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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.

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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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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), 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