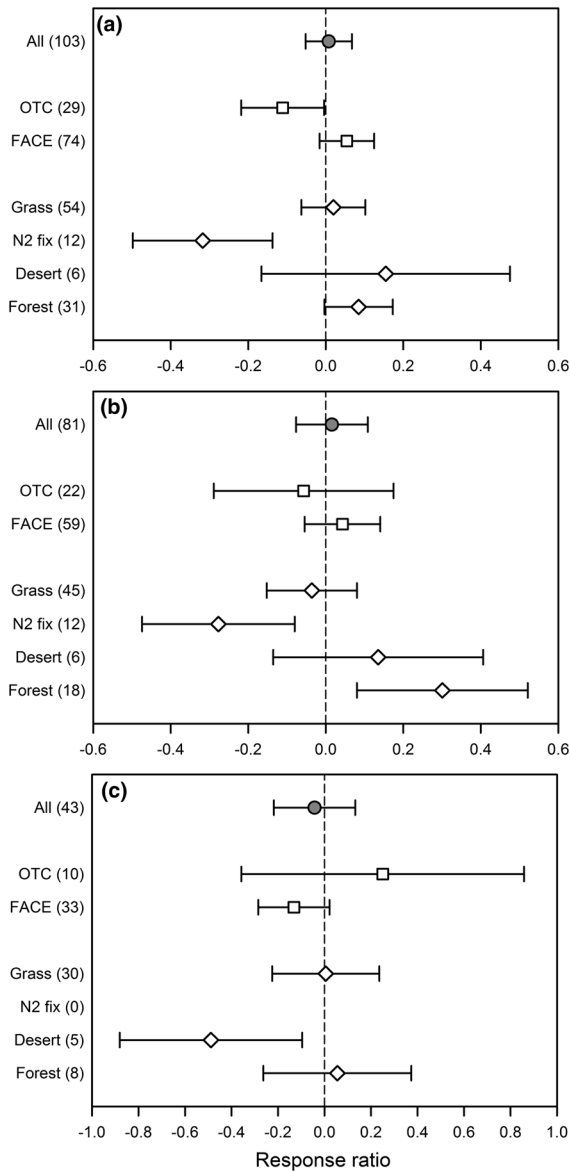
Fig. 1 Mean response ratios (*RR*) of gross N transformations under elevated CO_2 for mineralization (**a**), ammonium (NH_4^+) consumption (**b**) and nitrification (**c**). Data are means ± 95 % confidence intervals of the *RR* (see text for further explanation). Data are divided by exposure system (OTC open top chamber; FACE free air CO_2 enrichment) and ecosystem type. Number of data points is given in parentheses

None of the three considered soil N transformations were significantly affected by eCO_2 in the FACE studies when averaging all data points (Fig. 1). However, gross nitrification tended to decrease under eCO_2 ($p < 0.09$). Furthermore, the gross rates varied with ecosystem type in response to eCO_2. In forest

FACE studies both, gross NH_4^+ consumption ($p < 0.05$; not shown) and gross mineralization ($p < 0.06$; Fig. 2a) were increased under eCO_2. In contrast, the presence of eCO_2 tended to decrease gross mineralization in N_2 fixing communities ($p < 0.075$; Fig. 2a). Gross nitrification was significantly decreased in deserts and it is worth noticing the numerical decrease in gross nitrification in grassland FACE studies (Fig. 2b).

Does eCO_2 stimulate gross NH_4^+ consumption more than gross mineralization?

A stronger eCO_2 induced stimulation of gross (microbial) NH_4^+ consumption than gross mineralization would lead to decreased N availability for plants, which in turn could limit ecosystem productivity and C sequestration under rising CO_2 concentrations
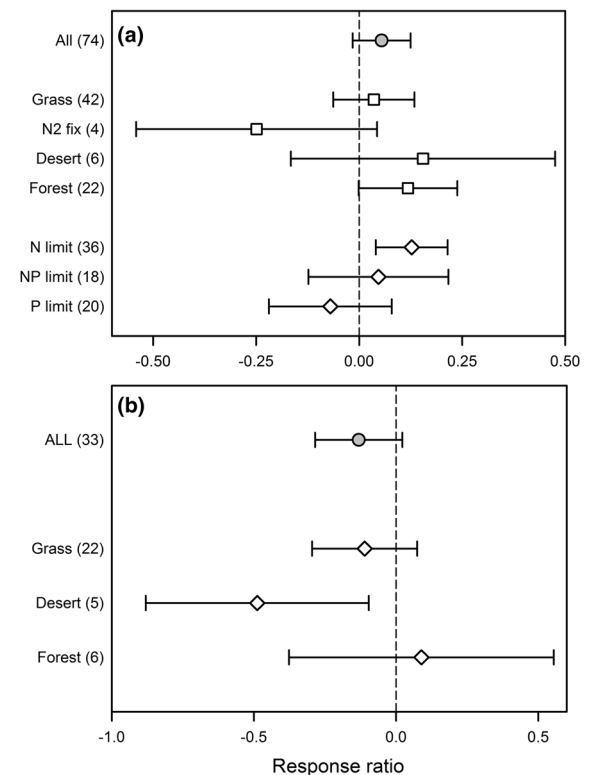

Fig. 2 Mean response ratios (*RR*) of gross mineralization (**a**) and nitrification (**b**) under elevated CO_2 in FACE experiments, divided into ecosystem types and nutrient limitation (see text for further explanation). Data are means ± 95 % confidence intervals of the *RR* and number of data points is given in parentheses

(Hungate et al. 2003). A positive linear relationship between RR of gross NH_4^+ consumption and mineralization was observed for all four ecosystems ($r^2 = 0.34$–0.97; Suppl. Table 1) and none of the slopes were significantly different from unity (Suppl. Table 1). Moreover, the ecosystems exhibited a common slope of 0.95 (CI 0.85–1.22), which also was not different from unity (Fig. 3). This indicates that gross mineralization was as much stimulated by eCO_2 as NH_4^+ consumption; hence N supply to plants can be expected to be sustained under rising CO_2 concentrations.

Both NH_4^+ production from mineralization and the fate of NH_4^+ are important for ecosystem N availability. Two microbial processes compete for NH_4^+ in soil: microbial immobilization (assimilation) and NH_4^+ oxidation (nitrification). Partitioning NH_4^+ consumption between these two processes is important, as nitrification leads to formation of nitrate (NO_3^-), which is more prone to be lost from ecosystems than NH_4^+. The ratio between nitrification and NH_4^+ immobilization (N/I) has been suggested as a proxy for the susceptibility of an ecosystem to N losses (Tietema and Wessel 1992). Unfortunately, the N/I ratio could not be calculated for most of the studies reporting on gross N transformations, due to methodological issues. Most studies conducted ^{15}N pool dilution experiments, which only allows quantification of gross NO_3^- production (=total nitrification) and total gross NH_4^+ consumption (Schimel 1996). For calculation of the N/I ratio, process specific rates for NH_4^+ oxidation and NH_4^+ immobilization are required, which can be quantified by conducting ^{15}N tracing experiments in conjunction with numerical data analysis (Rütting et al. 2011). Three such experiments have been conducted for grassland FACE sites (Björsne et al. 2014; Müller et al. 2009; Rütting et al. 2010). Notably, in all three experiments N/I decreased in response to eCO_2 from 0.44 to 0.20 ($p = 0.056$, paired t test; Suppl. Table 2). This indicates a lower potential of ecosystem N losses and a generally tighter N cycle under eCO_2, which can additionally contribute to alleviating PNL.

Ecosystem nutrient limitation governs responses of gross mineralization to eCO_2

As discussed above, in FACE studies the responses of gross mineralization to eCO_2 vary with ecosystem type (Fig. 2a). This poses the question, what is causing these contrasting and variable responses? Barnard et al. (2006) suggested, based on ^{15}N labelling experiments, that eCO_2 effects on N turnover differ between the short- and long-term. However, in the present data set no correlation between RR of gross N transformation rates and duration of eCO_2 exposure were observed (not shown). Rather, we suggest that differences in nutrient limitation cause the observed variation in N transformation responses. Due to the lack of an accepted quantitative measure for ecosystem nutrient limitation, we classified FACE sites qualitatively as being either N or P limited or co-limited by both nutrients (NP limited), based on the judgment of the authors of the original studies (see Table 1). We found that gross mineralization rates increased significantly under eCO_2 in N-limited ecosystems, but were unaffected in P-limited ecosystems with NP-limited ecosystems in-between (Fig. 2a). Besides the N_2 fixing plant communities, which were classified as P-limited, only one grassland FACE (JRGCE; Dukes et al. 2005) was reported to be P-limited. Considering therefore only grasslands the same response pattern as for the entire FACE data set was found (Suppl. Figure 1). However, the low number of P-limited study sites limits the generalization of our finding. Consequently, more studies on eCO_2 effects in P limited ecosystems are needed. Based on these existing FACE study results we propose a new conceptual model on how eCO_2 affects
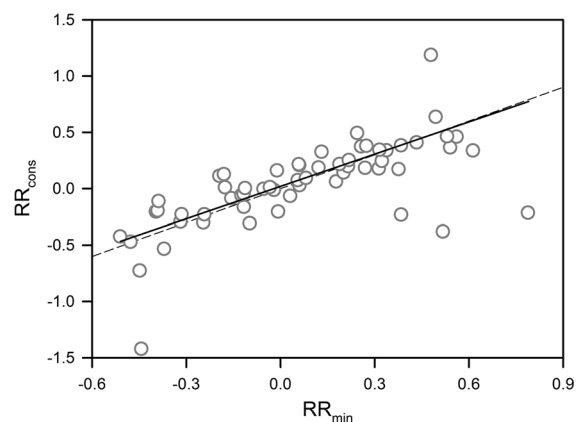

Fig. 3 Results from bivariate line fitting (*solid line*) between the response ratios of gross ammonium consumption (RR_{cons}) and gross mineralization (RR_{min}) under elevated CO_2 in FACE experiments. *Dashed line* indicates the 1:1 line of the ratios

gross N mineralization depending on nutrient limitation (Fig. 4).

In *P limited* ecosystems (not dominated by N_2 fixing plant species), we propose that gross N mineralization is unaffected by eCO_2 (Fig. 2a). An increase in rhizodeposition in these ecosystems, as a results of eCO_2, would not lead to additional SOM decomposition due to priming, but would rather cause additional P mobilization (Dijkstra et al. 2013). Increased P mobilization resulting from eCO_2 can occur via two processes: (1) increased desorption of P from charged soil particles due to higher rhizodeposition of organic acids and humic substances or (2) due to increased P mineralization from SOM (Lloyd et al. 2001). Since P mineralization, unlike N mineralization, is not coupled to SOM decomposition (McGill and Cole 1981), increased P mineralization would not lead to an increase in N mineralization, which consequently remains unaffected by eCO_2 in P limited ecosystems (Fig. 4).

In ecosystems with N_2 *fixing* plant communities, we propose that additional C input will stimulate BNF to meet the higher plant N demand (Hartwig and Sadowsky 2006). This in turn will decrease the C available for heterotrophic microorganism and, hence, gross N mineralization. Such a scenario does not comply with the finding that N_2 fixation is generally unaffected by eCO_2 (De Graaff et al. 2006; Hungate et al. 2004). However, the two eCO_2 experiments with N_2 fixing communities that investigated gross N

mineralization (Hungate et al. 1999; Richter et al. 2003) both showed an increase in N_2 fixation rates (Hartwig and Sadowsky 2006; Hungate et al. 1999), which supports our proposed concept. These contrasting findings for N_2 fixation might be related to the extent and type of nutrient limitation or the duration of eCO_2. Hungate et al. (2004) suggested that the enhanced N_2 fixation of the vine *Galactia elliottii* (Hungate et al. 1999) was not sustained over time due to molybdenum limitation. Edwards et al. (2006) found in a mesocosm study that N_2 fixation was not enhanced at P limitation and in the mixed grassland of the NZ-FACE N_2 fixation by white clover (*Trifolium repens*) was reduced likely due to P limitation (Watanabe et al. 2013). The latter grassland is though generally N limited and showed enhanced gross N mineralization (Rütting et al. 2010), indicating opposing responses of N_2 fixation and N mineralization to eCO_2. Of particular interest is the result from the Swiss FACE experiment, in which gross N transformations were investigated separately for soil planted with perennial rye grass (*Lolium perenne*) or white clover. While gross mineralization rates decreased in the clover swards (-22 %), they increased significantly in the N-limited grass sward ($+23$ %) (Richter et al. 2003). Again, this supports the proposition that decreased mineralization in N_2 fixing communities is due to increased N supply via BNF (Fig. 4).

Finally, in *N limited ecosystems* we propose that enhanced rhizodeposition under eCO_2 will cause rhizosphere priming to increased SOM decomposition, which will in turn stimulate N mineralization (Fig. 4). This is consistent with the increases in gross mineralization observed in N-limited ecosystems (Fig. 2a) and has been previously proposed (De Graaff et al. 2009; Rütting et al. 2010). The PNL hypothesis initially proposed has considered soil N dynamics to a limited extend (Luo et al. 2004). However, it has been pointed out that the likelihood of PNL is highest in ecosystems with low external N inputs (Hu et al. 2006). To date few studies have documented the development of an ecosystem PNL under eCO_2 (Newton et al. 2010; Norby et al. 2010), with the majority of studies demonstrating no support for PNL (e.g. McCarthy et al. 2010; Reich and Hobbie 2013; Talhelm et al. 2014). The scenario presented here offers a mechanism to explain why PNL does not develop, even in N limited ecosystems with low external N inputs: accelerated N mineralization
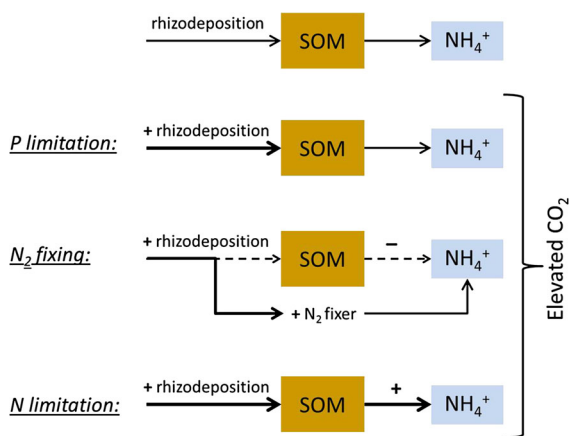

Fig. 4 Conceptual model of the effect of elevated CO_2 on gross nitrogen mineralization (NH_4^+ production from soil organic matter—SOM) depending on nutrient limitation of the ecosystem (see text for further explanations)

dynamics under eCO_2 results in a continuous N supply, which could satisfy the increased plant N demand without additional external N inputs.

Further research needs

While the present review advances our understanding of eCO_2 effects on the biogeochemical N cycle, there are still some urgent research needs. Most importantly, more studies of gross N transformations under eCO_2 are required, particularly in P limited ecosystems, in order to test the proposed conceptual model. Also N_2 fixing plant communities are underrepresented and for those it seems crucial that gross mineralization is investigated concurrently with N_2 fixing rates. Other ecosystems are entirely lacking in our data set on gross N transformations, namely arable fields, peatlands and (sub-)tropical ecosystem of all types. Particularly the latter ones are of interest for future investigations, as many tropical ecosystems are P-limited and contain numerous N_2 fixing plant species.

It is now widely recognized that plants not only take up inorganic N, but also organic N, such as amino acids (Näsholm et al. 2009). Indeed, it has been argued that the rate limiting step of the N cycle is not mineralization but depolymerization (Schimel and Bennett 2004). If the SOM depolymerization rates increase under eCO_2 concurrently with enhanced plant uptake of organic N, then increased plant N demand can be met even without the stimulation of N mineralization, by short-circuiting the inorganic N cycle. Experimental work using ^{15}N tracing suggest increased or unchanged plant uptake of amino acid N under eCO_2 (Andresen et al. 2009; Hofmockel et al. 2007; Jin and Evans 2010). However, increased plant uptake of amino acids can only alleviate PNL if the supply of amino acids via depolymerization is also stimulated by eCO_2. In the Duke FACE it was shown that potential amino acid (alanine) production was unaffected by eCO_2 (Hofmockel et al. 2007). However, as potential rates do not provide information on the actual rates of biogeochemical processes (e.g. Prosser and Nicol 2012), investigation of gross amino acid production rates under eCO_2 are still urgently needed. No such study has so far been conducted, but recent methodological developments now permit investigation of gross amino acid production (Wanek et al. 2010). Therefore, dedicated experiments are needed to

simultaneously quantify gross turnover of inorganic and organic N species as well as investigating the eCO_2 effect on plant uptake of a wider range of amino acids, since only a few specific amino acids (i.e. alanine and glycine) have until now been tested.

Conclusions

When combining all data eCO_2 did not alter gross N transformations, which agrees with earlier reviews (Barnard et al. 2005; De Graaff et al. 2006; Reich et al. 2006; Zak et al. 2003). However, our present study provides a novel and more detailed understanding on the variation in responses to eCO_2 by proposing a new conceptual model: gross N mineralization is stimulated in N-limited ecosystems only, but is unaffected in P-limited and is decreased in N_2 fixing plant communities. The implication of this new concept is that N-limited ecosystems are less prone to PNL than earlier suggested, as the stimulation of gross mineralization is a mechanism that may sustain N availability for plants. This is further indicated by the fact that gross mineralization was equally stimulated by eCO_2 as microbial NH_4^+ consumption. On a global scale, if fewer N-limited ecosystems are prone to PNL, sustained enhanced NPP can be expected, as has indeed been found in several long-term eCO_2 studies (McCarthy et al. 2010; Reich 2009; Schneider et al. 2004), which will also increase litter production and formation of new SOM (Drake et al. 2011; van Groenigen et al. 2014). The increased litter input has been shown to balance the faster SOM decomposition under eCO_2, leading to unchanged SOM content (van Groenigen et al. 2014). Global climate models have recently incorporated the biogeochemical N cycle (Friedlingstein and Prentice 2010; Zaehle and Dalmonech 2011) and the models assume ecosystem N limitation produces a reduced terrestrial C sink and higher global warming than earlier expected (e.g. Wang and Houlton 2009). However, the conceptual model proposed here—increased gross N mineralization sustaining N availability and avoiding PNL—would mean that the global climate models potentially overestimate the magnitude of climate warming.

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