



## Tansley review

# Ecosystem responses to elevated CO<sub>2</sub> governed by plant–soil interactions and the cost of nitrogen acquisition

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## Summary

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**Key words:** CO<sub>2</sub>, Free-Air CO<sub>2</sub> enrichment (FACE), mycorrhizas, N<sub>2</sub>-fixation, nitrogen, photosynthesis, soil carbon, soil organic matter (SOM).

Land ecosystems sequester on average about a quarter of anthropogenic CO<sub>2</sub> emissions. It has been proposed that nitrogen (N) availability will exert an increasingly limiting effect on plants' ability to store additional carbon (C) under rising CO<sub>2</sub>, but these mechanisms are not well understood. Here, we review findings from elevated CO<sub>2</sub> experiments using a plant economics framework, highlighting how ecosystem responses to elevated CO<sub>2</sub> may depend on the costs and benefits of plant interactions with mycorrhizal fungi and symbiotic N-fixing microbes. We found that N-acquisition efficiency is positively correlated with leaf-level photosynthetic capacity and plant growth, and negatively with soil C storage. Plants that associate with ectomycorrhizal fungi and N-fixers may acquire N at a lower cost than plants associated with arbuscular mycorrhizal fungi. However, the additional growth in ectomycorrhizal plants is partly offset by decreases in soil C pools via priming. Collectively, our results indicate that predictive models aimed at quantifying C cycle feedbacks to global change may be improved by treating N as a resource that can be acquired by plants in exchange for energy, with different costs depending on plant interactions with microbial symbionts.

## I. Introduction

The atmospheric CO<sub>2</sub> concentration has risen to > 40% above its pre-industrial level, and it is expected to continue rising for decades (Ciais *et al.*, 2013) even under the most ambitious climate-change

mitigation scenarios (Smith *et al.*, 2016). Although it is well established that elevated CO<sub>2</sub> (eCO<sub>2</sub>) stimulates photosynthesis at the leaf level (Ainsworth & Long, 2005), there is considerable uncertainty about the extent to which plants will sustain elevated levels of productivity and continued carbon (C) storage as CO<sub>2</sub>

concentrations rise. This uncertainty reflects incomplete understanding of how eCO<sub>2</sub> alters plant C allocation, decomposition of soil organic matter (SOM), and plant mortality and biomass turnover (Malhi *et al.*, 2015) – all processes modulated by the availability of soil resources.

One of the largest areas of uncertainty about the magnitude of the eCO<sub>2</sub> fertilization effect concerns the role of nutrient availability (Hungate *et al.*, 2003). Relatively tight stoichiometric constraints imply that if the nutrient requirements to increase plant growth are not met (Fay *et al.*, 2015), nutrient availability will inevitably limit the terrestrial C sink (Huang *et al.*, 2015). Nitrogen (N) availability, in particular, appears to limit plant productivity in many terrestrial ecosystems at present (Vitousek & Howarth, 1991; LeBauer & Treseder, 2008; Menge *et al.*, 2012), and is widely considered to be among the most important factors limiting the productivity response of ecosystems to eCO<sub>2</sub> (Körner, 2006; Reich *et al.*, 2006a; Huang *et al.*, 2015; Terrer *et al.*, 2016).

Although numerous experiments have been conducted over the past two decades to investigate the role of N in constraining CO<sub>2</sub>-induced stimulation of photosynthesis and primary production, there is still no general explanation for the disparity of responses observed among different ecosystems (Bazzaz, 1990; Saxe *et al.*, 1998; Nowak *et al.*, 2004; Körner, 2006; Reich *et al.*, 2006b; Norby & Zak, 2011). In some studies, low N availability was found to be the primary constraint responsible for the transient, small or nonexistent CO<sub>2</sub> fertilization effect (Schneider *et al.*, 2004; Norby *et al.*, 2010; Reich & Hobbie, 2013; Sigurdsson *et al.*, 2013). In other studies, plant production was stimulated by eCO<sub>2</sub> despite apparent N-limitation (McCarthy *et al.*, 2010; Hungate *et al.*, 2013; Talhelm *et al.*, 2014). As such, most reviews have concluded that the magnitude of the CO<sub>2</sub> effect varies on a site-by-site basis, leaving the observed inter-site variation unexplained.

One hypothesis predicts that the N-limitation on plant responses to eCO<sub>2</sub> is modulated by the type of N-acquisition strategy, which, in turn, is largely determined by symbiotic plant–microbial interactions (Alberton *et al.*, 2005; Drake *et al.*, 2011; Phillips *et al.*, 2013; Terrer *et al.*, 2016). For example, ecosystems where the dominant plants can acquire ‘additional N’ by stimulating biological N<sub>2</sub>-fixation (BNF) or accelerating SOM decomposition (e.g. via priming effects) are predicted to sustain high rates of net primary productivity (NPP) under elevated CO<sub>2</sub>. In a recent meta-analysis, Terrer *et al.* (2016) found that N availability and the type of microbial symbiont associated with the plant roots were important factors explaining the observed changes in standing biomass across eCO<sub>2</sub> experiments, with a strong and significant interaction between these two factors. Plants associated with ectomycorrhizal (ECM) fungi showed an eCO<sub>2</sub>-driven *c.* 28% enhancement in biomass even under low N. By contrast, plants associated with arbuscular mycorrhizal (AM) fungi were unresponsive to eCO<sub>2</sub> (*c.* 0%) under low N, unless associated with N<sub>2</sub>-fixers (*c.* 8%). These conclusions proved consistent for aboveground productivity as well as biomass (Terrer *et al.*, 2017).

Although greater numbers of long-term eCO<sub>2</sub> experiments with both AM and ECM trees are needed to further test this hypothesis (Norby *et al.*, 2017), differences in the nutrient economies of *symbiotic types* may offer a consistent framework to better

understand and model the interactions between the C and N cycles (Phillips *et al.*, 2013; Lin *et al.*, 2017). By symbiotic types we refer to the capacity of plant species to employ symbionts in their N-acquisition strategy, such as N-uptake mediated through AM and ECM fungi or symbiotic BNF. Nevertheless, the conclusions of Terrer *et al.* (2016) raise additional hypotheses: (1) do ECM plants and N<sub>2</sub>-fixers take up more N than AM plants in response to eCO<sub>2</sub>? (2) Is the role of N availability in constraining the eCO<sub>2</sub> effect on plant biomass caused by limitations on leaf-level photosynthesis? And (3) how do changes in N availability under eCO<sub>2</sub> affect soil C stocks and the ecosystem C balance?

Here, we explore these questions by reviewing observations from eCO<sub>2</sub> experiments with a focus on the C cost of N-acquisition. We acknowledge that other factors such as water availability (Morgan *et al.*, 2004) or phosphorus (P) availability (Ellsworth *et al.*, 2017) may be equally important in mediating terrestrial ecosystem responses to eCO<sub>2</sub>. These are, however, beyond the scope of the current review, which focuses on the effects of N availability, the most commonly limiting nutrient globally (LeBauer & Treseder, 2008). Importantly, we do not treat N-limitation as an ‘on–off’ property but rather refer to the cost of N-acquisition – or, its inverse, the return on investment – as a continuum. As such, our plant economics approach can be applied to other soil resources, provided that the necessary data are sufficiently available. In Section II we define and apply the return on investment approach, which is used in Section III as a link driving ecosystem-level effects triggered by eCO<sub>2</sub>. In Section IV we discuss the conclusions and propose a conceptual framework, with indications of productive directions for model and experimental improvements.

## II. The return on investment approach

### 1. Methods

We define the *return on investment* as a ratio of the marginal relative increase in N-acquisition (N<sub>acq</sub>) and the marginal relative increase in belowground C allocation (C<sub>bg</sub>). We quantify the return on investment with data from eCO<sub>2</sub> experiments using differences in measured N<sub>acq</sub> and C<sub>bg</sub> under elevated (‘ele’) and ambient (‘amb’) CO<sub>2</sub> treatments:

$$\text{Return on investment} = \frac{\frac{\partial N_{\text{acq}}}{N_{\text{acq}}}}{\frac{\partial C_{\text{bg}}}{C_{\text{bg}}}} \approx \frac{\frac{N_{\text{acq}}(\text{ele}) - N_{\text{acq}}(\text{amb})}{N_{\text{acq}}(\text{amb})}}{\frac{C_{\text{bg}}(\text{ele}) - C_{\text{bg}}(\text{amb})}{C_{\text{bg}}(\text{amb})}} = \psi_N^{-1}, \quad \text{Eqn 1}$$

$\psi_N$  can be interpreted as the C cost of acquiring N, and corresponds to the inverse of the return on investment. It quantifies how plants’ N<sub>acq</sub> rates relate to increasing belowground C allocation, and thereby estimates the degree to which aboveground growth is limited by N.

Although N<sub>acq</sub> is often measured in eCO<sub>2</sub> experiments (e.g. Feng *et al.*, 2015), estimating C<sub>bg</sub> (C investment in N<sub>acq</sub>) remains a conceptual and methodological challenge. C<sub>bg</sub> is not confined to root production (C<sub>root</sub>), but also includes C transferred to root

exudates, mycorrhizal fungi and symbiotic N-fixing bacteria ( $C_{transfer}$ ; see Vicca *et al.*, 2012), and is therefore indicative of ‘investments’ for N uptake (or nutrient uptake in general):

$$C_{bg} = C_{root} + C_{transfer} \quad \text{Eqn 2}$$

$C_{transfer}$  implies a cost for the plant by reducing the C available for biomass productivity (BP):

$$BP = NPP - C_{transfer} \quad \text{Eqn 3}$$

We therefore refer to  $C_{transfer}$  as the component of the C budget that may be used by plants to acquire N. Several lines of evidence suggest that is not allocated to plant biomass and, indeed, plants increase allocation to  $C_{transfer}$  as soil resources decrease in availability (Treseder, 2004; Hobbie, 2006; Högberg *et al.*, 2010; Drake *et al.*, 2011; Phillips *et al.*, 2011; Aoki *et al.*, 2012; Nouri *et al.*, 2014), and that such increases in allocation to  $C_{transfer}$  come at the expense of plant biomass production (Vicca *et al.*, 2012) and can reduce net ecosystem productivity (Fernández-Martínez *et al.*, 2014). This may explain why root colonization by mycorrhizal fungi is often increased by  $eCO_2$  (increased N demand) but decreased by N-fertilization (decreased N demand), indicating that plants increase the investment in  $C_{transfer}$  as a means to meet N requirements (Treseder, 2004). Moreover, differences in the C cost of nutrient acquisition may also explain why the proportion of C allocated to  $C_{bg}$  (and by extension  $C_{transfer}$ ) is inversely related to N availability at global scales (Gill & Finzi, 2016), with greater belowground investment in boreal relative to tropical regions.

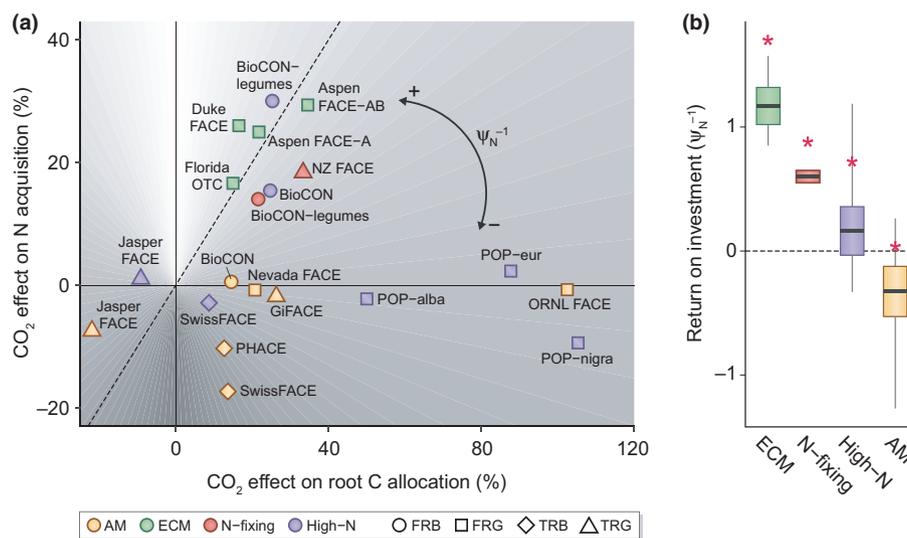
Here, we estimated  $\psi_N^{-1}$  (Fig. 1; Eqn 1) for as many  $eCO_2$  studies as possible, that is, those with data on both  $N_{acq}$  and  $C_{bg}$ . Even though  $C_{transfer}$  represents a fraction of 10–40% of NPP (Chapin *et al.*, 2011; Pritchard, 2011), there have been few measurements of C allocation to fungi and exudates in  $eCO_2$  experiments (Phillips *et al.*, 2011). We used fine-root production, fine-root biomass or root biomass as a proxy for  $C_{bg}$ , thus assuming a constant ratio of  $C_{transfer}$  to  $C_{root}$  and therefore:

$$\frac{\partial C_{bg}}{C_{bg}} = \frac{\partial C_{root}}{C_{root}} \quad \text{Eqn 4}$$

Eqn 4 is supported for several ECM species (Hobbie, 2006; Hobbie & Hobbie, 2008), but uncertainties regarding its validity remain for AM and N-fixing species. We included data from previous syntheses on  $eCO_2$ -driven  $N_{acq}$  (Finzi *et al.*, 2007; Feng *et al.*, 2015), and searched from the Web of Science for  $C_{bg}$  data, recent additional years and additional field studies Free-Air  $CO_2$  enrichment (FACE) and open top chamber (OTC) with available data on both  $N_{acq}$  and  $C_{bg}$ . In total, we used observations from 20 grassland and forest ecosystem experiments corresponding to 12 different sites (Table 1). For species in the Aspen-FACE experiment (Table 1) we excluded all years before canopy development was complete, as recommended elsewhere (Norby *et al.*, 2005).

## 2. Results

In the absence of N-fertilization,  $N_{acq}$  increased significantly (+24%,  $P < 0.001$ ) under  $eCO_2$  in ECM plants, whereas the effect was not significant (−5.6%,  $P = 0.1056$ ) in AM plants. In Fig. 1(a),



**Fig. 1** Plant economics spectrum of the efficiency of plants in acquiring additional nitrogen (N) under elevated  $CO_2$ . (a) Relationship between the elevated  $CO_2$  ( $eCO_2$ )-induced relative change (%) in root carbon ( $C_{root}$ ) (‘investments’) and aboveground N-acquisition (‘returns’). (b) Mean, SE, max and min return on investment ( $\psi_N^{-1}$ , Eqn 1). Colours represent four different N-acquisition strategies characterized by the type of symbiotic association, that is: arbuscular mycorrhizas (AM), ectomycorrhizas (ECM) and N-fixing species (N-fixing), or high N availability (High-N). Shapes in (a) represent the type of root data used to estimate belowground C allocation ( $C_{bg}$ ), that is: fine-root biomass (FRB), fine-root growth (FRG), total-root biomass (TRB) or total-root growth (TRG). Black dashed line in (a) represents the 1 : 1 line. The slope of the grey lines in the background in (a) represents  $\psi_N^{-1}$ , with lower returns (higher costs) as dark grey. Asterisks in (b) are  $\psi_N^{-1}$  estimates at Duke FACE (ECM) and BioCON (AM, N-fixing, and High-N) using  $C_{bg}$  instead of  $C_{root}$  data (Eqn 2).  $N_{acq}$ , product of total or aboveground biomass production and N concentration. When sites include data at the species-level, the site name is followed by a species code (Table 1). Sources of site-level data are given in Table 1.

the slope represents  $N_{\text{acq}}$ -efficiency ( $\psi_{\text{N}}^{-1}$ ), with lighter shading representing higher 'returns'. Most ECM experiments plotted close to the 1 : 1 line, suggesting proportionality between the relative changes in investment and acquisition (e.g. a 1% increase in C investment belowground translates into a 1% increase in  $N_{\text{acq}}$ ). Systems where  $N_2$ -fixers were present exhibited a similar relationship between  $N_{\text{acq}}$  and  $C_{\text{bg}}$  as ECM systems. This finding is based on two experiments: plots from the BioCON experiment with legume species only (Reich & Hobbie, 2013), and all plots from the New Zealand (NZ) FACE experiment, with a mix of  $N_2$ -fixers *Trifolium repens* L. and *Trifolium subterraneum* L. and other grassland AM-species (Newton *et al.*, 2014). AM plants achieved a much lower enhancement in  $N_{\text{acq}}$  than ECM plants and  $N$ -fixers for a given amount of C invested belowground. In some cases, AM plants acquired less N under elevated than ambient  $\text{CO}_2$  despite increasing belowground C investments (Fig. 1a). This relates to results by Feng *et al.* (2015), who found reduced  $N_{\text{acq}}$  under  $\text{eCO}_2$ . The simultaneous increase in  $C_{\text{bg}}$  indicates a strong reduction in  $N_{\text{acq}}$  efficiency.  $N$ -fertilization generally increased  $\psi_{\text{N}}^{-1}$  compared to nonfertilized AM systems (e.g. BioCON, SwissFACE), but it did not consistently help plants achieve the high  $\psi_{\text{N}}^{-1}$ -levels of ECM and  $N_2$ -fixers in this dataset (Fig. 1b).

$C_{\text{bg}}$  data in Fig. 1 are limited by the lack of  $C_{\text{transfer}}$  data (Eqn 2). In order to test the validity of Eqn 4 and the patterns in Fig. 1, we estimated  $\psi_{\text{N}}^{-1}$  using data from four experiments where  $C_{\text{bg}}$  ( $C_{\text{root}} + C_{\text{transfer}}$ ) was inferred from plant C balance (Litton *et al.*, 2007). These data can be used to estimate the cost of  $N_{\text{acq}}$  without assuming Eqn 4, in relative (asterisks in Fig. 1b) and absolute terms. For example, in the Duke FACE experiment (ECM), Drake *et al.* (2011) estimated that plants under  $\text{eCO}_2$  invested 88 g of  $C_{\text{bg}} \text{ g}^{-1}$  of  $N_{\text{acq}}$ , including 12 g of  $C_{\text{transfer}}$ . At BioCON (AM), the estimated cost of  $N_{\text{acq}}$  under  $\text{eCO}_2$  and low N was 2033 g  $C_{\text{bg}} \text{ g}^{-1} N_{\text{acq}}$  (Adair *et al.*, 2009) resulting from the low capacity of plants to acquire additional N. In  $N_2$ -fixing legumes, however,  $\text{eCO}_2$  stimulated  $N_{\text{acq}}$  at a rate of 97 g  $C_{\text{bg}} \text{ g}^{-1} N_{\text{acq}}$ , similar to ECM-trees at Duke. These patterns (asterisks in Fig. 1b) using both  $C_{\text{root}}$  and  $C_{\text{transfer}}$  data, indicate that the cost of  $N_{\text{acq}}$  varies across  $N_{\text{acq}}$ -strategies, supporting the conclusions in Fig. 1. Although assessing the assumption of a constant  $C_{\text{root}} : C_{\text{transfer}}$  ratio (Eqn 4) is a key need for this field, its uncertainty does not stand in the way of the exercise presented here, yet it does indicate uncertainty about the exact slope in Fig. 1(a). Regardless of the slope, marginal N-gains in ECM are larger than in AM plants (Sulman *et al.*, 2017). In order to estimate the true costs, however, more data about the investment in symbiotic associations ( $C_{\text{transfer}}$ ) under  $\text{eCO}_2$  are necessary (see list of data limitations of the approach in Table 2).

In view of these results, the ability of plants to acquire additional N under  $\text{eCO}_2$  appears to vary among symbiotic types and levels of N availability. The important role of mycorrhizal fungi as factors determining ecosystem processes (under current climate) is becoming increasingly apparent (Wurzburger *et al.*, 2017), with ECM fungi generally associated with more beneficial effects on their plant host's fitness than AM fungi (Bennett *et al.*, 2017; Teste *et al.*, 2017). Current evidence suggests that the role of AM fungi in  $N_{\text{acq}}$  depends on soil N availability, as the fungi may have limited

capacity to take up (or transfer) N when in low supply (Reynolds *et al.*, 2005; Johnson *et al.*, 2015). On the one hand,  $\text{eCO}_2$  did not commonly enhance aboveground  $N_{\text{acq}}$  in AM plants under low N in this dataset (Fig. 1a), whereas root investment was increased, leading to a negative mean  $\psi_{\text{N}}^{-1}$  (Fig. 1b). This is consistent with the hypothesis that AM fungi associate with plants along a continuum of interactions ranging from beneficial to parasitic (Johnson *et al.*, 1997), with negative effects for the plant under low N availability (Reynolds *et al.*, 2005; Johnson *et al.*, 2015). On the other hand, AM fungi are commonly associated with enhanced plant  $N_{\text{acq}}$  when N availability is moderate or high (Johnson *et al.*, 2015; Thirkell *et al.*, 2016). The negative  $\psi_{\text{N}}^{-1}$  in AM under low N may also reflect increased tissue C : N ratios and N-use efficiency under  $\text{eCO}_2$ . Whether this is a plant strategy controlled by acclimation of photosynthesis or merely a consequence of insufficient  $N_{\text{acq}}$  is unclear. ECM species in this dataset could acquire additional N 'on demand' via increased C investments, which may be explained by the capacity of many ECM fungal species to produce extracellular enzymes that break down SOM and transfer organic and inorganic forms of N to the host plant (Lindahl & Tunlid, 2015; Shah *et al.*, 2015).

### III. $\text{CO}_2$ response spectrum

Here we focus on the return on investment approach to summarize findings regarding the role of  $N_{\text{acq}}$  in shaping leaf-level photosynthesis (1), plant biomass production (2) and SOM decomposition (3) – all factors that influence ecosystem responses to  $\text{eCO}_2$  and ecosystem feedbacks to climate change. This approach allows us to characterize systems within a response spectrum spanned by the return on investment.

#### 1. $\text{eCO}_2$ effects on photosynthetic capacity

**Background** Theoretical considerations based on optimal use of resources predict a decrease in the maximum rate of carboxylation ( $V_{\text{cmax}}$ ) under  $\text{eCO}_2$  (Wang *et al.*, 2017). This prediction arises because the actual rate of assimilation under average field conditions is necessarily limited by available light, and because the response of light-limited assimilation to the leaf-internal partial pressure of  $\text{CO}_2$  ( $c_i$ ) is less steep than the response of  $V_{\text{cmax}}$ -limited assimilation. Therefore, if light availability and the ratio of  $c_i$  to ambient  $\text{CO}_2$  partial pressure ( $c_a$ ) are unchanged, an increase in  $c_a$  means that a lower  $V_{\text{cmax}}$  is required for the  $V_{\text{cmax}}$ -limited rate to match the light-limited rate. However, existing theories do not explicitly consider the costs of achieving and maintaining a given value of  $V_{\text{cmax}}$ , related to the cost of  $N_{\text{acq}}$  because Rubisco constitutes a substantial proportion of total foliar N (Spreitzer & Salvucci, 2002).

**Question** Is the role of N availability in constraining the  $\text{eCO}_2$  effect on biomass caused by limitations on leaf-level photosynthesis?

**Observations** The downregulation of  $V_{\text{cmax}}$  by  $\text{eCO}_2$  in nonfertilized soils is inversely related to  $\psi_{\text{N}}^{-1}$  (Fig. 2a,  $P < 0.01$ ), suggesting

**Table 1** List of Free-Air CO<sub>2</sub> enrichment (FACE) and open top chamber (OTC) sites analysed in this review, along with some site characteristics and sources for data used in Figs 1–4

Site	Location	Ecosystem, species	<i>n</i>	Symbiont	Root data	<i>N</i> <sub>acq</sub>	<i>V</i> <sub>cm<sup>max</sup></sub> , <i>A</i> <sub>sat</sub>	ANPP	Soil C
Aspen FACE	Rhineland, WI, USA	Forest (deciduous): <i>Populus tremuloides</i> (A) & <i>Betula papyrifera</i> (B)	Low–medium	ECM	Talhelm <i>et al.</i> (2014)*	Talhelm <i>et al.</i> (2014)	Ellsworth <i>et al.</i> (2004); Darbah <i>et al.</i> (2010)	Talhelm <i>et al.</i> (2014)	Talhelm <i>et al.</i> (2014)
Duke FACE	Durham, NC, USA	Forest (conifer): <i>Pinus taeda</i>	Low	ECM	McCarthy <i>et al.</i> (2010); Drake <i>et al.</i> (2011); A. C. Finzi, pers. comm.*	Finzi <i>et al.</i> (2007); A. C. Finzi, pers. comm.	Ellsworth <i>et al.</i> (2012)	A. C. Finzi, pers. comm.	Lichter <i>et al.</i> (2008)
Florida OTC	Cape Canaveral, FL, USA	Forest (deciduous): <i>Quercus myrtifolia</i> , <i>Q. geminata</i> and <i>Q. chapmanii</i>	Low	ECM	Hungate <i>et al.</i> (2013); B. A. Hungate, pers. comm.*	Hungate <i>et al.</i> (2013); B. A. Hungate, pers. comm.	Li <i>et al.</i> (1999)	Hungate <i>et al.</i> (2013); B. A. Hungate, pers. comm.	van Groenigen <i>et al.</i> (2014)
Nevada FACE	Las Vegas, NV, USA	Desert scrub dominated by <i>Larrea tridentata</i> and <i>Ambrosia dumosa</i>	Low	AM	Ferguson & Nowak (2011)*	Housman <i>et al.</i> (2012); Smith <i>et al.</i> (2014)	Ainsworth & Long (2005)	Smith <i>et al.</i> (2014)	Evans <i>et al.</i> (2014)
ORNL FACE	Oak Ridge, TN, USA	Forest (deciduous): <i>Liquidambar styraciflua</i>	Low	AM	Norby <i>et al.</i> (2010); R. J. Norby, pers. comm.*	Norby <i>et al.</i> (2010); R. J. Norby, pers. comm.	Warren <i>et al.</i> (2015)	Norby <i>et al.</i> (2010); R. J. Norby, pers. comm.	Iversen <i>et al.</i> (2012)
PHACE	Cheyenne, WY, USA	Mixed-grass prairie	Low	AM	Mueller <i>et al.</i> (2016)***; P. B. Reich, pers. comm.**	D. M. Blumenthal, pers. comm.	Blumenthal <i>et al.</i> (2013)	D. M. Blumenthal, pers. comm.	–
BioCON	Cedar Creek, MN, USA	Grassland dominated by C <sub>3</sub> , C <sub>4</sub> grasses, legumes and forbs	Low (ambient) & medium (4)	AM, N-fixing	P. B. Reich, pers. comm.**	P. B. Reich, pers. comm.	Crous <i>et al.</i> (2010); Lee <i>et al.</i> (2011)	Reich & Hobbie (2013); P. B. Reich, pers. comm.	http://www.cedarcreek.umn.edu/research/data/dataset?ache141
NZ FACE	Bulls, Manawatu, New Zealand	Grassland dominated by legumes, C <sub>3</sub> and C <sub>4</sub> grasses	Low	N-fixing, AM	Allard <i>et al.</i> (2005)***	P. C. D. Newton, pers. comm.	von Caemmerer <i>et al.</i> (2001)	P. C. D. Newton, pers. comm.	Ross <i>et al.</i> (2013)
Swiss FACE	Eschikon, Switzerland	Ryegrass dominated by <i>Lolium perenne</i>	Medium (14) and high (56)	AM	Bazot <i>et al.</i> (2006)***	Schneider <i>et al.</i> (2004); M. K. Schneider, pers. comm.	Rogers <i>et al.</i> (1998)	Schneider <i>et al.</i> (2004)	van Kessel <i>et al.</i> (2006)
POP	Tuscany, Italy	Forest (deciduous): <i>Populus alba</i> , <i>P. nigra</i> & <i>P. euramericana</i>	High	ECM + AM	Finzi <i>et al.</i> (2007)*	Finzi <i>et al.</i> (2007)	Hovenden (2003)	Finzi <i>et al.</i> (2007)	Hoosbeek & Scarascia-Mugnozza (2009)
Jasper FACE	San Mateo, CA, USA	California grassland dominated by annual nonnative grasses	Low (ambient) and high (7)	AM	Zhu <i>et al.</i> (2016)***	B. A. Hungate, pers. comm.	–	Zhu <i>et al.</i> (2016)	B. A. Hungate, pers. comm.
GI FACE	Giessen, Germany	Grassland, including legumes (< 1% initially)	Medium (4)	AM, N-fixing	Janze (2006)***	C. I. Kammann, pers. comm.	–	Andresen <i>et al.</i> (2017)	Lenhart <i>et al.</i> (2016)

The amount of N-fertilization applied is indicated in parentheses (units in g m<sup>-2</sup> yr<sup>-1</sup>).  
ECM, ectomycorrhiza; AM, arbuscular mycorrhiza.  
\*Fine-root growth; \*\*fine-root biomass; \*\*\*root growth; \*\*\*\*root biomass.

**Table 2** List of major gaps in the framework outlined here concerning the interactions between the carbon (C) and nutrient cycles under elevated CO<sub>2</sub>, and recommendations for experiments and methods to fill some of these gaps

Gap	Recommendations
Quantification of the C cost of N-acquisition under eCO <sub>2</sub>	Improve the quantification of the plant C investment (in response to eCO <sub>2</sub> ) in N-acquisition (C <sub>bg</sub> ) by systematically measuring fine-root production and estimating fine-root transfers to exudation and microbial symbionts. Mycorrhizal growth can be used as a proxy for C <sub>transfer</sub> to mycorrhizas Extend the quantification and report of measurements of plant total N-acquisition Quantification of N derived from N <sub>2</sub> -fixation eCO <sub>2</sub> experiments with ericoid mycorrhizal plants eCO <sub>2</sub> experiments with AM and ECM trees in the same site Quantification of the bottom range of N availability for ECM-mutualistic N-acquisition
Quantification of the C cost of P acquisition under eCO <sub>2</sub>	eCO <sub>2</sub> experiments in tropical forests are highly needed Study the role of AM and ECM fungi as above but under P-limitations
Quantification of soil C storage under eCO <sub>2</sub>	Quantification of changes in soil C pools Quantification of autotrophic and heterotrophic soil respiration Analysis of C stabilization pathways for litters with different C : N ratio
Methodological bias in eCO <sub>2</sub> experiments	Mesocosm experiments are excellent tools to quantify allocation to exudates and symbionts Field experiments should make use of natural and undisturbed soils Quantification of soil parameters pH, %N, %C, P% and other nutrients to assess nutrient availability Minimize the effect of expanding canopies, prioritising mature plants in steady-state Minimum of 5–10 yr of eCO <sub>2</sub> fumigation to allow soil dynamics start developing

C, carbon; N, nitrogen; C<sub>bg</sub>, belowground carbon; eCO<sub>2</sub>, elevated CO<sub>2</sub>; P, phosphorus; AM, arbuscular mycorrhiza; ECM, ectomycorrhiza.

that the decline of  $V_{\text{cmax}}$  under eCO<sub>2</sub> is generally less pronounced in plants that can acquire N more efficiently. This is consistent with meta-analyses that suggest that downregulation is related to low N supply, with a stronger  $V_{\text{cmax}}$  decline under low N (–22%, Ainsworth & Long, 2005) than under high N (–12%, Ainsworth & Long, 2005), and a stronger reduction in grasses (AM, –17%, Ainsworth & Long, 2005) than in trees (most of which were ECM, –6%, Ainsworth & Long, 2005) and legumes (N<sub>2</sub>-fixers, –12%, Ainsworth & Long, 2005) (Nowak *et al.*, 2004; Ainsworth & Long, 2005; Ainsworth & Rogers, 2007).

Despite downregulation of  $V_{\text{cmax}}$ , a stimulating effect of eCO<sub>2</sub> on leaf-level photosynthesis ( $A_{\text{sat}}$ ) in C<sub>3</sub> plants is observed (Fig. 2b), with an overall stimulation of 35%, similar to the 31% effect from the meta-analysis by Ainsworth & Long (2005). Following the same pattern as for  $V_{\text{cmax}}$ , the eCO<sub>2</sub> effect on  $A_{\text{sat}}$  is generally larger in ECM than in AM plants (Fig. 2b). For example, in the Duke FACE experiment, downregulation of  $V_{\text{cmax}}$  was not significant, and eCO<sub>2</sub> increased  $A_{\text{sat}}$  in pine (ECM) by an average of 67% despite moderately low soil fertility (Ellsworth *et al.*, 2012). At the AM-forest FACE experiment in Oak Ridge (ORNL), eCO<sub>2</sub>

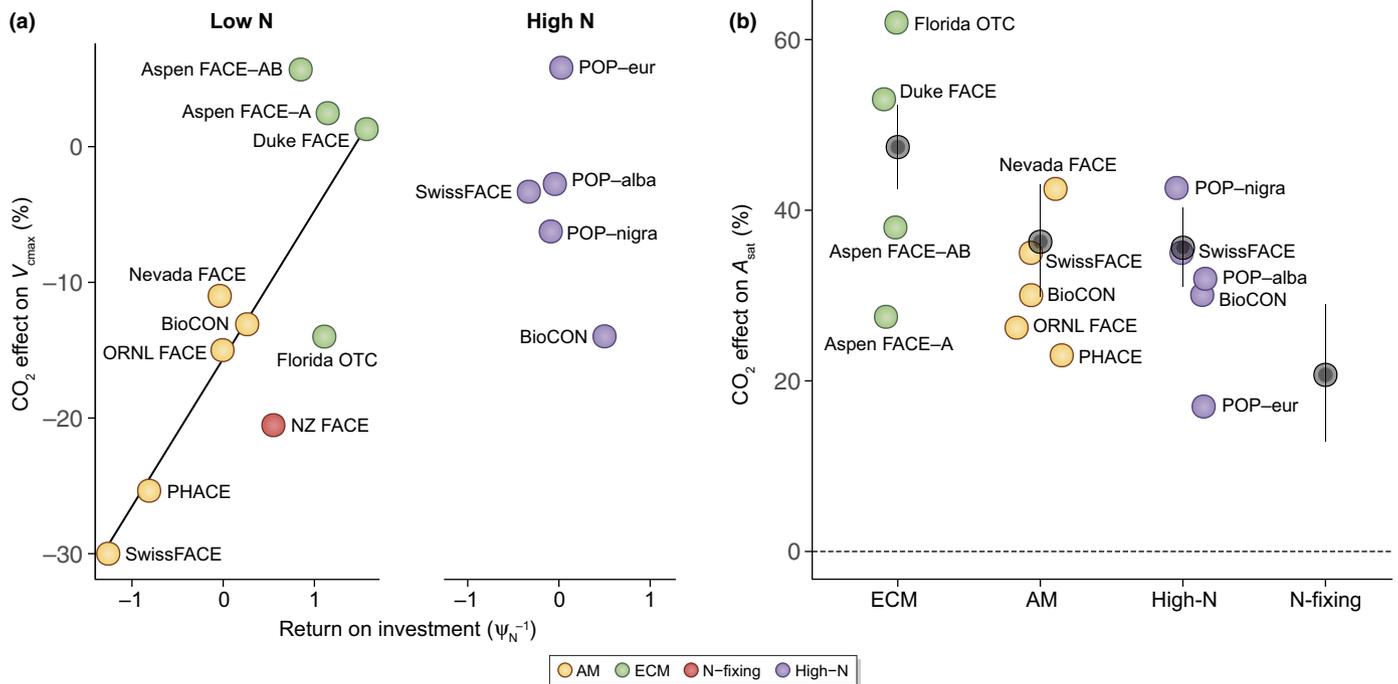
reduced foliar N (due to low N availability), and resulted in a 21% stimulation of  $A_{\text{sat}}$  (Warren *et al.*, 2015) (although with small sample sizes and only occasional measurements rendered this effect nonsignificant).

The effect of eCO<sub>2</sub> on  $A_{\text{sat}}$  in legumes (Ainsworth & Long, 2005; Wang *et al.*, 2012) and N-fertilized plants, however, was not higher than in AM nonfertilized plants (Fig. 2b), contrary to our expectation. For example, at the Swiss and BioCON FACE experiments, AM-associated grassland species growing under eCO<sub>2</sub> had eCO<sub>2</sub> effects on  $A_{\text{sat}}$  of similar magnitude for both low and high N treatments (Rogers *et al.*, 1998; Lee *et al.*, 2011). We speculate that  $A_{\text{sat}}$  did not increase with N-fertilization at BioCON because the downward shift in leaf %N with eCO<sub>2</sub> was larger in the N-fertilized than in the ambient treatments (–14% vs –9%) (Lee *et al.*, 2011), perhaps because N-fertilization was modest and plants under eCO<sub>2</sub> and high N increased growth (and thus demand) and remained both C and N limited (Reich & Hobbie, 2013). The lower effect on  $A_{\text{sat}}$  in legumes than in grasses (Fig. 2b, Ainsworth & Long, 2005) could have resulted from light limitation for legumes in dense canopy conditions or limitations from other soil resources beyond N; further research will be required to elucidate the mechanisms.

The ecosystem-level effect on photosynthesis (gross primary productivity, GPP) requires scaling the leaf-level response taking into account leaf area index (LAI). If eCO<sub>2</sub> decreases LAI, GPP might not increase despite a positive leaf-level effect. Negative effects of eCO<sub>2</sub> on LAI are not common. Rather, a meta-analysis showed that eCO<sub>2</sub> enhanced LAI by 21% in trees, with no significant effect in grasslands (Ainsworth & Long, 2005). Norby & Zak (2011) suggested that only trees with low LAI (< 3.5 m<sup>2</sup> leaf m<sup>-2</sup> ground) could increase LAI further in response to eCO<sub>2</sub>, although this effect might disappear when nutrient availability is low (Duursma *et al.*, 2016).

Another important factor to consider is the temporal acclimation of the photosynthetic response to eCO<sub>2</sub>. Stomatal density has been shown to decrease with historical CO<sub>2</sub> concentrations (Peñuelas & Matamala, 1990; Franks *et al.*, 2013), but a meta-analysis of eCO<sub>2</sub> experiments did not find a significantly negative effect for an average [CO<sub>2</sub>] of 571 ppm (Ainsworth & Rogers, 2007). Furthermore, a meta-analysis found that eCO<sub>2</sub> increased the number of leaves (Ainsworth & Long, 2005), an effect that might compensate for any potential reduction on stomatal density at the ecosystem level. The experiments shown in Fig. 2(b) did not generally find a decreasing  $A_{\text{sat}}$  response over time, but the long-term acclimation to eCO<sub>2</sub> requires further investigation (Franks *et al.*, 2013).

**Conclusions** Although the influence of N on the eCO<sub>2</sub> effect on  $V_{\text{cmax}}$  has been long known, it has commonly been linked to plant functional groups rather than to actual N<sub>acq</sub>-strategies (e.g. Ainsworth & Long, 2005). We have shown that the strength of the  $V_{\text{cmax}}$  decline under eCO<sub>2</sub> changes with the efficiency of plants in acquiring extra N ( $\psi_{\text{N}}^{-1}$ ), with the strongest decline under low N in AM systems where N-acquisition costs might increase most strongly. This affects leaf-level photosynthesis, with a smaller effect of eCO<sub>2</sub> in AM than in ECM plants. However, the role of N-fertilization and N<sub>2</sub>-fixation on the eCO<sub>2</sub> effect on  $A_{\text{sat}}$  needs



**Fig. 2** Effects of elevated CO<sub>2</sub> on leaf-level photosynthesis and its modulation by nitrogen (N)-acquisition efficiency. (a) Relationship between the effect of elevated CO<sub>2</sub> on maximum rate of carboxylation (V<sub>cmax</sub>) and the N return on investment (ψ<sub>N</sub><sup>-1</sup>, Eqn 1) under low (left panel) and high (right panel) N availability. (b) Summary of the effect of elevated CO<sub>2</sub> on light saturated photosynthesis (A<sub>sat</sub>). The black dots in (b) are mean effects ± CI from a meta-analysis by Ainsworth & Long (2005) for trees, grasses, N-fertilized plants and legumes. Sources of site-level data are given in Table 1.

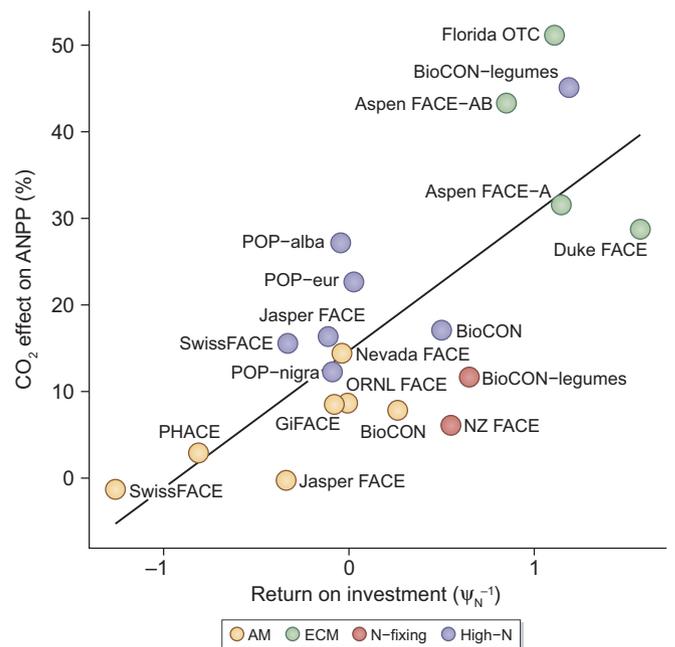
further investigation. In any case, despite partial downregulation of V<sub>cmax</sub>, N availability does not usually preclude an effect of eCO<sub>2</sub> on A<sub>sat</sub>. Hence, the lack of a significant eCO<sub>2</sub> effect on plant biomass in AM communities under low N (Terrer *et al.*, 2016) cannot be fully explained by downregulation of leaf-level photosynthesis; changes in C allocation are hence crucial for understanding these responses.

## 2. CO<sub>2</sub> effects on biomass production

**Background** When N availability is low, a positive growth enhancement effect of eCO<sub>2</sub> depends on a plant's ability to (1) increase its rate of N<sub>acq</sub> from the soil (Oren *et al.*, 2001; Finzi *et al.*, 2007), and/or (2) use the assimilated N more efficiently. The N-use efficiency (NUE) of growth can be defined as biomass produced per unit of N<sub>acq</sub>, and is reflected in the overall plant C : N stoichiometry and retranslocation efficiency of N upon leaf shedding. Zaehle *et al.* (2014) found that models' predicted enhancement of productivity under eCO<sub>2</sub> is commonly associated with an increase in NUE, in conflict with the conclusions from observational studies that found the effect driven by increased N<sub>acq</sub> (Finzi *et al.*, 2007; Feng *et al.*, 2015).

**Question** What are the mechanisms that drive the differences among sites in the magnitude of the CO<sub>2</sub> fertilization effect on biomass production?

**Observations** We found a significantly positive relationship between ψ<sub>N</sub><sup>-1</sup> and the eCO<sub>2</sub> effect on aboveground biomass productivity (ANPP) (Fig. 3, P < 0.001), resulting in the largest



**Fig. 3** Relationship between the effect of elevated CO<sub>2</sub> on aboveground biomass production (ANPP) and the nitrogen (N) return on investment (ψ<sub>N</sub><sup>-1</sup>, Eqn 1). Sources of site-level data are given in Table 1.

eCO<sub>2</sub>-driven ANPP enhancement in ECM > N-fertilized > N<sub>2</sub>-fixing > AM strategies. This suggests that N<sub>acq</sub>-efficiency is a primary driver of the eCO<sub>2</sub> effect on productivity. Note that although the change in biomass is part of the ψ<sub>N</sub><sup>-1</sup> calculation,

increased C investment belowground reduces  $\psi_N^{-1}$ ; thus, the positive relationship in Fig. 3 is not necessarily an artefact of using  $C_{\text{root}}$  in both (see also Feng *et al.*, 2015).

ECM plants consistently showed the largest increases in ANPP, and this was associated with the highest  $\psi_N^{-1}$  (Fig. 3). For example, FACE experiments with ECM-associated loblolly pine (Duke FACE) and aspen (Aspen FACE) trees showed a large (22–39%) and sustained effect on total biomass productivity despite moderate–low N availability (McCarthy *et al.*, 2010; Talhelm *et al.*, 2014). Furthermore, N-fertilization in the Duke FACE experiment did not increase productivity further (McCarthy *et al.*, 2010), consistent with the observation of increased aboveground growth in most AM trees in response to N-deposition, but not in ECM trees (Thomas *et al.*, 2010). Efficient  $N_{\text{acq}}$  stimulated trees at the Duke and Aspen FACE experiments to increasingly allocate more C to wood (with low [N]), enhancing NUE (Zaehle *et al.*, 2014) as a consequence of this biomass allocation shift.

Under high N availability, *Populus alba*, *P. euramericana* and *P. nigra* in the POP-FACE experiment in Italy, dominated by both ECM and AM fungi, showed a lower  $\psi_N^{-1}$  than other ECM species (Figs 1, 3) due to the lack of an  $e\text{CO}_2$ -driven  $N_{\text{acq}}$  enhancement;  $N_{\text{acq}}$  was already high in both  $\text{CO}_2$  treatment plots due to previous agricultural use and irrigation (Liberloo *et al.*, 2006). Instead, trees at POP-FACE sustained the  $e\text{CO}_2$  fertilization effect by increasing NUE (Finzi *et al.*, 2007), which was likely influenced by increased allocation to wood (low [N]).

AM systems showed a wider range of responses, presumably driven by their variable capacity to acquire N, either through N-fertilization or association with  $\text{N}_2$ -fixers. For example, AM-grassland *Lolium perenne* at SwissFACE showed a positive  $\text{CO}_2$ -induced aboveground biomass enhancement under high N, but not in low N plots (Schneider *et al.*, 2004), consistent with the lower cost of  $N_{\text{acq}}$  associated with N-fertilization (Fig. 3). *Medicago sativa* in this same experiment, however, showed a positive effect on ANPP and  $N_{\text{acq}}$  even under low N, consistent with its  $\text{N}_2$ -fixing capacity (Lüscher *et al.*, 2000) (data not included in Fig. 3 because no indication of  $C_{\text{bg}}$  was found). Likewise at BioCON, the  $e\text{CO}_2$ -enhancement in productivity was larger in  $\text{N}_2$ -fixing legumes than in nonlegume AM species (Fig. 3; see Mueller *et al.*, 2013).

AM trees at ORNL FACE apparently showed the opposite pattern to that of Aspen and Duke FACE ECM trees. As AM fungi may have little effect on plant  $N_{\text{acq}}$ , we speculate that these trees relied primarily on increased allocation to fine roots (with high [N]) to explore a larger proportion of the soil (Norby *et al.*, 2010; Iversen *et al.*, 2012), thus allocating less C to wood and decreasing NUE. Because this strategy caused only a slight, initial stimulation of total  $N_{\text{acq}}$ , and because NUE was already high from the start (Finzi *et al.*, 2007), the trees at the ORNL site could not meet the higher N demand imposed by higher  $\text{CO}_2$  supply – thus limiting the stand's capacity to increase ANPP (Fig. 3). Interestingly, the authors reported an increasing abundance of the  $\text{N}_2$ -fixer *Elaeagnus umbellata* by the end of the experiment, with evidence for  $\text{N}_2$ -fixation (Norby & Zak, 2011).

Although N return on investment is a primary factor determining the ANPP response to  $e\text{CO}_2$ , nutrients other than N, as well as water, are required for plant growth and may increase variability in

Fig. 3. For example, the ANPP response of AM species in the Nevada Desert FACE from 1998 to 2007 (Fig. 3) showed pronounced interannual variation because growth was limited by water availability, with stronger increases in ANPP under  $e\text{CO}_2$  in wet than dry years (Housman *et al.*, 2006; Smith *et al.*, 2014; see also Fatichi *et al.*, 2016). However, these periodic increases in productivity did not result in increased above- or belowground biomass at the end of the experiment (Newingham *et al.*, 2013). Opposite responses have been found for other grassland experiments in dry regions, with greater biomass responses to  $e\text{CO}_2$  in dry than wet years (Morgan *et al.*, 2004, 2011). Results from the TasFACE experiment, however, suggest that these contrasting results might have been driven by the effects of seasonal precipitation on the N cycle (Hovenden *et al.*, 2014), with spring rainfall causing negative effects on N availability, thus limiting the  $e\text{CO}_2$ -response.

The  $e\text{CO}_2$  effect on plant growth and its relationship with symbiotic type may also be prone to environmental factors other than N, including P availability, climatic conditions and disturbance. The role of symbiotic types in acquiring P under  $e\text{CO}_2$  is uncertain, as only few experiments have been conducted in low-P conditions. For example, ECM-dominated *Eucalyptus* trees in a water- and P-limited soil showed a positive leaf-level photosynthesis response to  $e\text{CO}_2$ , but no increase in aboveground growth (Ellsworth *et al.*, 2017) despite enhanced P and N availability (Hasegawa *et al.*, 2016; Ochoa-Hueso *et al.*, 2017). More research is needed to investigate whether AM plants may acquire P more efficiently and show a stronger  $e\text{CO}_2$  response than ECM plants under low-P. An indication of the influence of weather and disturbance may be provided by the scrub-oak OTC experiment in Florida, which showed the largest increase in ANPP (Fig. 2). There,  $N_{\text{acq}}$  in the ECM species may have been additionally stimulated by disturbance, initially by fire and later by a hurricane, both associated by a pulse of belowground resource availability (Hungate *et al.*, 2013).

Although ECM ecosystems typically showed a strong  $e\text{CO}_2$  response of ANPP and a high  $\psi_N^{-1}$ , this pattern may not persist under extremely N-scarce conditions. For example, a Norway spruce in Sweden on moraine soil and with a very thin soil organic layer did not show a significant  $e\text{CO}_2$ -effect on aboveground growth except when N-fertilized (Sigurdsson *et al.*, 2013). Following the mutualism–parasitism continuum hypothesis (Johnson *et al.*, 1997), and as suggested by some models for boreal N-poor forests (Franklin *et al.*, 2014; Baskaran *et al.*, 2017), there may be a point at the lower range of N availability below which ECM fungi do not transfer enough N to the plant to elicit and sustain higher rates of  $e\text{CO}_2$ -growth.

**Conclusion** Although several factors likely modulate growth responses to  $e\text{CO}_2$ , N return on investment is a primary control explaining the variety of responses observed in  $e\text{CO}_2$  experiments. Under low N availability, a sustained  $\text{CO}_2$  effect requires a mechanism by which plants can increase  $N_{\text{acq}}$ , via association with ECM fungi or  $\text{N}_2$ -fixers. AM plants generally do not increase  $N_{\text{acq}}$  under  $e\text{CO}_2$  (Fig. 1), so increases in productivity (Fig. 3), if any, are sustained through increased NUE. In soils with high N availability

where  $N_{\text{acq}}$  is already high, plants may sustain enhanced growth rates through increased NUE too. But changes in NUE also respond to shifts in competition strategies, with greater allocation to leaves (high [N]) during stand development, and greater allocation to wood (low [N]) after canopy closure, leading to increased NUE as trees age (Gholz *et al.*, 1985). Therefore, there is generally limited scope for enhanced NUE as a strategy to sustain increased demand under  $e\text{CO}_2$  in the long-term, which rather seems to be a consequence of changes in allocation to the different plant biomass pools. If enhanced root exploration or symbiotic uptake do not result in efficient  $N_{\text{acq}}$ , the  $\text{CO}_2$  effect disappears when available N in the rhizosphere does not meet plant N demand.

### 3. $e\text{CO}_2$ effects on priming and soil C content

**Background** In previous sections, we discussed the capacity of ECM and  $\text{N}_2$ -fixing plants to acquire additional N under  $e\text{CO}_2$ , which feeds back on plant productivity. Both N-acquisition through SOM decomposition (outputs) and productivity (inputs) affect soil C storage. Meta-analyses show that, indeed,  $e\text{CO}_2$  increases belowground C inputs through enhanced fine-root production by 44% (Dieleman *et al.*, 2010) and rhizodeposition by 37.9% (Nie *et al.*, 2013). Although greater inputs of root-derived C may increase soil C storage, much of the C that is released to the soil can also stimulate microbes to accelerate SOM decay and N release via ‘priming effects’ (Cheng *et al.*, 2014; Finzi *et al.*, 2015). Indeed, meta-analyses have shown that increases in soil C inputs under  $e\text{CO}_2$  are offset by losses (Hungate *et al.*, 2009; van Groenigen *et al.*, 2014). These studies, however, did not account for potential differential effects among symbiotic types. The quantification of priming effects has important implications on the magnitude of the terrestrial  $\text{CO}_2$  sink, but these effects are difficult to measure and model (Georgiou *et al.*, 2015).

**Question** How do changes in N availability under  $e\text{CO}_2$  affect soil C storage?

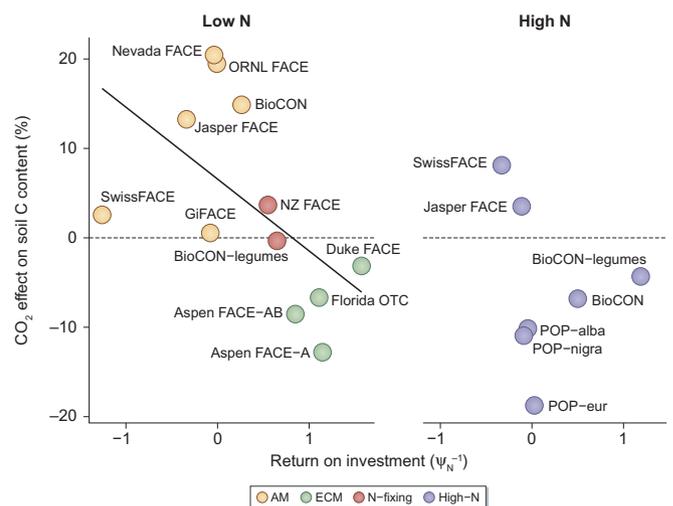
**Observations** We found a pattern of changes in soil C storage across N-acquisition strategies, with  $e\text{CO}_2$  generally stimulating soil C losses in ECM, and soil C storage in AM systems under low N availability. The marginally significant relationship between soil C storage and  $\psi_{\text{N}}^{-1}$  (Fig. 4;  $P=0.0503$ ), however, highlights that other factors beyond  $\psi_{\text{N}}^{-1}$  are at play.

Enhanced N-mining activity in ECM under  $e\text{CO}_2$  involves  $\text{CO}_2$  release through heterotrophic respiration, minimizing net accumulation of soil C with  $e\text{CO}_2$  (Fig. 4). For example, the large  $\text{CO}_2$  fertilization effect on ANPP in Duke FACE (ECM) (McCarthy *et al.*, 2010) was likely driven by increased allocation to ECM fungi (Drake *et al.*, 2011) and root exudation (Phillips *et al.*, 2011), which stimulated microbial activity and SOM decomposition (priming), increasing N availability to plants (see also Cheng *et al.*, 2014). This, however, was accompanied by increased soil respiration (Oishi *et al.*, 2014), reducing soil C content (Fig. 4). In the *Populus tremuloides* (ECM) community from the Aspen FACE experiment,  $e\text{CO}_2$  increased litter inputs, but also decreased soil C content (Fig. 4), suggesting strong stimulation in SOM

decomposition (Talhelm *et al.*, 2014). Likewise in the Florida OTC experiment,  $e\text{CO}_2$  increased plant productivity of scrub oaks (ECM) under low N availability (Fig. 3) through enhanced N-mineralization (Langley *et al.*, 2009), but the stimulation of SOM decomposition yielded no effect on C storage at the ecosystem level (Hungate *et al.*, 2013).

By contrast, several AM-ecosystems under low N have shown limited  $e\text{CO}_2$ -effects on N-mineralization and plant productivity, together with significant increases in soil C content. For example, the lack of a significant  $e\text{CO}_2$  effect on biomass after 10 yr in the Nevada Desert FACE (AM) (Newingham *et al.*, 2013) was accompanied by a significantly positive effect on soil C content (Evans *et al.*, 2014), with increased fungal activity (Jin & Evans, 2010), but not fine-root inputs (Ferguson & Nowak, 2011) – suggesting  $C_{\text{transfer}}$  as the main driver of this effect (Jin & Evans, 2010). The same pattern of smaller than average biomass responses but soil C accumulation was observed, for example, in an AM-forest ecosystem at ORNL (Iversen *et al.*, 2012), an AM-grassland ecosystem in Australia (Pendall *et al.*, 2011) and a shortgrass steppe in the US (Pendall & King, 2007), accompanied by a doubling in rhizodeposition (Pendall *et al.*, 2004).

Other AM ecosystems, however, do not follow this pattern. In the SwissFACE experiment, neither the AM grass *Lolium perenne* nor the  $\text{N}_2$ -fixer *Trifolium repens* showed an increase in soil C storage after 10 yr of  $e\text{CO}_2$  (van Kessel *et al.*, 2006), despite a positive effect on photosynthesis (Ainsworth *et al.*, 2003) and a lack of N-mineralization and ANPP response under low N availability (Schneider *et al.*, 2004).  $e\text{CO}_2$  did not increase soil C content at GiFACE either (Lenhart *et al.*, 2016), but the presence of legumes may have contributed to an increase in the allocation of  $C_{\text{transfer}}$  to  $\text{N}_2$ -fixation, rather than soil C stabilization, which would explain the strong increase in abundance of legume species from *c.* 1% at the beginning of the experiment to 10% in later years, together with an increasingly positive overall effect on plant biomass (Andresen *et al.*, 2017). A certain degree of  $\text{CO}_2$ -driven enhancement of



**Fig. 4** Relationship between the effect of elevated  $\text{CO}_2$  on soil carbon (C) content (%) and the nitrogen (N) return on investment ( $\psi_{\text{N}}^{-1}$ , Eqn 1). Sources of site-level data are given in Table 1.

N-mineralization in grasslands might also follow from increased soil water (e.g. Pendall *et al.*, 2003).

Although there have been reports of AM plants accelerating litter decomposition under eCO<sub>2</sub> (Cheng *et al.*, 2012), there is little evidence that AM plants can increase the decay of SOM under eCO<sub>2</sub>, particularly in low N soils. Thus, CO<sub>2</sub>-induced priming effects in AM systems are likely to be more short-lived relative to those occurring in ECM-dominated ecosystems (Sulman *et al.*, 2017).

An intermediate situation might be found for N<sub>2</sub>-fixers (Fig. 4), which can obtain (additional) N from the atmosphere. eCO<sub>2</sub> generally increases growth in legumes (Fig. 3; Ainsworth & Long, 2005), and thus likely also enhances soil C inputs, but whether SOM decomposition offsets additional inputs is uncertain. For example, eCO<sub>2</sub> increased C inputs through biomass and productivity (Fig. 3) in a grassland FACE experiment with N<sub>2</sub>-fixers in New Zealand. But eCO<sub>2</sub> also increased N-mineralization (Rütting *et al.*, 2010) and N availability (Newton *et al.*, 2010), yielding a modest increase in soil C storage (Ross *et al.*, 2013; Fig. 4). Various factors are probably at play to determine the balance between inputs and outputs, including species composition, litter quality, climate and nutrient and water availability.

The eCO<sub>2</sub> effects on soil C under high N availability do not appear to follow a clear pattern in this dataset (Fig. 4). Meta-analyses show that N-fertilization may increase the positive effects of eCO<sub>2</sub> on soil respiration further (Zhou *et al.*, 2016), but the effect of N has been shown to be negative in trees (Janssens *et al.*, 2010), and positive in grasslands and croplands (Zhou *et al.*, 2014). Whether this variability indicates different effects of N-fertilization among N-acquisition strategies or plant functional types remains to be disentangled.

These differences in the sign and magnitude of the effects of eCO<sub>2</sub> on N-mineralization, priming and soil C storage across symbiotic types might explain the large variability and non-significance of these effects found in several meta-analyses (de Graaff *et al.*, 2006; Hungate *et al.*, 2009; van Groenigen *et al.*, 2014). The reasons for these different patterns among symbiotic types, however, remain elusive. Recent empirical observations and model analyses suggest that labile litter (low C : N) is quickly assimilated by microbes, and this microbial necromass contributes to the formation of stable SOM in greater proportion than recalcitrant litter (high C : N), which decomposes slowly (Knicker, 2011; Castellano *et al.*, 2015; Cotrufo *et al.*, 2015). On the other hand, the stabilization of labile litter in SOM should protect plant material, constraining the eCO<sub>2</sub>-driven priming effect (Sulman *et al.*, 2014, 2017). Thus, recalcitrant litter should be more easily primed provided that it is 'unprotected'. A recent meta-analysis showed that, overall, AM trees produce litter that is significantly more labile than ECM trees (Lin *et al.*, 2017). Therefore, AM litter may be more easily stabilized by microbes, protecting new C from priming, whereas recalcitrant ECM litter may be more susceptible to priming, stimulating N-mineralization and N availability. This would explain the limited CO<sub>2</sub>-driven priming observed in some AM experiments, together with increased soil C content in AM-low N systems.

**Conclusions** Evidence from eCO<sub>2</sub> experiments suggests that mycorrhizal status plays a key role in determining the sign of the eCO<sub>2</sub> effect on soil C storage. Under low N availability, some AM- and ECM-dominated ecosystems show opposite patterns. In some AM-dominated ecosystems, eCO<sub>2</sub>-driven priming is more limited than in ECM-dominated ecosystems, which results in lower C losses in the former. By contrast, many ECM systems show strong priming effect and N-acquisition in response to eCO<sub>2</sub>. This mechanism, however, enhances SOM decomposition and may thus partially offset the increase in biomass storage and limit CO<sub>2</sub> sequestration at the ecosystem level. The result is a C-allocation shift in AM vs ECM ecosystems, which may result in enhanced soil-C gains in AM and enhanced biomass-C gains in ECM. It is, however, the final balance between the (changes in) C inputs and outputs that eventually determines whether soil C storage increases, decreases or remains unaltered.

#### IV. Discussion

We used a plant economics approach to quantify the C cost of N-acquisition and explore how this relates to the eCO<sub>2</sub>-response in different measured variables. Under eCO<sub>2</sub>, plants in nutrient-limited ecosystems may allocate part of the additional assimilation permitted by eCO<sub>2</sub> in ways that increase N<sub>acq</sub>: (1) allocation to fine roots (Iversen, 2010), (2) allocation to mycorrhizal fungi (Drake *et al.*, 2011) and (3) allocation to root exudates to increase soil priming (Phillips *et al.*, 2012). Therefore, N<sub>acq</sub> is a process that requires C resources that could otherwise be allocated to growth. Given the diversity of N<sub>acq</sub> strategies of investigated plants, soil conditions, and N-fertilization treatments, we expected different costs associated with N<sub>acq</sub> in plants exposed to eCO<sub>2</sub>. These costs might help explain discrepant responses in processes that require or are affected by N, such as leaf-level photosynthetic capacity, plant-level growth and soil C storage, and place different systems within a continuous spectrum of ecosystem responses to eCO<sub>2</sub>.

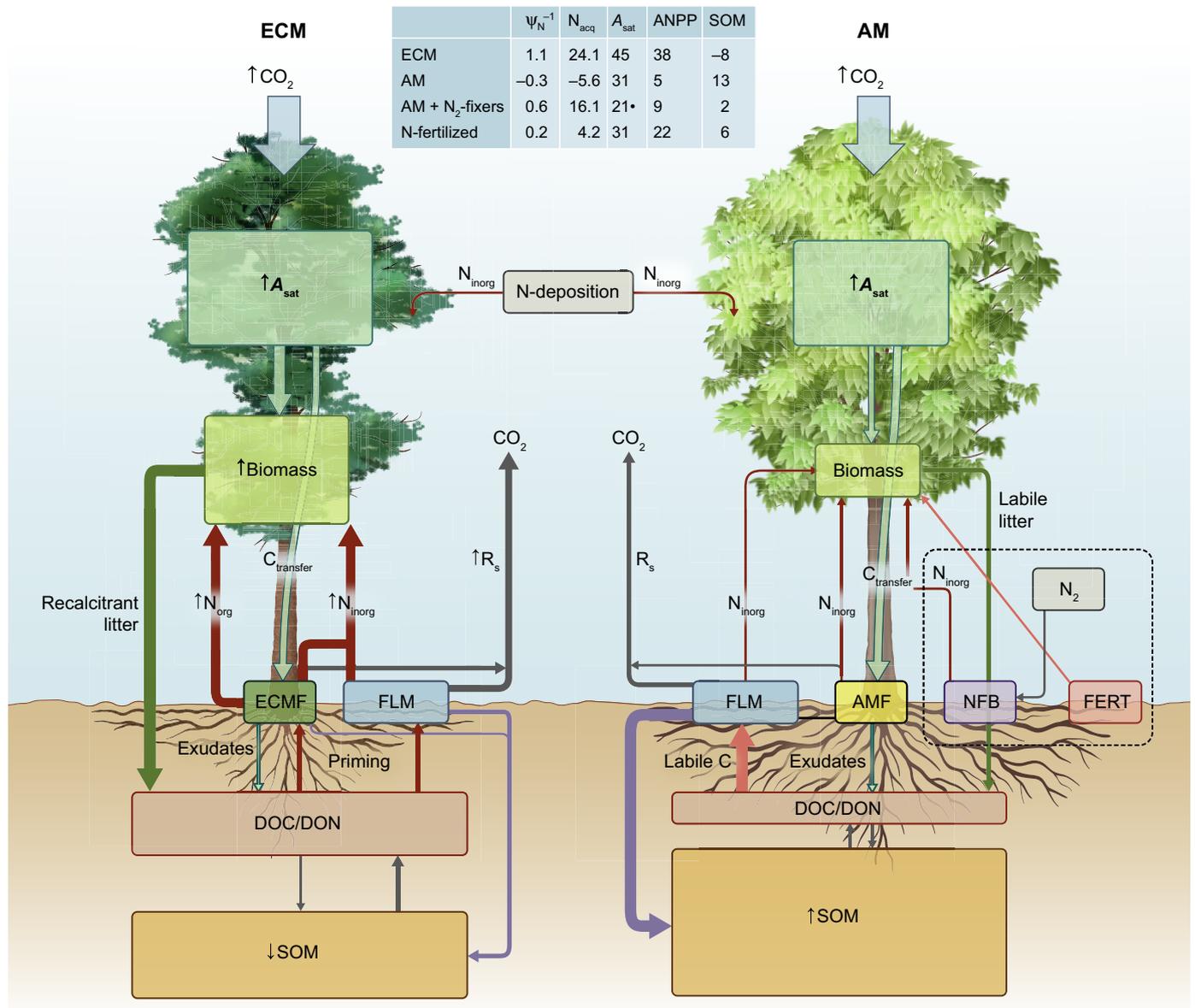
We show that the type of plant mycorrhizal association and N-fixing capability determines their position within this spectrum. ECM plants can acquire N more efficiently than AM plants under eCO<sub>2</sub>, although N<sub>acq</sub> by AM plants can be enhanced when grown with N<sub>2</sub>-fixing plants or when N-fertilized. This efficiency in N<sub>acq</sub> partly explains the magnitude of the eCO<sub>2</sub> effects on leaf-level photosynthesis, aboveground productivity and soil C storage. eCO<sub>2</sub> generally increases the amount of assimilates that plants produce per unit leaf area, even in plants with high costs associated with N<sub>acq</sub>. However, the eCO<sub>2</sub> stimulation of aboveground growth tends to be smaller when the cost of N<sub>acq</sub> is high, and vice versa. Contrarily to aboveground growth responses, the eCO<sub>2</sub> effect on soil C storage tends to decrease with decreasing costs.

Elevated CO<sub>2</sub> generally increases leaf-level photosynthesis regardless of N<sub>acq</sub>-costs, but the cost of N<sub>acq</sub> strongly affects the C allocation patterns. When costs are low (ECM in Fig. 5), plants can efficiently acquire N and sustain a growth response, which, on the other hand, can reduce SOM. We hypothesized that plants that

associate with ECM fungi acquire N more efficiently than those with AM for two reasons: (1) many ECM fungi have the enzymes necessary to mine organic N (Shah *et al.*, 2015), and (2) litter produced by ECM plants has a high C:N ratio (Lin *et al.*, 2017) that promotes slow decomposition (Cotrufo *et al.*, 2015) and facilitates priming (Sulman *et al.*, 2014, 2017). A similar effect can be achieved by AM plants when N availability is high or in the presence of N<sub>2</sub>-fixers (Fig. 5). The effects of eCO<sub>2</sub> on litter

production, root exudation and allocation to ECM, as well as potentially increasing litter C:N ratios, may amplify these effects.

When costs are high (AM in Fig. 5), a positive growth response to eCO<sub>2</sub> cannot be sustained as a consequence of insufficient N uptake. This is because (1) AM fungi do not produce the enzymes required to increase priming in response to eCO<sub>2</sub> (Hodge & Storer, 2015), and (2) litter produced by AM plants has a lower C:N ratio (Lin *et al.*, 2017), promoting



**Fig. 5** Conceptual framework, representing the effects of elevated CO<sub>2</sub> under low nitrogen (N)-acquisition costs in ectomycorrhizal (ECM) systems (left) and high costs in arbuscular mycorrhizal (AM) systems (right). The area within dashed lines represents plant N-acquisition through N<sub>2</sub>-fixation and external N-fertilization. N inputs through N<sub>2</sub>-fixation and N-fertilization are relevant in ECM systems as well, but not drawn here. Tabulated values represent the inverse of the carbon (C) cost of N-acquisition ( $\psi_N^{-1}$ , Eqn 1) and mean CO<sub>2</sub>-effects (%) on N-acquisition ( $N_{acq}$ ), leaf-level photosynthesis ( $A_{sat}$ ), aboveground biomass production (ANPP) and soil organic matter (SOM) for ECM, AM, AM with N<sub>2</sub>-fixing capacity and N-fertilized systems derived from Figs 2–4. The CO<sub>2</sub> effect on  $A_{sat}$  for AM + N<sub>2</sub>-fixers corresponds to the value reported in the meta-analysis by Ainsworth & Long (2005) for legumes.  $C_{transfer}$ , C exported to mycorrhizas, root exudation and symbiotic N<sub>2</sub>-fixation; ECMF, ectomycorrhizal fungi; AMF, arbuscular mycorrhizal fungi; FLM, free-living microbes; DOC, dissolved organic carbon; DON, dissolved organic nitrogen;  $R_s$ , soil respiration; N<sub>2</sub>, atmospheric N; NFB, N<sub>2</sub>-fixing bacteria; FERT, N-fertilization. Differences in box-size between AM and ECM systems represent differentiated changes in pool or flux size by elevated CO<sub>2</sub>, and arrows inside boxes represent the sign of the CO<sub>2</sub> effect.

greater stabilization of SOM (Sulman *et al.*, 2014, 2017). Thereby, AM plants have limited ability to prime the labile SOM that they live on. If soil C inputs into the soil are higher than C losses, however, eCO<sub>2</sub> may result in an increase in soil C storage. These allocation patterns of eCO<sub>2</sub>-driven extra C in AM and ECM plants result in a spectrum of ecosystem responses to eCO<sub>2</sub>, driven primarily by the cost of N<sub>acq</sub>.

It has been observed in several studies that an eCO<sub>2</sub>-driven increase in photosynthesis did not translate into an increase in plant biomass production (Bader *et al.*, 2013; Newingham *et al.*, 2013; Sigurdsson *et al.*, 2013; Ellsworth *et al.*, 2017). This has raised the question: 'Where does the carbon go?' Potential candidates are autotrophic respiration ( $R_a$ ) and  $C_{transfer}$ . The majority of experiments do not show a positive effect of eCO<sub>2</sub> on  $R_a$  (Smith, 2017), and there is no evidence that the  $R_a$ :GPP ratio consistently increases under eCO<sub>2</sub> (van Oijen *et al.*, 2010; Smith & Dukes, 2013). This implies that any increase in GPP without an increase in biomass production most likely increases the proportion of GPP allocated to  $C_{transfer}$  ( $GPP = BP + C_{transfer} + R_a$ ). Indeed, root exudation and mycorrhizal abundance have been observed to increase under eCO<sub>2</sub> (Treseder, 2004; Alberton *et al.*, 2005; Phillips *et al.*, 2011; Nie *et al.*, 2013), pointing at  $C_{transfer}$  as an important flux of the 'missing' C.

A large part of the framework outlined here (see Fig. 5) is not represented in the current generation of Dynamic Global Vegetation Models (Sitch *et al.*, 2015). Although these models may produce eCO<sub>2</sub>-induced increases in growth that are consistent in magnitude with observations (but see De Kauwe *et al.*, 2017), the importance of underlying mechanisms governing N constraints are inappropriately represented (Zaehle *et al.*, 2014). Common to most modelling approaches is to account for the limiting effects of N by reducing the ratio of NPP to GPP, hence increasing  $R_a$ , and to increase the C:N ratio of new tissue production to match the plant C and N budgets under *a priori* defined stoichiometric constraints (Zaehle *et al.*, 2014; Thomas *et al.*, 2015). Models do not generally consider  $C_{transfer}$  as a separate component of the plant C budget (Medlyn *et al.*, 2015), and 'spill-over'  $R_a$  has no effects on modelled N<sub>acq</sub>. Furthermore, little or no adjustment of above- vs belowground C allocation is simulated in response to shifts in the availability of above- and belowground resources (De Kauwe *et al.*, 2014; Zaehle *et al.*, 2014). Indeed, Zaehle *et al.* (2014) found that the eCO<sub>2</sub>-induced increase in simulated N<sub>acq</sub> was strongly underestimated in the Duke FACE experiment.

In order to better represent the effects of eCO<sub>2</sub> discussed here, a next generation of models for the coupled C and nutrient cycles in land ecosystems should be centred around nutrient cost considerations to simulate flexible C allocation in response to changing above- and belowground resource availabilities. Key mechanisms that determine these relationships are the capacity for BNF, mycorrhizal type-specific plant–soil interactions, rhizosphere  $C_{transfer}$  and its effects on SOM decomposition rates. In Table 2 we suggest some examples of types of observational data required to further explore some of the gaps detected here.

Our results suggest that the N-limitation on ecosystem responses to eCO<sub>2</sub> are most likely displayed in a continuum, in which the ability of the plants to acquire additional N in exchange for energy

(carbon) plays a key role. Many ecosystems with ECM-associated plants and N<sub>2</sub>-fixers have the capacity to enhance N<sub>acq</sub> under increasing demand, highlighting the importance of plant-mediated control on N availability, as opposed to the traditional view of a rigid N-limitation. Due to the limited temporal coverage of available experiments, the persistence of enhanced plant growth rates under eCO<sub>2</sub> remains uncertain. Our findings underline the importance of the cost of N-acquisition, an avenue that if explored by experimentalists and modellers working together may provide a way forward to better understand the interactions between the C and N cycles under rising CO<sub>2</sub>.

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## References

- Adair EC, Reich PB, Hobbie SE, Knops JMH. 2009. Interactive effects of time, CO<sub>2</sub>, N, and diversity on total belowground carbon allocation and ecosystem carbon storage in a grassland community. *Ecosystems* 12: 1037–1052.
- Ainsworth EA, Davey PA, Hymus GJ, Osborne CP, Rogers A, Blum H, Nösberger J, Long SP. 2003. Is stimulation of leaf photosynthesis by elevated carbon dioxide concentration maintained in the long term? A test with *Lolium perenne* grown for 10 years at two nitrogen fertilization levels under Free Air CO<sub>2</sub> Enrichment (FACE). *Plant, Cell & Environment* 26: 705–714.
- Ainsworth EA, Long SP. 2005. What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytologist* 165: 351–372.
- Ainsworth EA, Rogers A. 2007. The response of photosynthesis and stomatal conductance to rising [CO<sub>2</sub>]: mechanisms and environmental interactions. *Plant, Cell & Environment* 30: 258–270.
- Alberton O, Kuypers TW, Gorissen A. 2005. Taking myco-centrism seriously: mycorrhizal fungal and plant responses to elevated CO<sub>2</sub>. *New Phytologist* 167: 859–868.
- Allard V, Newton PCD, Lieffering M, Soussana JF, Carran RA, Matthew C. 2005. Increased quantity and quality of coarse soil organic matter fraction at elevated

- CO<sub>2</sub> in a grazed grassland are a consequence of enhanced root growth rate and turnover. *Plant and Soil* 276: 49–60.
- Andresen LC, Yuan N, Seibert R, Moser G, Kammann CI, Luterbacher J, Erbs M, Müller C. 2017. Biomass responses in a temperate European grassland through 17 years of elevated CO<sub>2</sub>. *Global Change Biology*. doi: 10.1111/gcb.13705.
- Aoki M, Fujii K, Kitayama K. 2012. Environmental control of root exudation of low-molecular weight organic acids in tropical rainforests. *Ecosystems* 15: 1194–1203.
- Bader MKF, Leuzinger S, Keel SG, Siegwolf RTW, Hagedorn F, Schleppi P, Körner C. 2013. Central European hardwood trees in a high-CO<sub>2</sub> future: synthesis of an 8-year forest canopy CO<sub>2</sub> enrichment project. *Journal of Ecology* 101: 1509–1519.
- Baskaran P, Hyvönen R, Berglund SL, Clemmensen KE, Ågren GI, Lindahl BD, Manzoni S. 2017. Modelling the influence of ectomycorrhizal decomposition on plant nutrition and soil carbon sequestration in boreal forest ecosystems. *New Phytologist* 213: 1452–1465.
- Bazot S, Ulff L, Blum H, Nguyen C, Robin C. 2006. Effects of elevated CO<sub>2</sub> concentration on rhizodeposition from *Lolium perenne* grown on soil exposed to 9 years of CO<sub>2</sub> enrichment. *Soil Biology and Biochemistry* 38: 729–736.
- Bazzaz F. 1990. The response of natural ecosystems to the rising global CO<sub>2</sub> levels. *Annual Review of Ecology and Systematics* 21: 167–196.
- Bennett JA, Maherali H, Reinhart KO, Lekberg Y, Hart MM, Klironomos J. 2017. Plant–soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* 355: 181–184.
- Blumenthal DM, Resco V, Morgan JA, Williams DG, LeCain DR, Hardy EM, Pendall E, Bladyka E. 2013. Invasive forb benefits from water savings by native plants and carbon fertilization under elevated CO<sub>2</sub> and warming. *New Phytologist* 200: 1156–1165.
- von Caemmerer S, Ghannoum O, Conroy JP, Clark H, Newton PC. 2001. Photosynthetic responses of temperate species to free air CO<sub>2</sub> enrichment (FACE) in a grazed New Zealand pasture. *Functional Plant Biology* 28: 439–450.
- Castellano MJ, Mueller KE, Oik DC, Sawyer JE, Six J. 2015. Integrating plant litter quality, soil organic matter stabilization, and the carbon saturation concept. *Global Change Biology* 21: 3200–3209.
- Chapin FS III, Matson PA, Vitousek P. 2011. *Principles of terrestrial ecosystem ecology*. New York, NY, USA: Springer Science & Business Media.
- Cheng L, Booker FL, Tu C, Burkey KO, Zhou L, Shew HD, Rufty TW, Hu S. 2012. Arbuscular mycorrhizal fungi increase organic carbon decomposition under elevated CO<sub>2</sub>. *Science* 337: 1084–1087.
- Cheng W, Parton WJ, Gonzalez Meler MA, Phillips R, Asao S, McNickle GG, Brzostek E, Jastrow JD. 2014. Synthesis and modeling perspectives of rhizosphere priming. *New Phytologist* 201: 31–44.
- Ciais P, Sabine C, Bala G, Bopp L, Brovkin V, Canadell J, Chhabra A, DeFries R, Galloway J, Heimann M *et al.* 2013. Carbon and other biogeochemical cycles. In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM, eds. *Climate Change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK & New York, NY, USA: Cambridge University Press, 465–570.
- Cotrufo MF, Soong JL, Horton AJ, Campbell EE, Haddix ML, Wall DH, Parton WJ. 2015. Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience* 8: 776–779.
- Crous KY, Reich PB, Hunter MD, Ellsworth DS. 2010. Maintenance of leaf N controls the photosynthetic CO<sub>2</sub> response of grassland species exposed to 9 years of free-air CO<sub>2</sub> enrichment. *Global Change Biology* 16: 2076–2088.
- Darbah JNT, Sharkey TD, Calfapietra C, Karnosky DF. 2010. Differential response of aspen and birch trees to heat stress under elevated carbon dioxide. *Environmental Pollution* 158: 1008–1014.
- De Kauwe MG, Medlyn BE, Walker AP, Zaehle S, Asao S, Guenet B, Harper AB, Hickler T, Jain AK, Luo Y *et al.* 2017. Challenging terrestrial biosphere models with data from the long-term multifactor Prairie Heating and CO<sub>2</sub> Enrichment experiment. *Global Change Biology* 348: 895.
- De Kauwe MG, Medlyn BE, Zaehle S, Walker AP, Dietze MC, Wang Y-P, Luo Y, Jain AK, El Masri B, Hickler T *et al.* 2014. Where does the carbon go? A model-data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO<sub>2</sub> enrichment sites. *New Phytologist* 203: 883–899.
- Dieleman WIJ, Luysaert S, Rey A, De Angelis P, Barton CVM, Broadmeadow MSJ, Broadmeadow SB, Chigwerewe KS, Crookshanks M, Dufrene E *et al.* 2010. Soil [N] modulates soil C cycling in CO<sub>2</sub>-fumigated tree stands: a meta-analysis. *Plant, Cell & Environment* 33: 2001–2011.
- Drake JE, Gallet Budynek A, Hofmockel KS, Bernhardt ES, Billings SA, Jackson RB, Johnsen KS, Lichter J, McCarthy HR, McCormack ML *et al.* 2011. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO<sub>2</sub>. *Ecology Letters* 14: 349–357.
- Duursma RA, Gimeno TE, Boer MM, Crous KY, Tjoelker MG, Ellsworth DS. 2016. Canopy leaf area of a mature evergreen Eucalyptus woodland does not respond to elevated atmospheric [CO<sub>2</sub>] but tracks water availability. *Global Change Biology* 22: 1666–1676.
- Ellsworth DS, Anderson IC, Crous KY, Cooke J, Drake JE, Gherlenda AN, Gimeno TE, Macdonald CA, Medlyn BE, Powell JR *et al.* 2017. Elevated CO<sub>2</sub> does not increase eucalypt forest productivity on a low-phosphorus soil. *Nature Climate Change* 320: 279–282.
- Ellsworth DS, Reich PB, Naumburg ES, Koch GW, Kubiske ME, Smith SD. 2004. Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO<sub>2</sub> across four free-air CO<sub>2</sub> enrichment experiments in forest, grassland and desert. *Global Change Biology* 10: 2121–2138.
- Ellsworth DS, Thomas R, Crous KY, Palmroth S, Ward E, Maier C, DeLucia E, Oren R. 2012. Elevated CO<sub>2</sub> affects photosynthetic responses in canopy pine and subcanopy deciduous trees over 10 years: a synthesis from Duke FACE. *Global Change Biology* 18: 223–242.
- Evans RD, Koyama A, Sonderegger DL, Charlet TN, Newingham BA, Fenstermaker LF, Harlow B, Jin VL, Ogle K, Smith SD *et al.* 2014. Greater ecosystem carbon in the Mojave Desert after ten years exposure to elevated CO<sub>2</sub>. *Nature Climate Change* 4: 394–397.
- Faticchi S, Leuzinger S, Paschalis A, Langley JA, Donnellan Barraclough A, Hovenden MJ. 2016. Partitioning direct and indirect effects reveals the response of water-limited ecosystems to elevated CO<sub>2</sub>. *Proceedings of the National Academy of Sciences, USA* 113: 12757–12762.
- Fay PA, Prober SM, Harpole WS, Knops JMH, Bakker JD, Borer ET, Lind EM, MacDougall AS, Seabloom EW, Wrapp PD *et al.* 2015. Grassland productivity limited by multiple nutrients. *Nature Plants* 1: 15080.
- Feng Z, Rütting T, Pleijel H, Wallin G, Reich PB, Kammann CI, Newton PCD, Kobayashi K, Luo Y, Uddling J. 2015. Constraints to nitrogen acquisition of terrestrial plants under elevated CO<sub>2</sub>. *Global Change Biology* 21: 3152–3168.
- Ferguson SD, Nowak RS. 2011. Transitory effects of elevated atmospheric CO<sub>2</sub> on fine root dynamics in an arid ecosystem do not increase long-term soil carbon input from fine root litter. *New Phytologist* 190: 953–967.
- Fernández-Martínez M, Vicca S, Janssens IA, Sardans J, Luysaert S, Campioli M, Chapin FS III, Ciais P, Malhi Y, Obersteiner M *et al.* 2014. Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change* 4: 471–476.
- Finzi AC, Abramoff RZ, Spiller KS, Brzostek ER, Darby BA, Kramer MA, Phillips RP. 2015. Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. *Global Change Biology* 21: 2082–2094.
- Finzi AC, Norby RJ, Calfapietra C, Gallet Budynek A, Gielen B, Holmes WE, Hoosbeek MR, Iversen CM, Jackson RB, Kubiske ME *et al.* 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO<sub>2</sub>. *Proceedings of the National Academy of Sciences, USA* 104: 14014–14019.
- Franklin O, Näsholm T, Höglberg P, Höglberg MN. 2014. Forests trapped in nitrogen limitation – an ecological market perspective on ectomycorrhizal symbiosis. *New Phytologist* 203: 657–666.
- Franks PJ, Adams MA, Amthor JS, Barbour MM, Berry JA, Ellsworth DS, Farquhar GD, Ghannoum O, Lloyd J, McDowell N *et al.* 2013. Sensitivity of plants to changing atmospheric CO<sub>2</sub> concentration: from the geological past to the next century. *New Phytologist* 197: 1077–1094.
- Georgiou K, Koven CD, Riley WJ, Torn MS. 2015. Toward improved model structures for analyzing priming: potential pitfalls of using bulk turnover time. *Global Change Biology* 21: 4298–4302.

- Gholz HL, Fisher RF, Prichett WL. 1985. Nutrient dynamics in slash pine plantation ecosystems. *Ecology* 66: 647–659.
- Gill AL, Finzi AC. 2016. Belowground carbon flux links biogeochemical cycles and resource-use efficiency at the global scale. *Ecology Letters* 19: 1419–1428.
- de Graaff M-A, van Groenigen KJ, Six J, Hungate B, van Kessel C. 2006. Interactions between plant growth and soil nutrient cycling under elevated CO<sub>2</sub>: a meta-analysis. *Global Change Biology* 12: 2077–2091.
- van Groenigen KJ, Qi X, Osenberg CW, Luo Y, Hungate BA. 2014. Faster decomposition under increased atmospheric CO<sub>2</sub> limits soil carbon storage. *Science* 344: 508–509.
- Hasegawa S, Macdonald CA, Power SA. 2016. Elevated carbon dioxide increases soil nitrogen and phosphorus availability in a phosphorus-limited Eucalyptus woodland. *Global Change Biology* 22: 1628–1643.
- Hobbie EA. 2006. Carbon allocation to ectomycorrhizal fungi correlates with belowground allocation in culture studies. *Ecology* 87: 563–569.
- Hobbie EA, Hobbie JE. 2008. Natural abundance of <sup>15</sup>N in nitrogen-limited forests and tundra can estimate nitrogen cycling through mycorrhizal fungi: a review. *Ecosystems* 11: 815–830.
- Hodge A, Storer K. 2015. Arbuscular mycorrhiza and nitrogen: implications for individual plants through to ecosystems. *Plant and Soil* 386: 1–19.
- Högberg MN, Briones MJI, Keel SG, Metcalfe DB, Campbell C, Midwood AJ, Thornton B, Hurry V, Linder S, Näsholm T *et al.* 2010. Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. *New Phytologist* 187: 485–493.
- Hoosbeek MR, Scarascia-Mugnozza GE. 2009. Increased litter build up and soil organic matter stabilization in a poplar plantation after 6 years of atmospheric CO<sub>2</sub> enrichment (FACE): final results of POP-EuroFACE compared to other forest FACE experiments. *Ecosystems* 12: 220–239.
- Housman DC, Killingbeck KT, Dave Evans R, Charlet TN, Smith SD. 2012. Foliar nutrient resorption in two Mojave Desert shrubs exposed to Free-Air CO<sub>2</sub> Enrichment (FACE). *Journal of Arid Environments* 78: 26–32.
- Housman DC, Naumburg E, Huxman TE, Charlet TN, Nowak RS, Smith SD. 2006. Increases in desert shrub productivity under elevated carbon dioxide vary with water availability. *Ecosystems* 9: 374–385.
- Hovenden MJ. 2003. Photosynthesis of coppicing poplar clones in a free-air CO<sub>2</sub> enrichment (FACE) experiment in a short-rotation forest. *Functional Plant Biology* 30: 391–400.
- Hovenden MJ, Newton PCD, Wills KE. 2014. Seasonal not annual rainfall determines grassland biomass response to carbon dioxide. *Nature* 511: 583–586.
- Huang W, Houlton BZ, Marklein AR, Liu J, Zhou G. 2015. Plant stoichiometric responses to elevated CO<sub>2</sub> vary with nitrogen and phosphorus inputs: evidence from a global-scale meta-analysis. *Scientific Reports* 5: 18 225.
- Hungate BA, Dijkstra P, Wu Z, Duval BD, Day FP, Johnson DW, Megonigal JP, Brown ALP, Garland JL. 2013. Cumulative response of ecosystem carbon and nitrogen stocks to chronic CO<sub>2</sub> exposure in a subtropical oak woodland. *New Phytologist* 200: 753–766.
- Hungate BA, Dukes JS, Shaw MR, Luo Y, Field CB. 2003. Nitrogen and climate change. *Science* 302: 1512–1513.
- Hungate BA, van Groenigen KJ, Six J, Jastrow JD, Luo Y, de Graaff M-A, van Kessel C, Osenberg CW. 2009. Assessing the effect of elevated carbon dioxide on soil carbon: a comparison of four meta-analyses. *Global Change Biology* 15: 2020–2034.
- Iversen CM. 2010. Digging deeper: fine-root responses to rising atmospheric CO<sub>2</sub> concentration in forested ecosystems. *New Phytologist* 186: 346–357.
- Iversen CM, Keller JK, Garten CT Jr, Norby RJ. 2012. Soil carbon and nitrogen cycling and storage throughout the soil profile in a sweetgum plantation after 11 years of CO<sub>2</sub>-enrichment. *Global Change Biology* 18: 1684–1697.
- Janssens IA, Dieleman W, Luysaert S, Subke JA, Reichstein M, Ceulemans R, Ciais P, Dolman AJ, Grace J, Matteucci G *et al.* 2010. Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience* 3: 315–322.
- Janze S. 2006. *Auswirkungen von erhöhtem CO<sub>2</sub> auf die Vegetation eines Grünlandes (Effects of increased CO<sub>2</sub> concentrations on the vegetation of a temperate grassland)*. Giessen, Germany: Giessener Elektronische Bibliothek, Universität Giessen.
- Jin VL, Evans RD. 2010. Microbial <sup>13</sup>C utilization patterns via stable isotope probing of phospholipid biomarkers in Mojave Desert soils exposed to ambient and elevated atmospheric CO<sub>2</sub>. *Global Change Biology* 16: 2334–2344.
- Johnson NC, Graham JH, Smith FA. 1997. Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *New Phytologist* 135: 575–585.
- Johnson NC, Wilson GWT, Wilson JA, Miller RM, Bowker MA. 2015. Mycorrhizal phenotypes and the Law of the Minimum. *New Phytologist* 205: 1473–1484.
- van Kessel C, Boots B, De Graaff M-A, Harris D, Blum H, Six J. 2006. Total soil C and N sequestration in a grassland following 10 years of free air CO<sub>2</sub> enrichment. *Global Change Biology* 12: 2187–2199.
- Knicker H. 2011. Soil organic N – an under-rated player for C sequestration in soils? *Soil Biology and Biochemistry* 43: 1118–1129.
- Körner C. 2006. Plant CO<sub>2</sub> responses: an issue of definition, time and resource supply. *New Phytologist* 172: 393–411.
- Langley JA, McKinley DC, Wolf AA, Hungate BA, Drake BG, Megonigal JP. 2009. Priming depletes soil carbon and releases nitrogen in a scrub-oak ecosystem exposed to elevated CO<sub>2</sub>. *Soil Biology and Biochemistry* 41: 54–60.
- LeBauer DS, Treseder KK. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* 89: 371–379.
- Lee TD, Barrott SH, Reich PB. 2011. Photosynthetic responses of 13 grassland species across 11 years of free-air CO<sub>2</sub> enrichment is modest, consistent and independent of N supply. *Global Change Biology* 17: 2893–2904.
- Lenhart K, Kammann C, Boeckx P, Six J, Müller C. 2016. Quantification of ecosystem C dynamics in a long-term FACE study on permanent grassland. *Rapid Communications in Mass Spectrometry* 30: 963–972.
- Li JH, Dijkstra P, Hinkle CR, Wheeler RM, Drake BG. 1999. Photosynthetic acclimation to elevated atmospheric CO<sub>2</sub> concentration in the Florida scrub-oak species *Quercus geminata* and *Quercus myrtifolia* growing in their native environment. *Tree Physiology* 19: 229–234.
- Liberloo M, Calfapietra C, Lukac M, Godbold D, Luo ZB, Polle A, Hoosbeek MR, Kull O, Marek M, Raines C *et al.* 2006. Woody biomass production during the second rotation of a bio-energy *Populus* plantation increases in a future high CO<sub>2</sub> world. *Global Change Biology* 12: 1094–1106.
- Lichter J, Billings SA, Ziegler SE, Gaindh D, Ryals R, Finzi AC, Jackson RB, Stemmler EA, Schlesinger WH. 2008. Soil carbon sequestration in a pine forest after 9 years of atmospheric CO<sub>2</sub> enrichment. *Global Change Biology* 14: 2910–2922.
- Lin G, McCormack ML, Ma C, Guo D. 2017. Similar below-ground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests. *New Phytologist* 213: 1440–1451.
- Lindahl BD, Tunlid A. 2015. Ectomycorrhizal fungi – potential organic matter decomposers, yet not saprotrophs. *New Phytologist* 205: 1443–1447.
- Litton CM, Raich JW, Ryan MG. 2007. Carbon allocation in forest ecosystems. *Global Change Biology* 13: 2089–2109.
- Lüscher A, Hartwig UA, Suter D, Nösberger J. 2000. Direct evidence that symbiotic N<sub>2</sub> fixation in fertile grassland is an important trait for a strong response of plants to elevated atmospheric CO<sub>2</sub>. *Global Change Biology* 6: 655–662.
- Malhi Y, Doughty CE, Goldsmith GR, Metcalfe DB, Girardin CAJ, Matthews TR, del Aguila-Pasquel J, Aragão LEOC, Araujo-Murakami A, Brando P *et al.* 2015. The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. *Global Change Biology* 21: 2283–2295.
- McCarthy HR, Oren R, Johnsen KH, Gallet Budyněk A, Pritchard SG, Cook CW, LaDeau SL, Jackson RB, Finzi AC. 2010. Re-assessment of plant carbon dynamics at the Duke free-air CO<sub>2</sub> enrichment site: interactions of atmospheric [CO<sub>2</sub>] with nitrogen and water availability over stand development. *New Phytologist* 185: 514–528.
- Medlyn BE, Zaehle S, De Kauwe MG, Walker AP, Dietze MC, Hanson PJ, Hickler T, Jain AK, Luo Y, Parton W *et al.* 2015. Using ecosystem experiments to improve vegetation models. *Nature Climate Change* 5: 528–534.
- Menge DNL, Hedin LO, Pacala SW. 2012. Nitrogen and phosphorus limitation over long-term ecosystem development in terrestrial ecosystems. *PLoS ONE* 7: e42045.
- Morgan JA, LeCain DR, Pendall E, Blumenthal DM, Kimball BA, Carrillo Y, Williams DG, Heisler-White J, Dijkstra FA, West M. 2011. C<sub>4</sub> grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* 476: 202–205.
- Morgan JA, Pataki DE, Körner C, Clark H, Del Grosso SJ, Grünzweig JM, Knapp AK, Mosier AR, Newton PCD, Niklaus PA *et al.* 2004. Water relations in

- grassland and desert ecosystems exposed to elevated atmospheric CO<sub>2</sub>. *Oecologia* 140: 11–25.
- Mueller KE, Blumenthal DM, Pendall E, Carrillo Y, Dijkstra FA, Williams DG, Follett RF, Morgan JA. 2016. Impacts of warming and elevated CO<sub>2</sub> on a semi-arid grassland are non-additive, shift with precipitation, and reverse over time. *Ecology Letters* 19: 956–966.
- Mueller KE, Hobbie SE, Tilman D, Reich PB. 2013. Effects of plant diversity, N fertilization, and elevated carbon dioxide on grassland soil N cycling in a long-term experiment. *Global Change Biology* 19: 1249–1261.
- Newingham BA, Vanier CH, Charlet TN, Ogle K, Smith SD, Nowak RS. 2013. No cumulative effect of 10 years of elevated [CO<sub>2</sub>] on perennial plant biomass components in the Mojave Desert. *Global Change Biology* 19: 2168–2181.
- Newton PCD, Lieffering M, Bowatte WMSD, Brock SC, Hunt CL, Theobald PW, Ross DJ. 2010. The rate of progression and stability of progressive nitrogen limitation at elevated atmospheric CO<sub>2</sub> in a grazed grassland over 11 years of Free Air CO<sub>2</sub> enrichment. *Plant and Soil* 336: 433–441.
- Newton PCD, Lieffering M, Parsons AJ, Brock SC, Theobald PW, Hunt CL, Luo D, Hovenden MJ. 2014. Selective grazing modifies previously anticipated responses of plant community composition to elevated CO<sub>2</sub> in a temperate grassland. *Global Change Biology* 20: 158–169.
- Nie M, Lu M, Bell J, Raut S, Pendall E. 2013. Altered root traits due to elevated CO<sub>2</sub>: a meta-analysis. *Global Ecology and Biogeography* 22: 1095–1105.
- Norby RJ, De Kauwe MG, Walker AP, Werner C, Zaehle S, Zak DR. 2017. Comment on 'Mycorrhizal association as a primary control of the CO<sub>2</sub> fertilization effect'. *Science* 355: 358–358.
- Norby RJ, DeLucia EH, Gielen B, Calfapietra C, Giardina CP, King JS, Ledford J, McCarthy HR, Moore DJP, Ceulemans R *et al.* 2005. Forest response to elevated CO<sub>2</sub> is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences, USA* 102: 18 052–18 056.
- Norby RJ, Warren JM, Iversen CM, Medlyn BE, McMurtrie RE. 2010. CO<sub>2</sub> enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences, USA* 107: 19 368–19 373.
- Norby RJ, Zak DR. 2011. Ecological lessons from free-air CO<sub>2</sub> enrichment (FACE) experiments. *Annual Review of Ecology and Systematics* 42: 181–203.
- Nouri E, Breuillin-Sessoms F, Feller U, Reinhardt D. 2014. Phosphorus and nitrogen regulate arbuscular mycorrhizal symbiosis in *Petunia hybrida*. *PLoS ONE* 9: e90841.
- Nowak RS, Ellsworth DS, Smith SD. 2004. Functional responses of plants to elevated atmospheric CO<sub>2</sub> – do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist* 162: 253–280.
- Ochoa-Hueso R, Hughes J, Delgado-Baquero M, Drake JE, Tjoelker MG, Piñero J, Power SA. 2017. Rhizosphere-driven increase in nitrogen and phosphorus availability under elevated atmospheric CO<sub>2</sub> in a mature Eucalyptus woodland. *Plant and Soil* 1: 1.
- van Oijen M, Schapendonk A, Höglind M. 2010. On the relative magnitudes of photosynthesis, respiration, growth and carbon storage in vegetation. *Annals of Botany* 105: 793–797.
- Oishi AC, Palmroth S, Johnsen KH, McCarthy HR, Oren R. 2014. Sustained effects of atmospheric [CO<sub>2</sub>] and nitrogen availability on forest soil CO<sub>2</sub> efflux. *Global Change Biology* 20: 1146–1160.
- Oren R, Ellsworth DS, Johnsen KH, Phillips N, Ewers BE, Maier C, Schäfer KV, McCarthy H, Hendrey G, McNulty SG *et al.* 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO<sub>2</sub>-enriched atmosphere. *Nature* 411: 469–472.
- Pendall E, Del Grosso S, King JY, LeCain DR, Milchunas DG, Morgan JA, Mosier AR, Ojima DS, Parton WA, Tans PP *et al.* 2003. Elevated atmospheric CO<sub>2</sub> effects and soil water feedbacks on soil respiration components in a Colorado grassland. *Global Biogeochemical Cycles* 17: 1046.
- Pendall E, King JY. 2007. Soil organic matter dynamics in grassland soils under elevated CO<sub>2</sub>: insights from long-term incubations and stable isotopes. *Soil Biology and Biochemistry* 39: 2628–2639.
- Pendall E, Mosier AR, Morgan JA. 2004. Rhizodeposition stimulated by elevated CO<sub>2</sub> in a semi-arid grassland. *New Phytologist* 162: 447–458.
- Pendall E, Osanai Y, Williams AL, Hovenden MJ. 2011. Soil carbon storage under simulated climate change is mediated by plant functional type. *Global Change Biology* 17: 505–514.
- Peñuelas J, Matamala R. 1990. Changes in N and S leaf content, stomatal density and specific leaf area of 14 plant species during the last three centuries of CO<sub>2</sub> increase. *Journal of Experimental Botany* 41: 1119–1124.
- Phillips RP, Brzostek E, Midgley MG. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytologist* 199: 41–51.
- Phillips RP, Finzi AC, Bernhardt ES. 2011. Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO<sub>2</sub> fumigation. *Ecology Letters* 14: 187–194.
- Phillips RP, Meier IC, Bernhardt ES, Grandy AS, Wickings K, Finzi AC. 2012. Roots and fungi accelerate carbon and nitrogen cycling in forests exposed to elevated CO<sub>2</sub>. *Ecology Letters* 15: 1042–1049.
- Pritchard SG. 2011. Soil organisms and global climate change. *Plant Pathology* 60: 82–99.
- Reich PB, Hobbie SE. 2013. Decade-long soil nitrogen constraint on the CO<sub>2</sub> fertilization of plant biomass. *Nature Climate Change* 3: 278–282.
- Reich PB, Hobbie SE, Lee T, Ellsworth DS, West JB, Tilman D, Knops JMH, Naeem S, Trost J. 2006a. Nitrogen limitation constrains sustainability of ecosystem response to CO<sub>2</sub>. *Nature* 440: 922–925.
- Reich PB, Hungate BA, Luo Y. 2006b. Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology, Evolution, and Systematics* 37: 611–636.
- Reynolds HL, Hartley AE, Vogelsang KM, Bever JD, Schultz PA. 2005. Arbuscular mycorrhizal fungi do not enhance nitrogen acquisition and growth of old-field perennials under low nitrogen supply in glasshouse culture. *New Phytologist* 167: 869–880.
- Rogers A, Fischer B, Bryant J, Frehner M, Blum H, Raines C, Long S. 1998. Acclimation of photosynthesis to elevated CO<sub>2</sub> under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-Air CO<sub>2</sub> enrichment. *Plant Physiology* 118: 683–689.
- Ross DJ, Newton PCD, Tate KR, Luo D. 2013. Impact of a low level of CO<sub>2</sub> enrichment on soil carbon and nitrogen pools and mineralization rates over ten years in a seasonally dry, grazed pasture. *Soil Biology and Biochemistry* 58: 265–274.
- Rütting T, Clough TJ, Müller C, Lieffering M, Newton PCD. 2010. Ten years of elevated atmospheric carbon dioxide alters soil nitrogen transformations in a sheep-grazed pasture. *Global Change Biology* 16: 2530–2542.
- Saxe H, Ellsworth DS, Heath J. 1998. Tree and forest functioning in an enriched CO<sub>2</sub> atmosphere. *New Phytologist* 139: 395–436.
- Schneider MK, Lüscher A, Richter M, Aeschlimann U, Hartwig UA, Blum H, Frossard E, Nösberger J. 2004. Ten years of free-air CO<sub>2</sub> enrichment altered the mobilization of N from soil in *Lolium perenne* L. swards. *Global Change Biology* 10: 1377–1388.
- Shah F, Nicolás C, Bentzer J, Ellström M, Smits M, Rineau F, Canbäck B, Floudas D, Carleer R, Lackner G *et al.* 2015. Ectomycorrhizal fungi decompose soil organic matter using oxidative mechanisms adapted from saprotrophic ancestors. *New Phytologist* 209: 1705–1719.
- Sigurdsson BD, Medhurst JL, Wallin G, Eggertsson O, Linder S. 2013. Growth of mature boreal Norway spruce was not affected by elevated [CO<sub>2</sub>] and/or air temperature unless nutrient availability was improved. *Tree Physiology* 33: 1192–1205.
- Sitch S, Friedlingstein P, Gruber N, Jones SD, Murray-Tortarolo G, Ahlström A, Doney SC, Graven H, Heinze C, Huntingford C *et al.* 2015. Recent trends and drivers of regional sources and sinks of carbon dioxide. *Biogeosciences* 12: 653–679.
- Smith NG. 2017. Plant respiration responses to elevated CO<sub>2</sub>: an overview from cellular processes to global impacts. In: Govindjee, Sharkey TD, Tcherkez G, Ghashghaie J, eds. *Contribution to Advances in Photosynthesis and Respiration special volume on plant respiration*. New York, NY, USA: Springer, in press.
- Smith NG, Dukes JS. 2013. Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO<sub>2</sub>. *Global Change Biology* 19: 45–63.
- Smith P, Davis SJ, Creutzig F, Fuss S, Minx J, Gabrielle B, Kato E, Jackson RB, Cowie A, Krieger E *et al.* 2016. Biophysical and economic limits to negative CO<sub>2</sub> emissions. *Nature Climate Change* 6: 42–50.
- Smith SD, Charlet TN, Zitzer SF, Abella SR, Vanier CH, Huxman TE. 2014. Long-term response of a Mojave Desert winter annual plant community to a

- whole-ecosystem atmospheric CO<sub>2</sub> manipulation (FACE). *Global Change Biology* 20: 879–892.
- Spreitzer RJ, Salvucci ME. 2002. RUBISCO: structure, regulatory interactions, and possibilities for a better enzyme. *Annual Review of Plant Biology* 53: 449–475.
- Sulman BN, Brzostek ER, Medici C, Shevliakova E, Menge DNL, Phillips RP. 2017. Feedbacks between plant N demand and rhizosphere priming depend on type of mycorrhizal association. *Ecology Letters* 102: 1043–1053.
- Sulman BN, Phillips RP, Oishi AC, Shevliakova E, Pacala SW. 2014. Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO<sub>2</sub>. *Nature Climate Change* 4: 1099–1102.
- Talhelm AF, Pregitzer KS, Pregitzer KS, Kubiske ME, Kubiske ME, Zak DR, Company CE, Burton AJ, Dickson RE, Hendrey GR *et al.* 2014. Elevated carbon dioxide and ozone alter productivity and ecosystem carbon content in northern temperate forests. *Global Change Biology* 20: 2492–2504.
- Terrer C, Vicca S, Hungate BA, Phillips RP, Prentice IC. 2016. Mycorrhizal association as a primary control of the CO<sub>2</sub> fertilization effect. *Science* 353: 72–74.
- Terrer C, Vicca S, Hungate BA, Phillips RP, Reich PB, Franklin O, Stocker BD, Fisher JB, Prentice IC. 2017. Response to Comment on 'Mycorrhizal association as a primary control of the CO<sub>2</sub> fertilization effect'. *Science* 355: 358.
- Teste FP, Kardol P, Turner BL, Wardle DA, Zemunik G, Renton M, Laliberté E. 2017. Plant–soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science* 355: 173–176.
- Thirkell TJ, Cameron DD, Hodge A. 2016. Resolving the 'nitrogen paradox' of arbuscular mycorrhizas: fertilization with organic matter brings considerable benefits for plant nutrition and growth. *Plant, Cell & Environment* 39: 1683–1690.
- Thomas RQ, Brookshire ENJ, Gerber S. 2015. Nitrogen limitation on land: how can it occur in Earth system models? *Global Change Biology* 21: 1777–1793.
- Thomas RQ, Canham CD, Weathers KC, Goodale CL. 2010. Increased tree carbon storage in response to nitrogen deposition in the US. *Nature Geoscience* 3: 13–17.
- Treseder KK. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO<sub>2</sub> in field studies. *New Phytologist* 164: 347–355.
- Vicca S, Luysaert S, Peñuelas J, Campioli M, Chapin FS III, Ciais P, Heinemeyer A, Högberg P, Kutsch WL, Law BE *et al.* 2012. Fertile forests produce biomass more efficiently. *Ecology Letters* 15: 520–526.
- Vitousek P, Howarth R. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* 13: 87–115.
- Wang D, Heckathorn SA, Wang X, Philpott SM. 2012. A meta-analysis of plant physiological and growth responses to temperature and elevated CO<sub>2</sub>. *Oecologia* 169: 1–13.
- Wang H, Prentice IC, Davis TW, Keenan T, Wright IJ, Peng C. 2017. Photosynthetic responses to altitude: an explanation based on optimality principles. *New Phytologist* 213: 976–982.
- Warren JM, Jensen AM, Medlyn BE, Norby RJ, Tissue DT. 2015. Carbon dioxide stimulation of photosynthesis in *Liquidambar styraciflua* is not sustained during a 12-year field experiment. *AoB Plants* 7: plu074.
- Wurzburger N, Brookshire ENJ, McCormack ML, Lankau RA. 2017. Mycorrhizal fungi as drivers and modulators of terrestrial ecosystem processes. *New Phytologist* 213: 996–999.
- Zaehle S, Medlyn BE, De Kauwe MG, Walker AP, Dietze MC, Hickler T, Luo Y, Wang Y-P, El Masri B, Thornton P *et al.* 2014. Evaluation of 11 terrestrial carbon–nitrogen cycle models against observations from two temperate Free-Air CO<sub>2</sub> Enrichment studies. *New Phytologist* 202: 803–822.
- Zhou L, Zhou X, Shao J, Nie Y, He Y, Jiang L, Wu Z, Bai SH. 2016. Interactive effects of global change factors on soil respiration and its components: a meta-analysis. *Global Change Biology* 22: 3157–3169.
- Zhou L, Zhou X, Zhang B, Lu M, Luo Y, Liu L, Li B. 2014. Different responses of soil respiration and its components to nitrogen addition among biomes: a meta-analysis. *Global Change Biology* 20: 2332–2343.
- Zhu K, Chiariello NR, Tobeck T, Fukami T, Field CB. 2016. Nonlinear, interacting responses to climate limit grassland production under global change. *Proceedings of the National Academy of Sciences, USA* 113: 10589–10594.



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