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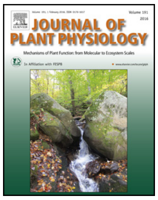

Review

Nutrient constraints on terrestrial carbon fixation: The role of nitrogen

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ABSTRACT

Carbon dioxide (CO_2) concentrations in the earth's atmosphere are projected to rise from current levels near 400 ppm to over 700 ppm by the end of the 21st century. Projections over this time frame must take into account the increases in total net primary production (NPP) expected from terrestrial plants, which result from elevated CO_2 (eCO_2) and have the potential to mitigate the impact of anthropogenic CO_2 emissions. However, a growing body of evidence indicates that limitations in soil nutrients, particularly nitrogen (N), the soil nutrient most limiting to plant growth, may greatly constrain future carbon fixation. Here, we review recent studies about the relationships between soil N supply, plant N nutrition, and carbon fixation in higher plants under eCO_2, highlighting key discoveries made in the field, particularly from free-air CO_2 enrichment (FACE) technology, and relate these findings to physiological and ecological mechanisms.

Contents

1. Introduction

Atmospheric CO_2 concentrations (C_a) have increased by nearly 50% since pre-industrial times, to values currently approaching 400 ppm. Socio-biogeochemical models have predicted that C_a may reach 550 ppm by the middle of the century, and may well surpass 700 ppm by 2100 (Pachauri et al., 2014; Le Quéré et al., 2015). Such levels have not been known to occur on Earth since the early Miocene, some 24 million years ago (Pagani et al., 2009). Closely associated with these forecasts are predictions of disastrous changes in the Earth's climate (*e.g.* Yin, 2013; Cai et al., 2014),

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Abbreviations: A', daily integrated CO_2 uptake; A_{net}, net photosynthesis; A_{sat}, light-saturated CO_2 uptake; BNF, biological N_2 fixation; C_a, atmospheric CO_2 concentrations; CUEe, ecosystem carbon-use efficiency; eCO_2, elevated atmospheric CO_2; FACE, free-air CO_2 enrichment; GPP, gross primary production; g_s, stomatal conductance; MSX, methionine sulfoximine; NEP, net ecosystem production; N_m, concentration of N in plant dry mass; NPP, net primary production; Nr, reactive nitrogen; OTC, open-top chambers; PEPC, phospho*enol*pyruvate carboxylase; PNL, progressive nitrogen limitation; PNUE, photosynthetic N-use efficiency; SLA, specific leaf area; SOM, soil organic matter.

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even if all anthropogenic emissions were to halt today (Frölicher et al., 2014). Accordingly, much recent attention has been focused on the consumption and storage of CO_2 by terrestrial biomes, where as much as a third of all anthropogenic CO_2 emissions (currently ~10 Pg C yr^{-1}) is captured (Reay et al., 2008; Andres et al., 2012; Le Quéré et al., 2015).

It is well established that elevated atmospheric CO_2 (eCO_2) can stimulate net primary production (NPP) in photosynthetic organisms (Harley et al., 1992; Norby et al., 2005; McCarthy et al., 2010; Franks et al., 2013; see also Fig. 1). Indeed, crop cultivation in greenhouses routinely involves the enrichment of greenhouse air with CO_2, which is applied at levels as high as 1000 ppm, and results in growth and yield increases of as much as 30% (Becker and Kläring, 2016). In field experiments, eCO_2 (at ~550 ppm) has been shown to generally increase carbon gain and biomass increases in a wide range of C_3 plant systems, by amounts that vary from study to study. For instance, in a meta-analysis of FACE (Free-Air CO_2 Enrichment) studies, Leakey et al. (2009) found biomass increases of about 19–46%, compared to growth under present-day CO_2 conditions. Lee et al. (2011), examining 13 grassland species, found a more modest increase of about 10%. By contrast, the photosynthetic apparatus of C_4 plants is already saturated under current CO_2 concentrations, and therefore elevated CO_2 does not have a great impact on the growth of this functional group (Lee et al., 2011; Kant et al., 2012), which includes important agricultural crops such as corn and sorghum. In addition to increases in plant biomass due to a 'CO_2 fertilization effect', eCO_2 has been linked to stimulated photosynthetic output, reduced stomatal conductance and transpiration, and increases in the efficiencies of water, light, and nitrogen (N) use (Curtis and Wang, 1998; Drake et al., 1997; Leakey et al., 2009).

However, constraints imposed on eCO_2-enhanced carbon fixation and plant productivity due to soil nutrient limitations, particularly that of N, have also long been observed (Evans, 1989; Vitousek and Howarth, 1991; Drake et al., 1997; LeBauer and Treseder, 2008). Higher rates of growth lead to increased demand for nutrients, especially N, which represents the most frequently growth-limiting soil nutrient in terrestrial ecosystems (*cf.* Sardans and Peñuelas, 2015). Moreover, although initially elevated rates of NPP under eCO_2 become downregulated in the longer term, involving the process of photosynthetic acclimation (Sage, 1994; Stitt and Krapp, 1999; see also Section 3; Fig. 2), they decrease to a much lesser extent when N supply is abundant (Stitt and Krapp, 1999; Fig. 1). Despite the importance of nutrient limitations on carbon fixation, they are frequently ignored in biogeochemical models, including in the case of N (Vitousek and Howarth, 1991; Hungate et al., 2003; Luo et al., 2004; Körner, 2006). For instance, a recent analysis of the Coupled Model Intercomparison Project (CMIP5), one of the most highly regarded multi-model datasets available for predicting future changes in atmospheric CO_2, concluded that CMIP5 has underestimated the atmospheric CO_2 burden projected for the year 2100 by 26–61 ppm, due to a neglect of terrestrial N limitation (Zaehle et al., 2015). Models that, by contrast, incorporate C-N interactions, indicate that the potential for terrestrial C capture could be reduced by 50% or more due to limitations in the nitrogen cycle (Sokolov et al., 2008; Thornton et al., 2009; Arneth et al., 2010; Zaehle et al., 2010). In fact, some models even suggest the terrestrial biosphere could turn into a net carbon source by the end of the century (Wieder et al., 2015; Mystakidis et al., 2016), given the numerous factors linked to climate change, including changing precipitation, temperature, ozone levels, microbial interactions, disease risk, and nutrient cycles (Melillo et al., 1993; Cramer et al., 2001; Harvell et al., 2002; Ciais et al., 2005; Hyvönen et al., 2007; Sitch et al., 2007, 2013; Reich et al., 2014).

In this review, we discuss the patterns of eCO_2 on terrestrial plant and ecosystem production, in the context of N limitation, and examine mechanisms occurring at various levels of organization that may explain some of the most pronounced effects. These include N- and eCO_2-dependent changes in growth and yield in grassland, forest, and agricultural systems, N uptake, assimilation, and accumulation under eCO_2, and progressive nitrogen limitation (PNL) and related soil processes.

2. N constraints on plant-growth responses to eCO_2

At the ecosystem level, eCO_2-associated increases in net ecosystem production (NEP, the difference between gross primary production (GPP) and ecosystem respiration, *i.e.* the sum of heterotrophic and autotrophic respiration) have been observed in many reports. The strongest effects are often seen at higher latitudes (>40°N; Forkel et al., 2016), which is largely attributable to high-latitude warming trends in addition to eCO_2, manifesting as a "greening" trend of increased vegetation cover at such latitudes (Myneni et al., 1997; Lucht et al., 2002). N constraints on soil-ecosystem production are also more prevalent at high latitudes (temperate, boreal, and tundra regions), where biological N_2 fixation (BNF) is naturally low, although the deposition of anthropogenically-derived reactive nitrogen (Nr) can be quite high in these regions (Vitousek and Howarth, 1991; Reich and Oleksyn, 2004; LeBauer and Treseder, 2008; Zaehle, 2013). Coincidentally, the majority of CO_2—N studies at the ecosystem level have been conducted in grassland and forest biomes of higher latitudes, in addition to agricultural systems (Table 1).

In the following discussion, we focus on eCO_2-induced stimulations of NPP in forest, grassland, and agricultural systems (Norby et al., 2005; Luo et al., 2006; Matthews, 2007; Leakey et al., 2009; Franks et al., 2013; *cf.* Dukes et al., 2005; Inauen et al., 2012), as well as the constraints imposed by N limitations (Reich et al., 2006a; Norby et al., 2010; Reich and Hobbie, 2013; Feng et al., 2015). We also look at soil respiration, which has been shown to consistently increase under eCO_2, and which varies widely in response to varied N levels from one ecosystem to another (Janssens et al., 2010; Adair et al., 2011; Maaroufi et al., 2015; Yue et al., 2016). Because soil respiration releases roughly 10 times more CO_2 into the atmosphere than all combined anthropogenic sources (Schlesinger and Andrews, 2000; Raich et al., 2002), even a modest deviation in soil respiration has the potential to greatly exacerbate or mitigate CO_2 emissions.

2.1. Methodological note

We begin with a brief consideration of methods used to study the effects of eCO_2 on plant carbon fixation. Early investigations relied on growth and physiological analyses conducted using growth chambers, greenhouses, or open-top chambers (OTCs; for review, see Leadley and Drake, 1993; Drake et al., 1997; Curtis and Wang, 1998; Medlyn et al., 1999; Wand et al., 1999; Ainsworth et al., 2002; Jablonski et al., 2002). It has been argued that major limitations arise with such techniques, including size constraints of the chambers, limited growing periods, and difficulties in extrapolating small-scale findings to larger, "real-world", environments (*e.g.* Ainsworth et al., 2002; Long et al., 2004; Ainsworth and Long, 2005; Bunce, 2012). More recent developments in FACE technology, by contrast, have allowed plants to grow under more natural, fully open-air conditions (Ainsworth and Long, 2005; Leakey et al., 2009). FACE imposes fewer restrictions on plant growth, notably root growth, and is especially well suited to the study of large, long-lived plants, such as trees (Arp, 1991; Curtis and Wang, 1998; McLeod and Long, 1999). However, others have argued that the benefits of FACE may be overstated, and that, as long as strict and realistic consideration of growth conditions are monitored (especially with respect to soil nutrients), techniques using OTCs may

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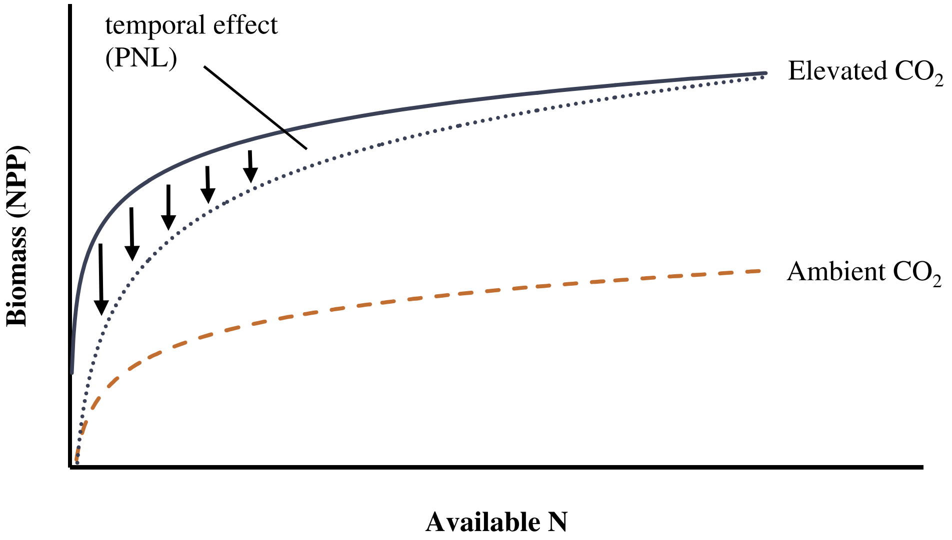

Fig. 1. The CO_2 fertilization effect in relation to N nutrition. Plant biomass increases with available N to a greater extent in plants grown on elevated CO_2 (solid line) relative to ambient CO_2 (dashed line). However, with long-term exposure to elevated CO_2, progressive N limitation (PNL) down-regulates biomass gains, which is more pronounced under low-N conditions (dotted line). Redrawn from Wong, 1979; and modified based on Bowler and Press, 1996; Reich et al., 2006b (*cf.* Hofmockel et al., 2011; Feng et al., 2015).

be appropriate (Körner, 2006; and references therein). Moreover, FACE technology can be costly (Messerli et al., 2015) and conditions may be difficult to control (such as with N addition). In addition, they often entail significant variations in CO_2 levels in addition to the frequent practice of not providing eCO_2 at night, both of which can have pronounced effects on plant growth (Bunce, 2012, 2014). Nevertheless, because of their scale, duration, and overall fidelity to natural conditions, FACE-type systems have become a preferred means of providing information inputs for models simulating and projecting the effects of eCO_2 on plant growth. Thus, the majority of studies discussed below are ones that have utilized FACE technology (see also Table 1). It may be noted that, as yet, FACE studies are relatively uncommon, in particular those which measure interactions between C and N over decennial timescales (Feng et al., 2015). In addition, FACE studies tend to be geographically biased towards temperate ecosystems of North America and Europe, while much work remains to be done in boreal and tropical regions, which have great significance for C sink and storage activity (Leakey et al., 2012; Jones et al., 2014; Norby et al., 2016), and where climate warming is most pronounced (see above).

The choice among methodologies is not trivial; overall, FACE studies have indicated a substantially lower (in many cases by 50% or more) eCO_2 fertilization effect for a wide variety of crops and herbaceous plants (although, in the case of trees, FACE studies often show a larger effect), with disquieting implications for climate-change mitigation and the future of humanity's food supply (Ainsworth and Long, 2005; Long et al., 2006; Leakey et al., 2009; Weigel and Manderscheid, 2012; *cf.* Tubiello et al., 2007). It is interesting to note, however, in the context of the present article, that nitrogen status may be more important for their growth responses to eCO_2 than the experimental system used (Yin, 2013; Pleijel and Högy, 2015).

2.2. Grasslands

Multiple studies have indicated that C_3 grasses respond positively to eCO_2 in terms of biomass gain, and that this response is frequently N-limited. For instance, in a study of 13 grassland species over 11 years at the BioCON (Biodiversity, CO_2, and Nitrogen) FACE site (Table 1), it was shown that net photosynthesis (A_{net}) was stimulated by about 10% with eCO_2 (Lee et al., 2011). Superimposed on this was a strong and persistent N limitation on eCO_2-induced biomass gain, as indicated by a marked reduction in growth stimulation in plots lacking N fertilization (Reich et al., 2006a; Reich and Hobbie, 2013; Figs. 1 and 3). Intriguingly, however, no significant $CO_2 \times N$ interactions were observed in the majority of the response variables tested: A_{net}, specific leaf area (SLA), stomatal conductance (g_s), instantaneous water-use efficiency, or photosynthetic N-use efficiency (PNUE) (Lee et al., 2011). In another seminal long-term grassland study, the SwissFACE experiment investigated $CO_2 \times N$ effects in a perennial ryegrass (*Lolium perenne*) sward, with similar results. In this setting, Schneider et al. (2004) observed an increased harvestable biomass (+32%) under eCO_2 but only at high N supply ($56\,g\,N\,m^{-2}\,yr^{-1}$ *vs.* $14\,g\,N\,m^{-2}\,yr^{-1}$). An earlier study in the SwissFACE plot showed no significant $CO_2 \times N$ interaction in daily integrated CO_2 uptake (A'), light-saturated CO_2 uptake (A_{sat}), or g_s (Ainsworth et al., 2003); however, low-N plants exhibited twice the extent of photosynthetic acclimation (down-regulation) over the course of long-term eCO_2 application (see Section 3.1; Figs. 2 and 3). The question of whether leaf-level $CO_2 \times N$ interactions (especially those pertaining to photosynthetic activity and capacity) scale to overall plant production (NPP), and further to ecosystem carbon capture (NEP), remains a subject of considerable debate (Reich et al., 2006b; Fernández-Martínez et al., 2014; Körner, 2015). As pointed out by Reich et al. (2006b), C-N interactions may manifest less prominently at the small (leaf) scale than at the large (ecosystem-wide) scale, due to the added effects of growth and decay dynamics of root systems and tree canopies. Körner (2015) has argued that the widespread assumption that photosynthesis is the rate-controlling factor of plant growth, may be mistaken; instead, it was proposed that sink capacity (tissue growth) controls C fixation based on demand.

Biomass gains with eCO_2 are not ubiquitous in grasslands, however. Shaw et al. (2002) showed that plants indeed responded to eCO_2 in terms of increased NPP in a California grassland, but only when eCO_2 was used as a single-factor treatment. Multi-factor combinations of eCO_2 and increased temperature, precipitation, and N deposition, on the other hand, actually decreased NPP, relative to ambient CO_2 conditions. The authors hypothesized that other soil nutrient limitations may be at play, perhaps due to gradual immobilization of nutrients by soil microorganisms, or decreased root allocation, which would limit the capacity of plants

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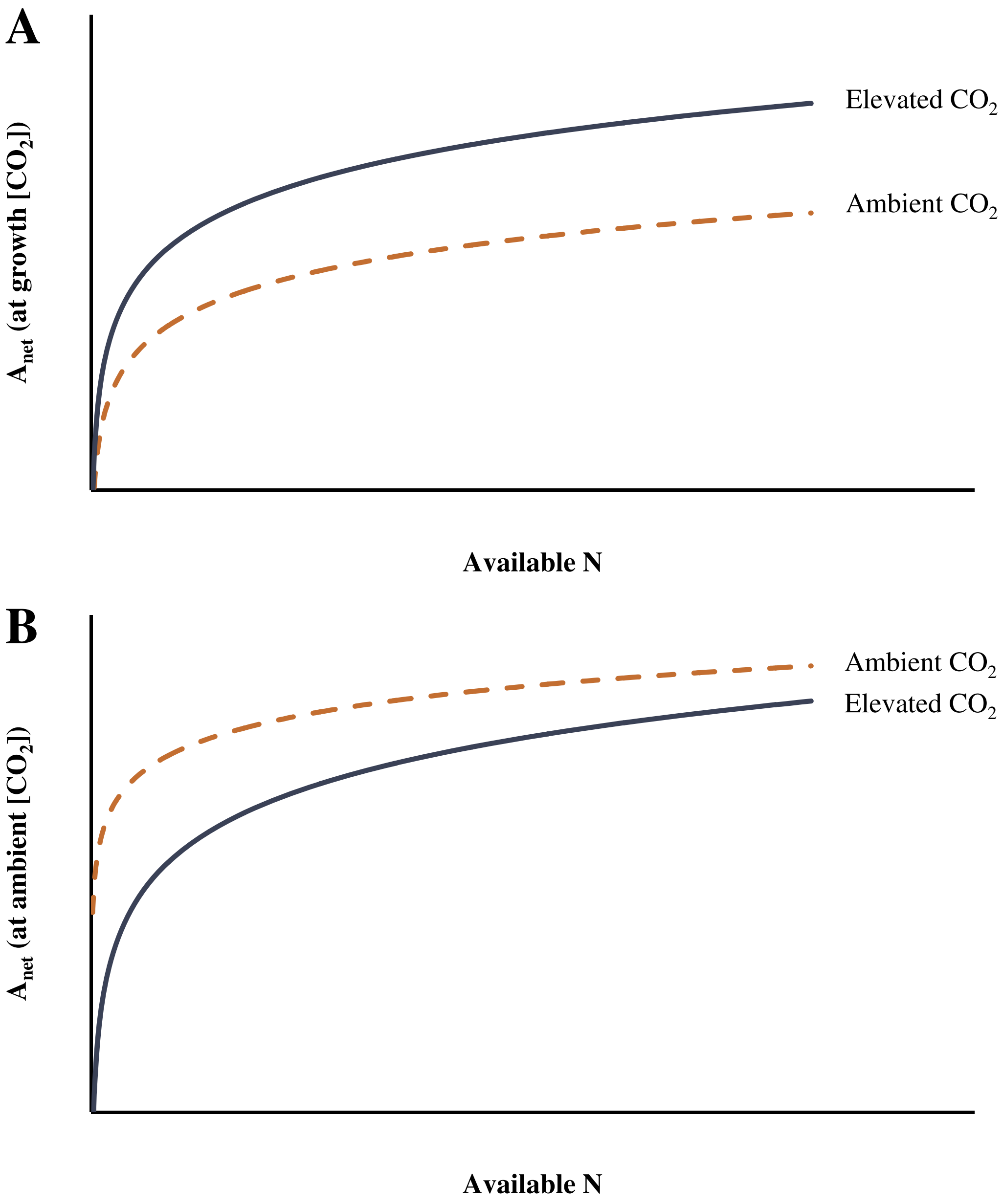

Fig. 2. Photosynthetic response to CO_2 enrichment and available N. (A) CO_2 assimilation rate, measured at growth [CO_2] (ambient or elevated; dashed and solid lines, respectively), as a function of available N. (B) CO_2 assimilation rate, measured at ambient [CO_2], as a function of available N. Note, photosynthetic acclimation occurs in plants grown on elevated CO_2 and is most pronounced under low-N conditions. Redrawn from Wong, 1979 (see also Sage, 1994; Bowler and Press, 1996; Miglietta et al., 1996; Stitt and Krapp, 1999; *cf.* Farage et al., 1998).

to forage for nutrients. Similarly, Dukes et al. (2005) found no biomass gains with eCO_2, irrespective of N supply, and suggested that phosphorus (P) limitations may be central to this observation, because eCO_2 reduced total plant P uptake. Inauen et al. (2012) also showed no growth stimulation by eCO_2 irrespective of N fertilization in nine species of plants collected from a glacier forefield (secondarily successional bare land, exposed by glacial retreat). However, they did observe a drastic change in root-shoot biomass partitioning, with aboveground biomass reduced by 35% across all species, and higher biomass allocated to the roots. The authors suggested that these alpine plants were not carbon-limited under current conditions. It is worth noting as well that land-use intensity (*e.g.* livestock grazing, fertilizer usage, etc.) can be a dominant driver of soil C sequestration in grasslands (Chang et al., 2016). Overall, these findings emphasize the need for a better understanding of soil nutrient constraints on plant and ecosystem production under eCO_2.

Ecosystem respiration is consistently stimulated in response to eCO_2 in grasslands (Luo et al., 1996; Zak et al., 2000; Craine et al., 2001; Adair et al., 2011). In a dramatic example, Adair et al. (2011) found that eCO_2 increased soil respiration by 45% in the BioCON plot. This large effect was found to be the result of increased C inputs and availability, rather than a result of changing soil water availability (eCO_2 has been found to reduce stomatal conductance and plant water use, and thereby increase soil moisture; Adair et al., 2011). However, unlike plant biomass production, soil respiration was found not to be strongly N-limited in BioCON (Adair et al., 2011). Unfortunately, there is currently a lack of similar multi-factor studies proceeding over a longer time frame, particularly with respect to soil respiration in grasslands. It is critical that such studies be

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Table 1
Survey of studies examining $CO_2 \times N$ interactions on biomass and photosynthetic response.

Study/System	Species/Ecosystem	Age/Time frame	Treatments	Biomass response	Photosynthetic response	References
Swiss FACE	*Lolium perenne* L. swards	10 years	360 and 600 ppm CO_2, 14 and 56 g $NH_4NO_3\,m^{-2}\,yr^{-1}$	Increased CO_2 effect with high N (decline over time).	No effect on A_{sat}, A', g_s, or J_{max}. Significant decrease in $V_{c,max}$ in low-N plants.	Ainsworth et al. (2003) and Schneider et al. (2004)
BioCON FACE	Perennial grassland (legumes, non-leguminous forbs, C_3 and C_4 grasses)	5–10 years	360 and 560 ppm CO_2, ambient and +4 g $NH_4NO_3\,m^{-2}\,yr^{-1}$	Increased CO_2 effect with high N after 4–6 years.	No effect on A_{net}, A_{sat}, SLA, or g_s.	Lee et al. (2001), Reich et al. (2006a,b), Lee et al. (2011), Reich and Hobbie (2013) and Reich et al. (2014)
Oak Ridge National Laboratory (ORNL) FACE	Sweetgum (*Liquidambar styraciflua*)	11 years	Ambient and 550 ppm CO_2, ambient and +200 kg urea-N $ha^{-1}\,yr^{-1}$	Stimulation in wood increment with N fertilization and eCO_2.	N/A	Norby et al. (2005, 2010)
Duke FACE	Loblolly pine (*Pinus taeda*)	10 years	Ambient and 550 ppm CO_2, ambient and +11 g urea-N $m^{-2}\,yr^{-1}$	Increased NPP with eCO_2 and N fertilization.	N/A	Finzi et al. (2007), McCarthy et al. (2010) and Drake et al. (2011)
Jasper Ridge Global Change Experiment	Annual grasses (*A. barbata*, *B. hordeaceus*) and forbs (*G. dissectum*, *E. botrys*)	3–5 years	Ambient and 680 ppm CO_2, ambient and +3.5 g $Ca(NO_3)_2\,m^{-2}\,yr^{-1}$	Reduced NPP under eCO_2 compared to ambient CO_2.	N/A	Shaw et al. (2002), Zavaleta et al. (2003) and Dukes et al. (2005)
Cedar Creek FACE	Herbaceous brackish wetland (C_3 sedge, C_4 grasses)	4 years	Ambient and 720 ppm CO_2, ambient and +25 g $NH_4Cl\ m^{-2}\,yr^{-1}$	eCO_2-induced increase in C_3 biomass and decrease in C_4 biomass with added N.	N/A	Langley and Magonigal (2010)
Japan Rice FACE	*Oryza sativa* L.	3 years	365 and 600 ppm CO_2, low (4), medium (8–9), and high (12–15 g m^{-2}) N (as $(NH_4)_2SO_4$)	*c.* 15% increase in grain yield with eCO_2 for medium- and high-N crops; no effect on total biomass; strong dependence on developmental stage.	N/A	Okada et al. (2001), Kim et al. (2003) and Shimono et al. (2008)
MeteoSwiss FACE/Mini FACE	Glacier forefield plants (graminoids, forbs, cushion)	3 years	385 and 580 ppm CO_2, ambient and +25 kg N $ha^{-1}\,yr^{-1}$	Aboveground biomass decline with eCO_2, irrespective of N supply.	Decline in A_{net}.	Inauen et al. (2012)
Wheat MiniFACE	Winter wheat	1 year	Ambient and 600 ppm CO_2, ambient and +15.6 g urea m^{-2}	N/A	Significant decrease in A_{net}, g_s, $V_{c,max}$ and J_{max} under eCO_2 and low N.	Miglietta et al. (1996)
Swiss model ecosystem OTC	Beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* Karst.)	5 years	370 and 570 ppm CO_2, 0.5 and 5 g $NH_4NO_3\ m^{-2}\,yr^{-1}$	Increased NPP.	N/A	Spinnler et al. (2002)
Chamber, pots	*Bromus mollis*	130 d	350 and 650 ppm CO_2, 0.37 and 1.87 mM NH_4NO_3	Increased seed biomass.	No effect on A_{net}.	Larigauderie et al. (1988)
Chamber, hydroponics	*Beta vulgaris* L.	7-weeks old	32 and 100 Pa CO_2, 7.5 mM NO_3^- or NH_4^+	Increase biomass with NO_3^-.	Increased A_{net} in NH_4^+-grown plants relative to NO_3^--grown plants.	Raab and Terry (1994)

eCO_2 = elevated CO_2; A' = daily integrated CO_2 uptake; A_{sat} = light-saturated CO_2 uptake rate; A_{net} = net photosynthesis; g_s = stomatal conductance; $V_{c,max}$ = maximum velocity of Rubisco carboxylation; J_{max} = maximum rate of electron transport; SLA = specific leaf area.

forthcoming, given the major impact soil C uptake and release has on the global C budget (Raich et al., 2002; Le Quéré et al., 2015).

2.3. Forests

Among terrestrial plants, trees are exceptionally strong "beneficiaries" of eCO_2, particularly when young. FACE studies have demonstrated increases in biomass approaching or even exceeding 50% under eCO_2 (Dijkstra et al., 2002; Ainsworth and Long, 2005; Ainsworth and Rogers, 2007). Thus, forests are an especially important terrestrial C sink due to their capacity to sequester large amounts of C from the atmosphere into long-lived biomass and into soil organic matter (SOM) *via* litter. Globally, forests cover more than 4 billion hectares of land area and possess an estimated total C-sink capacity of 2.4 ± 0.4 Pg C yr^{-1} (Pan et al., 2011). Although eCO_2 increases forest NPP (Norby et al., 2005; Hyvönen et al., 2007), soil N limitations can impose a major growth constraint, as in other ecosystems (Norby et al., 2010). For example, in an 11-year FACE experiment in a sweetgum (*Liquidambar styraciflua*) forest stand, eCO_2-induced NPP stimulation declined from 24% to 9% over the

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final 5 years of the study. This was attributed to the decline in soil N availability under eCO_2, as more N was sequestered into wood and SOM (an example of "progressive nitrogen limitation" (PNL); see Section 3.4), thus limiting tree growth (Norby et al., 2010). By contrast, PNL does not seem to have occurred in a decade-long FACE experiment with loblolly pine (*Pinus taeda*) in the Duke FACE plot (Finzi et al., 2007; Hofmockel et al., 2011). It is suggested that increased N acquisition (through some combination of increased fine root production, SOM decomposition, and C allocation to mycorrhizal associations) sustains the increases in NPP under eCO_2 (Finzi et al., 2007; Drake et al., 2011; Hofmockel et al., 2011; Phillips et al., 2011; see also Sections 3.3 and 3.4).

In general, forest production benefits from anthropogenic N deposition, and in several cases, soil N has been found to be the primary determinant of NEP in forested systems (Magnani et al., 2007; Norby et al., 2010; Fernández-Martínez et al., 2014; Maaroufi et al., 2015; Yue et al., 2016). In a study of 92 forests stands, including boreal, temperate, Mediterranean, and tropical forests, Fernández-Martínez et al. (2014) determined that only nutrient-rich forests increase carbon sequestration (NEP) *via* increasing carbon uptake. Ecosystem carbon-use efficiency (CUEe, *i.e.* the ratio of NEP to GPP) in nutrient-rich forests was found to be more than 5-fold higher than that in nutrient-deficient forests (33% *versus* 6%, respectively). The conclusions of this study, however, while striking, are in conflict with the great majority of global coupled carbon-climate models, which assume that C inputs *via* photosynthesis drive plant production and C sequestration. Rather, it emphasized that nutrient limitation is the single most important determinant of forest carbon sequestration globally (see Section 2.2; Körner, 2015).

The much lower CUEe in nutrient-poor forests observed in the Fernández-Martínez et al. (2014) study was attributed to a much larger proportion of GPP being lost to ecosystem respiration. The authors proposed that limited nutrient availability decreases C allocation to long-lived woody tissues, instead increasing C allocation to fungal root symbionts and root exudates, thus stimulating heterotrophic respiration in the rhizosphere (Janssens et al., 2010; Vicca et al., 2012), and stimulating overall ecosystem respiration. Conversely, several studies have shown that increased N deposition can mitigate the eCO_2-induced stimulation of soil respiration (Burton et al., 2004; Olsson et al., 2005; Janssens et al., 2010; Maaroufi et al., 2015; see also Fig. 3). However, exceptions do exist. For instance, Hasselquist et al. (2012) found that moderate N addition rates, similar to typical N deposition rates in boreal regions ($20\,kg\,N\,ha^{-1}\,yr^{-1}$), resulted in a doubling of soil respiration compared to control plots. This enhanced respiration was linked to increased autotrophic respiration. This study highlights the need for more investigation into $CO_2 \times N$ interactions in soil respiration, particularly exploring a range of realistic N deposition rates (as opposed to simple binary treatments).

Despite having the highest rates of NPP on Earth ($\sim 10\,Pg\,C\,yr^{-1}$; 30–40% of global NPP; Cleveland et al., 2015), tropical forests have been inadequately studied in terms of eCO_2 effects and nutrient limitation (Cleveland et al., 2011, 2015; Norby et al., 2016). In a recent meta-analysis of 113 tropical forest sites, Cleveland et al. (2011) suggest that P availability may be the most limiting nutrient to NPP in such systems; however many more studies, including those employing FACE (Norby et al., 2016), will be necessary to establish the chief limiting nutrients in different forest ecosystems (see also Vitousek, 1984; Wieder et al., 2015). A joint focus on N and P is clearly necessary.

2.4. Agriculture

As with natural ecosystems, many studies have shown that the productivity of agricultural C_3 plants, including major crops such as rice, wheat, potato, soybean, cotton, and tobacco, can be significantly increased by eCO_2, and such increases also depend on N availability in most cases (Kimball et al., 2002; Kim et al., 2003; Ainsworth and Long, 2005; Sakai et al., 2006; Ziska and Bunce, 2007; Fig. 3). For example, in a FACE experiment with wheat, Ma et al. (2007) found that the eCO_2-stimulated biomass under high N ($250\,kg\,N\,ha^{-1}$) was approximately double that under low N ($125\,kg\,N\,ha^{-1}$). In a survey of studies using FACE and earlier chamber-based methods, Kimball et al. (2002) showed that eCO_2 stimulated the growth of C_3 plants (wheat, perennial ryegrass, rice, white clover, potato, cotton, and grape) by 17%, on average, when N was adequately supplied, but only by 3% under low N (when the legume was excluded; see below); only in rare cases were exceptions to this general result found, such as in increases in the yield of perennial ryegrass, under low compared to high N.

By contrast, in a six-year FACE study of a crop rotation with winter barley, ryegrass, sugar beet, and winter wheat, Weigel and Manderscheid (2012) found that, contrary to expectations, eCO_2 effects on plant growth variables were independent of N supply. The authors noted that, in a handful of prior studies in rice, grain yield was also independent of N supply (Liu et al., 2008; Yang et al., 2009), although in one of these studies this independence only occurred between medium- and high-N provision, while an eCO_2-driven yield increase was still found between low- and medium-N treatments (Kim et al., 2003). In rice, yield stimulations or reductions in response to eCO_2 appear to be cultivar-dependent (Satapathy et al., 2014).

More broadly, the magnitude of crop responses to eCO_2 varies widely with the type of plant examined. Among C_3 plants, those with large C sinks in the form of carbohydrate storage organs, such as potato and cassava, and woody tissues such as cotton, can have particularly strong growth responses to eCO_2 (Ainsworth and Long, 2005; Rosenthal et al., 2012). In cassava, a 100% yield increase has been observed under eCO_2 with N fertilization (Rosenthal et al., 2012), and even with low N inputs tuber mass was shown to increase by 49% (Fernández et al., 2002). Because photosynthetic and growth responses of C_4 plants to eCO_2 are generally much lower than those of C_3 plants (Ainsworth and Long, 2005; *cf.* Wand et al., 1999), agricultural productivity increases for major C_4 crops such as corn, sugarcane, sorghum, and millet, may be limited in a CO_2-enriched atmosphere, except under drought conditions (Lopes et al., 2011). By contrast, positive eCO_2 effects on growth and yield in legume species tend to be particularly pronounced, due to their ability to fix organic N from atmospheric N_2 *via* root symbioses (Zanetti et al., 1996; Ainsworth et al., 2002; Rogers et al., 2006; Kant et al., 2012). However, whereas they may overcome N limitation in this way, legumes are often phosphorus limited (Rogers et al., 2009; see below), underscoring our earlier point on the necessity to examine not only N-, but also P-limitation effects under eCO_2.

A potential threat to agricultural production as C_a continues to rise is the reduction of N concentrations in tissues of crop plants, associated with increased biomass gains (see Section 3.1). In cereals, this is reflected in an 8–31% reduction in grain N, mostly in the form of organic N, *i.e.* protein and amino acids (Fangmeier et al., 1999; Kant et al., 2012; Pleijel and Uddling, 2012). The reduced protein levels in cereal grains can be gravely detrimental for human nutrition (Taub et al., 2008), as well as for the quality of bread flour produced from these grains (Högy et al., 2009).

3. Plant and soil N uptake and accumulation under eCO_2

3.1. Tissue N content

Many studies have indicated that plants grown under eCO_2 show decreased tissue concentrations of N relative to plants grown under ambient CO_2, although this condition can be alleviated by increased N supply, uptake, and -use efficiency (Stitt and Krapp,

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1999; Kant et al., 2012; Fig. 3). The decrease in the concentration of N in plant dry mass (N_m) varies between studies, but typically falls in the range of 9–16% depending on plant organ, species, functional group, or experimental method (Cotrufo et al., 1998; Curtis and Wang, 1998; Ainsworth and Long, 2005; Taub and Wang, 2008; Feng et al., 2015). Understanding the nature of this decrease is critical to the development of comprehensive models of carbon fixation, plant growth and yield, and ecosystem-level carbon sequestration (NEP) under eCO_2. Although the underlying mechanisms responsible for the decrease in N_m under eCO_2 are not fully understood, several hypotheses have been put forward (Taub and Wang, 2008; Bloom, 2015a; Feng et al., 2015).

The hypothesis most often put forward is that of 'biomass dilution' of tissue N_m, in response to increased photosynthetic assimilation of C under eCO_2 (Luo et al., 1994; Poorter et al., 1997; Farage et al., 1998; Gifford et al., 2000; Yin, 2002; Ellsworth et al., 2004; Taub and Wang, 2008; *cf.* Feng et al., 2015). Biomass dilution occurs when the biomass gains (NPP) under eCO_2 are greater than the corresponding changes in N uptake (see Section 3.3; it should be noted here that tissue N content per unit leaf area also declines; Ellsworth et al., 2004). However, this appears to be only partly responsible for the decrease in N_m. In a recent meta-analysis of studies in grassland, forest, and cropland ecosystems, Feng et al. (2015) asserted that the change in N_m in response to eCO_2 was in fact independent of the biomass (NPP) response to eCO_2. The authors suggest that the N limitations imposed on plant NPP gains under eCO_2 (and the corresponding decreases in N_m) are more likely to be linked to eCO_2-induced suppressions of plant N acquisition (Section 3.3), rather than to growth dilution of plant N or to processes related to progressive N limitation (Section 3.4). A further argument against the biomass dilution hypothesis is the disproportionate decrease in tissue N compared to decreases in tissue levels of other nutrients (*e.g.* potassium (K) and P; Poorter et al., 1997; Cortrufo et al., 1998; Taub and Wang, 2008; Jauregui et al., 2016), suggesting that processes other than biomass dilution are affecting N_m.

The well characterized decreases in ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) content under eCO_2 may account for some of the decreases observed in N_m (Long et al., 2004; McMurtrie et al., 2008; Taub and Wang, 2008). Approximately 25–30% of total leaf N is found in Rubisco, which is widely accepted to be the rate-limiting step of photosynthesis (Sage et al., 1987; Jensen, 2000; Spreitzer and Salvucci, 2002). With the increase in carboxylation efficiency under eCO_2 (due to the higher ratio of CO_2 to O_2 at the active site of Rubisco, favoring photosynthesis over photorespiration), C supply can exceed demand, particularly when N limitations constrain sink development; thus, it has been hypothesized that N from Rubisco can be recycled to offset limitations in sink development (Drake et al., 1997; Rogers et al., 1998; Long et al., 2004; McMurtrie et al., 2008). According to Moore et al. (1999), the reduced expression of genes encoding Rubisco are brought about by the hexokinase-mediated signaling of increased photosynthate levels. The eCO_2-induced declines in Rubisco are considered the basis of the acclimation response in which photosynthetic capacity is down-regulated under eCO_2, particularly under N-limiting conditions (Wong, 1979; Oberbauer et al., 1986; Arp, 1991; Sage, 1994; Drake et al., 1997; Rogers et al., 1998; Stitt and Krapp, 1999; Ainsworth and Rogers, 2007; see also Figs. 2 B and 3). However, it is worth noting that even when Rubisco levels are down-regulated under acclimation, eCO_2 still increases NPP in most cases (Leakey et al., 2009).

3.2. The effects of contrasting N sources

The relative proportions, and concentrations, of the major N sources available to plants, *i.e.* nitrate (NO_3^-), ammonium (NH_4^+), and organic N (*e.g.* amino acids), can vary substantially, and this can have profound effects on species distribution and plant performance in the field (Gigon and Rorison, 1972; Haynes and Goh, 1978; Kaye and Hart, 1997; Kronzucker et al., 1997; Hofmockel et al., 2007, 2010; Bloom, 2015b; Rubio-Asensio et al., 2015). Generally, low pH, low temperature, the accumulation of phenolic-based allelopathic compounds, and low oxygen supply favour net ammonification over nitrification in soils (Vitousek et al., 1982; Eviner and Chapin, 1997; Britto and Kronzucker, 2002). For example, late-successional forest soils are typically NH_4^+-dominated, in contrast to early-successional or post-disturbance forest soils, which are generally NO_3^--dominated (Smith et al., 1968; Rice and Pancholy, 1972; Klingensmith and Van Cleve, 1993; Kronzucker et al., 1997). Moreover, periodically flooded agricultural systems like rice paddies and cranberry fields are predominately NH_4^+-rich (Britto and Kronzucker, 2002; and references therein; see, however, Kirk and Kronzucker, 2005).

Plant responses to eCO_2 can be influenced by N source, although studies examining this are sparse and varied. In sugar beet (*Beta vulgaris*), net photosynthesis was substantially higher at elevated CO_2 (100 Pa *vs.* an ambient level of 32 Pa) in NH_4^+-grown plants compared to NO_3^--grown plants, due to an increase in photosynthetic enzymes, including Rubisco (Raab and Terry, 1994). Moreover, NH_4^+ plants showed a doubling of chloroplast volume, a ~60% rise in chlorophyll content, and a 4.3-fold higher accumulation of soluble proteins (see also Guo et al., 2007; for review). In cassava (*Manihot esculenta*), NO_3^--grown plants experienced significant photosynthetic acclimation, as opposed to NH_4^+-grown plants, which showed none; however, this was only the case in young (36-d-old) plants, but was not observed at more advanced ages, at which plants experienced NH_4^+-toxicity symptoms including severely reduced biomass (Cruz et al., 2014). By contrast, in two grass species, colonial bent (*Agrostis capillaris*) and matgrass (*Nardus stricta*), no significant effect of N form (NH_4^+ *vs.* NO_3^-) was found in any of the measured parameters under eCO_2: total biomass, carboxylation efficiency, A_{max}, leaf N content, specific leaf area, leaf area ratio, or soluble carbohydrate content (Bowler and Press, 1996).

It has been reported that NH_4^+ supply increases the rate of non-photosynthetic ("dark") carbon fixation in roots, in contrast to NO_3^- supply (Ikeda et al., 1992; Cramer et al., 1993; Koga and Ikeda, 2000; Balkos et al., 2010). This may be because, at elevated NO_3^- supply, NO_3^- that is not assimilated can be safely stored in root vacuoles (Salsac et al., 1987; Sechley et al., 1992), while, by contrast, NH_4^+ must be reduced immediately to avoid cytotoxicity (Givan, 1979; Oaks, 1994; Britto and Kronzucker, 2002). Products of dark carbon fixation, mediated mainly by phospho*enol*pyruvate carboxylase (PEPC), can anapleurotically provide the carbon skeletons necessary for NH_4^+ assimilation into organic N (Chollet et al., 1996; Huppe and Turpin, 1994). In fact, when NH_4^+ is supplied, PEPC activity and expression in roots has been shown to be significantly enhanced (Schweizer and Erismann, 1985; Arnozis et al., 1988; Koga and Ikeda, 2000; Balkos et al., 2010; Britto et al., 2014). In wheat seedlings, treatment with methionine sulfoximine (MSX), an inhibitor of glutamine synthetase (the enzyme that catalyzes primary NH_4^+ assimilation), suppressed CO_2 fixation in roots, suggesting a role for the products of NH_4^+ assimilation in the regulation of dark fixation (Koga and Ikeda, 2000). Although feeding plants with NH_4^+ may seem like a promising means of increasing CO_2 fixation under eCO_2, in tomato roots PEPC activity was shown to be suppressed by increased root-zone CO_2, despite being stimulated by NH_4^+ supply (Viktor and Cramer, 2005).

Bloom et al. (2010) reported that nitrate reductase (NR) activity in both *Arabidopsis* and wheat is limited under eCO_2. This effect was attributed to the decrease of photorespiration (which can stimulate the supply of reductant for NO_3^- reduction) under this condition, and also to the inhibition of nitrite (NO_2^-) transport from the cyto-

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sol to the chloroplast by elevated levels of bicarbonate ions in the leaf. The authors suggested that these effects may explain the differential responses observed in wheat and *Arabidopsis* to eCO_2 under contrasting N sources, where growth enhancement doubled under ammonium supply relative to NO_3^- supply, and shoot protein content declined in NH_4^+-grown plants to only half the extent observed in NO_3^--grown plants (Bloom et al., 2002, 2010). Moreover, it may explain the decline in plant NO_3^- acquisition and increase in soil NO_3^- availability, under eCO_2, and the lack of corresponding responses under NH_4^+ supply, as shown in a recent meta-analysis covering grasslands, forests, and croplands (Cheng et al., 2012). The decrease in organic N circulating from shoot to root as a result of decreased NR activity, however, may signal the root to, in fact, *increase* NO_3^- uptake (Imsande and Touraine, 1994; Jackson et al., 2008), as was observed by Jauregui et al. (2016), who found that N accumulation, and expression of several NO_3^- transporters in the root, were enhanced by eCO_2, while shoot NR activity was reduced. However, while the conclusions of Bloom et al. (2010) are based on converging results from five independent methods, some previous studies have indicated that NO_3^- assimilation does not decrease under eCO_2 except when NO_3^- supply is limiting (Nunes-Nesi et al., 2010). For example, several studies have shown a large stimulation of NR activity in tobacco plants under eCO_2 when NO_3^- provision was high, but not when it was low or when NH_4^+ was the N source (Geiger et al., 1998, 1999). Moreover, Kaiser and Forster (1989) showed that NO_3^- reduction was decreased under low CO_2 concentrations, and that this inhibition was reversed when CO_2 was added back to the system. More investigations are clearly warranted to address the apparent discrepancies in this complex interaction.

3.3. *Plant N acquisition*

The effects of eCO_2 on plant N acquisition are very likely to contribute to changes in plant N_m; however, N-acquisition responses to eCO_2 can be quite variable. Feng et al. (2015) observed a positive, linear, and strong relationship between the effect of eCO_2 on N acquisition and the effect of eCO_2 on plant production (in contrast to the response of N_m; see above). Interestingly, however, they also showed that N acquisition under eCO_2 decreased by up to ~10% relative to ambient-CO_2 levels when the corresponding plant production gains were nil or only modestly positive, regardless of N supply. According to the authors, this was likely due to plants having decreased access to N under these conditions.

Several hypotheses have been put forward to explain the decrease in N acquisition, where it occurs (*e.g.* Taub and Wang, 2008; Feng et al., 2015), including: (i) slower decomposition of plant litter with high C:N ratios, thus decreasing soil N availability over time (Luo et al., 2004), (ii) net N immobilization by a larger soil microbial biomass (de Graaff et al., 2006), (iii) shoot-to-root signaling of reduced aboveground N demand, either *via* inhibition of nitrate (NO_3^-) assimilation (Bloom et al., 2010; Bloom, 2015a; Jauregui et al., 2016) or decreased abundance of photosynthetic enzymes (especially Rubisco; Long et al., 2004; McMurtrie et al., 2008), (iv) decreased transpiration-driven mass flow of soil N to roots (McDonald et al., 2002; Cramer et al., 2009; McGrath and Lobell, 2013; Matimati et al., 2014), (v) decreased expression levels of root N transporters, such as NRT1.1. (Guo et al., 2013), and (vi) altered root system architecture, including increases in fine and coarse root mass, and root:shoot ratios (Beidler et al., 2015). By contrast, hypotheses for the stimulation in N acquisition include: (i) enhanced foraging by roots and increased whole-plant N sink strength (Finzi et al., 2007; Iversen et al., 2012), (ii) stimulated decomposition and N mineralization by a larger and/or more active microbial community (Dijkstra et al., 2008; Iversen et al., 2011; Phillips et al., 2011), (iii) increased biological N_2 fixation (Poorter et al., 1997; Rütting and Andresen, 2015; *cf.* Hungate et al., 2004), and (iv) increased N transporter activity and/or expression (Jauregui et al., 2016).

Despite the general observation of reduced N concentrations in plant tissues under eCO_2, however, N uptake by roots nevertheless appears to be enhanced under these conditions in many cases, although the extent of this enhancement is less than the increase in C fixation (Stitt and Krapp, 1999; Johnson, 2006; Lenka and Lal, 2012). Several earlier reviews reported no consistent pattern in terms of changes in the direction or extent of root nutrient absorption capacity under eCO_2, possibly due to variable experimental protocols and differences among species (*e.g.* BassiriRad et al., 2001), or the extent of N supply (Stitt and Krapp, 1999). More recent studies and reviews have generally indicated positive effects of eCO_2 on N uptake (Torbert et al., 2004; Yamakawa et al., 2004; Johnson, 2006; Finzi et al., 2007; Zak et al., 2007; Rennenberg et al., 2010; Hofmockel et al., 2011), with at times very large increases, for example a 33–34% greater total N in the case of sorghum and soybean (Torbert et al., 2004). Mechanistically, studies have tended to focus on changes in N uptake as a function of changes in soil-N availability, root-system size and architecture, and mass flow (*e.g.* Finzi et al., 2007; Hofmockel et al., 2011; McGrath and Lobell, 2013).

Relatively little work has examined changes in N acquisition under eCO_2 at the cellular or molecular level. Matt et al. (2001a,b) showed that, in tobacco, altered diurnal expression patterns of the genes encoding nitrate reductase and the nitrate transporter NRT2 resulted in overall higher N uptake and assimilation with NO_3^- as the N source (*cf.* Bloom et al., 2010). When grown on a mixed-N source (NH_4NO_3), however, the plants preferentially took up NH_4^+, which was suggested to be due to a large capacity for NH_4^+ assimilation brought about by eCO_2 and its release of photorespiratory demands on NH_4^+ re-assimilation (Raven et al., 1992; see also Section 3.2). In neither case was a reduction of tissue N concentration seen, indicating the presence of an adequate N supply (2 mM). In another example, yellow birch (*Betula alleghaniensis*) showed NO_3^- uptake was reduced and NH_4^+ uptake was unchanged with eCO_2, despite significant increases in total root length being observed in both conditions (Bauer and Berntson, 2001). By contrast, in the same study, no change in root system architecture with eCO_2 was observed in white pine (*Pinus strobus*), whereas both NH_4^+ and NO_3^- uptake were stimulated. A recent study by Jauregui et al. (2016) demonstrated large increases in the expression of genes encoding NO_3^- transporters in *Arabidopsis*, coinciding with a doubling of NO_3^- concentration in roots. By contrast, Guo et al. (2013) found that eCO_2 downregulated nitrate transport and transporter expression in the legume *Medicago truncatula*. Importantly, however, a proliferation of root nodules was also observed, with concomitant increases in expression of genes encoding N-fixation-related proteins as well as N fixation itself, resulting in higher tissue-N concentrations under eCO_2.

3.4. *Progressive N limitation (PNL) and N deposition*

The effects of eCO_2 on soil N levels and cycling have been highly variable, having been shown to decrease, remain stable, or increase under eCO_2 (Gill et al., 2002; Finzi and Schlesinger, 2003; Luo et al., 2004; Schneider et al., 2004; Reich et al., 2006a,b; Dijkstra et al., 2008; Langley et al., 2009; Phillips et al., 2009; Norby et al., 2010; Zak et al., 2011; Mueller et al., 2013; Rütting and Andresen, 2015).

The progressive nitrogen limitation (PNL) hypothesis proposes that long-term exposure to eCO_2 may result in feedbacks that suppress the availability of N, which in turn reduces the CO_2 fertilization effect (Luo et al., 2004; Dukes et al., 2005; Hungate et al., 2006; Reich et al., 2006b). This effect is particularly pronounced when N supply is low at the outset (Stitt and Krapp, 1999; Figs. 1 and 3). More specifically, PNL postulates that soil N availability becomes increasingly limited as it is sequestered into long-lived

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plant biomass (such as woody tissues) and recalcitrant fractions of SOM (Luo et al., 2004). In what is perhaps the most striking example of PNL, the decline in soil N availability was linked to the decline in eCO_2-stimulated NPP in the Oak Ridge National Laboratory (ORNL) FACE experiments (Norby et al., 2010; Norby and Zak, 2011; see Section 2.3). A similar conclusion was drawn in two grassland ecosystems (Reich et al., 2006a; Hovenden et al., 2008). By contrast, little evidence for PNL, even in the absence of N fertilization, has been found in the Duke FACE experiment, where loblolly pine has been growing at eCO_2-stimulated rates for over a decade (Finzi et al., 2007; McCarthy et al., 2010; Hofmockel et al., 2011; see below). In this system, it appears that PNL may be overcome by a combination of increased growth of deep roots, increased mineralization of N, and a shift in mycorrhizal fungal distribution towards deeper soil (Pritchard et al., 2008; Hofmockel et al., 2011). It is important to note, as Lenka and Lal (2012) point out, that turnover times of many of the recalcitrant biomass and SOM pools in question are typically much longer (*e.g.* >25 years; Parton et al., 1987) than the length of most FACE experiments (5–10 years), and, thus, much longer experiments are needed to fully understand the effects on soil nutrient cycles. Feng et al. (2015) even suggest that PNL may not be commonly occurring at all, since the effects of eCO_2 on plant production and N acquisition do not diminish over the decennial timescale in their meta-analysis.

Dieleman et al. (2012) caution that many PNL-related studies are based on single-factor treatments (*i.e.* eCO_2) and results may vary depending on co-factors. One critical factor in this context is soil warming. For example, when warming temperatures were considered in the meta-analysis of Dieleman et al. (2012), soil-N levels were found not to decline to the same extent as with eCO_2 alone, possibly due to warming-induced accelerations in litter decomposition (see also Melillo et al., 2011; Davidson and Janssens, 2006; Hovenden et al., 2008; Bai et al., 2013). In another study, soil warming (5 °C above ambient) for 7 years in a deciduous forest resulted in an average 45% annual increase in net nitrogen mineralization and a three-fold increase in nitrification since the start of the experiment (Butler et al., 2012). The warming-induced increases in bioavailable soil N resulted in significant increases in growth rate and foliar N content in the surrounding trees, especially red maples. Although it was not observed in the study, the increased availability and proportion of soil NO_3^- suggest that species adapted to this N source may be at a significant competitive advantage over NH_4^+-preferring species. Overall, these studies further highlight the importance of considering the multiple, and at times, contrasting, factors affecting ecosystem processes under eCO_2 and associated climate change.

Anthropogenic N deposition has had significant effects on the C cycle and plant carbon fixation, and is often recommended under PNL conditions; however, its net contribution to climate change remains widely debated (Galloway et al., 2008; Meyerholt and Zaehle, 2015). The extent of N deposition has increased tremendously since pre-industrial times, due to nitrogenous emissions from fossil fuel combustion and the industrial production of Nr species *via* the Haber-Bosch process, which consumes up to 5% of the world's natural gas (about 1% of total global energy supply), thus itself contributing to eCO_2 (Schlesinger, 2000; Smith, 2002; Smil, 2004). N deposition has increased from ~15 Tg N yr^{-1} in 1860 to ~187 Tg N yr^{-1} by 2005 (more than a 12-fold increase), and is projected to rise to ~267 Tg N yr^{-1} by 2050 (Galloway et al., 2004, 2008). Unfortunately, N-use efficiency by plants has also declined pervasively, resulting in a cascade of environmental and human-health problems resulting from high levels of Nr in water and land systems, and the human food supply (Vitousek et al., 1997; Britto and Kronzucker, 2002; Galloway et al., 2008). Moreover, while increases in anthropogenic N deposition have been increasing the size of terrestrial C sinks (Frey et al., 2014; Maaroufi et al., 2015), it is unlikely to keep pace with eCO_2 (Reay et al., 2008; Bala et al., 2013).

3.5. Biological N_2 fixation (BNF)

Legumes and other N_2-fixing plants are able to overcome soil N limitations *via* symbiotic association with diazotrophic bacteria, and many studies have indicated that the extent of N_2 fixation increases under eCO_2 (Johnson, 2006; Reich et al., 2006b; Rogers et al., 2006; Kant et al., 2012), although not universally (Arnone, 1999; Hungate et al., 2004; van Groenigen et al., 2006). This has been observed in grasslands (Zanetti et al., 1996; Luscher et al., 2000), agricultural crops such as soybean (Torbert et al., 2004), and N_2-fixing trees such alder (Koike et al., 2015). In addition, increased N_2 fixation has been observed among free-living cyanobacteria associated with rice roots in paddy soil (Hoque et al., 2001). Associated with this is a pronouncedly higher response in biomass

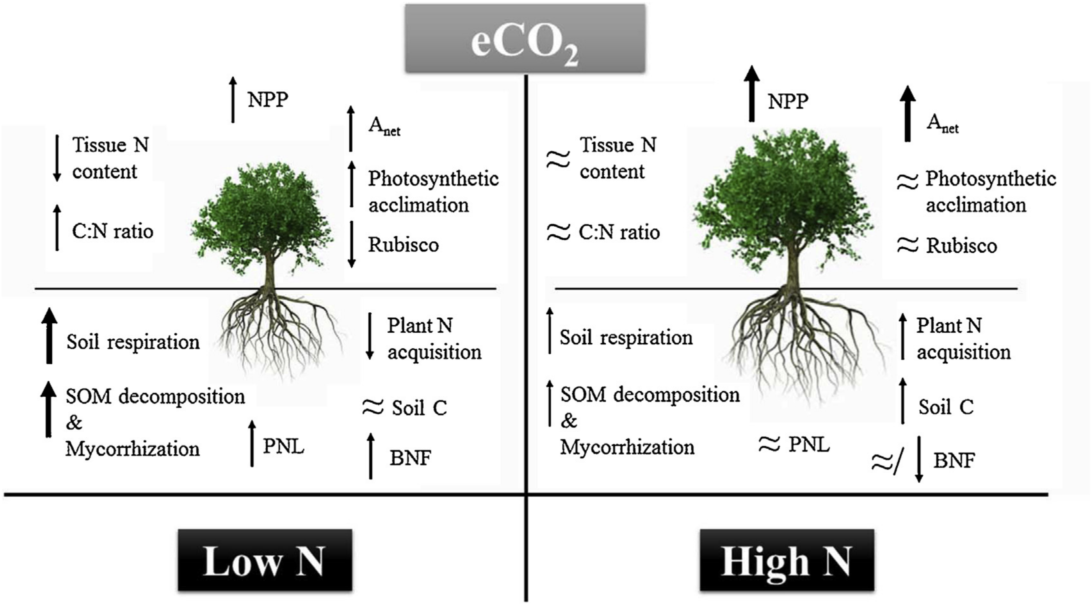

Fig. 3. Summary of the main aboveground and belowground responses to eCO_2 under low and high available N (see text for details).

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gain in N_2-fixers relative to non-fixers (Rogers et al., 2006; *cf.* van Groenigen et al., 2006). In addition to the increase in N supply *via* nodulation, the commensal association of plant roots with diazotrophs provides an additional sink for growth stimulation under eCO_2, in the form of photosynthate transferred from plant to bacterium (Ainsworth and Rogers, 2007). The reduction in tissue N generally observed for C_3 plants is often not pronounced in legumes; for instance, Torbert et al. (2004) found a 31% increase in the C:N ratio in sorghum, but no change in this ratio in soybean.

Soil N supply can also constrain the response of BNF to eCO_2. It is generally viewed that N-fixation rates decrease with increased soil N availability (Vitousek et al., 2002; *cf.* Pearson and Vitousek, 2001). This seems to be the case as well under eCO_2; for example, in a pine forest, N deposition was shown to suppress BNF under eCO_2, suppressing the diversity and abundance of N_2-fixing bacteria (Berthrong et al., 2014; Fig. 3). Indeed, the stimulation in growth of legumes and rates of BNF under eCO_2 are often seen only under N-limiting conditions (Hungate et al., 1999; Poorter and Navas, 2003; West et al., 2005). However, as West et al. (2005) demonstrate, this response can vary significantly across species, with some legumes showing significant biomass gains with eCO_2 regardless of soil N supply (Lee et al., 2003). It is important to note, in addition, that even N_2-fixing plants can be strongly nutrient-limited, typically by the low availability of soil P, K, Mg, and Mo (Hungate et al., 2004; Reich et al., 2006a; van Groenigen et al., 2006; Rogers et al., 2009).

4. Conclusion

In this review, we have discussed the effects of eCO_2 and N limitation on photosynthesis, respiration, N transport and assimilation, C and N accumulation, and growth and yield in a variety of plant systems and ecosystems. In addition, we have examined effects on soil N processes, including PNL, N mineralization, and BNF. The study and integration of these plant and soil processes is essential not only to the understanding of vegetation and agronomic responses to eCO_2 and how they intersect with N supply, but also to help design strategies by which to mitigate CO_2 emissions resulting from human activities.

While it is clear that eCO_2 increases the NPP of most C_3 plants particularly strongly when N supply is adequate, however, the approach to artificially fertilize natural ecosystems with N to increase their C-sink capacity would be problematic. As mentioned, the synthesis of N fertilizer is energetically costly, and the amount of N_2 fixed in this manner is already approximately equal to the total N_2 fixed by Earth's diazotrophs, having brought about a major shift in the global N cycle, and entailing a host of problems for environmental and human health (Vitousek and Howarth, 1991; Fowler et al., 2015). Particularly worth noting are eutrophication effects (Vitousek and Howarth, 1991), as well as the finding that, while eCO_2 can increase biodiversity (Reich, 2009), elevated N can lead to a loss of biodiversity (*e.g.* Langley and Megonigal, 2010; Isbell et al., 2013), which can negatively impact ecosystem functioning (Reich et al., 2001; Gamfeldt et al., 2013; Tilman et al., 2014). In one study, intermediate levels of species loss (21–40%) reduced primary production to levels comparable to that of climate warming, while higher levels of extirpation (41–60%) had effects comparable to ozone, acidification, eCO_2, and nutrient pollution (Hooper et al., 2012). Intermediate levels of species loss also had equal or greater effects on decomposition than eCO_2 or N deposition. In another study, decreases in grassland plant diversity influenced productivity at least as much as changes in nitrogen, water, CO_2, herbivores, drought, and fire (Tilman et al., 2012). Interestingly, in this study, the impact of biodiversity as a driver of ecosystem productivity increased over time, unlike the impact of other factors which either declined (*i.e.* nitrogen addition) or remained unchanged (all others).

In agricultural and silvicultural systems, where N is routinely supplemented, there may be potential for greenhouse-gas mitigation, as the growth and yield of crop species tend to respond well to eCO_2, especially so in the case of legumes (Jensen et al., 2012). Clearly, the intelligent management of soil resources will be required, such as the coordinated application of N at specific stages of plant development (Kim et al., 2001), and increases in the N-use efficiency of cropping systems, which currently stands at an average of only about 40% in the case of cereals (Kant et al., 2012). In addition, new attention will need to be focused on the source of N provided for fertilization, given the different responses of plants to NH_4^+ and NO_3^-, and possibly organic sources of N, under eCO_2 (Bauer and Berntson, 2001; Cruz et al., 2014; Bloom, 2015b). Secondly, advances in plant breeding to produce genotypes pre-adapted to changing environmental conditions will be very important in the coming decades. Target areas pertinent to the issues discussed here will include breeding plants with improved mineral nutrition, particularly that of N and P (Richardson et al., 2011; Pilbeam, 2015), and increased sink strength to maximize utilization of increasingly plant-available CO_2 (Wang et al., 2013). Advances in these areas specific to eCO_2 and N limitation will need to be coordinated with ongoing efforts to increase photosynthetic efficiency and productivity in plants to sustainably meet global food demands (Ort et al., 2015; White et al., 2016).

To conclude, we reiterate that accurate scientific models are critical to help policy makers design strategies to preserve, or increase, carbon sinks, and thus to mitigate eCO_2 and thereby climate change (Friedlingstein et al., 2011). Understanding the role of nutrient cycles in plant carbon fixation is essential to the development of reliable models (Zaehle et al., 2015), with a view to healthy natural-ecosystem function and the sustainable future of agricultural production, both of which are threatened by continued human population and resource-consumption growth and by the unprecedentedly rapid pace of global environmental change (Long et al., 2006; Lobell et al., 2011; Myers et al., 2014).

This review summarizes the effects of elevated atmospheric [CO_2] and N limitation on photosynthesis, respiration, N transport and assimilation, C and N accumulation, and growth and yield in a variety of plant systems and ecosystems. We highlight key studies from the field, particularly from free-air CO_2 enrichment (FACE) technology, and draw on both fundamental and novel physiological and ecological mechanisms for connection.

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