

The point-by-point response to the reviews

Response to reviews of manuscript “Leaf Area Index identified as a major source of variability in modelled CO₂ fertilization” (bg-2018-213). The original reviewers’ comments are italicized and our response to the reviewers’ comments follow.

Response to Associate Editor’s comments

Comments to the Author:

The revised version of this manuscript addresses many of the major concerns raised by reviewers. This assessment is supported by a follow-on review which also offers some suggestions for minor revisions. Before issuing a final acceptance I encourage the authors to consider incorporating these suggested revisions in a final version of the manuscript that I will review quickly once more.

Response: Thank you for your consistent encouragement. We have incorporated suggestions from the reviewer in the final version of our manuscript. We also devoted a lot of time and efforts to improving the language and readability in this version. We hope this version will lead to a satisfactory acceptance.

Reviewer 1: Overall, I think that the revisions the author's have carried out considerably improve the readability and framing for the reader, so I thank them for making those efforts. I think the addition of the CN and CNP is a nice contribution even if ultimately it does not change the interpretation; that message in itself is a useful one.

I have a few minor responses to their responses to my comments.

- In their revision the authors note: " β values at ecosystem levels are more variable with nutrient effects, LAI responses are still linearly correlated well with β GPP, β NPP and β cpool across different C3 PFTs in nutrient-coupled simulations as in C-only simulation, confirming the dominant role of LAI in regulating carbon cycle response under CO₂ fertilization"

Here, I think a valuable link with this conclusion would be to discuss current models simulate allocation to leaves (discussion perhaps?). For example, the EucFACE CO₂ experiment shows no increased LAI in response to CO₂ (Duursma et al. 2016), despite the roughly expected theoretical increase in leaf-level photosynthesis in response to CO₂ (Ellsworth et al. 2017). This would question a linear correlation between β GPP and LAI, I think? It is very likely that we have more to learn as we now begin to think further about mature ecosystems.

Duursma, R. A., Gimeno, T. E., Boer, M. M., Crous, K. Y., Tjoelker, M. G. and Ellsworth, D. S. (2016), Canopy leaf area of a mature evergreen Eucalyptus woodland does not respond to elevated atmospheric [CO₂] but tracks water availability. Glob Change Biol, 22: 1666-1676. doi:10.1111/gcb.13151

Ellsworth, D. S., Anderson, I. C., Crous, K. Y., Cooke, J., Drake, J. E., Gherlenda, A. N., & Tjoelker, M. G. (2017). Elevated CO₂ does not increase eucalypt forest productivity on a low-phosphorus soil. Nature Climate Change, 7, 279–282. <https://doi.org/10.1038/nclimate3235>

Response: We greatly appreciate the reviewer for sharing these important references with us. We think these references actually support our point that the responses at canopy and ecosystem level are significantly dominated by the response of LAI, rather than by leaf photosynthetic response to eCO₂. We have included these references into our discussion: “Some studies reported that LAI dynamics did not significantly change in specific FACE experiments, such as in a closed-canopy deciduous broadleaf forest (ORNL FACE; Norby et al., 2003) and in a mature evergreen broadleaf forest (EucFACE; Duursma et al., 2016). The negligible change of LAI at the EucFACE probably leads to insignificant response of productivity at this site, even though leaf photosynthesis rate significantly increases under eCO₂ (Ellsworth et al., 2017)” (Line 344-348).

Reviewer 1: - To my question about the CABLE simulations almost always being limited by RuBP-regeneration rate ... I agree that at elevated CO₂ concentrations this would be true, but I disagree this should be true when the CO₂ concentration is "391 ppm" as they stated. If one assumed a C_i/C_a of 0.7, then the C_i concentration would be ~270, which should make the model Rubisco limited (excluding the contribution of LAI). I do suggest they should check this point again. I guess my point is fundamentally about interpretation. A fraction of the readership will read their statement and begin to question whether there is an underlying issue with the model simulations. However, as the authors argue (citing Luo and Mooney), it probably does not matter, but I feel it would be useful to remove any doubt from the reader's

mind.

Response: We thank the reviewer for the careful check of our interpretation. We agree that removing “391 ppm” will make this sentence more accurate. We have changed the sentence to “We found photosynthesis rates are increasingly limited by RuBP regeneration under RCP 8.5 scenario” (Line 175).

Reviewer 1: - To the author's response about me asking how different levels of water-stress across models would affect their conclusions, they now state: "Our results show modelled ratio of C_i to atmospheric CO2 concentration (C_a) is relatively constant for each PFT with eCO_2 and varies little among PFTs (Table 1)". Here I refer them to my original point ... this may very well be true for CABLE, but what about if a model had twice as much water stress as CABLE? Whilst it may not be true that water stress has a bit impact on CABLE's results, it may not be true to conclude this factor does not impact a broader CMIP5 model ensemble which was their original comparison point. It is simply not true to asset that: "Wong et al. (1979) showed plant stomata could maintain a constant C_i/C_a across wide range of environmental conditions, including water stress condition. Therefore different vegetation types might have similar C_i for a given C_a in other models". The Wong study is not a model result, it may very well be theoretically true but models are known to disagree markedly on the impact on water stress, so they cannot have the a "similar C_i for given C_a " across models. In Fig 7, in De Kauwe et al. 2017, Global Change Biology (2017), doi: 10.1111/gcb.13643, I showed the average water stress for a range of models during the growing season. In these simulations C_a was increased in exactly the same way across models, so these differences must have equated to differences in C_i . Finally, they argue that Luo and Mooney showed insensitivity to a change in C_i/C_a from 0.8 to 0.6. But that is essentially without water stress, some of the models in the figure I referred to must have been considerably lower than 0.6. Frankly, a better argument to make to me here - is that water stress comes and goes and that it can be ignored as a factor when looking across years!

Response: We agree that Wong study is experimental results. We also greatly appreciate the reviewer for offering an alternative explanation that “water stress comes and goes and that it can be ignored as a factor when looking across years”. We have carefully studied the paper by De Kauwe et al. (2017) and Fig. 7 in the paper. The figure plots summer water availability factors in term of limiting productivity as water content declines for 10 models. Water influences on productivity through not only C_i/C_a ratio but also many other processes, such as canopy structure as explored in our study of this paper. It is hard to infer from that figure that C_i/C_a “must be lower than 0.6”.

We cited this paper in the revised manuscript:” Different models simulate diverse levels of water stress on productivity (De Kauwe et al., 2017)” (Line 424). We also added one sentence in our revised manuscript: “Land surface models might simulate relatively constant C_i/C_a ratios under water stress as well since photosynthesis and stomatal conductance are theoretically depicted based on experimental results” (Line 431-433).

Reviewer 1: - To their response on leaf temperature. I can't recall the details of the Luo and Mooney study, which they seem to know well. Whilst I do not take issue with their point on the impact of leaf temp on gamma star, I was actually thinking about the impact of the different resolved leaf temperatures on C_i , which is solved via the energy balance. However, this is most likely speculative (on my part) anyway, so can be ignored.

Response: The reviewer raised a good question. Actually there is not a clear relationship between leaf temperature and intercellular CO₂ concentration for C₃ plants (Fig. 1), indicating other factors such as the stomatal conductance might play an important role in regulating C_i .

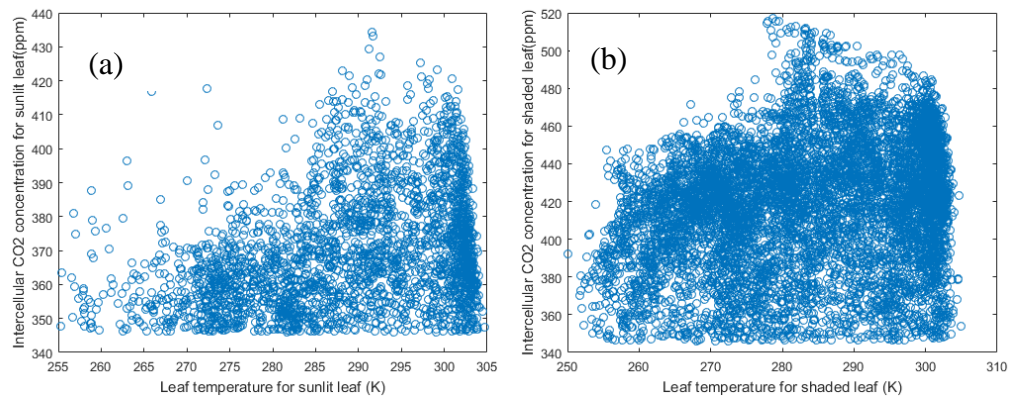


Fig. 1: Dependence of intercellular CO₂ concentration (C_i) on leaf temperature for sunlit leaf (a) and shaded leaf (b).

Reviewer 1: - In their reframing of the text in reference to the Hajima et al. paper, I wonder if the author's could go further in their explanations. This strikes me as a very important and interesting point, but as written is a little too superficial. The author's are arguing that one gets a different interpretation of β if one calculates it at the leaf-level vs. as canopy/stand-level, GPP/LAI. They appear to attribute this to the fact that the authors have ignored differences in the scaling in how the canopy is treated. If I follow, these are the only factors, or were there more? If these are the only factors, if the calculation is formulated on

a big-leaf vs a two-leaf vs a multi-layer, which one best matches the GPP/LAI formulation that Hajima used? Or which PFTs does this issue matter most for? These strike me as points worth making, or perhaps I've oversimplified?

Response: We thank the reviewer for the insightful comments. We believe that which canopy structure best fits GPP/LAI formulation that Hajima used is an interesting research question. Canopy structure is one of the important factors. We would like to expand on this point through explaining which PFTs this issue matters most for. We have reorganized this part into: "One possible issue of this calculation is that it ignores different canopy structure used by each CMIP5 model such as big-leaf, two-leaf or multiple-layer. Our results just show that the sensitivities of GPP/LAI are different from our mechanistic calculation of leaf-level β for different PFTs in a two-leaf model. β values estimated from GPP/LAI formulation are greatly underestimated for woody trees and slightly overestimated for C₃ grass and tundra, but best match for shrub if compared with our calculation (Fig. S8). Therefore, diagnostics such as C_i and Γ_* for leaf-level β are more desirable for woody trees" (Line 319-324).

The list of all relevant changes made in the manuscript

Here are the relevant changes made in the manuscript.

- (1) Page 8 line 158-159: we clarified the relationship between canopy GPP and big-leaf GPP.
- (2) Page 8 line 175: we modified the sentence as suggested by the reviewer.
- (3) Page 15 line 319-324: we added the discussion as suggested by the reviewer.
- (4) Page 16 line 344-348: we discussed the references as suggested by the reviewer.
- (5) Page 19 line 424: we cited the paper as mentioned by the reviewer.
- (6) Page 20 line 431-433: we discussed the references as suggested by the reviewer.

Leaf Area Index identified as a major source of variability in modelled CO₂ fertilization

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Abstract. The concentration-carbon feedback (β), also called the CO₂ fertilization effect, is a key unknown in climate-carbon cycle projections. A better understanding of model mechanisms that govern terrestrial ecosystem responses to elevated CO₂ is urgently needed to enable a more accurate prediction of future terrestrial carbon sink. We conducted C-only, carbon-nitrogen (C-N) and carbon-nitrogen-phosphorus (C-N-P) simulations of the Community Atmosphere Biosphere Land Exchange model (CABLE) from 1901 to 2100 with fixed climate to identify the most critical model process that causes divergence in β . We calculated CO₂ fertilization effects at various hierarchical levels from leaf biochemical reaction and leaf photosynthesis to canopy gross primary production (GPP), net primary production (NPP), and ecosystem carbon storage (*c_{pool}*) for seven C₃ plant functional types (PFTs) in response to increasing CO₂ under RCP 8.5 scenario. Our results show that β values at biochemical and leaf photosynthesis levels vary little across the seven PFTs, but greatly diverge at canopy and ecosystem levels in all simulations. The low variation of the leaf-level β is consistent with a theoretical analysis that leaf photosynthetic sensitivity to increasing CO₂ concentration is almost an invariant function. In the CABLE model, the major jump in variation of β values from leaf- to canopy- and ecosystem-levels results from divergence in modelled leaf area index (LAI) within and among PFTs. The correlation of β_{GPP} , β_{NPP} , or $\beta_{c_{pool}}$ each with β_{LAI} is very high in all simulations. Overall, our results indicate that modelled LAI is a key factor causing the divergence in β in the CABLE model. It is therefore urgent to constrain processes that regulate LAI dynamics in order to better represent the response of ecosystem productivity to increasing CO₂ in Earth System Models.

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1. Introduction

40 Terrestrial ecosystems take up roughly 30% of anthropogenic CO₂ emissions, and is of great uncertainty and vulnerable to global climate change (Cox et al., 2000; Le Quéré et al., 2018). Persistent increase of atmospheric CO₂ concentration will stimulate plant growth and ecosystem carbon storage, forming a negative feedback to CO₂ concentration (Long et al., 2004; Friedlingstein et al., 2006; Canadell et al., 2007). This concentration-carbon feedback (β), also called the CO₂ fertilization effect, has been identified as a major uncertainty in modeling terrestrial carbon-cycle response to historical climate change
45 (Huntzinger et al., 2017). In the Coupled Model Intercomparison Project (C4MIP) and the Coupled Model Intercomparison Project Phase 5 (CMIP5), all models agree that terrestrial carbon sink will gradually saturate in the future but disagree on the magnitude of β (Friedlingstein et al., 2006; Arora et al., 2013; Friedlingstein et al., 2015). Some studies pointed out that the contribution of β is 4 to 4.5 times larger, and more uncertain, than climate-climate feedback (γ) (Gregory et al., 2009; Bonan and Levis, 2010; Arora et al., 2013). Apart from the substantial uncertainty across different models, Smith et al. (2016)
50 suggested that Earth System Models (ESMs) in CMIP5 overestimate global terrestrial β values compared with remote sensing data and Free-Air CO₂ Enrichment (FACE) experimental results. Though satellite products they used may underestimate the effect of CO₂ fertilization on net primary productivity (De Kauwe et al., 2016), the large disparity between models and FACE experiments gives us little confidence in making policies to combat global warming.

55 The response of ecosystem carbon cycle to elevated CO₂ (eCO₂) is primarily driven by stimulation of leaf-level carboxylation rate in plants (Polglase and Wang, 1992; Long et al., 2004; Heimann et al., 2008). The CO₂ stimulation of carboxylation then translates into increasing gross primary production (GPP) and net primary production (NPP), possibly leading to increased biomass and soil carbon storage and slowing down anthropogenically driven increase in atmospheric CO₂ (Canadell et al., 2007; Iversen et al., 2012). The leaf-level CO₂ fertilization for C₃ plants is generally well characterized with models from
60 Farquhar et al. (1980), and the basic biochemical mechanisms have been adopted by most land surface models although some models implement variants of Farquhar et al. (1980) (Rogers et al., 2017). Previous research with both theoretical analysis and data synthesis from a large number of experiments has revealed that normalized CO₂ sensitivity of leaf-level photosynthesis,

65 which represents kinetics sensitivity of photosynthetic enzymes, varies little among different C₃ species at a given CO₂ concentration (Luo and Mooney, 1996; Luo et al., 1996). However, the CO₂ fertilization effects are considerably more variable at canopy- and ecosystem-level than at the leaf-level, because a cascade of uncertain processes, such as soil moisture feedback (Fatichi et al., 2016), canopy scaling (Rogers et al., 2017), nutrient limitation (Zaehle et al., 2014), allocation (De Kauwe et al., 2014), and carbon turnover process (Friend et al., 2014) influence the responses of GPP, NPP and carbon storage. Therefore, understanding which processes in ecosystem models amplify the variability in β from biochemical and leaf levels to canopy and ecosystem levels is quite important.

70 Leaf area index (LAI) largely affects canopy assimilation and plant growth under eCO₂. Many satellite products exhibit increasing trends of LAI over the past 30 years although marked disparity still exists among these products (Jiang et al., 2017). Zhu et al. (2016) has attributed global increases in satellite LAI primarily to increased CO₂ concentration. LAI plays a key role in scaling leaf-level biogeophysical and biogeochemical processes to global scale responses in ecosystem models, and the representation of LAI in models causes large uncertainty (Ewert, 2004; Hasegawa et al., 2017). Models generally predict that LAI dynamics will respond to eCO₂ positively due to enhanced NPP and leaf biomass (De Kauwe et al., 2014). But how the increasing LAI in turn feeds back to ecosystem carbon uptake as a result of more light interception has not been discussed in previous research. The relative contributions of the leaf-level photosynthesis and LAI to modelled β have been rarely quantified and compared.

80 The CO₂ fertilization effects depend on locations, vegetation types and soil nutrient conditions. The strongest absolute CO₂ fertilization effect has been found in tropical and temperate forests where the larger biomass presents than other regions. In comparison, the weakest response to eCO₂ occurs in boreal forests (Joos et al., 2001; Peng et al., 2014). But with gradual eCO₂, relative response in tropical forests might not be very high owing to light limitation caused by canopy closure (Norby et al., 2005). In addition, β might be overestimated by the neglect of nitrogen (N) limitations on plant growth (Luo et al., 2004; Thornton et al., 2009; Coskun et al., 2016). Several lines of evidence suggest that N availability also influences decomposition

of soil organic matter (Hunt et al., 1988; Neff et al., 2002; Averill et al., 2016). β will be reduced by 50–78% in C-N coupled simulations compared with C-only simulations in land surface models (Thornton et al., 2007; Sokolov et al., 2008; Zaehle et al., 2010). Inadequate phosphorus (P) will also constrain terrestrial carbon uptake, especially in tropical area (Aerts and Chapin, 2000; Vitousek et al., 2010). It is reported that N limitation on carbon uptake is significant in boreal ecosystems, while P limitation has a profound influence in tropical ecosystems in CASA-CNP model (Wang et al., 2010). However, whether N and P limitations affect the variability of β across different vegetation types at different hierarchical levels from biochemistry to ecosystem carbon storage, have not been carefully examined.

In this study, we tried to answer the following questions: how variability, as measured by coefficient of variation (CV) within and across different plant functional types (PFTs), in the CO₂ fertilization effects changes at different hierarchical levels from leaf to canopy GPP, ecosystem NPP and total carbon storage levels? What is the most important process causing the variability of β for different geographical locations and PFTs? How nutrient limitations influence the variability of β at different hierarchical levels? We used Community Atmosphere Biosphere Land Exchange model (CABLE) to identify key mechanisms driving diverse β values under RCP 8.5 scenario.

2. Materials and methods

2.1 CABLE model description

CABLE (version 2.0) is the Australian community land surface model (Kowalczyk et al., 2006) and incorporates CASA-CNP to simulate global carbon (C), nitrogen (N) and phosphorus (P) cycles (Wang et al., 2010; Wang et al., 2011). Leaf photosynthesis, stomatal conductance, and heat and water transfer in CABLE are calculated using the two-leaf approach (Wang and Leuning, 1998) for both sunlit leaves and shaded leaves. The descriptions of photosynthesis module are in supplementary Text S1.

Leaf Area Index (LAI) is calculated as:

$$110 \quad LAI = C_{leaf} * SLA \quad (1)$$

Where C_{leaf} is leaf carbon pool, and SLA is specific leaf area.

In the CABLE model, leaf growth is divided into four phases. Phase 1 is from leaf budburst to the beginning of steady leaf growth, phase 2 is from the start of steady leaf growth to the start of leaf senescence, phase 3 is the period of leaf senescence, and phase 4 is from the end of leaf senescence to the start of leaf bud burst. During phase 1, allocation of available carbon to
115 leaf is fixed to 0.8, and allocation to wood and root are set to 0.1 for woody biomes, and 0 and 0.2 respectively for non-woody biomes. During steady leaf growth (phase 2), the allocation coefficients are constants but vary from biome to biome, taking their values from Fung et al. (2005). During phases 3 and 4, the leaf allocation is zero and available carbon is divided between wood and root in proportional to their allocation coefficients. For evergreen biomes, leaf phenology remains at phase 2 throughout the year (Wang et al., 2010). SLA is PFT-specific and does not change through time in this study.

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GPP is the sum of canopy net photosynthesis rate (A) and day respiration (R_d). NPP is calculated as the difference between GPP and autotrophic respiration (R_a) (including maintenance and growth respiration), and acts as an input to the compartmental nine-pool carbon cycle model. The network for carbon transfer in the compartmental model is based on CASA' model (Fung et al., 2005), including three vegetation pools (leaf, wood and root), three litter pools (metabolic litter, structure
125 litter and coarse wood debris), three soil pools (fast soil pool, slow soil pool and passive soil pools). Heterotrophic soil respiration (R_h) is calculated as the sum of the respired CO_2 from the decomposition of all litter and soil organic carbon pools (Wang et al., 2010).

Wang et al. (2012) and Zhang et al. (2013) provided details explaining how nutrient limitations are incorporated into carbon
130 cycle in CASA-CNP module in the CABLE model. In brief, NPP is calculated as:

$$NPP = GPP(L, V_{cmax}(N_i), J_{max}(N_i)) - \sum_i R_{mi}(N_i) - R_g\left(\frac{N_i}{P_i}\right) \quad (2)$$

Where L represents leaf area index, V_{cmax} and J_{max} are maximum carboxylation rate and maximum rate of electron transport of the top leaves, respectively, both are linearly dependent on leaf N (g N m^{-2}) according to the relationships developed by Kattge et al. (2009) for different plant functional types. R_{mi} is maintenance respiration rates of plant tissue (i =leaf, wood and root), contingent on nitrogen amount in each part of plant. R_g is growth respiration, which is described as a function of leaf nitrogen to phosphorus ratio. Heterotrophic respiration (R_h) is limited by the mineral N pool required for microbial soil carbon decomposition (Wang et al., 2010). Net ecosystem productivity ($\text{NEP} = \text{GPP} - R_a - R_h$) is the amount of carbon that is either sequestered or lost from ecosystems, and is controlled by N and P availability via abovementioned C-N-P interactions.

2.2 Experimental design

CABLE was run from 1901 to 2100 for C-only, C-N and C-N-P modes. C-only simulation was designed to identify the key carbon cycle processes that influence the variability of the CO_2 fertilization effects. C-N and C-N-P simulations were run to explore how nutrients affect the patterns of and mechanisms underlying the variability of the CO_2 fertilization effects. The respective effects of N and P can be calculated through the difference in the carbon uptake between C-N and C-only or C-N-P and C-N simulations. CABLE was first spun up by using meteorological forcing from Community Climate System Model (CCSM) simulations (Hurrell et al., 2013) during 1901 to 1910 until steady states were achieved for the C-only, C-N and C-N-P cases separately. Hourly meteorological driving data include: temperature, specific humidity, air pressure, downward solar radiation, downward long-wave radiation, rainfall, snowfall, and wind. In order to separate the CO_2 fertilization effect from the effect of climate change, climate forcing was held as the average annual cycle of CCSM meteorological data from 1901 to 2100. Atmospheric CO_2 concentrations from 1901 to 2100 were taken from the CMIP5 dataset, representing global annual averages and the RCP8.5 scenario after 2010 (Etheridge et al., 1996; MacFarling Meure et al., 2006). The spatial resolution of CABLE used here is $1.9^\circ \times 2.5^\circ$ (latitude vs longitude). N deposition is prescribed from atmospheric transport models (Lamarque et al., 2010, 2011), spatially explicit but fixed as the average from 1901 to 2100 in time. N fixation is prescribed from a process-based model, spatially explicit but constant in time (Wang and Houlton, 2009). P enters ecosystems through constant rates of weathering and atmospheric deposition (from Mahowald et al. (2008)).

155 2.3 Calculation of β values at five hierarchical levels

We aimed to analyze the CO₂ fertilization effects for biochemical reaction (\mathcal{L}), leaf photosynthesis rate (p), leaf-to-canopy scaling factor (S), leaf area index (LAI), sunlit leaf GPP (GPP_{sun}), shaded leaf GPP (GPP_{sha}), canopy GPP, NPP, and ecosystem carbon storage (c_{pool}) from C-only, C-N and C-N-P simulations of CABLE. Canopy GPP is the sum of sunlit leaf GPP and shaded leaf GPP. Ecosystem carbon storage is the sum of plant, litter and soil carbon stock. Since CO₂ concentration increases at yearly basis, annual carbon fluxes and storages such as GPP_{sun} , GPP_{sha} , canopy GPP, NPP and ecosystem carbon storage were calculated. Leaf-to-canopy scaling factor and LAI were averaged within a year. β values of these variables were calculated as the normalized sensitivities of those variables to atmospheric CO₂ concentration (C_a) as β_V :

$$\beta_V = \frac{1}{V} * \frac{dV}{dC_a} \quad (3)$$

165 Where V in the denominator represents average annual value of S_{sun} , S_{sha} , LAI, GPP, GPP_{sun} , GPP_{sha} , NPP and ecosystem carbon storage between two consecutive years. Subscripts “sun” and “sha” denote the sunlit and shaded components. dV is the difference of these variables between two consecutive years. dC_a is the difference of corresponding C_a . The unit of β_V is ppm⁻¹. It should be noted that β_V is the relative response, which is similar to the traditional definition of β factor by Bacastow and Keeling (1973), but different from the carbon-concentration feedback parameter in Friedlingstein et al. (2006). The relative response facilitates the comparison among PFTs with different initial biomass and the comparison across carbon fluxes and storages with different units.

175 Leaf biochemical response (\mathcal{L}) was first proposed by Luo et al. (1996). \mathcal{L} function is the normalized response of leaf photosynthesis rate to a small change in intercellular CO₂ concentration (C_i) and has been suggested to be an invariant function for C₃ plants grown in diverse environments. The rate of photosynthesis is typically RuBP-regeneration-limited under high CO₂ concentration. We found photosynthesis rates are almost all increasingly limited by RuBP-regeneration process globally under RCP8.5 scenario since 2011 when CO₂ concentration exceeds 390 ppm. Besides, theoretical analysis by Luo and Mooney (1996) showed that biochemical responses are similar for either Rubisco- or RuBP-limited photosynthesis. In this

study, \mathcal{L} can be used to indicate leaf biochemical response to $e\text{CO}_2$. For sunlit leaf and shaded leaf, formulations of \mathcal{L} under RuBP-regeneration-limitation are defined as:

$$180 \quad \mathcal{L}_{sun} = \frac{3 * \Gamma_{*sun}}{(C_{isun} + 2 * \Gamma_{*sun})(C_{isun} - \Gamma_{*sun})} \quad (4)$$

$$\mathcal{L}_{sha} = \frac{3 * \Gamma_{*sha}}{(C_{isha} + 2 * \Gamma_{*sha})(C_{isha} - \Gamma_{*sha})} \quad (5)$$

In this study, Γ_{*sun} and Γ_{*sha} are yearly average CO_2 compensation points in the absence of day respiration for sunlit leaf and shaded leaf, respectively. C_i varies significantly at sub-daily, intra-annual and inter-annual bases. We're interested in how C_i responds to $e\text{CO}_2$ on an inter-annual basis. So, we first outputted hourly C_i then calculated yearly GPP-weighted average C_i for sunlit leaf (C_{isun}) and shaded leaf (C_{isha}).

Then leaf-level β_p is defined as the product of \mathcal{L} and $\frac{dC_i}{dC_a}$. For sunlit leaf and shaded leaf, the formulations are:

$$\beta_{psun} = \mathcal{L}_{sun} * \frac{dC_{isun}}{dC_a} \quad (6)$$

$$\beta_{psha} = \mathcal{L}_{sha} * \frac{dC_{isha}}{dC_a} \quad (7)$$

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Leaf-to-canopy scaling factor (S) scales fluxes at the single top leaf of the canopy to whole canopy fluxes. The formulations of S for sunlit leaves and shaded leaves are:

$$S_{sun} = \frac{1 - \exp[-\text{LAI}(k_n + k_b)]}{k_n + k_b} \quad (8)$$

$$S_{sha} = \frac{1 - \exp(-k_n \text{LAI})}{k_n} - \frac{1 - \exp[-\text{LAI}(k_n + k_b)]}{k_n + k_b} \quad (9)$$

195 Where k_b is extinction coefficient of a canopy of black leaves for direct beam radiation. k_n is an empirical parameter used to describe the vertical distribution of leaf nitrogen in the canopy (Kowalczyk et al., 2006). In our simulation, k_n is uniformly

assigned as 0.001 for different PFTs. The leaf-to-canopy scaling factor varies with time because k_b is the function of sun angle, and LAI varies seasonally and inter-annually. The annual value of the leaf-to-canopy scaling factor was just calculated as the average ~~from~~of hourly leaf-to-canopy scaling factors in a year.

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Big-leaf $\beta_{GPP_{sun}}$ (or $\beta_{GPP_{sha}}$) can be decomposed as the sum of normalized sensitivity of photosynthesis rate: $\beta_{p_{sun}}$ (or $\beta_{p_{sha}}$) and leaf-to-canopy scaling factor: $\beta_{S_{sun}}$ (or $\beta_{S_{sha}}$) as shown in Eq. (10) and Eq. (11). Detailed mathematical derivations are in supplementary Text S2.

$$\beta_{GPP_{sun}} = \beta_{p_{sun}} + \beta_{S_{sun}} \quad (10)$$

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$$\beta_{GPP_{sha}} = \beta_{p_{sha}} + \beta_{S_{sha}} \quad (11)$$

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There are ten patches in each model grid in CABLE. Each patch consists of a certain land use type with a specific fraction. To study the variation of β across different C₃ PFTs, biome-level parameters such as Γ_{*sun} , C_{isun} , S_{sun} and LAI were calculated as mean values based on PFTs, whereas biome-level GPP, GPP_{sun} , GPP_{sha} , NPP and ecosystem carbon storage were integrated sums based on PFTs. Then \mathcal{L}_{sun} , \mathcal{L}_{sha} , $\beta_{p_{sun}}$, $\beta_{p_{sha}}$, β_{GPP} , β_{NPP} and β_{cpool} at the year 2023 (relative to 2022) for different C₃ PFTs were calculated and compared. Coefficients of variation (CVs) of β values were calculated across various C₃ PFTs for these hierarchical levels. The year 2023 was chosen because large oscillations of LAI occurred for shrub after 2025 in the C-N-P simulation (Fig. S1c). For C-N and C-N-P simulations, the time series of LAI, GPP, and NPP for shrub, C₃ grass and tundra underwent small short-term variability and therefore were smoothed using the “smooth” function in MATLAB software before the calculation of β . We also calculated β values for each patch and CV of β values across different geographical locations within a specific PFT at different hierarchical levels at the year of 2023 to explore the variability of β within the same PFTs. All abovementioned calculations were processed in MATLAB R2014b.

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3. Results

3.1 Temporal trends of β at ecosystem level for different PFTs

220 In C-only simulation, β_{cpool} values for different C₃ PFTs all decline with time from 2011 to 2100 under RCP8.5 scenario (Fig. 1a). However, the magnitudes of β_{cpool} differ among different PFTs, with the highest values occurring in deciduous broadleaf forest from 2011 to 2075 and in shrub after 2075, and lowest values occurring in deciduous needleleaf forest and tundra. β_{cpool} values for deciduous needleleaf forest and tundra nearly overlap over time. As compared with C-only simulation, values of β_{cpool} are reduced when N limitation is included as in C-N simulation for all C₃ PFTs except evergreen broadleaf forest (Fig. 1b). Deciduous broadleaf forest and evergreen broadleaf forest have the greatest β_{cpool} values, while deciduous needleleaf forest and tundra still have the lowest β_{cpool} values in C-N simulation. When both N and P limitations are taken into account as in C-N-P simulation, magnitudes and trends of β_{cpool} are similar to those in C-N simulation (Fig. 1c) as P limitation is quite weak under present condition in the current version of CABLE (Zhang et al., 2011).

3.2 Variations of intercellular CO₂ concentration and CO₂ compensation point

230 To reveal which processes cause the large disparity of β across PFTs as shown in Fig. 1, we first compared intercellular CO₂ concentration (C_i) and CO₂ compensation point in the absence of day respiration (Γ_*), which are critical parameters for leaf-level biochemical response. In C-only simulation, the ratio of C_i to C_a (C_i/C_a) is approximately constant with eCO₂ for each PFT (Fig. 2a, 2b). For sunlit leaf, C_i/C_a values range from 0.64 to 0.70 with CV=0.03 across different C₃ PFTs (Table 1). C_i/C_a values for shaded leaf are higher than those for sunlit leaf, and the range is 0.68 to 0.76 with CV=0.03 across different C₃ PFTs (Table 1). Evergreen broadleaf forest has the greatest C_i/C_a value, while deciduous needleleaf forest has the lowest C_i/C_a value. In C-N simulation, C_i/C_a values for sunlit leaf are lower than those for the same PFT in C-only simulation, while C_i/C_a values for shaded leaf change little as compared with those for the same PFT in C-only simulation (Table 1 and Fig. S2). C_i/C_a values for both sunlit and shaded leaves in C-N-P simulation are very similar to those in C-N simulation (Table 1 and Fig. S3).

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In all of the simulations, values of CO₂ compensation point in the absence of day respiration (Γ_*) for a specific PFT do not change over time since air temperature as an input to the model is not affected by the biophysical feedback in the offline model simulations (Fig. 2c, 2d, S2c, S2d, S3c, S3d). But there is a huge variance of Γ_* across different C₃ PFTs because of different leaf temperature which Γ_* values depend on.

245 3.3 Comparison of β at different hierarchical levels

To further trace the cause for the divergence of β across PFTs as shown in Fig. 1 at a specific time, \mathcal{L}_{sun} , \mathcal{L}_{sha} , $\beta_{p_{sun}}$, $\beta_{p_{sha}}$, β_{GPP} , β_{NPP} and β_{cpool} at the year 2023 for different C₃ PFTs in all simulations were plotted in Fig. 3. CV is marked above data points for each variable to indicate degree of variation across different C₃ PFTs. In C-only simulation (Fig. 3a), results show that at leaf biochemical level, \mathcal{L} values for sunlit leaf and shaded leaf range from 0.00055 ppm⁻¹ to 0.00097 ppm⁻¹.

250 Variations of \mathcal{L}_{sun} and \mathcal{L}_{sha} among PFTs are small (CV=0.15 and 0.13). At leaf photosynthesis level, $\beta_{p_{sun}}$ and $\beta_{p_{sha}}$ for the seven PFTs vary from 0.00041 ppm⁻¹ to 0.00072 ppm⁻¹, and the variations among different PFTs are not significant (CV=0.18 and 0.12). But β values are diverging when scaled up to GPP level with CV jumping to 0.49 among PFTs. β values of deciduous broadleaf forest and shrub greatly increase from leaf level to GPP level. However, canopy scaling effects do not significantly amplify β values at canopy levels (β_{GPP}) for deciduous needleleaf forest, tundra and evergreen broadleaf forest.

255 Magnitudes and variance of β_{NPP} are similar to those of β_{GPP} because NPP linearly correlates with GPP for all C₃ PFTs (Fig. S4). Magnitudes of β_{cpool} for all PFTs are decreased compared with those of β_{NPP} and β_{GPP} . Deciduous broadleaf forest and shrub have the highest β_{GPP} and β_{NPP} values (around 0.0026 ppm⁻¹). Deciduous broadleaf forest has the greatest β_{cpool} value (around 0.0018 ppm⁻¹) among all. Deciduous needleleaf forest has the lowest β_{GPP} , β_{NPP} and β_{cpool} values. CV of β_{cpool} among different PFTs reaches the highest (0.58) compared with CV of β values at other levels.

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In C-N and C-N-P simulations, magnitudes and variations of β at leaf biochemical and photosynthetic levels are comparable to those in C-only simulation because C_i and Γ_* values only slightly change under nutrient limitations (Fig. 3b, 3c, S2, S3). Nutrient-limited β_{GPP} values are smaller than those in C-only simulation, except for evergreen broadleaf forest. There is a

large divergence of nutrient-limited β_{GPP} across different PFTs, which is similar to C-only simulation. However, unlike in
265 C-only simulation, β_{NPP} values in nutrient-coupled simulations are reduced for most C₃ PFTs and diverge more compared
with β_{GPP} values. Coefficients of variation (CVs) of β_{cpool} in nutrient-coupled simulations exceed 0.8, larger than that in
C-only simulation.

Within-PFT variations of β in C-only simulation were listed in Table 2, including CVs for biochemical response \mathcal{L} , leaf-
270 level β_p , β_{GPP} , β_{NPP} and β_{cpool} across different geographical locations within each PFT. Variations of biochemical and
leaf-level responses are relatively smaller than those at canopy and ecosystem levels within all C₃ PFTs. β_{GPP} values greatly
differentiate across different geographical locations. Variations of β_{NPP} are very similar to those of β_{GPP} within all PFTs
except the evergreen needleleaf forest. CVs of β_{cpool} are lower than those of β_{NPP} within most PFTs except evergreen
broadleaf forest and tundra. Within-PFT variations of β in C-N and C-N-P simulations are similar to those in C-only
275 simulation (data not shown).

To further explore why β values at canopy and ecosystem levels are diverging across different C₃ PFTs, the correlations
between β_{GPP} and β_{LAI} , β_{NPP} and β_{LAI} , β_{cpool} and β_{LAI} for C-only, C-N and C-N-P simulations were plotted at the year
2023. Results show that β_{GPP} , β_{NPP} and β_{cpool} all have significant linear correlations with β_{LAI} across different C₃ PFTs
280 (Fig. 4). Results also show that β_{LAI} linearly correlates with β_{GPP} , β_{NPP} and β_{cpool} across patches within the same PFT,
although there are some discontinuous points within evergreen broadleaf forest where canopy of many patches closes (Fig.
S5-S7). Therefore variations of β values from leaf to ecosystem scale can be well explained by β_{LAI} , or the LAI response to
increasing CO₂.

3.4 β of sunlit and shaded leaves

285 To understand the in-depth mechanism for the influence of LAI on canopy GPP, we investigate the response of sunlit and
shaded leaf GPP separately from C-only simulation. Temporal trends of sunlit leaf GPP (GPP_{sun}) and shaded leaf GPP (GPP_{sha})

were plotted for each type of C_3 PFTs from 1901 to 2100 in Fig. 5. From the beginning of the simulation, GPP_{sha} is higher than GPP_{sun} for all C_3 PFTs. With significant increases of CO_2 concentration from 2011, GPP_{sha} responds more drastically than GPP_{sun} . Shaded leaf GPP of deciduous broadleaf forest and shrub responds to eCO_2 more significantly than other PFTs.

290 However, a single sunlit leaf has higher photosynthesis rate (p_{sun}) than a shaded leaf (p_{sha}) because of more radiation absorbed. Thus, the LAI-dependent canopy scaling factor of shaded leaves (S_{sha}) contributes more to the magnitude and sensitivity of canopy GPP than photosynthesis rate.

Then temporal trends were plotted for $\beta_{GPP_{sun}}$ ($\beta_{GPP_{sha}}$) and decomposing factors $\beta_{p_{sun}}$ ($\beta_{p_{sha}}$) and $\beta_{S_{sun}}$ ($\beta_{S_{sha}}$) for each PFT as Eq. (10) and Eq. (11) to further evaluate the above inference. Results show that both of the sensitivities of GPP_{sun} and GPP_{sha} tend to approach zero through time because the decomposing factors $\beta_{p_{sun}}$, $\beta_{p_{sha}}$, $\beta_{S_{sun}}$ and $\beta_{S_{sha}}$ all decline with time (Fig. 6). $\beta_{p_{sun}}$ and $\beta_{p_{sha}}$ overlap through time for each PFT. Magnitudes of $\beta_{GPP_{sha}}$ are higher than those of $\beta_{GPP_{sun}}$ for all C_3 PFTs. For deciduous needleleaf forest and tundra, both $\beta_{p_{sun}}$ ($\beta_{p_{sha}}$) and $\beta_{S_{sun}}$ ($\beta_{S_{sha}}$) contribute to the magnitudes and trends of $\beta_{GPP_{sun}}$ ($\beta_{GPP_{sha}}$). For evergreen needleleaf forest, deciduous broadleaf forest, shrub and C_3 grass, $\beta_{S_{sun}}$ ($\beta_{S_{sha}}$) dominates the magnitude and change of $\beta_{GPP_{sun}}$ ($\beta_{GPP_{sha}}$). For evergreen broadleaf forest, $\beta_{S_{sha}}$ predominates the magnitude and change of $\beta_{GPP_{sha}}$ before 2035.

4. Discussion

4.1 ~~Variation~~Variations of biochemical and photosynthetic responses to eCO_2

The direct CO_2 fertilization effect occurs at leaf level and is determined by kinetic sensitivity of Rubisco enzymes to internal leaf CO_2 concentration. In fact, the normalized short-term sensitivity of leaf-level photosynthesis to CO_2 is mainly regulated by C_i and slightly influenced by leaf temperature, regardless of light, nutrient availability, and species characteristics (Luo et al., 1996; Luo and Mooney, 1996). In our study, modelled C_i/C_a ratio is approximately constant with eCO_2 for a specific PFT, and varies little within and across PFTs in all simulations. This is in line with FACE experimental results which show almost

constant C_i/C_a values for different PFTs under CO₂ fertilization (Drake et al., 1997; Long et al., 2004). Γ_* varies little for
310 different species and only depends on leaf temperature (Luo and Mooney, 1996). Sensitivity analysis in a previous study has
shown that a $\pm 5^\circ\text{C}$ of leaf temperature changes caused approximately ± 7 ppm changes in Γ_* , leading to variation of 0.12 to
leaf-level β (Luo and Mooney, 1996). The overall variation of leaf-level β caused by variation in leaf temperature is still
quite small compared with that of β_{GPP} . Therefore, biochemical and leaf-level β values vary little within and among PFTs
in this study. Our results also illustrate that nutrient effects do not significantly change C_i and Γ_* , leading to similar
315 biochemical and leaf-level β values in all simulations, which is in accordance with Luo et al. (1996).

To identify the source of uncertainty of β in CMIP5 models, Hajima et al. (2014) decomposed β into several carbon cycle
components. They used GPP divided by LAI (GPP/LAI) as a proxy to represent leaf-level photosynthesis for CMIP5 models,
since there are no leaf-level process outputs of these models. They found the sensitivities of GPP/LAI to eCO₂ diverged a lot
among models. ThisOne possible issue of this calculation is likely debatable for ignoring that it ignores different canopy
structure used by each CMIP5 model such as big-leaf, two-leaf or multiple-layer. Our results just show that the sensitivities of
GPP/LAI are different from our mechanistic calculation of leaf-level β for different PFTs (Fig. S8)-in a two-leaf model. β
values estimated from GPP/LAI formulation are greatly underestimated for woody trees and slightly overestimated for C₃
grass and tundra, but best match for shrub if compared with our calculation (Fig. S8). Therefore diagnostics such as C_i and
325 Γ_* for leaf-level β are more desirable for woody trees. Another advantage of our calculation of leaf-level β is that the reason
for the divergence of leaf-level β across PFTs can be traced back to the difference from C_i and leaf temperature as shown
in Fig. 2.

4.2 ~~Variation~~ Variations of β at canopy and ecosystem levels

The two-leaf scaling scheme in CABLE is widely employed by many land surface models, such as Community Land Model
330 version 4.5 (CLM4.5, Oleson et al., 2013) and the Joint UK Land Environment Simulator version 4.5 (JULES4.5, Best et al.,
2011; Clark et al., 2011; Harper et al., 2016). We found the responses of ecosystem carbon cycle to eCO₂ diverge primarily

because the responses of LAI diverge within and among PFTs in all simulations. Besides, GPP of shaded leaves responds to eCO₂ stronger than GPP of sunlit leaves for all C₃ PFTs. This is because the portion of shaded leaves increase exponentially with increasing LAI (Fig. S9), leading to a rapid change of shaded leaf GPP. While for sunlit leaves, GPP shows a saturating response because of the decreasing portion of sunlit leaves with increasing LAI (Dai et al., 2004). Our results also indicate that saturation of GPP is not only regulated by the leaf-level photosynthetic response, but also by the response of the LAI-dependent scaling factor to eCO₂. For shaded leaves, the sensitivity of the LAI-dependent scaling factor contributes more to the magnitude and trend of $\beta_{GPP_{sha}}$ than that of photosynthesis rate. The evidence all suggests LAI is a key process in modeling the response of ecosystem carbon cycle to climate change.

It has been reported that different CMIP5 models have simulated diverse LAI during 1985-2006. And modelled LAI values in most CMIP5 models have been overestimated according to satellite ~~product~~products (Anav et al., 2013). Many global vegetation models simulated increasing LAI trends globally in response to eCO₂ during historical period (Zhu et al., 2016). Our modelling study also shows that LAI responds positively to eCO₂ for all C₃ PFTs in all simulations. But experimental results are not consistent. In one review paper with 12 FACE experimental results, trees had a 21% increase in LAI, herbaceous C₃ grasses did not show a significant change in LAI (Ainsworth and Long, 2005). Some studies reported that LAI dynamics did not significantly change in specific FACE experiments, such as in a high-LAI-closed-canopy deciduous broadleaf forest (ORNL FACE; Norby et al., 2003) and in a low-LAI-mature evergreen broadleaf forest (EucFACE; Duursma et al., 2016). The negligible change of LAI at the EucFACE probably leads to insignificant response of productivity at this site, even though leaf photosynthesis rate significantly increases under eCO₂ (Ellsworth et al., 2017). Besides the impact of LAI on global carbon cycle, the increasing trend of LAI exerts profound biophysical impacts to climate through altering the energy and water cycles on the Earth's surface (Forzieri et al., 2017; Zeng et al., 2017). But there is a great uncertainty in the relationships between LAI and biophysical processes among land surface models (Forzieri et al., 2018).

355 In this study, modelled nutrient-unlimited β_{GPP} and β_{NPP} values are higher than leaf photosynthetic responses for all C_3
PFTs in C-only simulation (Fig. 3a). Nutrient-limited β_{NPP} are still higher than photosynthetic responses for many PFTs in
C-N and C-N-P simulations (Fig. 3b, 3c). However, it is generally observed in experiments that the leaf-level response is
consistently larger than the whole plant response (Long et al., 2006; Leuzinger et al., 2011). One possible reason is that models
overestimate the response of LAI to eCO_2 , as this study has shown that LAI is an important factor in driving ecosystem
360 response to CO_2 fertilization. And it is also likely the overestimation of the response of LAI to eCO_2 is responsible for the
overestimation of CO_2 fertilization in ESMs reported by previous studies (Smith et al., 2015; Mystakidis et al., 2017).

The overall response of LAI to eCO_2 depends on several processes in this study: (1) NPP increase, (2) change in allocation of
NPP to leaf, (3) change in specific leaf area (SLA) in response to eCO_2 , (4) PFT-specific minimum and maximum LAI values
365 prescribed in the model. First, the low responses of LAI to eCO_2 for deciduous needleleaf forest and tundra can be attributed
to smaller NPP enhancements in cold areas. The large divergence of the response of LAI within PFTs is mainly due to the
large range of NPP increment across different geographical locations. The reduced magnitudes of β_{LAI} under nutrient
limitations is the direct outcome of reduced β_{NPP} . Accurate estimate of response of GPP and NPP is therefore fundamental to
realistic LAI modeling. Second, diverse allocation schemes influence the responses of LAI for different PFTs. And, results
370 from two FACE (Duke Forest and Oak Ridge) experiments indicate that the carbon allocated to leaves is decreased and more
carbon is allocated to woods or roots at higher CO_2 concentration (De Kauwe et al., 2014). Unfortunately, CABLE has fixed
allocation coefficients and likely overestimates LAI response, leading to overestimated responses of GPP, NPP and total carbon
storage. Third, we fixed SLA to calculate LAI in CABLE. But a reduction in SLA is a commonly observed response in eCO_2
experiments (Luo et al., 1994; Ainsworth and Long, 2005; De Kauwe et al., 2014). Tachiiri et al. (2012) also found SLA and
375 β values are most effectively constrained by observed LAI to smaller values in a model. Therefore, the fixed SLA may also
lead to over-prediction of the response of canopy cover to eCO_2 . Forth, in our results, LAI values for most C_3 PFTs are below
the maximum LAI limits with eCO_2 in C-only simulation. With only one exception, LAI values of many evergreen broadleaf
forest patches saturate at the prescribed maximum value under high CO_2 concentration (Fig. S1a and Table. S1). That's why

the sensitivity of LAI for evergreen broadleaf forest is low and thus leads to small relative GPP enhancements. If the preset
380 LAI upper limits are narrowed, β values are expected to be significantly reduced. Hence model parameters related to LAI
need to be better calibrated according to experiments and observations in order to better represent the response of ecosystem
productivity to eCO₂ (De Kauwe et al., 2014; Qu and Zhuang, 2018).

In this study, the almost identical values and variance of β_{NPP} as those of β_{GPP} within and across C₃ PFTs in C-only
385 simulation suggests carbon use efficiency (CUE) does not change with eCO₂, as autotrophic respiration is calculated from GPP
and plant carbon. In C-N and C-N-P simulations, magnitudes of β_{NPP} for all C₃ PFTs except evergreen broadleaf forest all
decline compared with those of β_{GPP} , indicating CUE also decline with eCO₂ under nutrient limitations. However, FACE
experimental results indicate that CUE values under eCO₂ are not changed in N-limited Duke site (Hamilton et al., 2002;
Schäfer et al., 2003), increase in fertile POPFACE site (Gielen et al., 2005) or decrease in fertile ORNL site (DeLucia et al.,
390 2005). Thus, representations of nutrient effects on GPP and autotrophic respiration in land surface models should be carefully
calibrated with experimental data (DeLucia et al., 2007). Our results also show that β_{NPP} values diverge more than β_{GPP}
values across different PFTs in nutrient-coupled simulations, because the different nutrient-limiting effects on autotrophic
respiration introduce additional variation across different PFTs. Although β values at ecosystem levels are more variable
with nutrient effects, LAI responses are still linearly correlated well with β_{GPP} , β_{NPP} and β_{cpool} across C₃ PFTs in nutrient-
395 coupled simulations as in C-only simulation, confirming the dominant role of LAI in regulating carbon cycle response under
CO₂ fertilization.

The reduced magnitudes of β_{cpool} compared with those of β_{GPP} and β_{NPP} in all simulations indicates carbon turnover
processes make ecosystems respond to eCO₂ less sensitively due to the slow allocation and carbon turnover processes. A
400 previous study using seven global vegetation models identified carbon residence time as the dominant cause for uncertainty in
terrestrial vegetation responses to future climate and atmospheric CO₂ change (Friend et al., 2014). The response of soil carbon
storage to eCO₂ also depends on soil carbon residence time (Harrison et al., 1993). In this study and many other models,

allocation coefficients are fixed over time (Walker et al., 2014). But allocation pattern to plant organs with different lifespan has been reported to change in response to eCO₂ in experiments, thereby altering carbon residence time in plants and soil (De
405 Kauwe et al., 2014). Therefore, the fixed allocation scheme we adopted in this study might lead to some biases in simulating the response of carbon residence time to eCO₂. In our study, soil decomposition rate is assumed not to be affected by CO₂ level, as in most other conventional soil carbon models (Friedlingstein et al., 2006; Luo et al., 2016). However, recent synthesis of experimental data suggests replenishment of new carbon into soil due to eCO₂ increases turnover rate of soil carbon (Van Groenigen et al., 2014; Van Groenigen et al., 2017). Within a certain PFT, the variation of β_{cpool} across different geographical
410 locations is usually smaller than that of β_{NPP} . While the greater variation of β_{cpool} than that of β_{NPP} across different C₃ PFTs in C-only simulation suggests other processes such as different carbon allocation patterns, plant carbon turnover, and the soil carbon dynamics of various PFTs, are responsible for the additional divergence. In nutrient-coupled simulations, the variations of β_{cpool} across different C₃ PFTs are only slightly larger than those of β_{NPP} , indicating that nutrients do not bring much differential effects on carbon turnover processes for different PFTs.

415 **4.3 Implication for understanding β in other models**

Although we analyze a single land-surface model in detail, the patterns of and mechanisms underlying the variability of β we found may be generally applicable to other models. The basic Farquhar photosynthesis model and two-leaf scaling scheme in the CABLE model are shared by many land surface models. Some models use variants of Farquhar photosynthesis model such as co-limitation approach described by Collatz et al. (1991). Inflection point from Rubisco- to RuBP- limited processes is an
420 important control of the absolute photosynthetic response to eCO₂ (Rogers et al., 2017). However, the relative photosynthetic responses for different ecosystems will converge to a small range because the normalized photosynthetic response to eCO₂ only depends on estimates of intercellular CO₂ concentration (C_i), Michaelis-Menten constants (K_c , K_o) and CO₂ compensation point (Γ_*), and the relative photosynthetic responses are similar for either Rubisco- or RuBP-limited photosynthesis (Luo et al., 1996; Luo and Mooney, 1996). Soil moisture availability is another key constraint on photosynthetic
425 response. Water stress on plants is generally alleviated under eCO₂ due to reduced stomatal conductance (Leuzinger and Körner,

2007; Fatichi et al., 2016). [Different models simulate diverse levels of water stress on productivity \(De Kauwe et al., 2017\).](#)

Water stress is simulated in many models to regulate stomatal conductance (Rogers et al., 2017; Wu et al., 2018). For example, the CABLE model represents water stress by an empirical relationship based on soil texture and limits the slope of the coupled relationship between photosynthesis rate and stomatal conductance as Eq. (S11). The influence of water stress is reflected by C_i . Synthesis of many empirical study results and our results in this study all show that ratio of C_i to C_a is relatively constant, probably due to homeostatic regulations through photosynthetic rate and stomatal conductance (Pearcy and Ehleringer, 1984; Evans and Farquhar, 1991). Wong et al. (1979) showed plant stomata could maintain a constant C_i/C_a [ratio](#) across wide range of environmental conditions, including water stress condition. [Land surface models might simulate relatively constant \$C_i/C_a\$ ratios under water stress as well since photosynthesis and stomatal conductance are theoretically depicted based on experimental results.](#) Moreover, Luo and Mooney (1996) found that changing C_i/C_a ratio from 0.6 to 0.8 caused less than variation of 0.08 in sensitivity of leaf photosynthesis to a unit of increase in C_a . K_c , K_o are variable among species, but only slightly affect leaf-level response (Luo and Mooney, 1996). Different leaf temperature will exert limited influence on the variability of leaf-level β as we discussed above. Therefore, leaf-level β values for different C_3 PFTs are more likely to converge in other land surface models.

A recent study used 16 crop models to simulate rice yield at two FACE sites (Hasegawa et al., 2017). These models have diverse representations of primary productivity. Their results showed that the variation of yield response across models was not much associated with model structure or magnitude of primary photosynthetic response to eCO_2 , but was significantly related with the estimations of leaf area. This is consistent with our conclusion and highlights the great need to improve prognostic LAI modeling. Other land-surface modelling groups may benefit from a similar analysis to identify major causes of variability of β across the hierarchical levels from biochemistry to land carbon storage. Candidate causes that can make substantial contributions to the variability include changes in changes in leaf area index, changes in carbon use efficiency and changes in land carbon residence times. If modelling groups can add leaf-level diagnostics in the next inter-model comparison project, it will greatly help disentangle the uncertainty of concentration-carbon feedback.

450 **5. Conclusions**

Exploring the variability of β at different hierarchical levels within and across different C₃ PFTs helps unravel model mechanisms that govern terrestrial ecosystem responses to elevated CO₂. Our study shows that the sensitivities of biochemistry and leaf-level photosynthesis to eCO₂ are very similar within and across C₃ PFTs in C-only, C-N and C-N-P simulations of CABLE, in accordance with previous theoretical analysis. While β values of GPP, NPP and ecosystem carbon storage diverge
455 primarily because the sensitivities of LAI significantly differ within and across different PFTs in all simulations. After decomposing β into photosynthetic and LAI components, we find LAI contributes more than photosynthesis to the magnitudes and trends of model responses. Our results indicate that processes related to LAI need to be better constrained with results from experiments and observations in order to better represent the responses of ecosystem carbon cycle processes to changes in CO₂ and climate.

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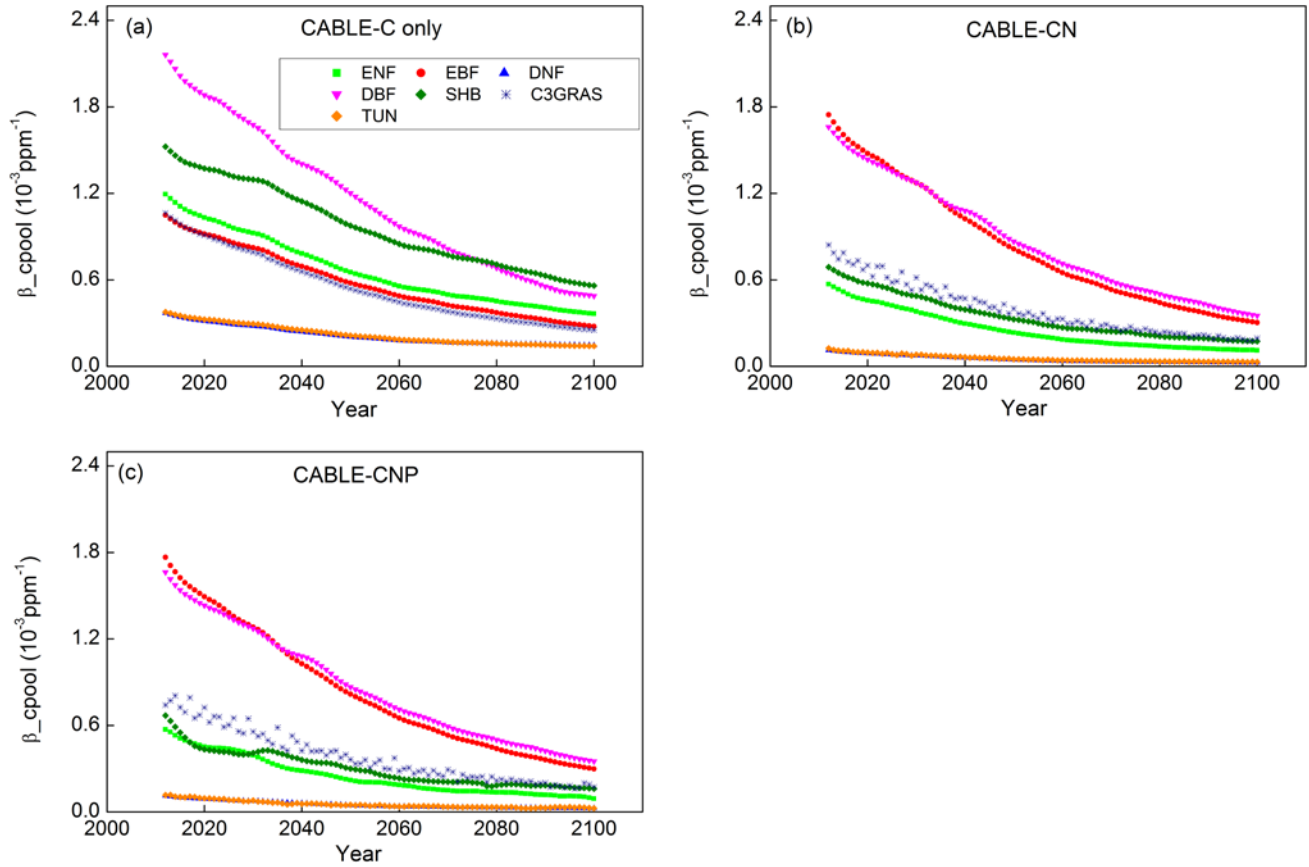
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Table 1. The ratio of intercellular CO₂ concentration (C_i) to atmospheric CO₂ concentration (C_a) for different C₃ PFTs, mean and coefficient of variation (CV) across these PFTs of C_i/C_a in C-only, C-N, C-N-P simulations of CABLE under RCP8.5 scenario. Values for shaded leaves are in brackets. Abbreviations are the same as Figure 1.

PFT	C_i/C_a (C-only) sunlit(shaded)	C_i/C_a (C-N) sunlit(shaded)	C_i/C_a (C-N-P) sunlit(shaded)
ENF	0.69(0.74)	0.66(0.74)	0.66(0.79)
EBF	0.70(0.76)	0.65(0.78)	0.65(0.78)
DNF	0.64(0.68)	0.61(0.67)	0.61(0.67)
DBF	0.67(0.73)	0.63(0.73)	0.64(0.73)
SHB	0.70(0.73)	0.65(0.73)	0.65(0.73)
C3GRAS	0.69(0.73)	0.63(0.73)	0.63(0.73)
TUN	0.68(0.71)	0.63(0.71)	0.63(0.71)
Mean	0.68(0.73)	0.64(0.73)	0.64(0.73)
CV	0.03(0.03)	0.03(0.05)	0.03(0.06)

Table 2. Coefficients of variation of \mathcal{L} , β_p , β_{GPP} , β_{NPP} and β_{cpool} across different geographical locations within each C₃ PFT at the year of 2023 in CABLE-C only simulation. The two numbers in the same unit are for sunlit leaves and shaded leaves respectively. Values for shaded leaves are in brackets. Abbreviations are the same as Figure 1.

PFT	CV(\mathcal{L})	CV(β_p)	CV(β_{GPP})	CV(β_{NPP})	CV(β_{cpool})
	sunlit(shaded)	sunlit(shaded)			
ENF	0.27(0.30)	0.41(0.42)	1.77	2.68	1.40
EBF	0.26(0.29)	0.24(0.28)	0.55	0.54	0.60
DNF	0.26(0.28)	0.25(0.28)	1.19	1.20	0.30
DBF	0.39(0.38)	0.42(0.37)	1.29	1.42	0.85
SHB	0.33(0.32)	0.30(0.49)	1.24	1.23	1.12
C3GRAS	0.38(0.34)	0.35(0.34)	1.12	1.10	0.98
TUN	0.35(0.34)	0.36(0.37)	1.86	1.85	1.92



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Figure 1. Temporal trends of β_{cpool} from 2011 to 2100 for C_3 PFTs from CABLE-C only (a), CABLE-CN (b), and CABLE-CNP (c) simulations. β_{cpool} values for different C_3 PFTs all decline with time from 2011 to 2100 under RCP8.5 scenario, but the magnitudes of β_{cpool} differ across them in all simulations. In C-N and C-N-P simulations, magnitudes of β_{cpool} are reduced compared with those in C-only simulation for all C_3 PFTs except evergreen broadleaf forest. ENF, Evergreen Needleleaf Forest (light green squares); EBF, Evergreen Broadleaf Forest (red circles); DNF, Deciduous Needleleaf Forest (dark blue triangles); DBF, Deciduous Broadleaf Forest (pink triangles); SHB, Shrub (dark green diamonds); C3GRAS, C_3 grass (dark blue stars); TUN, tundra (orange diamonds).

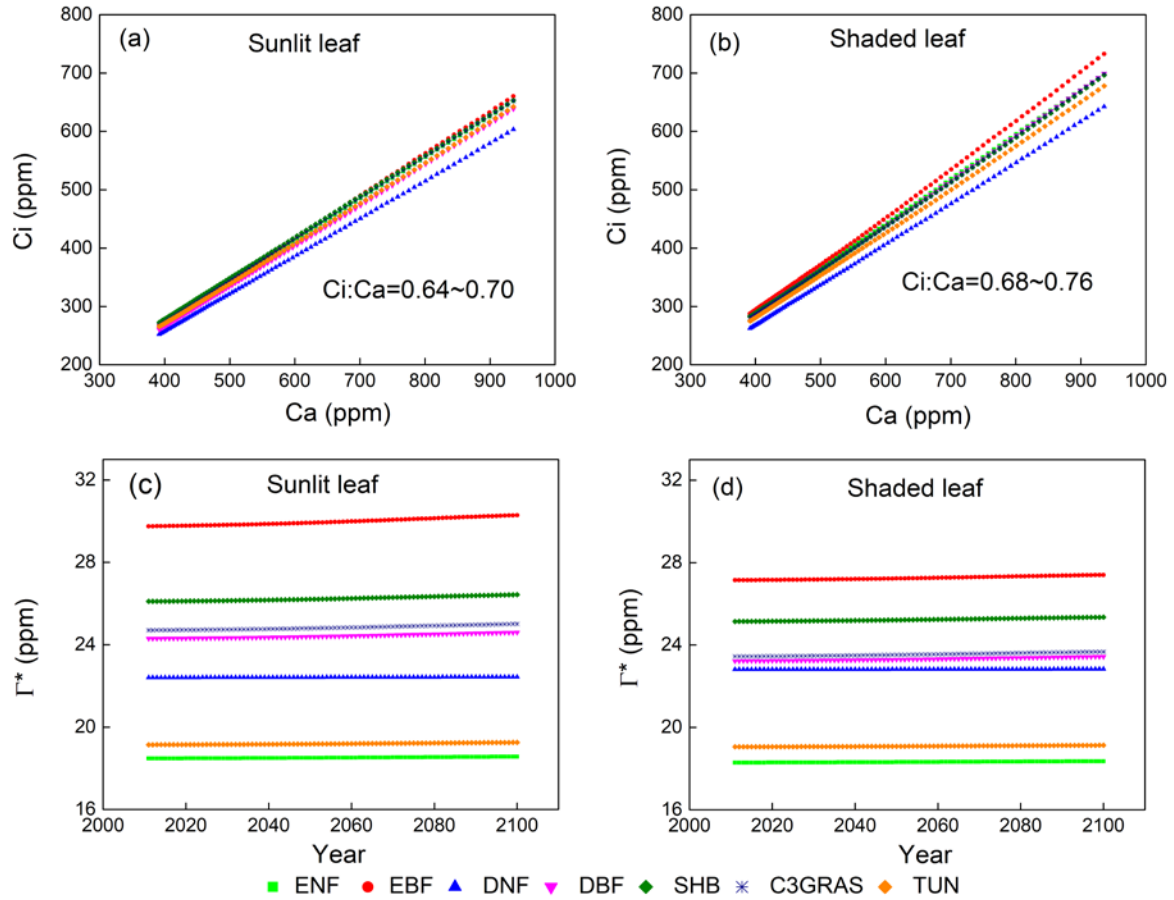
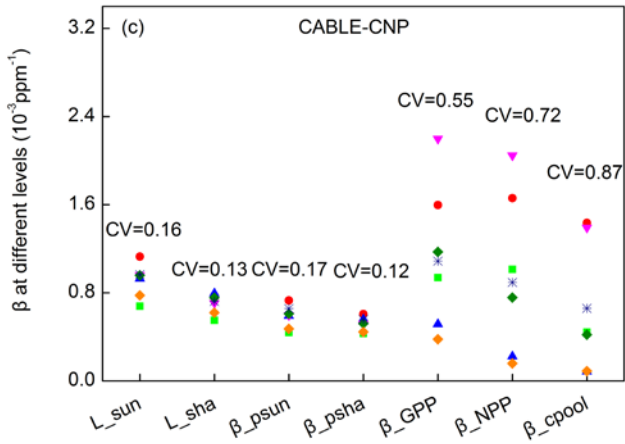
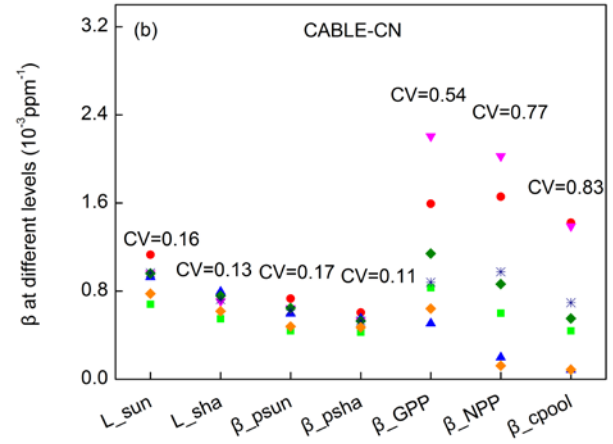
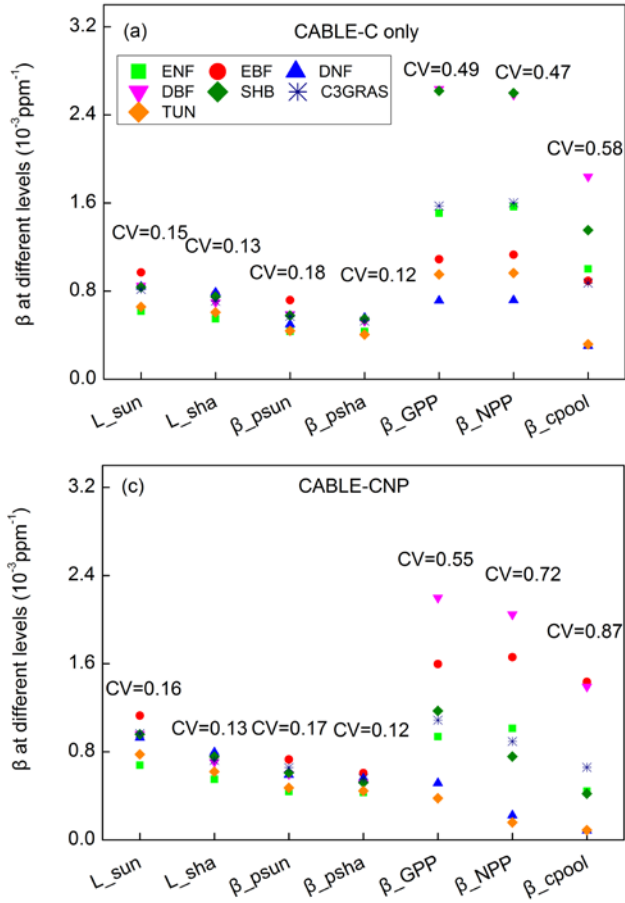


Figure 2. Responses of yearly intercellular CO₂ concentration (C_i) to eCO₂ of a single sunlit leaf (a) and shaded leaf (b) for C₃ PFTs from CABLE-C only simulation. Temporal trends of CO₂ compensation point in the absence of day respiration (Γ_*) for sunlit leaf (c) and shaded leaf (d) from 2011 to 2100 from CABLE-C only simulation. The ratio of C_i to C_a (C_i/C_a) is approximately constant with eCO₂ for each PFT and varies little across PFTs. Γ_* values vary across different PFTs, but do not change over time for each PFT. Abbreviations and symbols are the same as Figure 1.

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775 **Figure 3. Biome-level β values at different levels at the year 2023 from CABLE-C only (a), CABLE-CN (b), and CABLE-CNP (c) simulations. CV means coefficient of variation of biome-level β across C₃ PFTs. β values at biochemical (\mathcal{L}_{sun} and \mathcal{L}_{sha} for sunlit and shaded leaves) and leaf levels (β_{psun} and β_{psun}) are very similar across PFTs, but greatly diverge at canopy level (β_{GPP}), and ecosystem levels (β_{NPP} and β_{cpool}) in all simulations. Unlike in**
 780 **C-only simulation, β_{NPP} diverges more than β_{GPP} across different PFTs in nutrient-coupled simulations. Abbreviations and symbols are the same as Figure 1.**

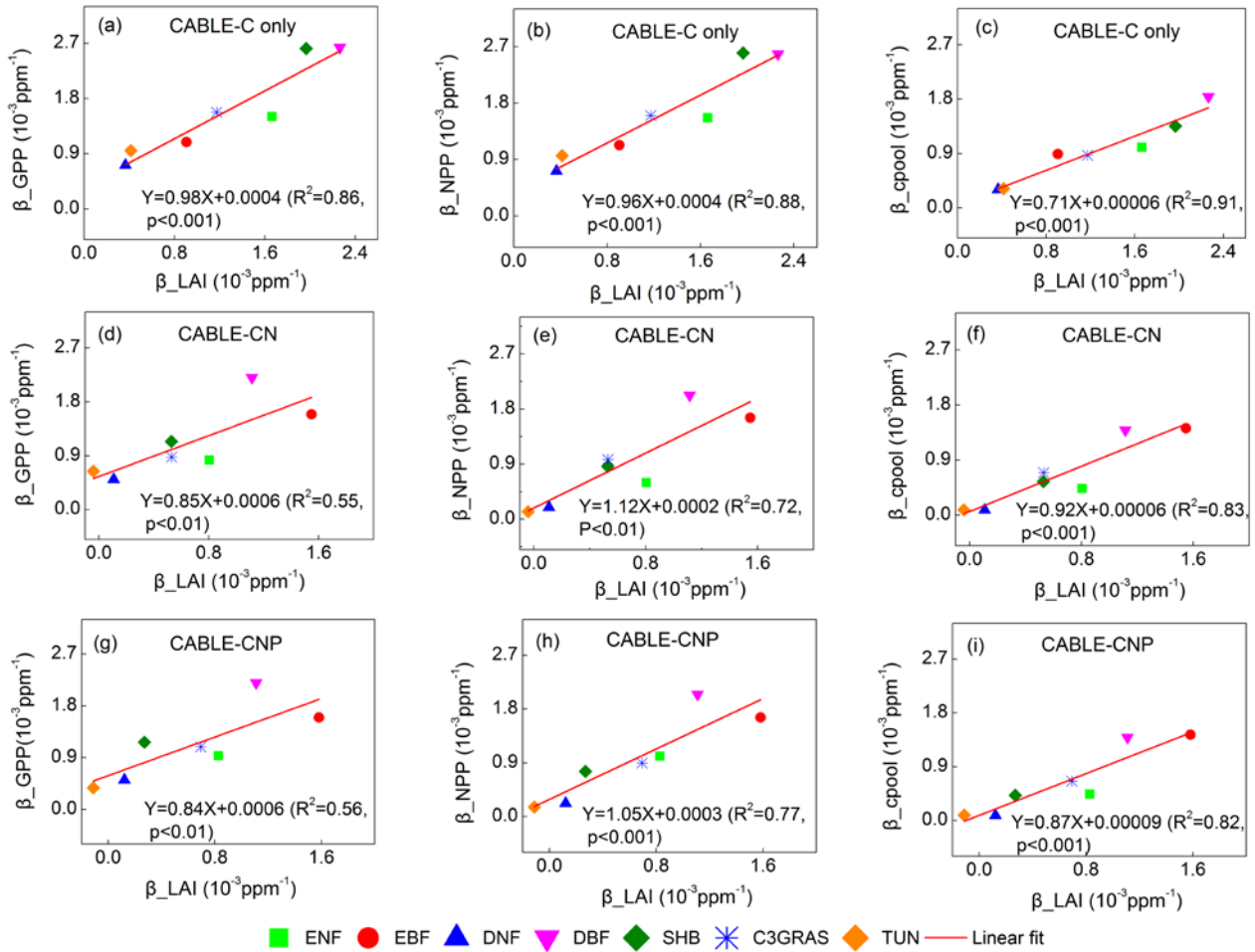
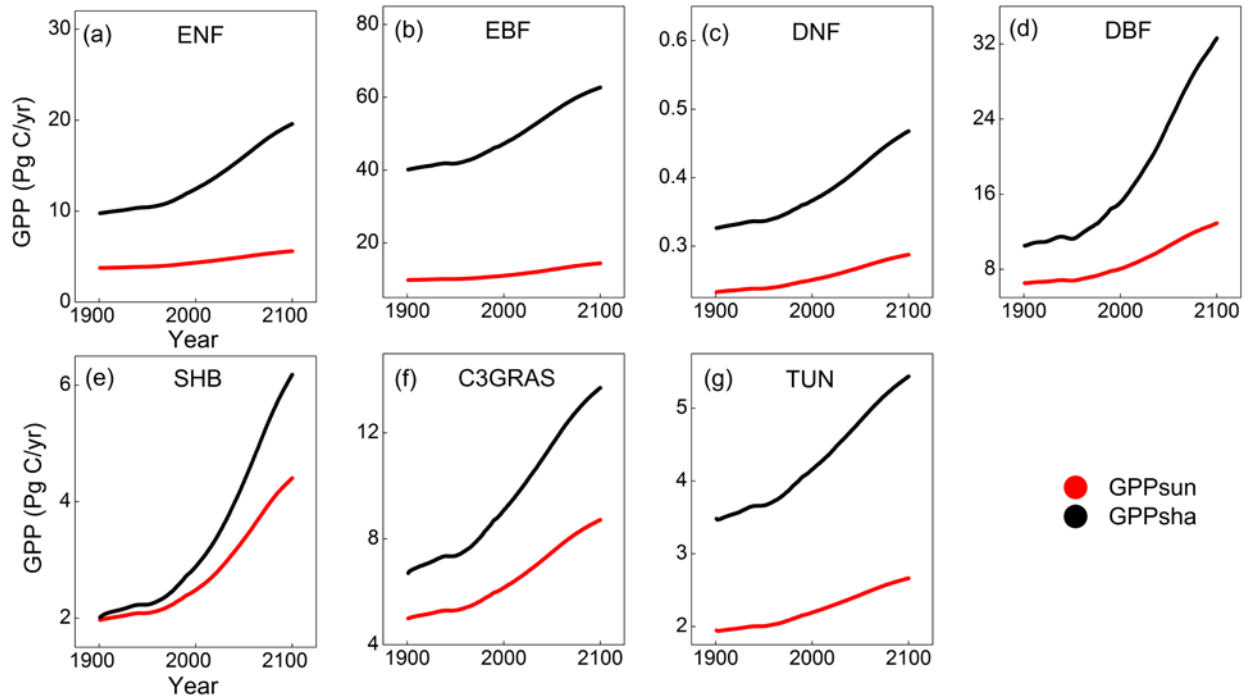


Figure 4. Correlations between β_{GPP} and β_{LAI} , β_{NPP} and β_{LAI} , β_{cpool} and β_{LAI} at the year 2023 across C_3 PFTs from CABLE C-only (a)~(c), CABLE-CN (d)~(f) and CABLE-CNP (g)~(i) simulations. β_{GPP} , β_{NPP} and β_{cpool} all have significant linear correlations with β_{LAI} in all simulations. Abbreviations and symbols are the same as Figure 1.

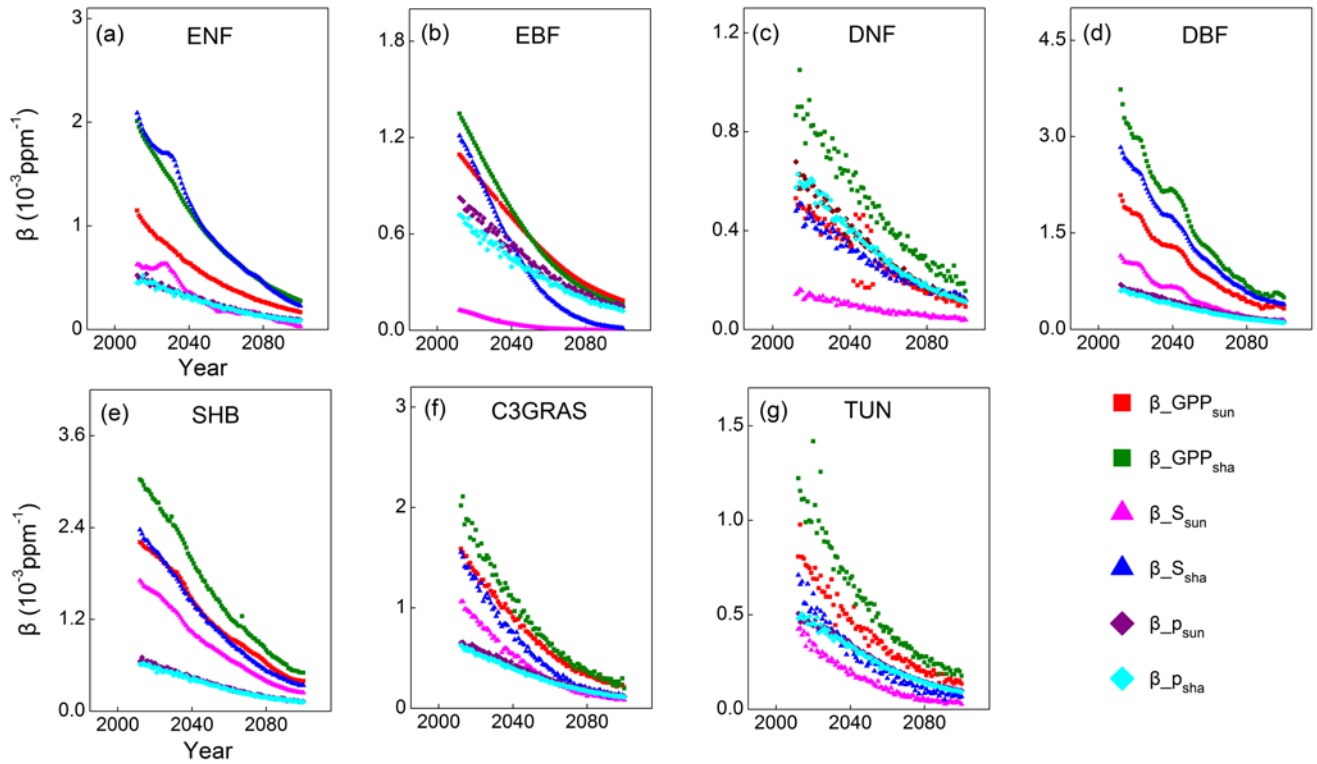
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Figure 5. Temporal trends of GPP_{sun} (red points) and GPP_{sha} (black points) for C₃ PFTs from 1901 to 2100 from CABLE C-only simulation. GPP_{sha} is higher than GPP_{sun} for all PFTs. With significant increase of CO₂ concentration from 2011, GPP_{sha} responds more drastically than GPP_{sun} .

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800 **Figure 6.** Temporal trends of $\beta_{GPP_{sun}}$ (sensitivity of sunlit leaf GPP; red squares), $\beta_{GPP_{sha}}$ (sensitivity of shaded leaf
 805 GPP; green squares), $\beta_{S_{sun}}$ (sensitivity of scaling factor for sunlit leaf; pink triangles), $\beta_{S_{sha}}$ (sensitivity of scaling
 factor for shaded leaf; dark blue triangles), $\beta_{p_{sun}}$ (photosynthetic response for sunlit leaf; purple diamonds) and
 $\beta_{p_{sha}}$ (photosynthetic response for shaded leaf; sky blue diamonds) for C_3 PFTs from CABLE C-only simulation. The
 sensitivities of GPP_{sun} and GPP_{sha} tend to approach zero through time because the decomposing factors $\beta_{p_{sun}}$,
 $\beta_{p_{sha}}$, $\beta_{S_{sun}}$ and $\beta_{S_{sha}}$ all decline with time. $\beta_{S_{sha}}$ determines the magnitudes and trends of $\beta_{GPP_{sha}}$ for almost all
 PFTs.