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Key Points:

- Ecosystem C sequestration responses to elevated CO₂ were simulated by seven models
- C sequestration variability was driven first by NPP and second by turnover
- Progressive N limitation depended on time scale and model N uptake assumptions

Supporting Information:

- Text S1 and Figures S1–S3

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Predicting long-term carbon sequestration in response to CO₂ enrichment: How and why do current ecosystem models differ?

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Abstract Large uncertainty exists in model projections of the land carbon (C) sink response to increasing atmospheric CO₂. Free-Air CO₂ Enrichment (FACE) experiments lasting a decade or more have investigated ecosystem responses to a step change in atmospheric CO₂ concentration. To interpret FACE results in the context of gradual increases in atmospheric CO₂ over decades to centuries, we used a suite of seven models to simulate the Duke and Oak Ridge FACE experiments extended for 300 years of CO₂ enrichment. We also determine key modeling assumptions that drive divergent projections of terrestrial C uptake and evaluate whether these assumptions can be constrained by experimental evidence. All models simulated increased terrestrial C pools resulting from CO₂ enrichment, though there was substantial variability in quasi-equilibrium C sequestration and rates of change. In two of two models that assume that plant nitrogen (N) uptake is solely a function of soil N supply, the net primary production response to elevated CO₂ became progressively N limited. In four of five models that assume that N uptake is a function of both soil N supply and plant N demand, elevated CO₂ led to reduced ecosystem N losses and thus progressively relaxed nitrogen limitation. Many allocation assumptions resulted in increased wood allocation relative to leaves and roots which reduced the vegetation turnover rate and increased C sequestration. In addition, self-thinning assumptions had a substantial impact on C sequestration in two models. Accurate representation of N process dynamics (in particular N uptake), allocation, and forest self-thinning is key to minimizing uncertainty in projections of future C sequestration in response to elevated atmospheric CO₂.

1. Introduction

We face a high CO₂ Earth and consequently a changing climate. Since the industrial revolution, atmospheric CO₂ has been increasing, primarily due to fossil fuel emissions (currently approximately 10 Pg C yr⁻¹ [Andres et al., 2012]) and that trend is likely to continue into the foreseeable future. CO₂ can stimulate plant productivity [Norby et al., 2005; McCarthy et al., 2010; Morgan et al., 2011; Franks et al., 2013], potentially increasing terrestrial carbon (C) storage (commonly known as C sequestration) and creating negative feedback on atmospheric CO₂ increase. The response of terrestrial ecosystems to increasing CO₂, and the strength of the feedback, is a large source of uncertainty in projecting the future of the Earth system [Arora et al., 2013; Friedlingstein et al., 2014]. While the direct physiological effects of elevated atmospheric CO₂ (eCO₂) are well understood [Arp, 1991; Stitt, 1991; Franks et al., 2013], it is uncertain how these physiological effects cascade through multiple ecosystem processes to affect ecosystem function across broader spatial and temporal scales [Arora et al., 2013; De Kauwe et al., 2014; Zaehle et al., 2014a]. Projections of terrestrial C uptake by multimodel ensembles, like the projections of the Coupled Model Intercomparison Project Phase 5 (CMIP5) ensemble [Arora et al., 2013], show an extremely wide range during the 21st century [Friedlingstein et al., 2014].

Free-Air CO₂ Enrichment (FACE) experiments have tested the effects of eCO₂ on a number of terrestrial ecosystems for over a decade. Initial responses of net primary production (NPP) appeared to be conserved across a range of forest ecosystems [Norby *et al.*, 2005]. However, the NPP responses at Duke and Oak Ridge FACE experiments deviated in the years after the initial synthesis by Norby *et al.* [2005], and carbon (C) sequestration responses at the two sites were very different [De Kauwe *et al.*, 2014; Zaehle *et al.*, 2014a]. The responses of two key ecological processes—nitrogen (N) cycle feedbacks and vegetation turnover—were shown to be key drivers of experimental and modeled NPP responses [McCarthy *et al.*, 2010; Norby *et al.*, 2010; Garten *et al.*, 2011; Zaehle *et al.*, 2014a] and C sequestration responses [De Kauwe *et al.*, 2014], respectively. We therefore hypothesize that variability in the way that terrestrial ecosystem and biosphere models (TEMs) represent the N cycle and vegetation turnover will explain much of the variability in the decadal to centennial ecosystem C sequestration projections of those TEMs.

Using a tractable ecosystem model, an early version of the Generic Decomposition and Yield (GDAY) model, Comins and McMurtrie [1993] demonstrated in a seminal theoretical study that the NPP response to eCO₂ became progressively limited by nitrogen over time (a concept known as progressive nitrogen limitation, PNL [see Luo *et al.*, 2004]). PNL occurred in GDAY because leaf C:N ratios increased at eCO₂, which decreased litter quality and increased the partitioning of litter to longer turnover soil organic matter (SOM) pools, thereby reducing soil organic matter (SOM) decomposition and N mineralization rates. Increased amounts of N were also sequestered in long-lived woody biomass. N cycling through the ecosystem slowed, further reducing leaf N and causing feedback that counteracted the physiological increase in photosynthetic efficiency at eCO₂.

For the purposes of this analysis, after Luo *et al.* [2004] we define PNL as a progressive decrease in the relative response of NPP to eCO₂ compared with ambient CO₂ conditions, caused by increasing N sequestration in long-lived organic matter, which consequently reduces N mineralization rates. The mechanism of PNL is analogous to the mechanism that causes N-limited productivity dynamics during forest stand development in some temperate ecosystems [Turner, 1981; Johnson, 2006].

Nitrogen dynamics were observed to play an important role in FACE experiments, in part, controlling the magnitude of the NPP response [Zak *et al.*, 2007; McCarthy *et al.*, 2010; Norby *et al.*, 2010; Garten *et al.*, 2011]. At Oak Ridge, PNL drove the NPP response to CO₂ to near zero by the end of the experiment [Norby *et al.*, 2010], albeit against a backdrop of PNL in the ambient treatment caused by stand development (for the concept, see Johnson [2006]). The data from Oak Ridge support the hypothesis generated by the model of Comins and McMurtrie [1993], but data from many other FACE experiments have shown no evidence for PNL under eCO₂, e.g., at Duke FACE [Drake *et al.*, 2011] and AspenFACE [Zak *et al.*, 2011]. Since Comins and McMurtrie [1993], many modeling studies using models with different N cycling assumptions have continued to support the hypothesis that N cycle feedbacks constrain NPP responses to CO₂ [Thornton *et al.*, 2007; Zaehle *et al.*, 2010, 2014a; Zhang *et al.*, 2011; Gerber *et al.*, 2013; Thomas *et al.*, 2013]. Most models used in the CMIP5 did not simulate an N cycle and have been shown to make unrealistic implicit assumptions of N availability [Hungate *et al.*, 2003; Wang and Houlton, 2009; Zaehle *et al.*, 2014b].

Models typically represent terrestrial ecosystems with a system of C pools and C fluxes between those pools [Parton *et al.*, 1987; Xia *et al.*, 2013]. C enters the system via photosynthesis and is allocated among the proximal set of pools. Turnover rates (τ) determine the longevity of C in each of these pools, and different turnover rates of each pool mean that C allocation among the pools affects the turnover rate of vegetation C. C allocation and turnover rates are key determinants of C sequestration within an ecosystem [Olson, 1963; Anav *et al.*, 2013; Friend *et al.*, 2013; Xia *et al.*, 2013; De Kauwe *et al.*, 2014]. Therefore, to identify key processes and potential causes of uncertainty in modeling terrestrial C sequestration, we analyzed a suite of models with various N cycling and C turnover assumptions.

FACE experiments are some of the most data-rich, long-term ecosystem manipulation experiments to date, and FACE experiments have recorded ecosystem responses to eCO₂ integrated over seconds to multiyear time scales. The FACE experiments are an invaluable resource, yet they are necessarily restricted in the temporal domain, and we need to use models to help extrapolate measurements made over a decade to decadal to centennial time scales. Temporal scales crucial to our understanding of global environmental change.

The goal of this study was to use models to project idealized responses at the Duke and Oak Ridge FACE sites 300 years into the future, informed by our preexisting knowledge of the sites and the models' behavior at

these sites [De Kauwe *et al.*, 2013, 2014; Walker *et al.*, 2014; Zaehle *et al.*, 2014a] to assess projected responses of temperate forest ecosystems to eCO₂. We also use modeling to assess the difference in employing a step change in CO₂ concentration, as was done in the FACE experiments, with a gradual rise in CO₂ that is currently occurring [Luo and Reynolds, 1999]. Thus, a further point of investigation relates to the impact of the treatment on the observed responses.

Using seven TEMs with well-understood CO₂ responses at the Duke and Oak Ridge FACE sites [De Kauwe *et al.*, 2013, 2014; Zaehle *et al.*, 2014a], we evaluate the potential long-term responses of carbon sequestration in temperate forest ecosystems in response to increasing atmospheric CO₂ by considering these two key processes: N cycle feedback and C turnover within the ecosystem. We aim to (1) assess how N feedback and C allocation and turnover affect quasi-equilibrium and the rate of change in ecosystem C sequestration; (2) determine the important model hypotheses and assumptions driving these changes; and (3) interpret results from step change experiments in the context of ecosystems responding to a gradual rise in CO₂ concentration and to inform future experiments. We ran the models from an equilibrium state rather than initializing the simulations in the transient state in which the experiments began as identifying the key modeling assumptions would be the harder when convolved with an ecosystem in a transient state.

2. Methods

The two FACE sites were chosen for the simulations as they represent different vegetation types, evergreen needle-leaved (*Pinus taeda* L.) versus broad-leaved trees (*Liquidambar styraciflua* L.), under a similar temperate climate and had contrasting responses to CO₂ enrichment. The models have been previously applied to these sites [Walker *et al.*, 2014], and the short-term model responses to eCO₂ at these sites are well understood [De Kauwe *et al.*, 2013, 2014; Zaehle *et al.*, 2014a]. The two sites are extensively described elsewhere [Norby *et al.*, 2001; McCarthy *et al.*, 2010; Walker *et al.*, 2014], and meteorological data have been archived [Norby *et al.*, 2015].

2.1. Simulations

Three land surface models CABLE [Wang *et al.*, 2011], CLM4 [Oleson *et al.*, 2010], and O-CN [Zaehle and Friend, 2010]; two dynamic vegetation models LPJ-GUESS [Smith *et al.*, 2014] and SDGVM [Woodward and Lomas, 2004]; and two ecosystem models DAYCENT [Parton *et al.*, 1998] and GDAY [Medlyn *et al.*, 2000] were used to simulate the response of the Duke and Oak Ridge forest ecosystems to increased CO₂ concentrations sustained over 300 years. Three simulations were performed at each site: constant CO₂ concentrations at 380 ppmv (amb), instantaneous step change in CO₂ to 550 ppmv at the start of the simulation (eStep), and CO₂ increasing exponentially (annual increase of 0.742%) to reach 550 ppmv 50 years after the beginning of the simulation (eGrad).

A CO₂ concentration of 550 ppmv was chosen because this was close to the elevated CO₂ concentrations of the two FACE experiments (571 ppmv at Duke and 545 ppmv at Oak Ridge). CO₂ concentrations in the eStep and eGrad scenarios were chosen to meet 50 years after commencement of enrichment as 550 ppmv is the predicted concentration of the “business-as-usual” RCP8.5 scenario around 2050 [Meinshausen *et al.*, 2011].

To apply the equilibrium analysis to diagnosing model responses, the models in all three scenarios were spun-up to an equilibrium state using a constant CO₂ concentration of 380 ppmv, constant N deposition of 0.24 g m⁻² y⁻¹, and a randomly repeated sequence of meteorological data measured at the sites.

Following spin-up, the simulations were run for 300 years beginning with the initial sequence of meteorological data from the two sites (1997–2007 at Duke and 1998–2008 at Oak Ridge) followed by a random 289 year sequence of the meteorological data (all models used the same random sequence). Simulated NPP, C_{veg}, and C_{soil} were in equilibrium following the spin-up as demonstrated by the steady state in these variables during the whole of the ambient CO₂ simulation (Figure S1 in the supporting information).

Site-specific soil and plant functional-type parameters were applied to each model as described in Walker *et al.* [2014]. As with previous simulations, in CLM4 the gaseous loss rate of soil mineral N was reduced from 0.5 day⁻¹ to 0.1 day⁻¹, which has also been shown to improve CLM4 N responses [Thomas *et al.*, 2013]. LPJ-GUESS was run with 200 forest patches with each patch subject to a potential 100% mortality event occurring with an annual probability of 0.01, which is a standard implementation of LPJ-GUESS (the meteorological data, protocols, and model data can be found at cdiac.ornl.gov/face/metdata1 [Norby *et al.*, 2015] and cdiac.ornl.gov/face/model1 [Walker *et al.*, 2015]).

Table 1. Key Modeling Assumptions That Determine Ecosystem C Sequestration

	CABLE	CLM4	DAYCENT	GDAY	LPJ-GUESS	O-CN	SDGVM
Key reference	Wang et al. [2010]	Oleson et al. [2010]	Parton et al. [1998]	Comins and McMurtrie [1993]	Smith et al. [2014]	Zaehle and Friend [2010]	Woodward et al. [1995]
Photosynthesis in relation to leaf N	$V_{\text{cmax}} = f(\text{leaf N})$	$V_{\text{cmax}} = f(\text{leaf N})$	None	$V_{\text{cmax}} = f(\text{leaf N})$	$V_{\text{cmax}} = f(\text{leaf N})$	$V_{\text{cmax}} = f(\text{leaf N})$	$V_{\text{cmax}} = f(\text{leaf N})$
N uptake	$f(\text{supply, demand})$	$f(\text{supply, demand})$	$f(\text{supply, demand})$	$f(\text{supply})$	$f(\text{supply, demand, root mass})$	$f(\text{supply, demand, root mass})$	$f(\text{soil C})$
N stoichiometry (leaves, wood, and roots)	Flexible within tight bounds	Fixed	Flexible	Flexible, unbounded (leaf and fine root; Fixed (wood))	Flexible within bounds (attempts to optimize canopy N)	Flexible within bounds	Flexible, unbounded (leaves only)
C allocation	Resource limitation	Fixed ratios, wood alloc = $f(\text{NPP})$	Prioritization and resource limitation	Fixed coefficients	Functional balance = pipe model and limitation	Functional balance = pipe model and limitation	Canopy optimization, fixed wood and root coefficients
C turnover	Fixed coefficients	Fixed coefficients	Fixed coefficients	Fixed coefficients	Fixed coefficients	Fixed coefficients	Wood and root = $f(\text{NPP})$
Mortality/self-thinning	Fixed coefficient	Fixed coefficient	Fixed coefficient	Fixed coefficient	Probabilistic disturbance, allometric self-thinning	Allometric self-thinning	Must satisfy minimal growth increment

2.2. Models and Their Assumptions

The models and their assumptions regarding C and N cycling have been described in detail elsewhere [De Kauwe et al., 2013, 2014; Walker et al., 2014; Zaehle et al., 2014a]. Here we provide an overview of the key model assumptions that describe the processes of N uptake, N stoichiometry, C allocation, and turnover rates (detailed in Table 1).

Each model simulates N uptake differently (for detail see Comins and McMurtrie [1993], Woodward et al. [1995], Oleson et al. [2010], Wang et al. [2010], Zaehle and Friend [2010], Smith et al. [2014], and Zaehle et al. [2014a]). A key difference that separates the models is whether N uptake is a function of soil N supply and plant N demand (CABLE, CLM4, DAYCENT, LPJ-GUESS, and O-CN) or simply a function of soil N supply (GDAY and SDGVM). Tissue C:N stoichiometry is simulated as fixed (CLM4), flexible within prescribed bounds (CABLE, DAYCENT, LPJ-GUESS, and O-CN), or entirely flexible (GDAY and SDGVM).

C allocation is also simulated differently by each model [De Kauwe et al., 2014]. The approaches taken [see Franklin et al., 2012; De Kauwe et al., 2014] are either fixed allocation fractions (GDAY), a resource limitations approach (CABLE and DAYCENT), a functional relationships approach (LPJ-GUESS and O-CN), a canopy optimization (SDGVM), and increasing the wood allocation fraction as NPP increases (CLM4). Both the resource limitations and functional relationships approaches alter allocation fractions based on resource limitation. The resource limitation approach simply increases allocation fractions to a particular organ (e.g., roots when N or water is limiting), while the functional balance approach alters target organ size ratios and allocation fractions accordingly to achieve those ratios.

C turnover of each tissue type is generally governed by a fixed coefficient, and the vegetation turnover rate can vary depending on the ratios of these tissues. Often, mortality is included in these turnover rates; however, some models also have additional dynamic turnover associated with self-thinning, C starvation, and disturbance. Self-thinning constraints (LPJ-GUESS, O-CN, and SDGVM) are a function of the size of the average crown size and the number of stems per unit ground area (stem density). In SDGVM, NPP must be sufficient to maintain a minimum stem diameter increment, and when this is not possible, stem density is reduced so that the constraint can be satisfied. LPJ-GUESS and O-CN preserve stem diameter to canopy diameter allometric relationships; when stand crown area exceeds a threshold ratio to ground area, stem density is reduced [Sitch et al., 2003]. LPJ-GUESS allows some flexibility in

the crown area to ground area ratio, while O-CN allows no flexibility. C starvation can also cause mortality in a number of these models (CABLE, LPJ-GUESS, O-CN, and SDGVM). Mortality in LPJ-GUESS is predominantly via disturbance and C starvation emerging from competition among trees for resources and rarely via self-thinning.

2.3. Analysis

Following *Rastetter et al.* [1992] and *Zaehle et al.* [2014a], we decompose NPP into component variables that describe two distinct but interrelated N constraints on NPP. The decomposition takes the form:

$$\text{NPP} = fN_{\text{up}} \cdot \text{NUE}, \quad (1)$$

where fN_{up} is the uptake of N from the soil and NUE is nitrogen use efficiency ($\text{NPP}/fN_{\text{up}}$) describing productivity per unit N taken up from the soil. Under $e\text{CO}_2$, an NPP response can be achieved with a response of either fN_{up} , NUE, or both. Therefore, N can constrain the NPP response through fN_{up} , NUE, or both.

We use two analyses to investigate the processes that result in increased C sequestration in response to $e\text{CO}_2$. The first describes a change in equilibrium C pools by a shift in either the flux into the pool (overall C fluxes and the partitioning of that flux to the pool in question) or the turnover rate of that pool. For a single pool with a single incoming flux and a single outgoing flux the rate of change in the size of that pool can be described by the simple linear differential equation [Olson, 1963]:

$$\frac{dC}{dt} = fC_i - fC_o, \quad (2)$$

where C is the pool size and fC_i and fC_o are the incoming and outgoing fluxes. For vegetation, fC_i and fC_o can be described by the equations:

$$fC_i = G_{\text{veg}} \text{NPP}, \quad (3)$$

$$fC_o = \tau_{\text{veg}} C, \quad (4)$$

where NPP is net primary production over a time interval, G_{veg} is the fraction of NPP going to tissue growth, and τ_{veg} is the fraction of the C pool that becomes litter over the time interval (i.e., the turnover rate). When the pool is at equilibrium, the fluxes are in balance and the rate of change in the pool size is zero. Setting dC/dt to zero in equation (2) and substituting in equations (3) and (4) gives:

$$C^e = \frac{G_{\text{veg}} \cdot \text{NPP}}{\tau_{\text{veg}}}, \quad (5)$$

where C^e is the pool size at equilibrium. Equation (5) can be used to describe the response of C^e to a steady perturbation, for our purposes, an increase in CO_2 concentration. The equation is a simple analogue of the biomass component of a forest, describing the relative change in C^e as a result of a relative change in either NPP, G , τ_{veg} , or any combination of the three.

We apply the analysis to C in wood (C_{wood}):

$$C_{\text{wood}}^e = \frac{G_{\text{wood}} \cdot \text{NPP}}{\tau_{\text{wood}}}, \quad (6)$$

where G_{wood} and τ_{wood} are the fraction of NPP partitioned to wood and the turnover rate of wood. We also apply this analysis to soil C:

$$C_{\text{soil}}^e = \frac{\tau_{\text{veg}} \cdot C_{\text{veg}}}{\tau_{\text{soil}}}, \quad (7)$$

where τ_{soil} is the soil turnover rate, calculated as heterotrophic respiration divided by C_{soil} . The numerator is the vegetation turnover rate multiplied by vegetation C as this describes the C inputs to the soil.

To describe the change in ecosystem C in terms of N constraints, we use the analysis of *Rastetter et al.* [1992]:

$$C_{\text{org}} = \left(f_{\text{veg}} \frac{C_{\text{veg}}}{N_{\text{veg}}} + (1 - f_{\text{veg}}) \frac{C_{\text{soil}}}{N_{\text{soil}}} \right) N_{\text{org}}, \quad (8)$$

where C_{org} and N_{org} are organic ecosystem C and N and f_{veg} is the fraction of ecosystem N in vegetation. Equation (8) describes how an increase in C_{org} can be achieved by (1) an increase in ecosystem N (N_{org}), an

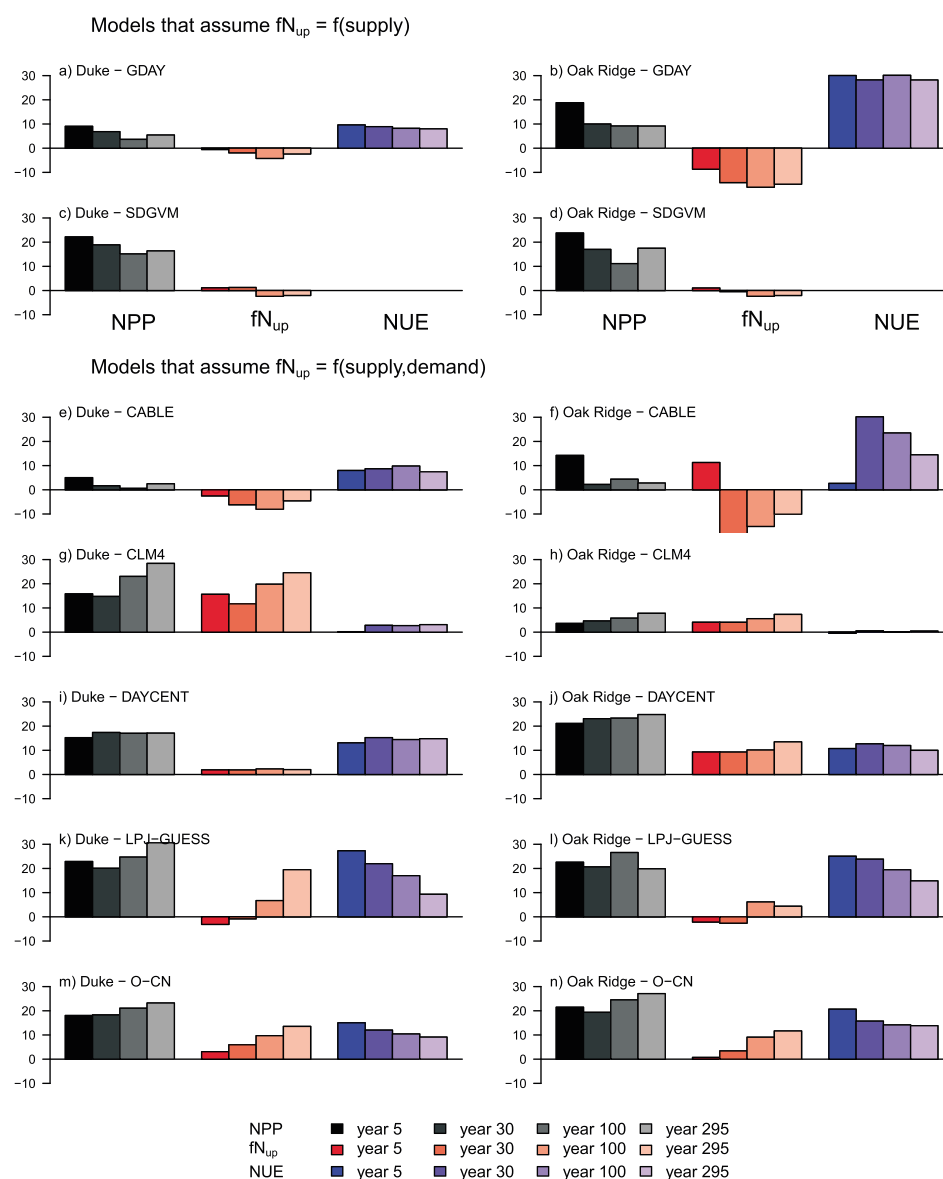


Figure 1. The percentage response of NPP (black bars), N_{up} (red bars), and NUE (blue bars) to a step change in CO_2 from 380 ppmv to 550 ppmv, after 5, 50, 100, and 295 years of CO_2 enrichment. Results are presented for (a, c, e, g, i, k, and m) Duke and (b, d, f, h, j, l, and n) Oak Ridge. Values are 9 year means.

increase in either (2) vegetation or (3) soil C:N ratios, or (4) an increase in f_{veg} which increases the proportion of N in the higher C:N ratio vegetation compared with the soil.

3. Results

3.1. N Constraints on the NPP Response

All models simulated increased NPP in response to eCO_2 , and the NPP response remained positive over 300 years of CO_2 enrichment (Figure 1). Responses for each model were consistent across both sites. Some models showed an increasing NPP trend as enrichment continued (CLM4, DAYCENT at Oak Ridge, LPJ-GUESS at Duke, and O-CN) and others a decreasing trend (CABLE, GDAY, and SDGVM).

We begin with models that assume that fN_{up} is simply a function of N supply (GDAY and SDGVM). GDAY simulates fN_{up} as a fixed fraction of soil mineral N concentration, and GDAY simulated a decrease in fN_{up} . NUE increased as GDAY assumes flexible leaf and fine root C:N ratios in response to increased C availability relative to N availability.

The fN_{up} and NUE response combined resulted in small ($<10\%$ after 30 years) NPP responses (Figures 1a and 1b). In GDAY, eCO_2 increased leaf and fine root C:N ratios increasing N partitioning to long-lived soil organic matter (SOM) pools which slowed N mineralization, the classic PNL described by *Comins and McMurtrie* [1993].

SDGVM assumes that canopy N is a decreasing function of soil C [Woodward *et al.*, 1995]. Increased NPP under eCO_2 resulted in increased litter production and higher soil C which reduced canopy N, decreased photosynthetic rates, and induced PNL of the NPP response to eCO_2 . SDGVM assumes no stoichiometric constraint of N on NPP; hence, NUE for SDGVM was not plotted in Figures 1c and 1d.

CABLE, CLM4, DAYCENT, LPJ-GUESS, and O-CN all assume that fN_{up} is a function of both soil N supply and plant N demand. CABLE simulated decreased fN_{up} in response to eCO_2 (Figures 1e and 1f). Shifts in allocation fractions under eCO_2 (described below) resulted in decreased leaf biomass (approximately 20%) and higher wood and root biomass. This change in allocation increased the C:N of litter inputs to the soil causing higher microbial N demand thus reducing net N mineralization, similar to GDAY. The shift in allocation to higher C:N ratio tissues also minimized any increase in N demand in response to eCO_2 . N demand increased sufficiently to shift allocation toward higher C:N ratio tissues which in turn reduced demand, not sufficiently to prevent the shift in allocation but sufficiently to minimize any increase in N uptake resulting from increased plant demand. Interestingly, it is the allocation scheme in CABLE that caused PNL by shifting litter partitioning to longer-lived SOM pools which reduced N mineralization rates and supply and increased overall plant C:N ratios thereby minimizing increases in plant N demand.

In contrast to CABLE, all the other models that assume that fN_{up} is a function of N supply and demand (CLM4, DAYCENT, LPJ-GUESS, and O-CN) simulated increased fN_{up} in response to eCO_2 . CLM4 simulated increased plant N demand resulting from increased photosynthetic assimilation efficiency and inflexible tissue stoichiometry (which also limits the NUE response). Increased N demand in CLM4 increased plant competitive ability for soil N relative to soil microbes, allowing greater plant N uptake. CLM4 assumes fixed tissue stoichiometry and simulated a small increase in NUE in response to eCO_2 at Duke ($<5\%$ after 30 years, Figure 1g), due to increased wood allocation fractions, but no change in NUE at Oak Ridge.

The responses of NPP, NUE, and fN_{up} simulated by LPJ-GUESS and O-CN were qualitatively very similar (Figures 1k–1n). The initial NPP response was achieved entirely with increased NUE, primarily as a result of flexible tissue stoichiometry [Zaehle *et al.*, 2014a]. Over the course of 300 years of eCO_2 the fN_{up} response gradually increased and the NUE response decreased. Both models simulate N uptake as a function of root mass and plant N demand [Zaehle and Friend, 2010; Smith *et al.*, 2014]. The initial increase in fN_{up} resulted from increased demand and increased root mass (resulting from both increased productivity and increased root allocation fractions caused by increased N limitation).

For CLM4, O-CN, and LPJ-GUESS at both sites, and DAYCENT at Oak Ridge, increased fN_{up} reduced N concentration in the soil solution and reduced ecosystem N losses (Figure 2), allowing N to accumulate in the ecosystem. N in SOM gradually increased allowing increased rates of mineralization, which gradually increased fN_{up} , relieving N stress and supporting higher productivity (Figures 1g–1n). We term this feedback on the NPP response to elevated CO_2 progressive release from N limitation (PRNL). GDAY also reduced ecosystem N losses at Oak Ridge (Figure 2) as a result of reduced mineralization rates but not of the same order of magnitude as the reduced losses caused by increased plant N demand in other models. CLM4 also increased N fixation in response to eCO_2 (up to approximately 0.1 gm^{-2} , N fixation is a function of NPP), but this was an order of magnitude lower than the reduced N losses.

In CLM4 the marked difference in NPP between the two sites resulted from phenological differences affecting turnover dynamics. Demand for N in CLM4 is instantaneous so that when plants are not photosynthesizing, there is no demand for N. In CLM4 deciduous systems, such as Oak Ridge, leaf turnover occurs during canopy senescence and the fine root turnover occurs simultaneously at the same rate, which is an unrealistic assumption [Abramoff and Finzi, 2015]. Decomposition is stimulated by the fresh C and N inputs, yet there is no plant N demand, so any newly mineralized N is extremely vulnerable to the high denitrification rates in CLM4 (note that denitrification rates were reduced in these simulations from the default 0.5 day^{-1} to 0.1 day^{-1} , so this will be an even larger issue in default model simulations). In evergreen systems such as at Duke, litter inputs are more evenly distributed through the year and covary more closely with plant and microbial N demand, so N losses are less vulnerable to denitrification.

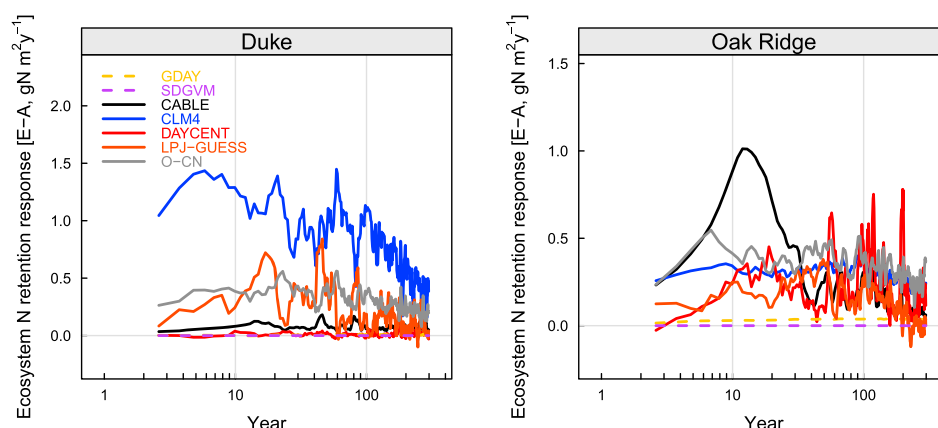


Figure 2. The absolute response of ecosystem N retention ($\text{g N m}^{-2} \text{yr}^{-1}$) to eCO_2 . Ecosystem N retention is defined as the difference between N inputs (deposition and fixation) and N outputs (leaching and gaseous emission). Axes are $\log_{10}$ transformed to illustrate responses at different time scales. Solid lines denote models that assume N uptake is a function of soil N supply and plant N demand. Dashed lines denote models that assume N uptake is a function of soil N supply.

In response to eCO_2 DAYCENT increased both NUE and fN_{up} to similar levels at Oak Ridge, while at Duke the NPP response was mostly achieved by increased NUE (Figures 1i and 1j). Increased root and wood allocation fractions immediately increased NUE due to the higher C:N ratios of these pools compared with leaves. Absolute increases in NPP were similar at both sites (Figures 5a and 5d); however, N requirements to supply the additional growth were higher at Oak Ridge due to lower C:N ratios in all tissues and greater allocation fractions to leaves, which have the lowest tissue C:N ratios. Thus, the site differences of the fN_{up} response were similar to the differences of the N demand response. DAYCENT showed no trend in the response of NPP, NUE, or fN_{up} at Duke and slight PRNL at Oak Ridge. DAYCENT simulates NPP as maximum potential NPP downregulated according to N availability. Maximum potential NPP is simulated as a function of environment, modified by a scalar at eCO_2 . In contrast with other models in which photosynthetic rates and GPP are functions of leaf N content, maximum potential NPP in DAYCENT does not increase with leaf N content. Therefore, once NPP attains the maximum potential NPP, N availability cannot further increase NPP. The stability in the responses simulated by DAYCENT reflects that NPP has reached maximum potential NPP. Slight PRNL occurred in DAYCENT at Oak Ridge as ecosystem N accumulated allowing NPP to approach maximum potential NPP.

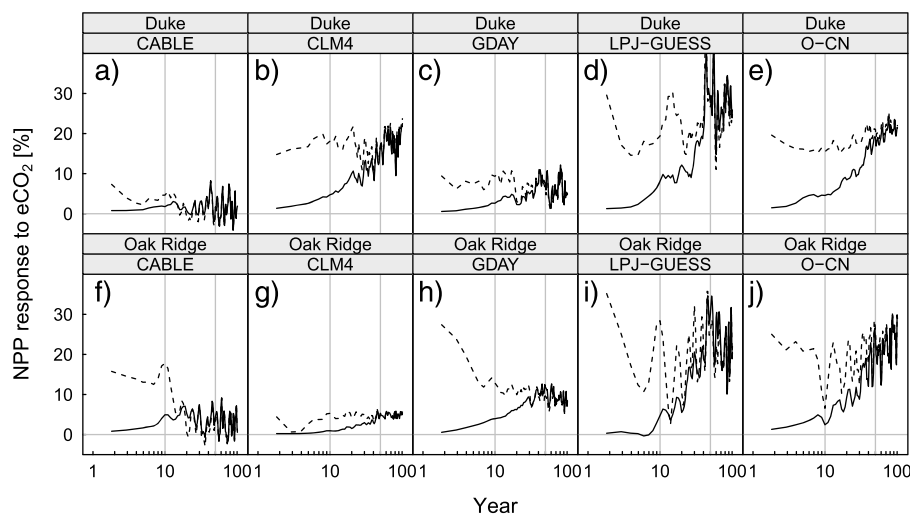


Figure 3. Percentage NPP response to eCO_2 after 2 to 100 years of enrichment in the eStep (black solid line) and eGrad (dashed line) for a reduced set of models. Values are 3 year means. Axes are $\log_{10}$ transformed to illustrate responses at different time scales.

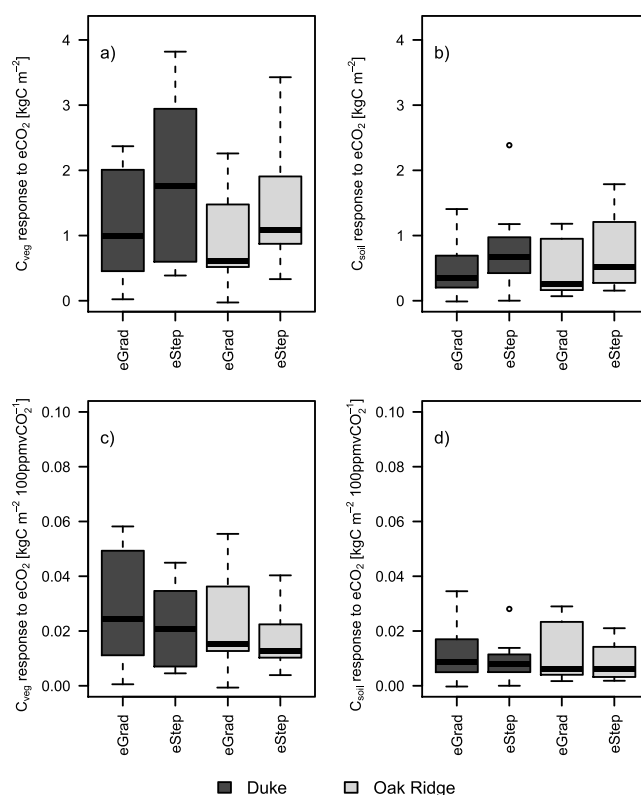


Figure 4. Box and whisker plots showing the distribution of model projections for (a, c) C_{veg} and (b, d) C_{soil} C sequestration after 50 years of CO_2 enrichment in the eStep and eGrad scenarios at Duke (dark grey) and Oak Ridge (light grey). Absolute values (Figures 4a and 4b) and values normalized by the integral of CO_2 enrichment over the 50 years (Figures 4c and 4d).

40–90 years (Figure 3), until the NPP response after 100 years was greater than the initial response, the PNRL we describe above.

3.3. C sequestration After 50 Years of CO_2 Enrichment

Figures 4a and 4b show the range of model projections of C in vegetation and soil in the eStep and eGrad scenarios 50 years after initiation of CO_2 enrichment, the first year in which the eGrad scenario CO_2 concentration reached that of the eStep scenario, i.e., 550 ppmv. Despite very different mean CO_2 concentrations over the first 50 years of each scenario (454 ppmv eGrad versus 550 ppmv eStep), the range of C_{veg} accumulation of both scenarios substantially overlap. That is to say that there was a greater difference in projections of vegetation C sequestration caused by model representations of responses to e CO_2 than caused by very different trajectories of CO_2 increase.

When normalized by the CO_2 addition, C sequestration was greater (for all but one model) in the eGrad scenario than in the eStep scenario (Figures 4c and 4d). This was because the C and N cycles remained more closely synchronized in eGrad, allowing fN_{up} and NUE to fulfill more completely the smaller annual increase in productivity under the eGrad scenario and allowing N to accumulate in the system (as described above) in closer synchronization with the rate of increase in CO_2 .

The models simulated a large range of NPP responses to e CO_2 in the eStep scenario, ranging from about 35% in LPJ-GUESS at Oak Ridge to <5% in CABLE (Figure 3). After 50 years of CO_2 enrichment, the majority of models simulated a similar NPP response in the eGrad scenario as that in the eStep scenario, with some models (GDAY and CABLE) simulating similar responses in each scenario in less than 50 years and only O-CN simulating a similar response after more than 70 years (Figure 3). The differences were due to N cycle feedbacks (discussed

3.2. PNL Under Stepwise or Gradual CO_2 Enrichment

Above we have shown that in response to a step change in CO_2 some models predict PNL while others predict PRNL, and some models predict both effects but at different time scales. Of the models that show PNL in response to a step change in e CO_2 (eStep scenario), none show PNL of the NPP response under gradual CO_2 increase (eGrad scenario, Figure 3). This is because the C and N cycles are desynchronized by the abrupt change in CO_2 concentration in the eStep scenario, equivalent to an environmental disturbance.

PNL was not simulated by any model in the eGrad scenario; i.e., there was no progressive decrease in NPP. However, for all models, NPP in the eGrad scenario met the NPP of the eStep scenario. Thus, for those models that show PNL in the eStep scenario, the NPP response in the eGrad scenario was still N limited, but the characteristic decrease in NPP of PNL was observed only under a step change in CO_2 . O-CN (and CLM at Oak Ridge) under a step change in CO_2 showed PNL in the first decade of enrichment, but this was gradually released over the next

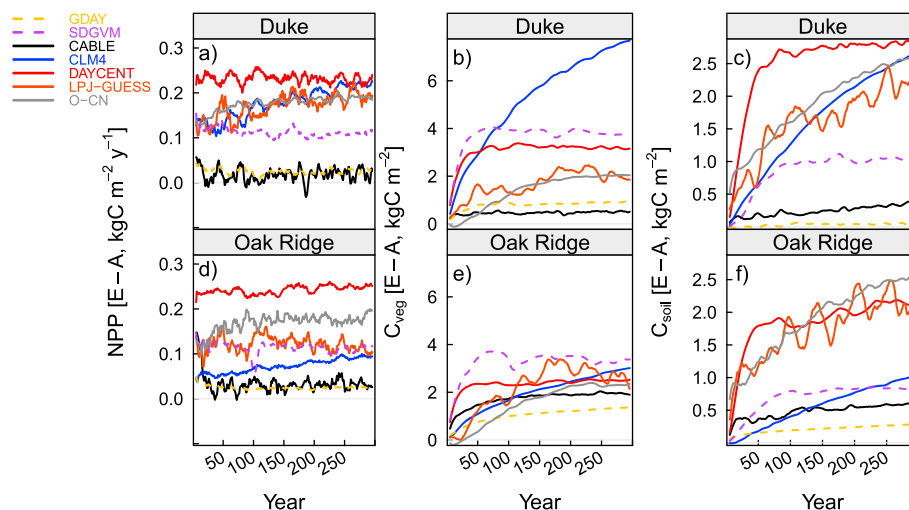


Figure 5. Absolute response of (a, c) NPP, (b, d) C_{veg} , and (c, f) C_{soil} to a step change in CO_2 over 300 years. Values are 9 year means. Solid lines denote models that assume N uptake is a function of soil N supply and plant N demand. Dashed lines denote models that assume N uptake is a function of soil N supply.

above) which limited NPP in GDAY and CABLE but slowly increased the response in O-CN causing a lag in ecosystem N retention under the eGrad scenario compared with eStep.

Depending on the transient response of τ_{veg} , the C_{veg} response was lower than the NPP response in some models (CLM4, GDAY, LPJ-GUESS, and O-CN) and greater than the NPP response in others (CABLE, DAYCENT, and SDGVM) (Figure S2). For CABLE and DAYCENT, the response of τ_{veg} decreased after 50 years, similar to the equilibrium response, which increases the rate of C_{veg} accumulation. For CLM4 and GDAY, the initial response of τ_{veg} was to increase, in contrast to the equilibrium response, in which the rate of C_{veg} accumulation decreased. Because allocation fractions to leaves and fine roots did not change and they equilibrated rapidly, τ_{veg} increased, due to their high τ , and contributed relatively more compared with equilibrium conditions to τ_{veg} than the woody biomass pools (with low τ). Slowing the rate of biomass accumulation, LPJ-GUESS and O-CN both immediately and substantially (approximately 20%) increased τ_{veg} due to their strong canopy area:ground area self-thinning assumptions. By contrast, SDGVM immediately decreased τ_{veg} allowing biomass to rapidly accumulate C. The mechanism was additional to that by which SDGVM reduced τ_{veg} at equilibrium (τ_{veg} is a decreasing function of NPP); the self-thinning constraint in SDGVM (a minimum diameter increment) was released in response to increased NPP. In summary, the transient dynamics of the τ_{veg} responses can be different from the equilibrium response, and they are important for determining C_{veg} after 50 years of CO_2 enrichment, a timeframe of interest for global C dynamics.

3.4. Quasi-Equilibrium Vegetation C

The NPP response of all models (with the exception of CLM4) reached quasi-equilibrium within the 300 years of eCO_2 , and the response ranged from 20 to $250 \text{ g C m}^{-2} \text{ y}^{-1}$ (Figures 5a and 5d). We use the term “quasi-equilibrium” as the true equilibrium of the ecosystem had not yet been reached (i.e., mainly in the “passive” soil C pools which have very slow turnover rates). All models simulated increased vegetation C (C_{veg} ; Figures 5b and 5e) which reached quasi-equilibrium in all but one model (again with the exception of CLM4). For all models at both Duke and Oak Ridge the C_{veg} response was greater and often more than double the C_{soil} response (Figures 5b and 5c and 5e and 5f and Table 2).

Figure 6 shows the quasi-equilibrium responses of C_{veg} (Figures 6a and 6b), C_{wood} (Figures 6c and 6d), and C_{soil} (Figures 6e and 6f) described by equations (5)–(7). The response of NPP to eCO_2 was the primary driver of the C_{veg} response (Figures 6a and 6b) although responses of τ_{veg} were also important and were the primary driver for CABLE and O-CN.

The assumption of fixed allocation fractions and turnover rates (GDAY) resulted in the C_{veg} response to eCO_2 being driven wholly by the NPP response. CLM4 makes very similar assumptions with the addition that

Table 2. Mean Ecosystem State at Ambient and Elevated CO₂ in the Final 50 Years of the Simulations

Site	Model	aCO ₂						eCO ₂					
		C _{veg}	C _{soil}	NPP	τ_{veg}	G _{wood}	τ_{wood}	C _{veg}	C _{soil}	NPP	τ_{veg}	G _{wood}	τ_{wood}
Duke	CABLE	11,394	25,528	1,200	0.11	0.3	0.04	11,905	25,874	1,222	0.10	0.31	0.04
	CLM4	25,158	9,693	785	0.03	0.63	0.03	32,673	12,256	1,003	0.03	0.65	0.03
	DAYCENT	16,243	16,274	1,358	0.08	0.61	0.07	19,420	19,101	1,586	0.08	0.64	0.07
	GDAY	17,350	8,504	487	0.03	0.70	0.02	18,264	8,545	514	0.03	0.70	0.02
	LPJ-GUESS	6,297	5,463	603	0.09	0.27	0.03	8,251	7,654	797	0.09	0.30	0.03
	O-CN	26,473	17,497	796	0.03	0.17	0.04	28,512	20,045	986	0.03	0.18	0.05
Oak Ridge	SDGVM	17,484	8,230	707	0.04	0.38	0.02	21,223	9,285	817	0.04	0.40	0.02
	CABLE	13,567	17,976	916	0.07	0.25	0.02	15,518	18,565	946	0.06	0.27	0.02
	CLM4	36,867	16,175	1,165	0.03	0.64	0.02	39,784	17,154	1,258	0.03	0.64	0.02
	DAYCENT	8,762	10,893	1,024	0.12	0.65	0.10	11,261	13,044	1,274	0.11	0.68	0.10
	GDAY	15,763	4,322	270	0.02	0.63	0.01	17,101	4,597	294	0.02	0.63	0.01
	LPJ-GUESS	8,422	8,056	560	0.06	0.52	0.04	10,976	10,303	671	0.06	0.55	0.04
	O-CN	27,609	18,019	728	0.03	0.19	0.04	29,905	20,554	909	0.03	0.20	0.05
	SDGVM	14,630	5,229	651	0.04	0.36	0.02	17,950	6,062	764	0.04	0.38	0.02

the wood allocation fraction is an increasing function of NPP [Oleson *et al.*, 2010]. Thus, the direct effect of NPP on C_{veg} also had an indirect effect through increasing wood allocation fractions which decreased τ_{veg} . This was not apparent at Oak Ridge due to the lower NPP response.

The canopy optimization, resource limitation, and functional balance assumptions all increased wood allocation. For models with fixed turnover rates (CABLE and DAYCENT) and with τ_{wood} as an increasing function of NPP (SDGVM), increased wood allocation fractions decreased τ_{veg} , contributing to increased C_{veg} (Figures 6a–6d). However, the assumption that self-thinning is a strict allometric function of crown area (O-CN) increased τ_{veg} in response to eCO₂, limiting the C_{veg} response. LPJ-GUESS also assumes self-thinning to be an allometric function, but allowing some canopy overlap and mortality in LPJ-GUESS is dominated by gap dynamics which caused the difference in τ_{veg} between the two sites in these simulations. SDGVM also assumes a self-thinning such that NPP must be sufficient to meet a minimum radial growth increment. The self-thinning routine is such that at a given tree radius vegetation turnover is not a function of NPP (see supporting information) so that eCO₂ does not affect self-thinning at quasi-equilibrium.

3.5. Quasi-Equilibrium Soil C

All models simulated increased soil C (C_{soil}; Figures 5c and 5f), although GDAY simulated very little change in C_{soil} at Duke. After 300 years the C_{soil} trajectories were increasing at a slower rate than initially, indicating that only the long-lived SOM pool remained at disequilibrium (Figures 5c and 5f). The analysis in equation (7) is designed for equilibrium pools, yet we apply the analysis with the caveat that C_{soil} was not completely equilibrated. A consequence of nonequilibrium is that turnover rates may be overestimated as the long-lived pools with low turnover rates are not yet at equilibrium pool size. Inputs to the soil are C_{veg} multiplied by τ_{veg} (equation (7)). While C_{veg} increased in all models, in most models (except O-CN) τ_{veg} decreased so the relative increase in the equilibrium C_{soil} pool size was expected to be smaller than the relative increase in the C_{veg} pool. In O-CN the relative increase in the equilibrium C_{soil} was expected to be larger than the C_{veg} increase, which occurred (Figures 6e and 6f) but the effect was largely counterbalanced by a large (~13%) increase in τ_{soil} (heterotrophic respiration divided by C_{soil}). All the other models also showed a small (1–10%) increase in τ_{soil} , and this factor reduced the relative increase in soil C.

As discussed above, the increase in τ_{soil} under elevated CO₂ could be related to the nonequilibrium state of the long-lived soil C pools. However, there were also several process responses to eCO₂ that were likely to have affected SOM decomposition (turnover). Higher soil water content following reductions in stomatal conductance [Medlyn *et al.*, 2011; De Kauwe *et al.*, 2013] occurred in most models (except DAYCENT at Duke; Figure S3) which would increase SOM decomposition rates. While soil C:N ratios increased in some models indicating that in these N-limited systems, N limitation of soil decomposition most likely increased under eCO₂ slowing decomposition rates. The results suggest that on balance the effect of soil water on decomposition was the stronger effect, although increased decomposition rates were also likely to be a product of the nonequilibrium state of the soils.

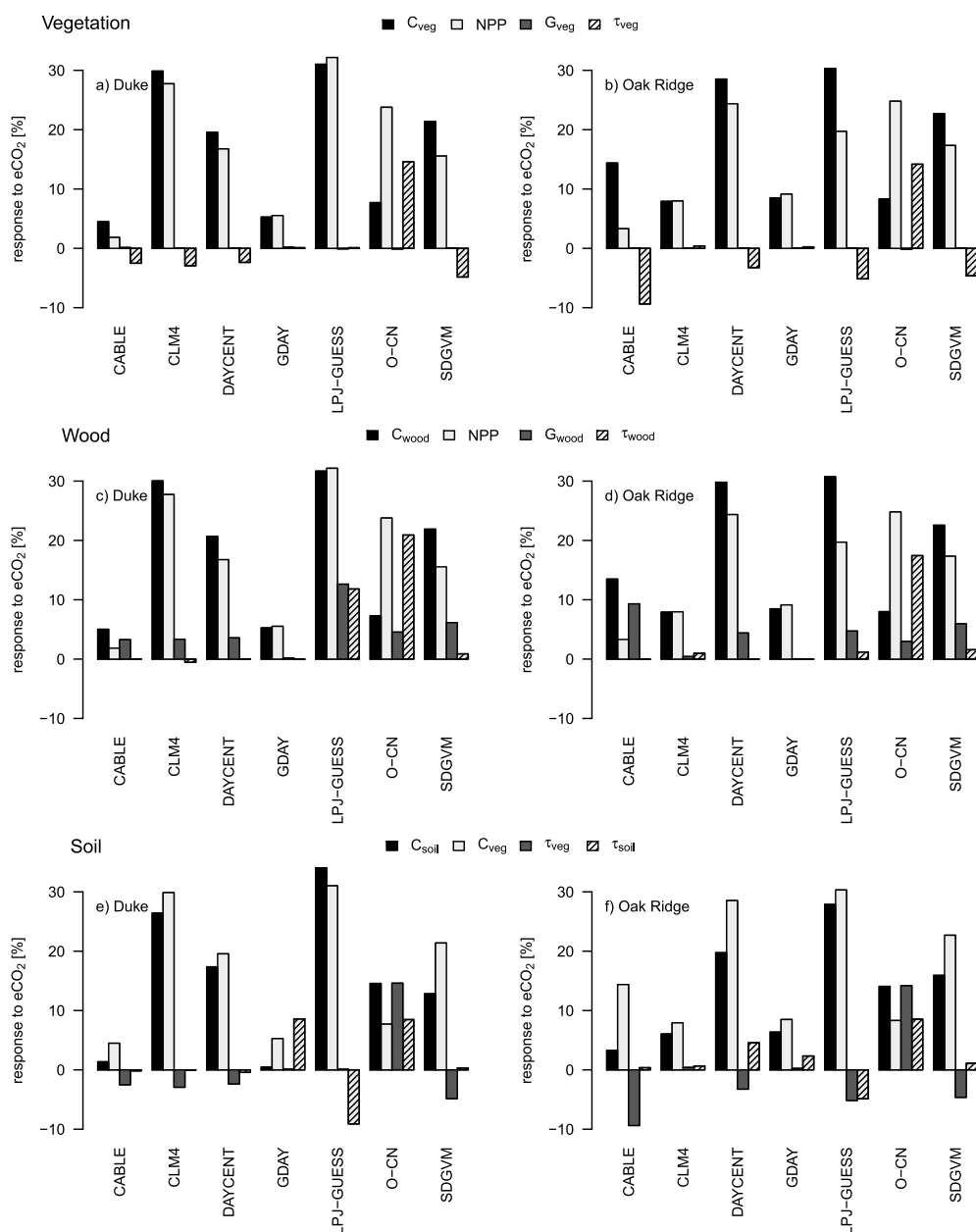


Figure 6. Equilibrium ecosystem C response to CO₂; variables shown are those in equations (a and b) (5), (c and d) (6), and (e and f) (7). Values are means of the final 50 years of the simulations.

3.6. N Constraints on Ecosystem C Sequestration

Ecosystem C sequestration in response to elevated CO₂ is constrained to limits set by the ecosystem's N stoichiometry and N availability. Four factors control the magnitude of C sequestration: (1) change in the ecosystem's N pool, (2) change in the vegetation's C:N ratios (C:N_{veg}), (3) change in the soil's C:N ratios (C:N_{soil}), or (4) change in the partitioning N from the low C:N soil to higher C:N vegetation [Rastetter *et al.*, 1992].

After 10 years of enrichment, models that assume flexible tissue stoichiometry (DAYCENT, GDAY, LPJ-GUESS, and O-CN) showed increased C:N_{veg} in response to N limitation and increased vegetation C sequestration. The assumption of fixed tissue C:N ratios (CLM4) decreased C:N_{veg} in the short term due to a relative increase in the lower C:N ratio leaf and root biomass compared with wood, which resulted from the different equilibration time scales of the biomass pools.

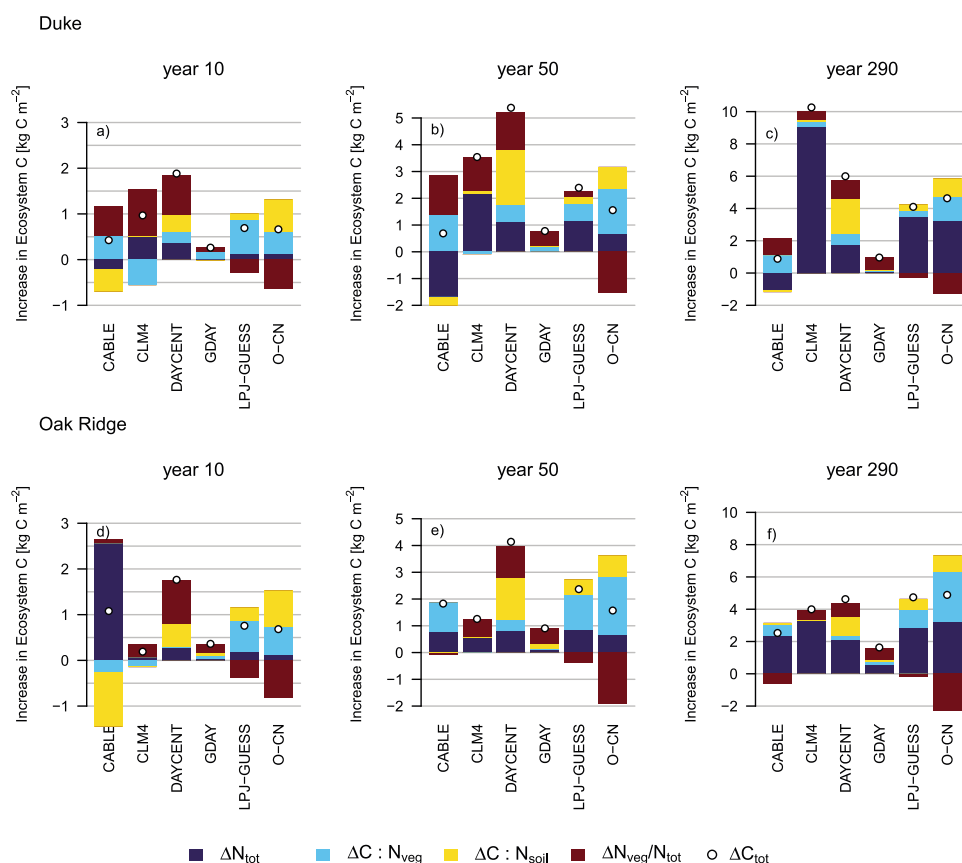


Figure 7. Total change in ecosystem organic carbon (ΔC_{org}) as a result of eCO_2 at the (a–c) Duke and (d–f) Oak Ridge FACE sites after 10 (Figures 7a and 7d), 50 (Figures 7b and 7e) and 290 (Figures 7c and 7f) years resulting from changes in the total organic ecosystem nitrogen (N) store (ΔN_{org}), vegetation and soil C:N ratios ($\Delta C:N_{veg}$ and $\Delta C:N_{soil}$), and changes in the partitioning of total ecosystem N between vegetation and soil (N_{veg}/N_{tot}). Results are 19 year means. SDGVM does not feature on this plot as N is not mass balanced and does not stoichiometrically constrain ecosystem C.

CLM4 assumes that increased plant N demand increases the competitive ability of plants to take up N relative to microbes, thereby reducing soil N immobilization and increasing N in vegetation relative to soil. A feedback caused by the CENTURY soil C decomposition model (employed by most of the models used in this study [see Parton *et al.*, 1987]) is that lower mineral soil N results in higher SOM C:N ratios. As a consequence, less N is required to decompose litter (see Zaehle *et al.* [2014a] for a detailed explanation). CABLE and DAYCENT increased N_{veg}/N_{tot} through increased N uptake which reduced mineral soil N. This also occurred in LPJ-GUESS and O-CN [Zaehle *et al.*, 2014a], but the effect was counteracted by increased litter C:N ratios which increased soil N partitioning to longer-lived turnover pools. GDAY also increased litter C:N ratios but makes the assumption that wood C:N is inflexible (while O-CN and LPJ-GUESS assume flexible wood C:N). The assumptions made on the stoichiometric flexibility of wood could be the reason behind the difference in sign of the N_{veg}/N_{tot} response.

The analysis shows that the contribution of each of these factors to ecosystem C sequestration differed depending on the time scale of interest (Figure 7). After 290 years of CO_2 enrichment, the sign of the effects of soil C:N and N_{veg}/N_{tot} persisted, but for models that simulated PRNL the key process relieving the N constraint on ecosystem C sequestration shifted to increased total ecosystem N (Figures 7c and 7f). For this set of models (CLM4, DAYCENT, LPJ-GUESS, and O-CN), increased total ecosystem N was the cumulative result of increased ecosystem N retention. Changes in total ecosystem N became a greater contributor to ecosystem C sequestration as time progressed (Figure 7). As a result, models that simulated unchanged N losses and thus simulated only small increases in total ecosystem N (CABLE at Duke and GDAY) showed very little increase in ecosystem C.

The models with the largest increases in C sequestration after 50 and 290 years were also those that were capable of increasing ecosystem N retention (CLM4, DAYCENT, LPJ-GUESS, and O-CN). The increase in soil C:N and decrease in N_{veg}/N_{tot} simulated by LPJ-GUESS and O-CN counteracted each other such that increases in ecosystem C were achieved by increased ecosystem N and increased vegetation C:N. Increased vegetation C:N also contributed to increased C sequestration, and this was due to the assumption that wood stoichiometry is flexible. By contrast, DAYCENT achieved C sequestration via increased soil C:N ratios and increased N_{veg}/N_{tot} , and as time progressed increased N_{veg}/N_{tot} contributed relatively less and increased ecosystem N becomes more prevalent. After 50 years in CLM4, increased ecosystem N and increased N_{veg}/N_{tot} contributed equally to C sequestration, and after 290 years increased ecosystem N was the primary driver of C sequestration.

4. Discussion

Seven terrestrial ecosystem models were used to simulate two temperate forests under two regimes of eCO_2 to understand the key processes that influence terrestrial C sequestration over decadal to centennial time scales and to identify the modeling assumptions that cause uncertainty in Earth system model projections. We have shown that the assumptions that describe the processes of N uptake, partitioning of litter among SOM pools, vegetation C allocation, and vegetation turnover are key determinants of ecosystem C sequestration in response to eCO_2 . We found that variability in productivity (NPP) was the primary driver of variability in ecosystem C sequestration. N uptake dynamics were the key drivers of variability in model projections of the NPP response to eCO_2 . Both progressive N limitation (PNL) and progressive release from N limitation (PRNL) were simulated. *Friend et al.* [2013] found that C turnover time was the larger driver of uncertainty in C sequestration compared with NPP in a suite of global simulations using models primarily without an N cycle (all but HYBRID). In contrast to the findings of *Friend et al.* [2013], our results suggest that when an N cycle becomes the norm in global models, NPP is likely to be a more substantial contributor to uncertainty in C sequestration, unless the uncertainty in the N cycle assumptions made across the models can be reduced.

All dynamic allocation assumptions (i.e., all assumptions except fixed allocation fractions) and canopy area: ground area self-thinning had a substantial impact on quasi-equilibrium C sequestration, though turnover was the primary driver for only two models (CABLE and O-CN). Most allocation assumptions resulted in decreased vegetation turnover in response to eCO_2 , thereby increasing C_{veg} to levels greater than would be expected from increased NPP alone. The strict self-thinning assumption (O-CN) increased vegetation turnover which strongly limited the magnitude of the C_{veg} response and was the primary driver of ecosystem C sequestration in O-CN. Relative increases in C_{soil} were generally smaller than the relative increases in C_{veg} as the C_{veg} turnover rate often decreased and the soil turnover rate increased, most likely as a result of increased soil water content under eCO_2 .

4.1. Modeling Assumptions That Require Attention: C and N Interactions

A key difference among the models used in this study is the N uptake assumption, in particular whether plant N demand is applied to N uptake or not. Using an early version of GDAY, *Comins and McMurtrie* [1993] showed that PNL of the CO_2 response was caused by a transfer of N to longer turnover time pools, primarily as a consequence of increasing litter C:N ratios. However, we have shown that the assumption that N uptake is solely a function of soil N supply was a key determinant of PNL (two models of two that make the assumption—GDAY and SDGVM). Four models (CLM4, DAYCENT, O-CN, and LPJ-GUESS) of five that assume N uptake is a function of both N supply and demand simulated a sustained or increasing CO_2 response over decadal time scales.

The concept of plant N demand also varies across these models. For CABLE, CLM4, and DAYCENT, demand is the stoichiometric N requirement to match the carbon available for growth in a single time step [*Oleson et al.*, 2010; *Wang et al.*, 2010]. For O-CN, demand is a function of N needed to provide a sufficient buffer to meet annual growth requirements [*Zaehle and Friend*, 2010]. LPJ-GUESS simulates N demand as the leaf N that will maximize canopy photosynthesis under current environmental conditions, multiplied by concomitant N ratios to other pools [*Smith et al.*, 2014]. Notwithstanding these differences, most of these representations of demand resulted in comparable trajectories of CO_2 uptake if N uptake was a function of demand.

CABLE was the only model with demand-based uptake that simulated PNL. CABLE was also the only model to simulate a decrease in leaf biomass (approximately 20%, the reasons for which are described below), not just a decrease in the leaf allocation fraction, which led to strongly increased litter C:N ratios as wood and root

litter inputs (with higher C:N ratios than leaves) were a substantially higher fraction of total litter. As with GDAY, increased litter C:N ratios increased partitioning to longer-lived SOM pools thus reducing N mineralization rates and restricting NPP gains in response to $e\text{CO}_2$. The decrease in low C:N ratio leaf biomass also minimized any increase in N demand which prevented a substantial increase in N uptake under $e\text{CO}_2$. However, increased vegetation C:N ratio in CABLE also increased NUE, which relaxed the stoichiometric N constraint on NPP, allowing increased C_{veg} per unit of N. Similarly, some models (e.g., O-CN) simulated increased wood C:N based on the assumption that wood C:N ratios are flexible. There was no evidence to suggest that wood C:N ratios were strongly affected by $e\text{CO}_2$ at either site [Norby and Iversen, 2006; Finzi et al., 2007]. Effects of $e\text{CO}_2$ on wood C:N has implications for both aboveground C sequestration and belowground SOM decomposition allowing for complex effects on overall ecosystem C sequestration. To accurately characterize terrestrial ecosystem C sequestration, we need to improve the representation of the flexibility of C:N stoichiometry in the face of a changing environment. Furthermore, increased soil water likely increased soil N turnover rates in many models, and all of these countervailing effects warrant further investigation.

Zaehle et al. [2014a] described the responses of C and N interactions in these models over the experimental (11 year) period. In general, all the models predicted PNL over this time scale, a prediction that was in contrast to the observations at Duke. A mechanism by which plants obtained N at both experimental sites was shown to be missing from the models [Zaehle et al., 2014a], most likely increased SOM decomposition rates under $e\text{CO}_2$, often referred to as priming, which has been shown to be common across many $e\text{CO}_2$ experiments [van Groenigen et al., 2014]. None of the seven models that we used include a priming mechanism that could reduce the effects of PNL. Nonetheless, it is likely that this effect would be unsustainable (as soil N stocks decline) and that supply versus supply and demand-based N uptake assumptions would still lead to the diverging NPP responses shown in this study.

A further model assumption contributing to preventing PNL through N demand-based N uptake is that the ecosystem loses N as a function of soil mineral N concentration [Thomas et al., 2013]. Under $e\text{CO}_2$, demand-based N uptake increased plant N uptake, which sustained the CO_2 response and reduced mineral N concentration in the soil solution. The subsequent reduction in concentration-dependent N losses under $e\text{CO}_2$ allowed the ecosystem to retain N and build N capital, which released some of the CO_2 response from N limitation.

Ecosystem N losses also occur through leaching of dissolved organic matter (DOM), an N loss pathway not considered by the suite of models employed in this study (nor more generally in this class of model). In natural ecosystems with minimal N deposition in Chile and Argentina, N loss via leaching of DOM can be up to 95% of leached N [Hedin et al., 1995; Perakis and Hedin, 2002]. In ecosystems of the northeastern U.S. where there are larger N deposition rates, while the absolute magnitude of N loss via leached DOM can be similar to low N deposition systems, the percentage contribution to total leached N can be less than 25% [Perakis and Hedin, 2002]. Plants have limited control over DOM N losses as they have limited capacity to take up organic N, though mycorrhizal symbionts can supply organic N to plants [McFarland et al., 2010]. Mycorrhizae are able to up regulate organic N uptake in response to C transfer from their plant symbiont [Fellbaum et al., 2012], which may increase under $e\text{CO}_2$ conditions [Chen et al., 2007; Drigo et al., 2013].

We have demonstrated that the capacity of forest trees to exhibit PNL or PRNL in response to $e\text{CO}_2$ depends on their capacity to reduce ecosystem N losses as a result of increased N demand. To determine the response of forests globally will require an understanding of the controls on fractionation of N loss between different pathways, how plant available the N is within these different pathways, including the capacity of plants and their mycorrhizal symbionts to increase DOM N uptake under $e\text{CO}_2$. Until we can accurately represent N uptake in a common framework across models, predictions of terrestrial C sequestration in response to $e\text{CO}_2$ are likely to continue to exhibit large uncertainty.

4.2. Modeling Assumptions That Require Attention: Allocation and Turnover

C_{veg} responses to $e\text{CO}_2$ were not solely driven by NPP responses. For example, SDGVM at Oak Ridge had a moderate NPP response but the largest C_{veg} response and although CLM4 and O-CN had similar NPP responses at Duke, their C_{veg} responses were very different (Figures 5a, 5b, and 6a). C_{veg} responses were also a result of changes in vegetation turnover rates (τ_{veg}). By either changing the intrinsic turnover rate of each vegetation biomass pool or by changing the relative contribution of each biomass pool to C_{veg} , τ_{veg} can shift, i.e., changing C allocation fractions. Other than the fixed coefficient assumption, all other model assumptions

increased wood allocation fractions in response to $e\text{CO}_2$, and the assumptions responsible for this are described in detail in *De Kauwe et al.* [2014]. CABLE was the only model that employed a slightly different allocation scheme in the simulations in this study to those of *De Kauwe et al.* [2014]. Instead of fixed coefficients that vary among phenological phases (described by *De Kauwe et al.* [2014]), CABLE employed a resource limitations approach during the second phenological phase. During the resource limitation phase, CABLE increases C allocation fractions to roots (and wood) in response to N or water stress after [*Friedlingstein et al.*, 1999]. Under $e\text{CO}_2$, CABLE increased root biomass in response to increased N limitation, yet despite the increase in root biomass, N limitation was not sufficiently relieved and the leaf allocation fraction and leaf biomass remained lower in response to $e\text{CO}_2$. By increasing vegetation and litter C:N ratios, the allocation response both limited soil N supply and restricted increases in plant N demand, reducing plant N uptake and inducing PNL. Furthermore, the allocation response increased NUE and decreased turnover rate such that almost the entirety of the CABLE response was due to the allocation response.

The assumption of fixed turnover rates had no impact on the CO_2 response. However, the canopy area:ground area constraint assumed by LPJ-GUESS and O-CN (and others in the LPJ clade) resulted in a strong self-thinning constraint which increased τ_{veg} in response to increased productivity under $e\text{CO}_2$. Similarly, *Bugmann and Bigler* [2011] assumed τ_{veg} to be an increasing function of growth rates and therefore predicted very little change in C_{veg} under $e\text{CO}_2$. SDGVM also employs a self-thinning constraint whereby a minimum growth increment must be satisfied. In SDGVM, there was no change in τ_{veg} once C_{veg} equilibrium had been reached, but during the transient phase self-thinning decreased substantially causing a rapid increase in C_{veg} in response to $e\text{CO}_2$.

Observational evidence shows that biomass to productivity relationships are nonlinear [*Keeling and Phillips*, 2007; *Quesada et al.*, 2012], and modeling studies have demonstrated that default model assumptions do not accurately reproduce regional patterns of biomass [*Delbart et al.*, 2010; *Castanho et al.*, 2013]. Both C allocation fractions and τ_{veg} are key drivers of terrestrial C sequestration, yet methods to simulate these processes are diverse [*McDowell et al.*, 2013; *De Kauwe et al.*, 2014], often have limited empirical support, and can produce unintended consequences [*De Kauwe et al.*, 2014].

Accurate simulation of terrestrial C sequestration over the coming century will depend on the response of τ_{veg} to increasing CO_2 , manifest by shifts in allocation, and perhaps direct changes in litterfall and mortality rates. It is imperative that we understand and generate mechanistic hypotheses to represent the process of allocation and the multiple processes that drive tree mortality.

4.3. Application to Experiments

FACE experiments necessarily employed a step change from ambient CO_2 concentrations (approximately 380 ppmv) to elevated CO_2 concentrations (approximately 550–600 ppmv) creating an abrupt change in the environment that could be viewed as an ecological disturbance [*Grime*, 1977]. By stimulating photosynthesis, the disturbance alters the rate of C entry into the ecosystem relative to the rate at which N becomes available within the ecosystem, similar to the desynchronization of N and phosphorus cycling following a disturbance described by *Rastetter et al.* [2013]. A period of recovery follows during which C and N cycles must resynchronize. During this recovery period, resynchronization of the C and N cycles caused a decrease in the NPP response, the classic PNL, in all models.

Simulations of a gradual rise in CO_2 concentrations did not result in PNL, suggesting that PNL could be a result of the CO_2 step change disturbance. However, in the period where eGrad and eStep had similar CO_2 concentrations, no model showed a difference between the eStep and eGrad scenarios. This suggests that the eGrad scenario was still N limited and that the mechanisms of N uptake, tissue stoichiometry, and litter partitioning had a very similar effect in the eGrad and eStep scenarios after 30–70 years. Key to the interpretation of the field experiments is that the response to a step change in CO_2 was not the same as the response 50 years into the gradual change scenario (i.e., when CO_2 concentrations were 550 ppmv). In models that showed PRNL, the NPP response to CO_2 in the first 1–3 years postenrichment in the eStep scenario was similar to the NPP response 50 years into the eGrad scenario. In contrast, for models that showed PNL the NPP response 50 years into the eGrad scenario was much lower than NPP in the first decade postenrichment in the eStep scenario. This difference was primarily a result of the model's capacity to reduce N losses, as a consequence of demand-based N uptake, and is key to the long-term interpretation of results from FACE experiments.

Stimulation of N uptake by plant N demand was a key contributor to model variability, and plant N uptake stimulated by demand is more consistent with current theory [Fisher *et al.*, 2010; Ning *et al.*, 2012]. The simulations show that the differences in terms of ecosystem-scale, annual N retention were small. Differentiation between PNL and PRNL trajectories resulting from changed losses would require measurements that detect changes in ecosystem N of the order of $0.2 \text{ g N m}^{-2} \text{ y}^{-1}$, measurements that would be challenging to make. N deposition was the primary source of the additional ecosystem N in these simulations. Sustained or PRNL of the NPP response depends on this supply of additional N. Also, increased soil decomposition rates were observed in many eCO_2 experiments [van Groenigen *et al.*, 2014] and were not captured by any of this suite of models [Zaehle *et al.*, 2014a], the dynamics of which are complex but could increase long-term ecosystem N recycling rates. However, we were unable to test those effects with the current suite of models.

Another process by which exogenous N may accumulate in the system is through increased N fixation. CABLE, CLM4, LPJ-GUESS, and O-CN all simulated N fixation in these simulations. However, CLM4 was the only model to simulate a response of N fixation to eCO_2 though it remained an order of magnitude lower than ecosystem N retention caused by reduced N losses (at Duke approximately $0.1 \text{ g m}^{-2} \text{ y}^{-1}$ compared with approximately $1 \text{ g m}^{-2} \text{ y}^{-1}$). There was evidence for nitrogen fixation in the Oak Ridge experiment, and an increasing presence of *Elaeagnus umbellata* (an invasive actinorhizal N fixing shrub) was noted in the final years at Oak Ridge experiment [Souza *et al.*, 2010]. There was no statistically significant effect of eCO_2 on *E. umbellata* abundance, but N was strongly limiting in both treatments [Norby *et al.*, 2010], so a substantial treatment effect may not be expected. In a scrub oak ecosystem, Hungate *et al.* [2004] noted an immediate stimulation of N fixation under eCO_2 ; however, the initial stimulation declined over time, most likely due to decreasing molybdenum availability. Increased N limitation under eCO_2 conditions could give N fixers a competitive advantage. Yet symbiotic N fixing trees are often absent from the canopies of N-limited, temperate forests [Vitousek *et al.*, 2002, 2013], and the global distribution of N fixers is tied to the acquisition of phosphorus (P) [Houlton *et al.*, 2008]. The limited response of N fixation to CO_2 in CLM, and zero response in other models, was because N fixation was not simulated as a function of N demand, or in the case of CABLE, demand was not stimulated.

As we have shown, and as others have shown before [Rastetter *et al.*, 1997; Kirschbaum *et al.*, 1998], the C sequestration response of forests depends on the openness of the N cycle and the ability of plants to reduce N losses under eCO_2 . When planning CO_2 experiments, researchers should attempt to quantify the openness of nutrient cycles and the ability of plants to reduce losses. An understanding of these factors across global biomes will help to accurately assess terrestrial ecosystem responses to rising CO_2 .

4.3.1. Summary List of Recommendations for Experiments and Modeling

1. The factors that determine N recycling rates within an ecosystem are keys to predicting the N constraints on ecosystem responses to eCO_2 ; these include the following: (a) quantification of plant N uptake at the ecosystem scale and how N supply and N demand interact to control N uptake need to be better understood. This includes improved theory of plant N demand, how demand relates to stoichiometry, the time scales over which demand is integrated, and the response of plant and mycorrhizal DOM N uptake to eCO_2 . (b) Understanding the controls on partitioning between different N loss pathways—leached mineral N and DOM N and gaseous losses—in both human-influenced and pristine ecosystems. (c) Understanding the controls on N entry into the ecosystem—deposition and N fixation. In particular, how N fixation will respond increased N demand resulting from eCO_2 with consideration for its potential colimitation by other nutrients.
2. The dynamics of C allocation and the strength of C allocation flexibility in the face of multiple limiting resources—light, nutrients, and water—must be better understood.
3. The controls on self-thinning and mortality of forest stands and how these might be influenced by eCO_2 should be studied.

Finally, the step change in CO_2 induced PNL in these models. Some models contained processes that lead to the release of PNL over time. Caution must therefore be applied when interpreting results from step change experiments in the context of the current, gradual rise in atmospheric CO_2 concentrations. The effects of eCO_2 on soil decomposition rates require further modeling and experimental study to compare the difference between a step and a gradual increase in CO_2 .

5. Conclusions

Current carbon cycle research aims to answer the question: how much atmospheric carbon is sequestered by terrestrial ecosystems and how will C sequestration change in response to rising atmospheric CO₂ and climate change? As the net flux of carbon into terrestrial ecosystems, NPP is clearly a major driver of terrestrial C sequestration. We show that models predict both PNL and PRNL of NPP depending on time scale and the N uptake assumptions made. The long-term sustainability of the CO₂ response depends on the capacity of the ecosystem to reduce N losses, build N capital, and increase internal N cycling rates. The ambiguity in the representation of N dynamics is a key source of uncertainty in model simulations of NPP, and work is needed to further understand plant N uptake from the soil at the ecosystem scale.

Ecosystem carbon sequestration is not solely a function of the inputs into the system (NPP) but also a function of outputs from the system or the turnover rate of carbon in the system. If the turnover rate of carbon in the ecosystem is affected by eCO₂, then there is the potential for additional feedback on atmospheric CO₂ concentrations that may amplify or damp the photosynthetic feedback. We have shown that models predict both positive and negative signs of this feedback through shifts in biomass partitioning toward wood or increases in the rate of biomass turnover, i.e., litterfall or mortality. It is imperative that we improve and reduce uncertainty in the modeling algorithms that represent the complex processes of allocation, litterfall, and mortality.

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