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RESEARCH ARTICLE

# Acclimation of Photosynthesis to $CO_2$ Increases Ecosystem Carbon Storage due to Leaf Nitrogen Savings

Nicholas G. Smith[1] | Qing Zhu[2] | Trevor F. Keenan[2,3] | William J. Riley[2]

[1]Department of Biological Sciences, Texas Tech University, Lubbock, Texas, USA | [2]Climate and Ecosystem Sciences, Lawrence Berkeley National Laboratory, Berkeley, California, USA | [3]Department of Environmental Science, Policy and Management, UC Berkeley, Berkeley, California, USA

**Correspondence:** Nicholas G. Smith (nick.smith@ttu.edu) | Qing Zhu (qzhu@lbl.gov)

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## ABSTRACT

Photosynthesis is the largest flux of carbon between the atmosphere and Earth's surface and is driven by enzymes that require nitrogen, namely, ribulose-1,5-bisphosphate (RuBisCO). Thus, photosynthesis is a key link between the terrestrial carbon and nitrogen cycle, and the representation of this link is critical for coupled carbon-nitrogen land surface models. Models and observations suggest that soil nitrogen availability can limit plant productivity increases under elevated $CO_2$. Plants acclimate to elevated $CO_2$ by downregulating RuBisCO and thus nitrogen in leaves, but this acclimation response is not currently included in land surface models. Acclimation of photosynthesis to $CO_2$ can be simulated by the photosynthetic optimality theory in a way that matches observations. Here, we incorporated this theory into the land surface component of the Energy Exascale Earth System Model (ELM). We simulated land surface carbon and nitrogen processes under future elevated $CO_2$ conditions to 2100 using the RCP8.5 high emission scenario. Our simulations showed that when photosynthetic acclimation is considered, photosynthesis increases under future conditions, but maximum RuBisCO carboxylation and thus photosynthetic nitrogen demand decline. We analyzed two simulations that differed as to whether the saved nitrogen could be used in other parts of the plant. The allocation of saved leaf nitrogen to other parts of the plant led to (1) a direct alleviation of plant nitrogen limitation through reduced leaf nitrogen requirements and (2) an indirect reduction in plant nitrogen limitation through an enhancement of root growth that led to increased plant nitrogen uptake. As a result, reallocation of saved leaf nitrogen increased ecosystem carbon stocks by 50.3% in 2100 as compared to a simulation without reallocation of saved leaf nitrogen. These results suggest that land surface models may overestimate future ecosystem nitrogen limitation if they do not incorporate leaf nitrogen savings resulting from photosynthetic acclimation to elevated $CO_2$.

## 1 | Introduction

Photosynthesis on land represents the largest flux of carbon between the atmosphere and the Earth's surface (Ciais et al. 2013) and thus represents a key process for understanding and predicting the rate and magnitude of atmospheric $CO_2$ change. However, photosynthetic processes are some of the largest sources of uncertainty in predictions of biosphere-atmosphere $CO_2$ feedbacks by land surface models (Ziehn et al. 2011; Booth et al. 2012). These models represent and parameterize photosynthetic processes differently (Smith and Dukes 2013; Rogers et al. 2017), reflecting uncertainty in mechanistic understanding.

Photosynthesis is important for connecting terrestrial carbon and nitrogen cycles because photosynthesis is driven by enzymes that require nitrogen to build (Arneth et al. 2010; Zaehle et al. 2014; Walker et al. 2021). Chief among these enzymes is ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), which is made up of ~20% nitrogen (Harrison et al. 2009) and constitutes ~18% of leaf nitrogen globally (Luo et al. 2021). As such, uncertainty in the parameterization of photosynthetic processes influences estimates of both future carbon and nitrogen cycling under global change.

Given the fact that a large amount of leaf nitrogen is required to support photosynthetic processes, many coupled carbon–nitrogen land surface models simulate photosynthesis as a function of leaf nitrogen, which is affected by soil nitrogen uptake and allocation processes (Smith and Dukes 2013; Rogers et al. 2017; Zhu et al. 2019). For example, leaf nitrogen has been widely used to directly scale the maximum rate of RuBisCO carboxylation ($V_{\mathrm{cmax}}$; Kattge et al. 2009; Walker et al. 2014) and thus leaf photosynthetic rates. This method has led to projections of photosynthetic rates becoming increasingly nitrogen-limited under elevated $CO_2$ conditions due to lower simulated leaf nitrogen concentrations (Thornton et al. 2007; Wieder et al. 2015), particularly when leaf carbon to nitrogen ratios are set to match observations (Hauser et al. 2023). Furthermore, the plant growth rate is also predicted to be reduced under elevated $CO_2$ due to reduced photosynthesis and direct nitrogen limitations to biomass production (Thornton et al. 2007; Wieder et al. 2015; Zhu et al. 2020), which has been observed in some free air $CO_2$ fertilization experiments (e.g., Norby et al. 2010; Jiang et al. 2020), but this response is not uniform across studies (e.g., McCarthy et al. 2010; Norby et al. 2024). Reductions in the stimulation of plant productivity under elevated $CO_2$ due to nitrogen limitations is part of so-called "progressive nitrogen limitation" (Luo et al. 2004), which posits that $CO_2$ fertilization of plant productivity will become increasingly limited by nitrogen availability.

Data from $CO_2$ fertilization experiments (e.g., Ainsworth and Long 2005; Ainsworth and Rogers 2007; Leakey et al. 2009) indicate that plants grown under elevated $CO_2$ have reduced leaf nitrogen concentration and amount per area, reduced leaf RuBisCO amount per area, and reduced leaf $V_{\mathrm{cmax}}$ per area than those grown under ambient $CO_2$ (Poorter et al. 2022). While these responses may be thought to support "progressive nitrogen limitation," they may instead be the result of photosynthetic acclimation to $CO_2$ (Bazzaz 1990). The observed decreases in the RuBisCO amount per leaf area under elevated $CO_2$ are consistent with a lower RuBisCO demand needed to use available light for photosynthesis (Bazzaz 1990; Smith and Dukes 2013; Dusenge, Duarte, and Way 2019). A recent analysis using data from 31 elevated $CO_2$ experiments showed that reduced $V_{\mathrm{cmax}}$ under elevated $CO_2$ is consistent with photosynthetic acclimation and not the result of nitrogen limitation (Smith and Keenan 2020). The reduced nitrogen investment in RuBisCO under elevated $CO_2$ hypothetically liberates nitrogen for use elsewhere in the plant.

Despite evidence that acclimation to elevated $CO_2$ is likely to reduce demand at the leaf level for nitrogen to build RuBisCO, models typically do not account for this downregulation (Smith and Dukes 2013). As such, these models might be overestimating future nitrogen demand for photosynthesis. Furthermore, the downregulation of RuBisCO nitrogen at the leaf level could liberate nitrogen and alleviate nitrogen limitation at the plant and ecosystem level. Importantly, reduced nitrogen limitation due to photosynthetic acclimation to elevated $CO_2$ could alter projections of future carbon uptake and storage and, thus, climate change.

Here, we assess whether acclimation of plant photosynthesis that results in RuBisCO and leaf nitrogen downregulation under elevated $CO_2$ will partially alleviate elevated $CO_2$-induced nitrogen limitation of productivity. To do so, we integrated a model of $C_3$ photosynthetic biochemistry acclimation (Smith et al. 2019; Smith and Keenan 2020; Stocker et al. 2020), based on developments of the least-cost theory of photosynthesis (Wright, Reich, and Westoby 2003; Wang et al. 2017) into the ELM land model (ELM; Zhu et al. 2019) of the Energy Exascale Earth System Model (E3SM; Golaz et al. 2019). We examined how downregulation of photosynthetic biochemistry that results from photosynthetic acclimation to elevated $CO_2$ would impact land surface processes related to carbon and nitrogen cycling. ELM was an appropriate testbed for asking this question because of its dynamic carbon and nutrient allocation scheme, which allows plants to utilize available nutrients to dynamically support processes based on demand and resource limitation constraints (Zhu et al. 2019). Briefly, we reconfigured the photosynthetic scheme in ELM such that $V_{\mathrm{cmax}}$ acclimates to a 10-day trailing average of aboveground climate (i.e., temperature and light) and atmospheric $CO_2$ and that plants allocated nitrogen to meet that demand for $V_{\mathrm{cmax}}$ in existing leaves. If that demand was met, any available nitrogen leftover was used to support other processes as dictated by the allocation scheme.

We ran two ELM simulations to examine the effect of optimal photosynthetic acclimation and use of the resulting nitrogen savings on global leaf, plant, and ecosystem processes. We forced the model with constant climate, but with projected high emission $CO_2$ changes to 2100 (RCP8.5; van Vuuren et al. 2011) to isolate the effect of elevated $CO_2$. Both simulations included acclimated photosynthesis following Smith and Keenan (2020) that allowed $V_{\mathrm{cmax}}$ to acclimate to a 10-day trailing average of aboveground climate and atmospheric $CO_2$. However, one simulation (Simulation A) did not allow for allocation to the rest of the plant of the excess leaf N beyond that required for $V_{\mathrm{cmax}}$ (i.e., excess nitrogen remained in the leaf). In contrast, Simulation B allowed for allocation of excess nitrogen to the rest of the plant (termed leaf nitrogen savings). The configuration of the two simulations is summarized in Table 1. We hypothesized the following:

1. Future elevated $CO_2$ would increase leaf net photosynthesis at a lower amount of leaf nitrogen due to acclimation of photosynthetic biochemistry in the simulation that allowed for allocation of leaf nitrogen savings (Simulation B) compared to the simulation that did not allow for that allocation (Simulation A).
2. Reductions in per-leaf-area nitrogen under elevated $CO_2$ in Simulation B would allow for more nitrogen to be used for

**TABLE 1** | Summarized configuration of ELM simulations.[a]

| | Simulation A | Simulation B | Difference |
|---|---|---|---|
| Time period | 1900–2100 | 1900–2100 | No |
| Climate forcing | 1901 to 2010: GSWP3 reanalysis forcing 2011–2100: 2001–2010 repeated climate forcings | 1901 to 2010: GSWP3 reanalysis forcing 2011–2100: 2001–2010 repeated climate forcings | No |
| $CO_2$ forcing | 1901–2010: transient $CO_2$ concentrations; 2011–2100: $CO_2$ concentrations from RCP8.5 | 1901–2010: transient $CO_2$ concentrations; 2011–2100: $CO_2$ concentrations from RCP8.5 | No |
| Photosynthesis | Farquhar, von Caemmerer, and Berry (1980) scheme with acclimation of $V_{cmax}$ following Smith and Keenan (2020) | Farquhar, von Caemmerer, and Berry (1980) scheme with acclimation of $V_{cmax}$ following Smith and Keenan (2020) | No |
| Leaf nitrogen | Leaf nitrogen savings from acclimated $V_{cmax}$ remain in the leaf | Leaf nitrogen savings from acclimated $V_{cmax}$ can be allocated throughout the plant | **Yes** |
| Whole-plant allocation | Dynamic allocation of carbon and nitrogen to leaf, stem, and root tissue in response to light, water, and nitrogen limitations (Friedlingstein et al. 1999) | Dynamic allocation of carbon and nitrogen to leaf, stem, and root tissue in response to light, water, and nitrogen limitations (Friedlingstein et al. 1999) | No |
| Nitrogen acquisition | Competition for soil nitrogen among plant, microbial immobilizers, nitrifiers, and denitrifiers resolved with equilibrium chemistry approximation (Zhu et al. 2016) | Competition for soil nitrogen among plant, microbial immobilizers, nitrifiers, and denitrifiers resolved with equilibrium chemistry approximation (Zhu et al. 2016) | No |

[a] Table contains relevant similarities and differences between the two simulations performed in this study. The full description of each simulation can be found in the Section 2. The key difference (indicated in bolded text) is whether leaf nitrogen savings under elevated $CO_2$ can be allocated throughout the plant (as in Simulation B).

supporting plant growth, ultimately increasing gross and net primary productivity globally as compared to Simulation A.

3. Nitrogen savings from photosynthetic biochemistry acclimation in Simulation B would increase simulated carbon stored on land in plants and in soil as a result of increased productivity as compared to Simulation A.

## 2 | Materials and Methods

### 2.1 | E3SM Land Model Overview

We used the ELM land model (Zhu et al. 2019) integrated in the E3SM to assess the impacts of photosynthetic acclimation to elevated $CO_2$ on ecosystem carbon dynamics through nitrogen savings. Important features of ELM include (1) flexible leaf nitrogen content that is prognostically simulated with observational constraints (Zhu et al. 2020); (2) dynamic allocation of carbon and nitrogen to leaf, stem, and root tissue in response to light, water, and nitrogen limitations (Friedlingstein et al. 1999); and (3) competition for soil nitrogen among plants, microbial immobilizers, nitrifiers, and denitrifiers resolved with equilibrium chemistry approximation (Zhu et al. 2016).

### 2.2 | Photosynthetic Acclimation and Leaf Nitrogen Predictions in ELM

Net photosynthesis ($A_n$; μmol m$^{-2}$ s$^{-1}$) of $C_3$ plants in ELM is simulated based on the Farquhar, von Caemmerer, and Berry (1980) scheme:

$$A_n = \min\{A_c, A_j\} - R_d \tag{1}$$

where $R_d$ is the rate of dark respiration (μmol m$^{-2}$ s$^{-1}$). $A_c$ is the RuBisCO carboxylation rate-limited photosynthesis:

$$A_c = V_{cmax} m_c \tag{2}$$

where $V_{cmax}$ (μmol m$^{-2}$ s$^{-1}$) is the maximum rate of RuBisCO carboxylation and

$$m_c = \frac{C_i - \Gamma^*}{C_i + K_c\left(1 + \frac{O_i}{K_o}\right)} \tag{3}$$

where $C_i$ (Pa) and $O_i$ (Pa) are the intercellular $CO_2$ and $O_2$ concentrations, respectively, $\Gamma^*$ is the $CO_2$ compensation point (Pa), and $K_c$ (Pa) and $K_o$ (Pa) are Michaelis–Menten constants for $CO_2$ and $O_2$, respectively. $C_i$ was predicted from stomatal conductance using the Ball et al. (1987) stomatal conductance scheme. $A_j$ (μmol m$^{-2}$ s$^{-1}$) is the electron transport rate-limited photosynthesis:

$$A_j = \frac{J}{4} m \tag{4}$$

where

$$m = \frac{C_i - \Gamma^*}{C_i + 2\Gamma^*} \tag{5}$$

and $J$ is the electron transport rate (μmol m$^{-2}$ s$^{-1}$), simulated as:

$$\theta J^2 - \left(\varphi I + J_{max}\right)J + \varphi I J = 0 \tag{6}$$

where $\theta$ (unitless) is the curvature of the light response curve assumed to be 0.85 as in Smith et al. (2019), $\varphi$ is the quantum efficiency of photosynthetic electron transport (mol mol$^{-1}$), and $J_{\mathrm{max}}$ (μmol m$^{-2}$ s$^{-1}$) is the maximum rate of electron transport.

The default ELM (Zhu et al. 2019) simulates the photosynthesis rate with an observed scaling relationship between the leaf nitrogen concentration and $V_{\mathrm{cmax}}$ (Walker et al. 2014), which is derived from present-day conditions (ambient $CO_2$ concentration). However, under elevated $CO_2$ conditions, this scaling relationship may be inappropriate because of the acclimation of $V_{\mathrm{cmax}}$ toward higher $CO_2$ concentrations. In fact, the required leaf nitrogen concentration to support the acclimated $V_{\mathrm{cmax}}$ should decrease under elevated $CO_2$, likely to values lower than the predicted leaf nitrogen concentrations in the default ELM. Thus, the excess leaf nitrogen could be used for other functions (e.g., growth and storage).

In order to evaluate the impacts of such nitrogen savings, we first implemented the acclimation of $V_{\mathrm{cmax}}$ to elevated $CO_2$ concentration based on least-cost optimality theory (Smith and Keenan 2020) in ELM. The theory posits that plants will strive to achieve the greatest rates of leaf-level photosynthesis at the least amount of nitrogen use for a given environment. Modeled leaves do this by adjusting their leaf biochemical traits such that they are equally limited by $A_{\mathrm{c}}$ and $A_{\mathrm{j}}$ (i.e., $A_{\mathrm{c}} = A_{\mathrm{j}}$) and are thus not overinvested in either process. Under the least-cost optimality theory, $V_{\mathrm{cmax}}$ and $J_{\mathrm{max}}$ were calculated using 10-day trailing averages for temperature, light, and $C_{\mathrm{i}}$ following Smith and Keenan (2020):

$$V_{\mathrm{cmax}} = J_{\mathrm{max}}\left(\frac{m}{m_{\mathrm{c}}}\right)\left(\frac{\omega^{*}}{8\theta\omega}\right) \tag{7}$$

$$J_{\mathrm{max}} = \varphi I \omega \tag{8}$$

where $\omega$ and $\omega^{*}$ are terms that describe the cost to maintain electron transport defined as:

$$\varpi^{*} = 1 + \varpi - \sqrt{(1+\varpi)^{2} - 4\theta\varpi} \tag{9}$$

$$\varpi = -(1-2\theta) + \sqrt{(1-\theta)\left(\frac{1}{\frac{4c}{m}\left(1-\theta\frac{4c}{m}\right)} - 4\theta\right)} \tag{10}$$

where $c$ (unitless) is a constant related to the cost of electron transport, set to 0.053 as determined in Smith et al. (2019). Modeled $\Gamma^{*}$, $K_{\mathrm{c}}$, and $K_{\mathrm{o}}$ were affected by temperature following Bernacchi et al. (2001) using 10-day running averages of temperature. $A_{\mathrm{n}}$ was simulated at each time step following Equation (1) using acclimated $V_{\mathrm{cmax}}$ and $J_{\mathrm{max}}$ values and environmental conditions at that time step. As such, acclimation was not instantaneous and lagged current conditions at any given time step.

ELM then infers the leaf carbon to nitrogen ratio (C:N$_{\mathrm{leaf}}$; gC gN$^{-1}$) required to support the acclimated $V_{\mathrm{cmax}}$. We first standardized the acclimated $V_{\mathrm{cmax}}$ to its rate at 25°C ($V_{\mathrm{cmax25}}$; μmol m$^{-2}$s$^{-1}$) following Kattge and Knorr (2007) and then calculated C:N$_{\mathrm{leaf}}$ as:

$$\mathrm{C{:}\,N_{leaf}} = \frac{a f_{\mathrm{lnr}}}{V_{\mathrm{cmax25}}\mathrm{SLA}} \tag{11}$$

where SLA is the specific leaf area (m$^2$ gC$^{-1}$; values are plant type-specific; Zhu et al. 2019), $a$ is the reference RuBisCO activity at 25°C (60 μmol gRubisco$^{-1}$ s$^{-1}$), and $f_{\mathrm{lnr}}$ is the amount of RuBisCO per gram of RuBisCO nitrogen (gRubisco gN$^{-1}$; values are plant type-specific; Zhu et al. 2019). The C:N$_{\mathrm{leaf}}$ will monotonically increase when $V_{\mathrm{cmax}}$ acclimates to higher $CO_2$ concentrations, indicating less demand for leaf nitrogen.

### 2.3 | Model Experiments

We conducted two ELM simulations (Table 1) to investigate the impacts of photosynthetic acclimation and associated leaf nitrogen dynamics under elevated $CO_2$ and its impact on ecosystem carbon and nitrogen cycles. Both simulations calculated photosynthetic carbon assimilation in the same way, following Farquhar, von Caemmerer, and Berry (1980; Equations 1–6), with photosynthetic biochemical acclimation following Smith and Keenan (2020; Equations 7–10). However, the simulations differed in their calculation of leaf nitrogen. Simulation A did not allow for allocation to the rest of the plant of the excess leaf N beyond that required for $V_{\mathrm{cmax}}$ (i.e., excess nitrogen remained in the leaf). In contrast, Simulation B allowed for allocation of excess nitrogen to the rest of the plant. The whole-plant allocation and nitrogen acquisition schemes were the same for both simulations (Table 1). For both simulations, we first conducted a 400-year accelerated spinup followed by 200 years regular spinup simulations forced by 1901–1920 repeated climate from Global Soil Wetness Project Phase 3 version 1.0 (GSWP3) reanalysis forcing (Dirmeyer et al. 2006) and constant atmospheric $CO_2$ mole fraction (285 ppm). The two-stage spinup approach accumulates soil and vegetation carbon pools and reaches a quasi-steady state condition for the land carbon cycle (Koven et al. 2013; Zhu et al. 2019). The simulations were then run in a transient mode from 1901 to 2010 with GSWP reanalysis forcing, transient $CO_2$ concentrations, nitrogen deposition (Lamarque et al. 2005), and phosphorus deposition (Mahowald et al. 2008). GSWP3 variable sets used were "huss_gswp3," "pr_gswp3," "ps_gswp3," "rlds_gswp3," "rsds_gswp3," "tas_gswp3," and "wind_gswp3." Lastly, we ran the simulations from 2011 to 2100 with $CO_2$ concentrations from the RCP8.5 high emission scenario and 2001–2010 repeated climate forcings. The future projections were used to evaluate the $CO_2$ fertilization effects on photosynthesis and ecosystem carbon and nitrogen cycling. We disentangled the $CO_2$ fertilization versus leaf nitrogen saving impacts on plant photosynthesis and ecosystem carbon and nitrogen cycles by comparing Simulations A and B. Both ELM simulations were performed at a 1.9° latitude by 2.5° longitude resolution.

## 3 | Results

### 3.1 | Leaf Level Photosynthesis Acclimation to Elevated $CO_2$

In accordance with the least-cost optimality theory of photosynthesis (Equations 5–8), regionally averaged $V_{\mathrm{cmax}}$ consistently declined with elevated $CO_2$ in both simulations. The reduction in $V_{\mathrm{cmax}}$ was greater than 30% in most regions by the end of 2100 and was more prominent in tropical and temperate biomes compared with boreal biomes (Figure 1). Even though $V_{\mathrm{cmax}}$

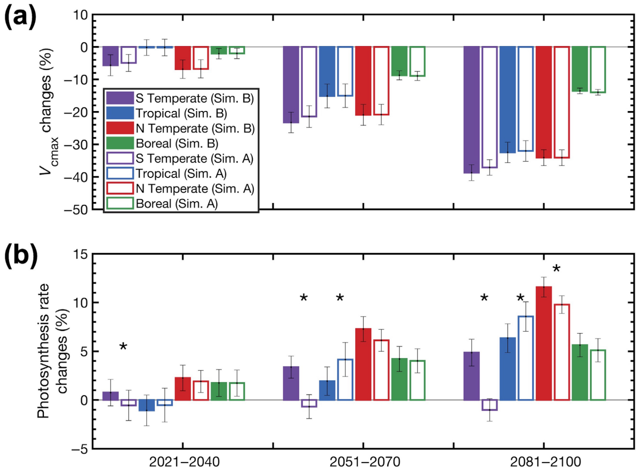

**FIGURE 1** | The change in (a) $V_{cmax}$ and (b) net photosynthesis rate from 2011 to 2021–2040 (left bars), 2051–2070 (middle bars), and 2081–2100 (right bars) in Southern Temperate (60S–30S; purple), Tropical (30S–30N; blue), Northern Temperate (30N–60N; red), and Boreal (60N–80N; green) regions driven by the RCP8.5 $CO_2$ concentration scenario. Filled bars represent the simulation with leaf nitrogen downregulation as a result of photosynthetic $CO_2$ acclimation (Simulation B; Table 1), while the open bars represent simulations without leaf nitrogen downregulation (Simulation A; Table 1). Asterisks (*) represent significantly different pairs of bars within time period and region between Simulation A and Simulation B from a *t*-test at an alpha level of 0.05.

declined, regionally aggregated net photosynthesis rates still remained the same or increased in all regions in both simulations under elevated $CO_2$ (Figure 1).

### 3.2 | Leaf Nitrogen Saving due to Photosynthetic Acclimation to Elevated $CO_2$

We found strong scaling relationships between modeled leaf area growth and changes in leaf nitrogen per unit ground area in both simulations. Plants continuously grew and expanded the leaf area under the RCP8.5 scenario, up to $0.4\,m^2\,m^{-2}$ leaf area index increases at the global scale, with corresponding increases in leaf nitrogen per ground area in both simulations (Figure 2). However, the change in the leaf nitrogen per unit ground area was lower in the scenario with allocation of saved leaf nitrogen to the rest of the plant (Simulation B, Figure 2, blue circles) as compared to the simulation where saved leaf nitrogen stayed in the leaf (Simulation A, Figure 2, red circles). Such downregulation of the leaf nitrogen per unit leaf area became progressively stronger throughout the 21st century. This result indicates that more and more leaf nitrogen was available for reallocation to other tissues (e.g., root and stem) due to leaf nitrogen savings.

### 3.3 | Plant Nitrogen Cycle Impacts From Photosynthetic Nitrogen Savings Under Elevated $CO_2$

There are two impacts of photosynthetic leaf nitrogen savings in response to elevated $CO_2$. First, lower nitrogen demand to support photosynthesis liberates nitrogen for plant growth and other functions. Second, plant allocation of saved nitrogen to root construction can increase plant nitrogen uptake. Based on our simulations, during the last decade of the 21st century (2091–2100), the leaf nitrogen savings case (Simulation B, Figure 3, blue lines) not only required 13.9 TgN less to support photosynthesis machinery but also acquired 22.0 TgN year$^{-1}$ more nitrogen through root uptake, indicating a positive feedback between leaf nitrogen savings and plant nitrogen uptake.

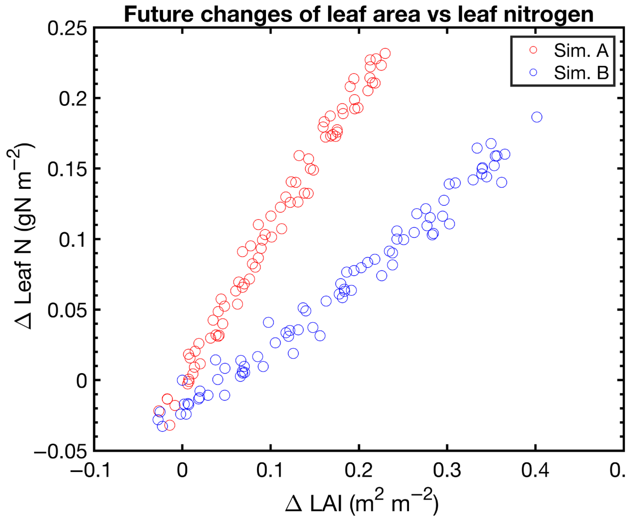

**FIGURE 2** | Scaling relationships between the changes (from 2021 to 2100) of leaf nitrogen (per unit of ground area) and leaf area index under the RCP8.5 high emission scenario, with (Simulation B, blue circles) and without (Simulation A, red circles) considering the leaf nitrogen downregulation.

### 3.4 | Ecosystem Carbon Cycle Impacts From Photosynthetic Nitrogen Savings Under Elevated $CO_2$

Leaf nitrogen savings had significant impacts on ecosystem carbon cycling and long-term carbon storage. Comparing Simulations A and B, we found that the reallocation of saved leaf nitrogen directly benefitted leaf production (*x*-axis values are greater at any *y*-axis value in Figure 2). The growth rate of leaf carbon was significantly higher when reallocation of saved leaf nitrogen was implemented versus when it stayed in the leaf (i.e., Simulation B vs. Simulation A; Figure 4a). Similarly, fine root and stem growth was higher in Simulation B than Simulation A. Averaged across the last decade of the 21st century (2091–2100), reallocation of saved leaf nitrogen (Simulation B) led to an accumulation of 16% more carbon in fine roots (Figure 4b), and 38% more carbon in living and dead stems as compared to Simulation A (Figure 4c).

Reallocation of saved leaf nitrogen also enhanced soil carbon storage (Figure 4d). On the one hand, plant biomass growth was significantly higher in the simulation with reallocation of saved leaf nitrogen (Simulation B), which generated more carbon inputs into soil when litter fell and woody biomass turned over as compared to Simulation A. On the other hand, reallocation of saved leaf nitrogen (i.e., Simulation B) enhanced plant nitrogen uptake competitiveness (more fine roots) and thus partially suppressed soil microbial nitrogen immobilization and soil organic matter turnover as compared to Simulation A. Overall, reallocation of saved leaf nitrogen (Simulation B) enhanced the whole ecosystem 21st century carbon storage by 50.3% as compared to Simulation A through storing carbon in relatively long-lived woody tissues and the soil (Figure 5).

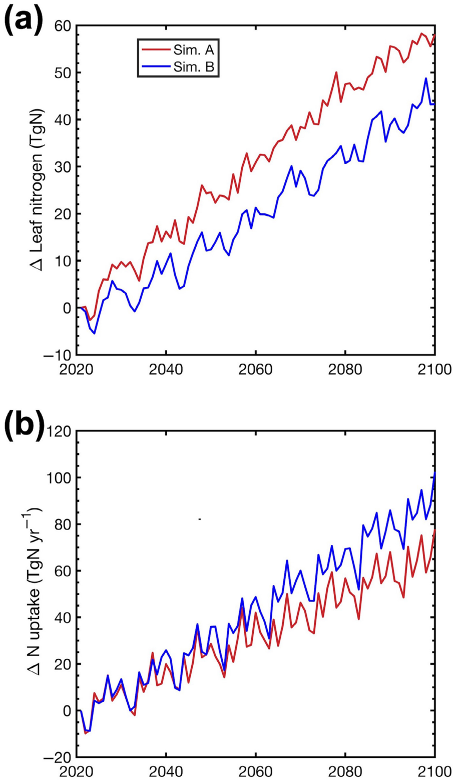

**FIGURE 3** | Changes (Δ) in (a) leaf nitrogen stock and (b) plant nitrogen uptake rates with (Simulation B, blue lines) and without (Simulation A, red lines) considering leaf nitrogen savings. Changes are represented as absolute changes from the year 2020.

## 4 | Discussion

We explored the impact of photosynthetic acclimation to elevated $CO_2$ on future terrestrial carbon and nitrogen cycle projections. To do this, we implemented photosynthetic acclimation (Smith and Keenan 2020) into the ELM land surface model (Zhu et al. 2019) and simulated terrestrial ecosystem processes under the RCP8.5 $CO_2$ concentration scenario from the present day to 2100. Our simulations showed an increase in leaf-level photosynthesis despite downregulation of $V_{\mathrm{cmax}}$. We explored the effects of nitrogen savings on carbon and nitrogen cycling within plants and ecosystems using simulations that differed in how leaf nitrogen was estimated (Table 1). The simulation that allowed for reallocation of saved leaf nitrogen as a result of RuBisCO downregulation under elevated $CO_2$ (Simulation B) showed increased leaf, stem, and fine root growth as compared to a simulation without reallocation of saved leaf nitrogen (Simulation A). The additional leaf growth enhanced canopy photosynthesis, while the additional root growth further alleviated nitrogen limitation at the whole-plant level. These effects combined to increase plant and soil carbon storage on land globally in Simulation B as compared to Simulation A. These results are discussed in more detail below.

### 4.1 | Future Photosynthesis Is Enhanced by Elevated $CO_2$ Even Under Optimal RuBisCO Downregulation

We found that our simulated rates of leaf-level photosynthesis were enhanced under elevated $CO_2$ despite simulated reductions in $V_{\mathrm{cmax}}$. These responses match those seen in elevated

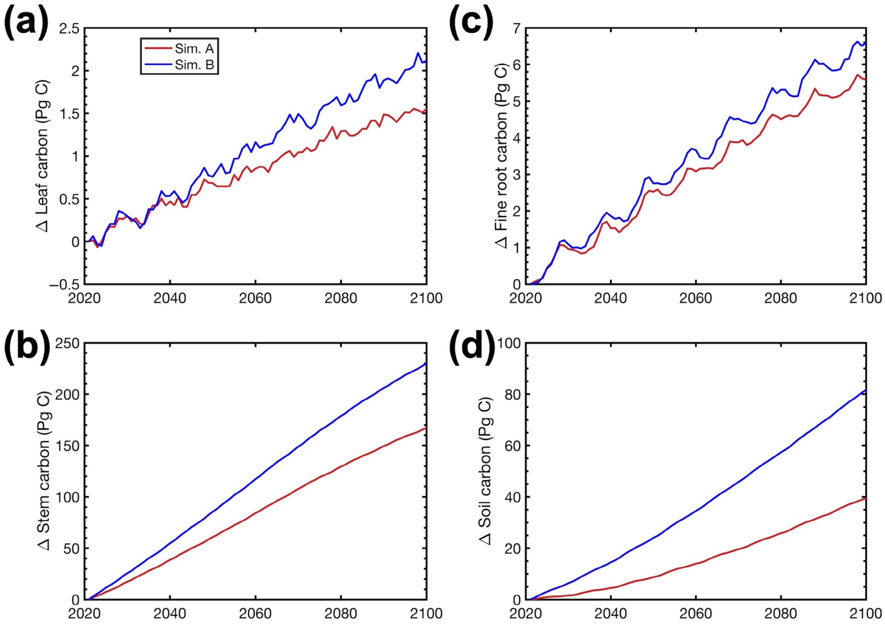

**FIGURE 4** | Changes (Δ) in global (a) leaf, (b) fine root, (c) stem, and (d) soil carbon stocks with (Simulation B, blue lines) and without (Simulation A, red lines) considering leaf nitrogen savings due to photosynthetic acclimation to elevated $CO_2$. Changes are represented as absolute changes from the year 2020.

$CO_2$ experiments (Ainsworth and Long 2005; Ainsworth and Rogers 2007; Leakey et al. 2009; Smith and Keenan 2020). The increase in photosynthesis with reduced $V_{cmax}$ under elevated $CO_2$ follows from the idea that, in $C_3$ plants, elevated $CO_2$ reduces photorespiration by enhancing the competitiveness of $CO_2$ for RuBisCO relative to $O_2$. Thus, plants can achieve higher rates of photosynthesis under elevated $CO_2$ at reduced amounts of RuBisCO (and reduced $V_{cmax}$). The $CO_2$ fertilization of photosynthesis is simulated by all land surface models that adopt the Farquhar, von Caemmerer, and Berry (1980) model of photosynthesis (Smith and Dukes 2013; Rogers et al. 2017), but the acclimation and downregulation of RuBisCO is not typically included.

Because $V_{cmax}$ was not determined from leaf nitrogen in our simulations, as is common in coupled C–N models (Smith and Dukes 2013), the simulated reduction in $V_{cmax}$ was not due to nitrogen limitation. Instead, our simulations employed the hypothesis that $V_{cmax}$ is determined by demand for, rather than supply of, nitrogen. This line of reasoning is not common in past studies that have provided implementations of leaf nitrogen–$V_{cmax}$ relationships for land surface models (Kattge et al. 2009; Walker et al. 2014). However, the demand-driven model used here has been shown to well-represent $V_{cmax}$ responses to elevated $CO_2$ in a meta-analysis of 31 experiments with and without soil nitrogen fertilization (Smith and Keenan 2020). This corroborates findings of global reductions in canopy demand for nitrogen under elevated $CO_2$ (Dong et al. 2022). Importantly, the approach used here suggests that changes in $V_{cmax}$ that result from changes in atmospheric $CO_2$ can be predicted independently from leaf nitrogen. This independence eliminates the need to predict the amount of leaf nitrogen in RuBisCO, which can be highly dynamic (Luo et al. 2021) and increase model uncertainty.

### 4.2 | RuBisCO Downregulation Under Elevated $CO_2$ Causes Leaf Nitrogen Savings and Indirectly Enhances Plant Nitrogen Uptake Through Increased Fine Root Allocation

Our simulated downregulation of RuBisCO reduced leaf demand for nitrogen and, ultimately, reduced leaf nitrogen per leaf area in the simulation that allowed for leaf nitrogen savings to be allocated throughout the plant (Simulation B), as compared to the simulation that kept saved leaf nitrogen in the leaf (Simulation A). This nitrogen in Simulation B was used to build plant tissues. Interestingly, the simulations suggested that plants used most of this saved nitrogen to build fine roots. The increase in relative fine root production under elevated $CO_2$ has been shown in previous experiments (Norby et al. 2004; Franklin et al. 2009; Iversen 2010). Our results suggest that this response may be underestimated by models that do not consider downregulation of leaf nitrogen under elevated $CO_2$.

The enhancement of fine root production in Simulation B compared to Simulation A suggests that reallocation of saved leaf nitrogen does not entirely alleviate nitrogen limitation of whole-plant growth under elevated $CO_2$. Our ELM simulations incorporated a dynamic allocation regime (Zhu et al. 2019), under which plants allocated resources to tissues limiting growth. Thus, the relative enhancement of allocation of saved nitrogen to the building of fine roots indicates that plants were still relatively nitrogen-limited. Thus, progressive nitrogen limitation (Luo et al. 2004) still persisted in our simulations.

Further, the enhanced fine root allocation increased plant nitrogen uptake in the simulation where saved leaf nitrogen could be allocated throughout the plant (Simulation B) relative to the simulation where saved leaf nitrogen stayed in the leaf (Simulation A). This additional nitrogen uptake showed that photosynthetic nitrogen savings reduced progressive nitrogen limitation, indicating that models that do not consider optimal downregulation of leaf nitrogen are overestimating future progressive nutrient limitation.

However, there is still more work needed to fully understand variation in progressive nutrient limitations spatially and temporally, as effects may differ due to many factors including successional age and background nutrient amounts (see discussion in Norby et al. 2024). Targeted experiments could be used to examine the role that leaf nitrogen savings due to acclimation to elevated $CO_2$ play in influencing nutrient limitations in different ecological contexts, particularly with regard to changes in plant resource allocation. However, care needs to be taken when examining the role of background plant nutrient availability, which can depend on a variety of factors including soil organic matter nutrient content, soil physical properties, soil biological processes, and nutrient losses. Soil nutrient manipulations can be used to directly impose variability in availability, but are limited in their reflection of real-world variability, which could be addressed by coupling ecological and modeling experiments (e.g., Wieder et al. 2019).

### 4.3 | Ecosystem Carbon Is Enhanced Under Elevated $CO_2$ by Optimal RuBisCO Downregulation

The leaf nitrogen savings from RuBisCO downregulation in Simulation B led to an increase in plant and soil carbon compared to the simulation that kept saved leaf nitrogen in the leaf (Simulation A). This result suggests that future progressive nutrient limitation may have been overestimated by previous model simulations (Wieder et al. 2015). As such, terrestrial ecosystems may act as greater carbon sinks in the future than previously suggested.

The land carbon sink is continuing to increase (Keenan and Williams 2018; Friedlingstein et al. 2022; Ruehr et al. 2023). Our results suggest that this is in part due to leaf nitrogen savings from optimal photosynthetic downregulation under elevated $CO_2$. Given that the land carbon sink offsets ~32% of fossil fuel emissions (Friedlingstein et al. 2022), it is critical to accurately project changes in this sink in the future.

It should be noted that our leaf nitrogen savings were calculated from $V_{cmax}$ and assuming a fraction of leaf nitrogen in RuBisCO that did not vary across our simulations. Experimental evidence shows that leaf nitrogen reductions are similar to reductions in $V_{cmax}$ under elevated $CO_2$ (Poorter et al. 2022), supporting our approach. However, we may have overestimated the leaf nitrogen savings effect if the fraction of nitrogen allocated to RuBisCO decreases with elevated $CO_2$, as is seen in response

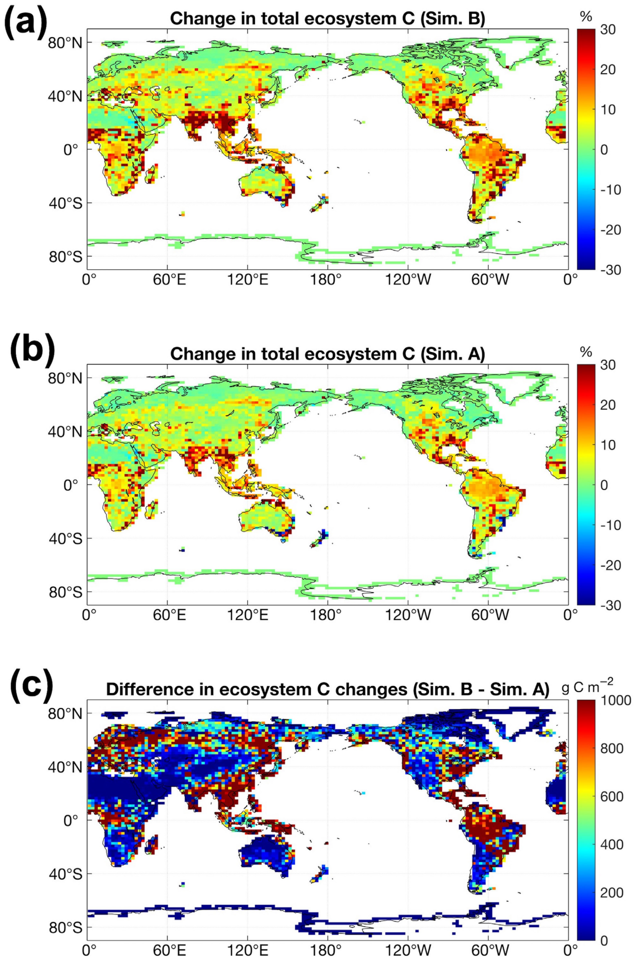

**FIGURE 5** | Change of total ecosystem carbon (2100 minus 2011) with (Panel (a); Simulation B) and without (Panel (b); Simulation A) considering leaf nitrogen savings due to photosynthetic acclimation to elevated CO2. (c) Absolute differences in ecosystem carbon between the two simulations (Simulation B − Simulation A; gC m-2). Map lines delineate study areas and do not necessarily depict national boundaries.

to other environmental factors (Luo et al. 2021). More research is needed to better understand the variability in leaf nitrogen partitioning under elevated $CO_2$.

It is important to note that our simulations only included future projected increases in atmospheric $CO_2$ and omitted projected changes in climate. This choice was taken to isolate the impact of optimal photosynthetic downregulation under elevated $CO_2$ on the global carbon cycle. That said, climate change will have important interactive effects with elevated $CO_2$ on global carbon cycling. For instance, warming may reduce canopy photosynthesis if temperature exceeds canopy optima (Duffy et al. 2021). However, warming may also lead to RuBisCO downregulation due to a reduction in photosynthetic enzyme demand that results from increased enzymatic speed under increased temperatures (Smith and Keenan 2020; Dong et al. 2022). Warming-induced downregulation in leaf nitrogen could additively impact the results found here. The effect of elevated $CO_2$ on photosynthesis should also increase with temperature due to alleviation of the enhanced respiration that occurs at higher temperatures (Dusenge, Duarte, and Way 2019). This interaction is considered in models that simulate photosynthesis with the Farquhar, von Caemmerer, and Berry (1980) model. In addition, elevated $CO_2$ can reduce water stress through reductions in stomatal opening (Ainsworth and Rogers 2007; Keenan et al. 2013). This effect is considered in models that implement a process-based representation of the coupling between photosynthesis and stomatal conductance and a representation of stomatal water stress.

### 4.4 | Eco-Evolutionary Optimality Is a Useful Approach for Improving Model Realism and Reliability

Eco-evolutionary optimality (EEO) theory for plant form and functioning is a growing field that is used to better understand plant trait variability over space and time (Harrison et al. 2021). EEO theory also provides an avenue for incorporating processes into models without sacrificing model reliability by adding uncertain parameters (Prentice et al. 2015; Kyker-Snowman et al. 2022). Here, we demonstrate how this can be done, specifically by leveraging an EEO-derived model of leaf photosynthetic biochemistry (Smith and Keenan 2020) to include photosynthetic acclimation to changing atmospheric $CO_2$. Importantly, the model we incorporated did not add any new parameters to ELM. Thus, model realism was increased by adding a new process ($CO_2$ acclimation) without adding parameter uncertainty.

## 5 | Conclusions

Here, we implemented an optimality-based representation of photosynthetic biochemical acclimation into the E3SM land model, ELM. Under elevated $CO_2$, the model simulated reductions in $V_{cmax}$ and, as a result, required leaf nitrogen These leaf nitrogen savings freed up nitrogen that enhanced plant growth, particularly that of fine roots that were used to uptake more nitrogen. Both factors alleviated nitrogen limitation under elevated $CO_2$ globally. The net effect was an increase in plant and soil carbon compared to a simulation that did not allow for saved leaf nitrogen to be used for other processes. Photosynthetic acclimation to elevated $CO_2$ and resulting leaf nitrogen savings are not simulated by any coupled model intercomparison project-participating land surface models (Smith and Dukes 2013; Rogers et al. 2017). Our results suggest that the inclusion of this process will reduce future simulated nitrogen limitation reductions in terrestrial ecosystem carbon uptake and storage.

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### Author Contributions

**Nicholas G. Smith:** conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, writing – original draft, writing – review and editing. **Qing Zhu:** conceptualization, data curation, formal analysis, methodology, resources, software, visualization, writing – review and editing. **Trevor F. Keenan:** conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing – review and editing. **William J. Riley:** conceptualization, methodology, supervision, writing – review and editing.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

All code used for the model simulations can be found at https://github.com/E3SM-Project/E3SM/tree/qzhu-lbl/lnd/photosynthesis_Nsaving (DOI: 10.5281/zenodo.13909764). All data used to drive the model simulations are publicly available, with GSWP3 climate forcings available at https://www.isimip.org/gettingstarted/input-data-bias-adjustment/details/4/ (DOI: 10.48364/isimip.886955) and RCP8.5 $CO_2$ data from Riahi, Grübler, and Nakicenovic (2007) available at https://tntcat.iiasa.ac.at/RcpDb/ and at https://zenodo.org/records/13931715 (https://doi.org/10.5281/zenodo.13931715).

## References

Ainsworth, E. A., and S. P. Long. 2005. "What Have We Learned From 15 Years of Free-Air $CO_2$ Enrichment (FACE)? A Meta-Analytic Review of the Responses of Photosynthesis, Canopy Properties and Plant Production to Rising $CO_2$." *New Phytologist* 165: 351–372.

Ainsworth, E. A., and A. Rogers. 2007. "The Response of Photosynthesis and Stomatal Conductance to Rising [$CO_2$]: Mechanisms and Environmental Interactions." *Plant, Cell & Environment* 30: 258–270.

Arneth, A., S. P. Harrison, S. Zaehle, et al. 2010. "Terrestrial Biogeochemical Feedbacks in the Climate System." *Nature Geoscience* 3: 525–532.

Bazzaz, F. A. 1990. "The Response of Natural Ecosystems to the Rising Global $CO_2$ Levels." *Annual Review of Ecology and Systematics* 21: 167–196.

Ball, J. T., I. E. Woodrow, and J. A. Berry. 1987. "A Model Predicting Stomatal Conductance and Its Contribution to the Control of Photosynthesis Under Different Environmental Conditions." In *Progress in Photosynthesis Research*, edited by J. Biggins, 221–224. Dordrecht: Springer.

Bernacchi, C. J., E. L. Singsaas, C. Pimentel, A. R. Portis Jr., and S. P. Long. 2001. "Improved Temperature Response Functions for Models of Rubisco-Limited Photosynthesis." *Plant, Cell & Environment* 24: 253–259.

Booth, B. B. B., D. J. Chris, C. Mat, et al. 2012. "High Sensitivity of Future Global Warming to Land Carbon Cycle Processes." *Environmental Research Letters* 7: 24002.

Ciais, P., C. Sabine, G. Bala, L. Bopp, V. Brovkin, and J. I. House. 2013. "Climate Change 2013: The Physical Science Basis." In *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by T. F. Stocker, D. Qin, G.-K. Plattner et al. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

Dirmeyer, P. A., X. Gao, M. Zhao, Z. Guo, T. Oki, and N. Hanasaki. 2006. "GSWP-2: Multimodel Analysis and Implications for Our Perception of the Land Surface." *Bulletin of the American Meteorological Society* 87: 1381–1398.

Dong, N., I. J. Wright, J. M. Chen, et al. 2022. "Rising $CO_2$ and Warming Reduce Global Canopy Demand for Nitrogen." *New Phytologist* 235: 1692–1700.

Duffy, K. A., C. R. Schwalm, V. L. Arcus, G. W. Koch, L. L. Liang, and L. A. Schipper. 2021. "How Close Are We to the Temperature Tipping Point of the Terrestrial Biosphere?." *Science Advances* 7: eaay1052.

Dusenge, M. E., A. G. Duarte, and D. A. Way. 2019. "Plant Carbon Metabolism and Climate Change: Elevated $CO_2$ and Temperature Impacts on Photosynthesis, Photorespiration and Respiration." *New Phytologist* 221: 32–49.

Farquhar, G. D., S. von Caemmerer, and J. A. Berry. 1980. "A Biochemical Model of Photosynthetic $CO_2$ Assimilation in Leaves of $C_3$ Species." *Planta* 149: 78–90.

Franklin, O., R. E. McMurtrie, C. M. Iversen, et al. 2009. "Forest Fine-Root Production and Nitrogen Use Under Elevated $CO_2$: Contrasting Responses in Evergreen and Deciduous Trees Explained by a Common Principle." *Global Change Biology* 15: 132–144.

Friedlingstein, P., G. Joel, C. B. Field, and I. Y. Fung. 1999. "Toward an Allocation Scheme for Global Terrestrial Carbon Models." *Global Change Biology* 5: 755–770.

Friedlingstein, P., M. O'sullivan, M. W. Jones, et al. 2022. "Global Carbon Budget 2022." *Earth System Science Data Discussions* 2022: 1–159.

Golaz, J.-C., P. M. Caldwell, L. P. van Roekel, et al. 2019. "The DOE E3SM Coupled Model Version 1: Overview and Evaluation at Standard Resolution." *Journal of Advances in Modeling Earth Systems* 11: 2089–2129.

Harrison, M. T., E. J. Edwards, G. D. Farquhar, A. B. Nicotra, and J. R. Evans. 2009. "Nitrogen in Cell Walls of Sclerophyllous Leaves Accounts for Little of the Variation in Photosynthetic Nitrogen-Use Efficiency." *Plant, Cell & Environment* 32: 259–270.

Harrison, S. P., W. Cramer, O. Franklin, et al. 2021. "Eco-Evolutionary Optimality as a Means to Improve Vegetation and Land-Surface Models." *New Phytologist* 23: 2125–2141.

Hauser, E., W. R. Wieder, G. B. Bonan, and C. C. Cleveland. 2023. "Flexible Foliar Stoichiometry Reduces the Magnitude of the Global Land Carbon Sink." *Geophysical Research Letters* 50: e2023GL105493.

Iversen, C. M. 2010. "Digging Deeper: Fine-Root Responses to Rising Atmospheric $CO_2$ Concentration in Forested Ecosystems." *New Phytologist* 186: 346–357.

Jiang, M., B. E. Medlyn, J. E. Drake, et al. 2020. "The Fate of Carbon in a Mature Forest Under Carbon Dioxide Enrichment." *Nature* 580: 227–231.

Kattge, J., and W. Knorr. 2007. "Temperature Acclimation in a Biochemical Model of Photosynthesis: A Reanalysis of Data From 36 Species." *Plant, Cell & Environment* 30: 1176–1190.

Kattge, J., W. Knorr, T. Raddatz, and C. Wirth. 2009. "Quantifying Photosynthetic Capacity and Its Relationship to Leaf Nitrogen Content for Global-Scale Terrestrial Biosphere Models." *Global Change Biology* 15: 976–991.

Keenan, T. F., D. Y. Hollinger, G. Bohrer, et al. 2013. "Increase in Forest Water-Use Efficiency as Atmospheric Carbon Dioxide Concentrations Rise." *Nature* 499: 324–327.

Keenan, T. F., and C. A. Williams. 2018. "The Terrestrial Carbon Sink." *Annual Review of Environment and Resources* 43: 219–243.

Koven, C. D., W. J. Riley, Z. M. Subin, et al. 2013. "The Effect of Vertically Resolved Soil Biogeochemistry and Alternate Soil C and N Models on C Dynamics of CLM4." *Biogeosciences* 10: 7109–7131.

Kyker-Snowman, E., D. L. Lombardozzi, G. B. Bonan, et al. 2022. "Increasing the Spatial and Temporal Impact of Ecological Research: A Roadmap for Integrating a Novel Terrestrial Process Into an Earth System Model." *Global Change Biology* 28: 665–684.

Lamarque, J., J. T. Kiehl, G. P. Brasseur, et al. 2005. "Assessing Future Nitrogen Deposition and Carbon Cycle Feedback Using a Multimodel Approach: Analysis of Nitrogen Deposition." *Journal of Geophysical Research: Atmospheres* 110: D19303.

Leakey, A. D. B., E. A. Ainsworth, C. J. Bernacchi, A. Rogers, S. P. Long, and D. R. Ort. 2009. "Elevated $CO_2$ Effects on Plant Carbon, Nitrogen, and Water Relations: Six Important Lessons From FACE." *Journal of Experimental Botany* 60: 2859–2876.

Luo, X., T. F. Keenan, J. M. Chen, et al. 2021. "Global Variation in the Fraction of Leaf Nitrogen Allocated to Photosynthesis." *Nature Communications* 12: 4866.

Luo, Y., B. Su, W. S. Currie, et al. 2004. "Progressive Nitrogen Limitation of Ecosystem Responses to Rising Atmospheric Carbon Dioxide." *Bioscience* 54: 731–739.

Mahowald, N., T. D. Jickells, A. R. Baker, et al. 2008. "Global Distribution of Atmospheric Phosphorus Sources, Concentrations and Deposition Rates, and Anthropogenic Impacts." *Global Biogeochemical Cycles* 22: GB4026.

McCarthy, H. R., R. Oren, K. H. Johnsen, et al. 2010. "Re-Assessment of Plant Carbon Dynamics at the Duke Free-Air $CO_2$ Enrichment Site: Interactions of Atmospheric [$CO_2$] With Nitrogen and Water Availability Over Stand Development." *New Phytologist* 185: 514–528.

Norby, R. J., J. Ledford, C. D. Reilly, N. E. Miller, and E. G. O'Neill. 2004. "Fine-Root Production Dominates Response of a Deciduous Forest to Atmospheric $CO_2$ Enrichment." *Proceedings of the National Academy of Sciences* 101: 9689–9693.

Norby, R. J., N. J. Loader, C. Mayoral, et al. 2024. "Enhanced Woody Biomass Production in a Mature Temperate Forest Under Elevated $CO_2$." *Nature Climate Change* 14: 983–988.

Norby, R. J., J. M. Warren, C. M. Iversen, B. E. Medlyn, and R. E. McMurtrie. 2010. "$CO_2$ Enhancement of Forest Productivity Constrained by Limited Nitrogen Availability." *Proceedings of the National Academy of Sciences* 107: 19368–19373.

Poorter, H., O. Knopf, I. J. Wright, et al. 2022. "A Meta-Analysis of Responses of C3 Plants to Atmospheric $CO_2$: Dose–Response Curves for 85 Traits Ranging From the Molecular to the Whole-Plant Level." *New Phytologist* 233: 1560–1596.

Prentice, I. C., X. Liang, B. E. Medlyn, and Y.-P. Wang. 2015. "Reliable, Robust and Realistic: The Three R's of Next-Generation Land-Surface Modelling." *Atmospheric Chemistry and Physics* 15: 5987–6005.

Riahi, K., A. Grübler, and N. Nakicenovic. 2007. "Scenarios of Long-Term Socio-Economic and Environmental Development Under Climate Stabilization." *Technological Forecasting and Social Change* 74: 887–935.

Rogers, A., B. E. Medlyn, J. S. Dukes, et al. 2017. "A Roadmap for Improving the Representation of Photosynthesis in Earth System Models." *New Phytologist* 213: 22–42.

Ruehr, S., T. F. Keenan, C. Williams, et al. 2023. "Evidence and Attribution of the Enhanced Land Carbon Sink." *Nature Reviews Earth and Environment* 4: 518–534.

Smith, N. G., and J. S. Dukes. 2013. "Plant Respiration and Photosynthesis in Global-Scale Models: Incorporating Acclimation to Temperature and $CO_2$." *Global Change Biology* 19: 45–63.

Smith, N. G., and T. F. Keenan. 2020. "Mechanisms Underlying Leaf Photosynthetic Acclimation to Warming and Elevated $CO_2$ as Inferred From Least-Cost Optimality Theory." *Global Change Biology* 26: 5202–5216.

Smith, N. G., T. F. Keenan, I. C. Prentice, et al. 2019. "Global Photosynthetic Capacity Is Optimized to the Environment." *Ecology Letters* 22: 506–517.

Stocker, B. D., H. Wang, N. G. Smith, et al. 2020. "P-Model v1.0: An Optimality-Based Light Use Efficiency Model for Simulating Ecosystem Gross Primary Production." *Geoscientific Model Development* 13: 1545–1581.

Thornton, P. E., J.-F. Lamarque, N. A. Rosenbloom, and N. M. Mahowald. 2007. "Influence of Carbon-Nitrogen Cycle Coupling on Land Model Response to $CO_2$ Fertilization and Climate Variability." *Global Biogeochemical Cycles* 21: GB4018.

van Vuuren, D. P., J. Edmonds, M. Kainuma, et al. 2011. "The Representative Concentration Pathways: An Overview." *Climatic Change* 109: 5–31.

Walker, A. P., A. P. Beckerman, L. Gu, et al. 2014. "The Relationship of Leaf Photosynthetic Traits—Vcmax and Jmax—To Leaf Nitrogen, Leaf Phosphorus, and Specific Leaf Area: A Meta-Analysis and Modeling Study." *Ecology and Evolution* 4: 3218–3235.

Walker, A. P., M. G. de Kauwe, A. Bastos, et al. 2021. "Integrating the Evidence for a Terrestrial Carbon Sink Caused by Increasing Atmospheric $CO_2$." *New Phytologist* 229: 2413–2445.

Wang, H., I. C. Prentice, T. F. Keenan, et al. 2017. "Towards a Universal Model for Carbon Dioxide Uptake by Plants." *Nature Plants* 3: 734–741.

Wieder, W. R., C. C. Cleveland, W. K. Smith, and K. Todd-Brown. 2015. "Future Productivity and Carbon Storage Limited by Terrestrial Nutrient Availability." *Nature Geoscience* 8: 441–444.

Wieder, W. R., D. M. Lawrence, R. A. Fisher, et al. 2019. "Beyond Static Benchmarking: Using Experimental Manipulations to Evaluate Land Model Assumptions." *Global Biogeochemical Cycles* 33: 1289–1309.

Wright, I. J., P. B. Reich, and M. Westoby. 2003. "Least-Cost Input Mixtures of Water and Nitrogen for Photosynthesis." *American Naturalist* 161: 98–111.

Zaehle, S., B. E. Medlyn, M. G. de Kauwe, et al. 2014. "Evaluation of 11 Terrestrial Carbon–Nitrogen Cycle Models Against Observations From Two Temperate Free-Air $CO_2$ Enrichment Studies." *New Phytologist* 202: 803–822.

Zhu, Q., W. J. Riley, C. M. Iversen, and J. Kattge. 2020. "Assessing Impacts of Plant Stoichiometric Traits on Terrestrial Ecosystem Carbon Accumulation Using the E3SM Land Model." *Journal of Advances in Modeling Earth Systems* 12: e2019MS001841.

Zhu, Q., W. J. Riley, J. Tang, et al. 2019. "Representing Nitrogen, Phosphorus, and Carbon Interactions in the E3SM Land Model: Development and Global Benchmarking." *Journal of Advances in Modeling Earth Systems* 11: 2238–2258.

Zhu, Q., W. J. Riley, J. Tang, and C. D. Koven. 2016. "Multiple Soil Nutrient Competition Between Plants, Microbes, and Mineral Surfaces: Model Development, Parameterization, and Example Applications in Several Tropical Forests." *Biogeosciences* 13: 341–363.

Ziehn, T., J. Kattge, W. Knorr, and M. Scholze. 2011. "Improving the Predictability of Global $CO_2$ Assimilation Rates Under Climate Change." *Geophysical Research Letters* 38: L10404.