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 CO_2 fertilization" (bg-2018-213).

Dear Editor,

We appreciate the insightful comments on our manuscript by all reviewers, and accordingly made substantial revision to improve this manuscript. We hope that our point-by-point responses below satisfactorily address the concerns raised by reviewers. The major proposed changes we made include:

(1) We included results from carbon-nitrogen (C-N) coupled and carbon-nitrogen-phosphorus (C-N-P) coupled simulations of CABLE to study how the CO_2 fertilization effects (β) at different levels change with nutrient limitations for different plant functional types. Our results from C-N and C-N-P coupled simulations support our original conclusion reached from C only simulations.

(2) We clarified the motivation and contribution of our study as the reviewers suggested.

(3) We carefully corrected language errors in our revised manuscript.

The original reviewers' comments are italicized and our response to the reviewers' comments follow.

Response to Associate Editor's comments

Associate Editor: The revisions proposed in the response letter go a long way to address the critiques raised by reviewers and a duly revised manuscript is correspondingly welcomed. Adding the nutrient dynamics to the simulation system, and comparing those results to the original C-dynamics-only simulations, will add a good deal of value to the paper. The paper's contributions will also be deepened by including text from the response letters in the paper's results and discussion sections, where appropriate.

Response: We deeply appreciate you for the encouragement and giving us an opportunity to revise our manuscript. We have included text from the response letters in the paper's results and discussion sections. Please see more details in our response comments to the reviewers.

The work has the potential to make a valuable contribution, providing useful insights into the model mechanisms that govern terrestrial ecosystem responses to elevated CO2. However, as noted when handling the BG_2018_153 version of this manuscript, care must be taken to ensure that the paper's major interpretations and conclusions are framed to accurately match the methods and findings. My understanding of what this study mainly shows is that beta factors vary (a) across hierarchical levels of C-fluxes and stocks, and (b) across PFTs in a way that is largely attributable to variations in LAI dynamics across PFTs. This finding is framed as if it sheds light on across model spread in beta but that is not correct. The methods and results do not pinpoint LAI as a leading source of across-model spread or uncertainty in the land carbon cycle response to elevated CO2. The authors attempt to make a conceptual and motivational link between the across-model spread in beta factors shown in other studies and the findings presented in this paper however this is misleading. Consider this - it is possible that all of models in some MIP would show the same kind of across-PFT variation in beta, and that those models still having large across-model disagreement in the overall beta factors for different ecosystems and for the global biosphere. Some of the response comments still seem to misunderstand this point. Again, the paper has a contribution to make, particularly with the revisions in response to reviews, but I would reiterate that the introductory framing, interpretations and conclusions may still need to modified to match its methods and findings if the paper is to be ultimately accepted for publication.

Response: Thanks a lot for your comments and suggestions. We agree with you that previous frame of the manuscript is a little confusing. We particularly focused on this issue in the revised manuscript. We have made corresponding adjustments in the Abstract (Line 20-21), Introduction (Line 95-100), Discussion (411-431) and Conclusion (Line 443-444) to make them more compatible with our methods and results.

Response to reviewer#1

Reviewer 1: Li et al. use the CABLE model to explore the role of LAI in variability in the CO2 fertilisation response. The analysis has some interesting aspects which I'm sure will be of interest to the modelling community, in particular I thought fig 5 was interesting. However, I think the manuscript could be carefully revised for greater impact and insight. I have a number of specific points below but also 4 key issues with the analysis as presented:

Response: We thank the reviewer for the positive comments. His suggestions are very important for improving our manuscript.

Reviewer 1: 1. I don't understand the logic of using a model which simulates N and P cycles and then switching this functionality off to understand the CO2 fertilisation response? In my eyes, this is one of the great strengths of this model. So to not compare C against N and P, or C against N, is a missed opportunity. Whilst I'm realistic enough to envisage the authors won't rethink this strategy, I do feel this requires some further justification.

Response: We appreciate the reviewer's critical comments. This concern has been raised by two reviewers. The reason why we didn't originally include nitrogen and phosphorus cycles in our previous study is that we tried to find the most important factor causing the variations of β within and across different plant functional types (PFTs) with minimal confounding effects of other processes.

However, we totally agree with the reviewers that carbon-nutrient interactions should be considered when studying the CO_2 fertilization effects. C-N and C-N-P simulations were useful to explore how nutrients affect the patterns of and mechanisms underlying the variability of the CO_2 fertilization effects. We have conducted C-N and C-N-P coupled simulations of CABLE and added related descriptions and analyses in the revised manuscript. Results show that 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 different C_3 PFTs in nutrient-coupled simulations as in C-only simulation, confirming the dominant role of LAI in regulating carbon cycle response under CO_2 fertilization. The related major changes in the revised manuscript are:

(1) In the Abstract part, we clarified our simulation designs with nutrient cycles (Line 21-23).

(2) In the Introduction part, we reviewed the effects of nutrient limitations on CO_2 fertilization effects in Line 85-93. We proposed the scientific questions related to carbon-nutrient interactions in Line 98-99.

(3) In the Materials and Methods part, we introduced how nutrient limitations were incorporated into carbon cycle in the CABLE model in Line 129-138. We clarified our experimental design and calculation in Line 140-154 and 212-215.

(4) In the Results part, we presented temporal trends of β at ecosystem level for different vegetation types in C-N and C-N-P simulations in Line 223-228, Fig. 1b and Fig. 1c. We showed variations of intercellular CO_2 concentration and CO_2 compensation point under nutrient limitations in Line 236-244, Fig. S2 and Fig. S3. We compared β values at different hierarchical levels in nutrient-coupled simulations in Line 261-267, Fig. 3b and Fig. 3c. Correlations between β_{GPP} and β_{LAI}, β_{NPP} and β_{LAI}, β_{cpool} and β_{LAI} in nutrient-coupled simulations were discussed in Line 277-280 and Fig. 4.

(5) In the Discussion part, we discussed about why magnitudes of biochemical and leaf-level β with nutrient-limitations are similar to those without nutrient limitations in Line 314-315. We discussed the nutrient effects on the magnitudes and variations of β_{NPP} in Line 381-391. We also discussed about the variability of nutrient-limited β_{cpool} in Line 407-409.

(6) In the Conclusion part, we clarified our simulation designs and results with nutrient cycles (Line 444-446).

Reviewer 1: It is stated that CABLE is largely RuBP-limited (line 179) and this point is given no further analysis. This is interesting and it isn't clear why this would be the case? Do the authors envisage that *this is also true of other models? I would suggest it isn't but would be keen to read the authors thoughts on this. Surely this shapes the analysis (responsiveness to CO2)? So it warrants more than a single sentence that simply says "not shown" ...*

Response: We thank the reviewer for this comment. It is an important prerequisite in our study. We agree it should be clarified in our manuscript. The formulation of leaf-level β depends on the intercellular CO_2 concentration (Farquhar et al., 1980). Generally, photosynthesis rate is RuBP-regeneration limited (limited by light) when CO_2 concentration exceeds a certain level. And we coded a variable indicating which process (Rubisco activity, RuBP regeneration or sink) limits photosynthesis rate at each running step in the original CABLE code. Then we outputted this variable. We found photosynthesis rates are almost all limited by RuBP-regeneration process globally since 2011 when CO_2 concentration is 391 ppm. Then leaf-level biochemical β can be expressed as an equation of intercellular CO_2 concentration and CO_2 compensation point. We didn't show the results because of the large volume of data (56560 model grids × 8760 hours in a year in total). Moreover, theoretical analysis by Luo and Mooney (1996) showed that leaf-level β values are similar for either Rubisco- or RuBP-limited photosynthesis. We have added these points in the revised manuscript (Line 174-177).

Reviewer 1: The paper is about CABLE but surely the aim is to make the result general (otherwise the title would have the word CABLE...)? However, I wonder if I was developing JULES or CLM, (etc) what my take home messages would be? The authors urge other modelling groups to repeat their analysis, but could they also make suggestions as to the implications for other modelling groups? How do these results help us to understand model responses to CO2? The CMIP5 concentration-carbon feedback factor?

Response: We thank the reviewer for the suggestion to highlight the take-home messages more clearly. We believe our conclusions about the across-PFT variation of β and the dominant role of LAI for the variability of β in CABLE is generally applicable to other models. According to the comments from the Associate Editor, in order to match our methods and findings, we will not extend the implication of our study to the uncertainty of CMIP5 concentration-carbon feedback factor. But we have discussed about the implication for across-PFT variation of β in other models in the revised manuscript (Line 411-431).

Reviewer 1: I didn’t take much in the way of insight from the current section on this topic, i.e. section 4.3. For example, the authors assert that "It can be inferred that normalized leaf-level ð˙I ˙ Z¡ values would diverge little across different land surface models as long as they use ...". Is that true? If the models had different levels of water stress (which they almost always do) they would get very different values of Ci even with the same model assumptions. As the authors also show, leaf temperature affects gamma_star, so I see no reason to assume that models would predict similar leaf temperatures. Leaf temperature itself is dependent on a whole range of assumptions. I’ve never seen any evidence that models with different architectures, with different assumptions about leaf –to-boundary conductance, etc, would predict similar leaf temperatures. If the authors disagree they should support these assumptions. The authors cite the Hasegawa et al study as an example of a consistent result of their conclusion. But wouldn’t a number of the other model CO2 paperls that point to marked divergence argue otherwise. My sense is their conclusion here is too simplistic.

Response: Thank the reviewer for pointing out this issue. We agree with the reviewer that different models have diverse levels of water stress on photosynthesis (De Kauwe et al., 2017). Water stress is applied to regulate stomatal conductance in many models (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 (Eq. (S11)). The influence of water stress is reflected by intercellular CO_2 concentration (C_i). Our results show modelled ratio of C_i to atmospheric CO_2 concentration (C_a) is relatively constant for each PFT with eCO_2 and varies little among PFTs (Table 1). This modelling result is consistent with the concept of 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 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. 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. We have added the above discussions into our revised manuscript (Line 419-429).

It's also true that different model might simulate different leaf temperatures as the reviewer pointed out. Sensitivity analysis in a previous study has shown that a ±5°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}. We have added the above discussions into our revised manuscript (Line 309-313).

Based on our literature review, only few studies like Hasegawa et al. (2017) have explored why different models simulated diverse responses of plant productivity to eCO_2. We will greatly appreciate it if the reviewer can show us some related references.

Reviewer 1: The authors argue for the importance of LAI but don't really consider the role of allocation or turnover in great detail. Surely this is the key reason different models arrive at different LAI values? Even if you ignore changes in allocation/turnover due to CO2, this impacts on the scaling terms that the authors focus on.

Response: The reviewer made a great point. Changes in LAI are related to changes in allocation/turnover under eCO_2. The response of allocation to eCO_2 will influence β in two ways. The first way is through altering the portion of carbon allocated to leaf, then changing LAI. We have discussed more about this point in the revised manuscript: "Second, diverse allocation schemes influence the responses of LAI for different PFTs. And, results 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" (Line 364-368).

The second way is by changing the allocation pattern to plant organs with different lifespan, thereby altering carbon turnover time in plants and soil. It has been discussed in the revised version Line 397-401:"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 eCO_2 in experiments, thereby altering carbon residence time in plants and soil (De 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 eCO_2".

Reviewer 1: 4. The results are considered on a PFT level, but presumably they vary in interesting ways within a PFT (i.e. in space). Would this be worth showing or exploring further?

Response: Actually in the previously submitted manuscript, we have analyzed within-PFT variations of β at different levels in Table 1, Results 3.3, and Fig. S1-S3. In the revised manuscript, the related parts are in Line 215-217, 269-275, 280-282, 361-362, Table 2 and Fig. S5-S7.

Reviewer 1:

Specific comments =================

- Line 43: Could you explain the CO2 fertilising effect further? The text as written expects the casual reader has significant background knowledge for the second sentence of your manuscript.

Response: Agree. We added the following sentences in the first paragraph: "Persistent increase of atmospheric CO_2 concentration will stimulate plant growth and ecosystem carbon storage, forming a negative feedback to CO_2 concentration (Long et al., 2004; Friedlingstein et al., 2006; Canadell et al., 2007). This concentration-carbon feedback (β), also called the CO_2 fertilization effect, has been identified as a major uncertainty in modelling terrestrial carbon-cycle response to historical climate change (Huntzinger et al., 2017)" (Line 41-45).

Reviewer 1: - Line 48: 4 or 4.5? What does that mean, do you mean 4 to 4.5? How can it be OR?

Response: Sorry for the ambiguity. Actually, the contribution of β is 4 times larger than that of carbon-climate feedback (γ) in Gregory et al. (2009) and Bonan and Levis (2010), but is 4.5 times larger in Arora et al. (2013). We have changed this sentence to "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)" (Line 47-49).

Reviewer 1: - Line 49: the reference to the Smith et al. paper ignores a technical comment on this paper: De Kauwe et al. (2016). Satellite based estimates underestimate the effect of CO2 fertilization on net primary productivity. Nature Climate Change, 6, 892-893. This is important as the authors are using this study to leverage their question. See also point on line 340.

Response: We thank the reviewer for pointing to the related comment paper by De Kauwe et al. (2016). It is indeed an important reference to supplement the point we were trying to make. We have modified the last sentence in the first paragraph to "Though satellite products they used may underestimate the effect of CO_2 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" (Line 51-53).

Reviewer 1: - Line 51: it isn't "reality" - the satellite estimates are also model estimates.

Response: Agree. See the response above.

Reviewer 1: - Line 54: "increasing temperature in models" why is temperature being introduced as a factor here? Isn't the focus solely on the CO2 fertilisation effect rather than the than carbon-climate feedback factor? There are further studies cited in this paragraph which should be removed if the focus of this paper does not consider the carbon-climate feedback factor.

Response: Agree. We have removed the γ-related part in the revised manuscript.

Reviewer 1: - Line 67: Despite models using apparently similar photosynthesis models, Rogers et al. (A roadmap for improving the representation of photosynthesis in Earth system models. New Phytologist, 213, 22-42.) showed some important differences. It would be worthwhile highlighting this study in the context of the section of the text.

Response: We thank the reviewer for sharing us this important reference. We have adjusted the sentence to a more accurate one: "The leaf-level CO_2 fertilization for C_3 plants is generally well characterized with models from 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)" (Line 59-61). We also discussed about how those different implementations influence photosynthetic response in the Discussion: "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 important control of the absolute values of photosynthetic response to eCO_2 (Rogers et al., 2017). However, the relative photosynthetic responses for different ecosystems will converge to a small range because the normalized photosynthetic response to eCO_2 only depends on estimates of intercellular CO_2 concentration (C_i), Michaelis-Menten constants (K_c, K_o) and CO_2 compensation point (Γ_*), and relative leaf-level responses are similar for either Rubisco- or RuBP-limited photosynthesis (Luo et al., 1996; Luo and Mooney, 1996)” (Line 413-419).

Reviewer 1: - Line 72: what does carbon storage have to do with this sentence?

Response: Thanks for pointing out what we have missed. Besides NPP, allocation and carbon turnover process can influence carbon storage. We have changed this sentence to “However, the CO_2 fertilization effects are considerably more variable at canopy- and ecosystem-level than at the leaf-level, because a cascade of uncertain factors, 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” (Line 64-67).

Reviewer 1: - Line 76/7: seems a narrow characterisation of the literature, the De Kauwe et al. 2014 study that the authors cite, explored these issues in depth.

Response: We have added related references as the reviewer suggested: “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 eCO_2 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” (Line 73-78).

Reviewer 1: - Line 81: Why would a high "basic" (delete basic) NPP necessarily lead to tropical regions having the highest stimulation by CO2? Wouldn’t the opposite be expected? These regions have a high LAI and so would predominantly be light-limited and so have a more limited capacity to respond to CO2? Either way, the authors need to expand on this assertion.

Response: We agree this sentence is not very clear. This sentence in this paragraph has now been changed into "The strongest absolute CO_2 fertilization effect has been found in tropical and temperate forests where the larger biomass presents than other regions. In comparison, the weakest response to eCO_2 occurs in boreal forests (Joos et al., 2001; Peng et al., 2014). But with gradual eCO_2, relative response in tropical forests might not be very high owing to light limitation caused by canopy closure (Norby et al., 2005)" (Line 81-85).

Reviewer 1: - Line 89: Improved on what?

Response: We will change this sentence to: "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)" (Line 103-104).

Reviewer 1: - Line 124: The assumption that Jmax25 = 2 x Vcmax25. Did the authors consider varying this assumption? Other models would make quite different assumptions about this ratio.

Response: It's true that the ratio of the maximum electron transport rate ($J_{max,25}$) to maximum photosynthetic capacity ($V_{cmax,25}$) are different in models (Rogers et al., 2017). But difference of this ratio will not change the conclusion because β values in our study are normalized values, irrespective of $J_{max,25}$ or $V_{cmax,25}$.

Reviewer 1: - Line 155: is there a citation, web link for "Community Climate System Model (CCSM) simulations"

Response: We have added a citation "Hurrell, J. W., Holland, M., Gent, P., Ghan, S., Kay, J. E., Kushner, P., Lamarque, J.-F., Large, W., Lawrence, D., Lindsay, K., Lipscomb, W. H., Long, M. C., Mahowald, N., Marsh, D. R., Neale, R. B., Rasch, P., Vavrus, S., Vertenstein, M., Bader, D., Collins, W. D., Hack,

J. J., Kiehl, J., and Marshall, S.: The community earth system model: a framework for collaborative research, Bull. Am. Meteorol. Soc., 94, 1339–1360, 2013." (Line 145, 571-574).

Reviewer 1: - Line 168: the definition of S (line 171) needs to be moved up to this line.

Response: Agree. Please see related changes in Line 191-194.

Reviewer 1: - Line 215: just to clarify when the authors say total carbon storage - do they mean the soils too? Or just the plant? Or just the foliage pool? The equation isn't very clear. This also makes Fig 1 hard for me to interpret as I'm unclear what is being shown, I'm going to assume it is total plant carbon...

Response: Total carbon storage is the sum of plant, litter and soil carbon pools. We have made it clear in the revised manuscript (Line 158-159).

Reviewer 1: - Fig 1. Does it make sense to normalise these PFT lines? The authors say they decline but the magnitudes differ, the point is that the initial starting points are different too. This makes it hard for the eye to gauge.

Response: Indeed, the CO_2 fertilization effects at different levels in our manuscript are all normalized values. See Eq. (3) in Line 163.

Reviewer 1: - As a general comment the results need work, particularly in terms of transition text. For example 3.1 talks about the temporal trend in Bcpool and then switches immediately to the Ci/Ca ratio in 3.2? It is hard to follow the logic of the transition, is there is meant to be any connection for the reader?

Response: Section 3.1 is about β at ecosystem level, showing that β values differ among different PFTs and decrease over time. It stimulates the following study that calculating β values from leaf biochemical level to ecosystem level in order to identify the key processes for the divergent β at ecosystem level. We have added one transition sentence at the beginning of Section 3.2: "To reveal which processes cause the large disparity of β across PFTs as shown in Fig. 1, we first compared intercellular CO_2 concentration (C_i) and CO_2 compensation point in the absence of day respiration (Γ_*), which are critical parameters for leaf-level biochemical response" (Line 230-232).

Reviewer 1: - What is the point of Fig. 2? It isn't clear what this figure has to do with the story of the paper?

Response: Please see the above response.

Reviewer 1: - The text around line 261 which refers to Fig 4 could do with further explanation. I personally don't find this particularly surprising, but the reader isn't offered much as the way of explanation. Presumably the change in slope as you move from B_GPP to B_NPP relates to respiration assumptions and then to B_cpool, allocation/turnover assumptions? I think the authors could go further in assisting the reader with interpretation. As currently written, the text simply highlights that the slope changes.

Response: After thinking carefully about this concern, we agree that the slopes of the three fitting lines are not making much sense so we have removed this sentence in the revised manuscript.

Reviewer 1: - I think figure 5 is very interesting.

Response: Thank the reviewer for the positive comment.

Reviewer 1: - Line 290: I think this discussion of Fig S5 is interesting but I'm not sure I follow the interpretation? The LAI is the emergent outcome of the model assumptions - 1 leaf, 2leaf, multi-layer.

Of course this assumption will lead to differences? But why you do the analysis on the leaf-level? Surely you're interested in the emergent outcome – the LAI. Most likely I simply misunderstood this point but I think it could also be explained further as it seems like an important point the authors are making.

Response: The discussion of Fig. S5 (Fig. S8 in the revised manuscript) is primarily triggered by the comparison between our results and Hajima et al. (2014). We believe that leaf-level photosynthesis cannot be simplified as GPP/LAI for CMIP5 models as Hajima et al. (2014) did since CMIP5 models use different canopy structure such as big-leaf, two-leaf or multiple-layer. Most previous studies focused on variation in β for the land carbon storage, the standard definition of β as in Friedlingstein et al. (2006). But diagnosis of leaf-level response has not been attempted by modelling groups before. And CMIP5 model outputs have limited information for identifying mechanisms for model uncertainty since there are no leaf-level process outputs. So we did the analysis on the leaf-level processes. We have reorganized this part to make our manuscript more concise: "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 eCO_2 diverged a lot among models. This calculation is likely debatable for ignoring 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)" (Line 317-322).

Reviewer 1: - Line 295: I don't fully follow that interpretation? Your differences in Ci/Ca were small across PFTs? And the differences in leaf temp would be expected between PFTs? Certainly, fig 2 doesn't show any within PFT variation.

Response: We would like to express that the leaf-level β computed in our study can be mechanistically traced back to intercellular CO_2 concentration and leaf temperature. Since Fig. 2 shows the results across different PFTs, we have changed this sentence to: “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” (Line 322-324).

Reviewer 1: - Line 362: This is an assumption of the model and might not necessarily be true!

Response: Agree. We have added the following sentences in the manuscript: “However, FACE experimental results indicate that CUE values under eCO_2 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., 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)” (Line 382-386).

Reviewer 1:

Technical corrections =====================

- Abstract: "vegetation types is 0.15-0.13", presumably you meant 0.13 to 0.15? Also, why don’t the other variables (e.g. BetaGPP) have ranges too?

Response: Yes, we meant 0.13 and 0.15 for shaded leaf and sunlit leaf, respectively. We did not show the coefficients of variation in Abstract in the revised manuscript. In this sentence, we did not differentiate sunlit leaves and shaded leaves for canopy GPP, so there is only one value for β_{GPP}.

Reviewer 1: - First line of the introduction, makes no sense. You can’t start a sentence with Terrestrial carbon sink and then a comma.

Response: Agree. We have changed the first sentence to: “Terrestrial ecosystems take up roughly 30%

of anthropogenic CO_2 emissions, and is of great uncertainty and vulnerable to global climate change (Cox et al., 2000; Le Quéré et al., 2018)” (Line 40-41).

Reviewer 1: - Line 45: In Coupled -> In the Coupled

Response: Agree (Line 45).

Reviewer 1: - Line 138: In CABLE model -> in the cable model

Response: Agree (Line 112).

Response to reviewer#2

Reviewer 2:

Synopsis:

In this paper, the authors run CABLE for seven C3 vegetation types, without nutrient cycling, and calculate CO2 fertilization for the RCP 8.5 scenario. CCSM simulations from 1901 to (the paper says 1910; I assume they mean 2010) holding carbon-climate feedbacks constant (driving the model with the averaged meteorology-I’m guessing average annual cycle, although the authors do not say) and feeding CABLE increasing CO2 concentration from the CCSM RCP 8.5 results.

They find that CO2 fertilization differs between PFTs, and decreases with time during the period 2011-2100. Fertilization is relatively constant both between PFTs and when the calculation is made on a per-unit leaf level, and shows much larger diversity both across PFTs and when the CO2 fertilization is calculated on a unit-leaf vs. integrated canopy basis. The authors close with the claim that simulated LAI is critical to the calculation of CO2 fertilization in climate simulations.

Response: We thank the reviewer for the time she or he spent on reviewing our manuscript. The above paragraphs are a good summary of what we did for this study. While most of the summary is accurate, we would like to clarify here that CABLE model has been run from 1901 to 2100. Before that, CABLE was spun up by using meteorological forcing from 1901 to 1910 repetitively until a steady state was achieved. And we indeed used the average annual cycle of meteorological forcing data to fix carbon-climate feedbacks. We have clarified these points in our revised manuscript (Line 140, 144-146).

Reviewer 2:

Review:

I have 2 major problems with this paper. Either one by itself, I believe, is fatal, but taken together I cannot make any recommendation for this paper other than rejection.

Response: We have made significant changes to the both the text and simulations (by including nutrient-enabled CABLE simulations). We hope that major criticisms have been addressed in our revised manuscript.

Reviewer 2:

Problem #1: *There is a rich body of literature from the FACE experiments that claims, pretty much unequivocally, that nutrient cycling and/or limitation becomes more and more important to CO2 fertilization as CO2 concentrations rise. Yet, in this experiment CABLE is run with nutrient cycling turned off!*

Response: We may not have made our research objective quite clear. In the revised manuscript, we now stated that our study was to examine how variability, as measured by coefficient of variation (CV) within and across different plant functional types (PFTs), in the CO_2 fertilization effect (i.e., CV of β) changes from leaf to canopy GPP, ecosystem NPP and total carbon storage levels. Our study was not intended to quantify the CO_2 fertilization effect itself. We have clarified our goal in the revised manuscript Line 95-

100.

We agree with the reviewer that nutrient limitations are universally observed in experiments. Nutrient cycling influences the CO_2 fertilization effect. When comparing the carbon-only simulations with nutrient (N, or NP) enabled simulations using CABLE, we find that the previous conclusion about CV of the CO_2 fertilization effects was not significantly changed. Thus, we hope this reviewer will re-evaluate our manuscript, particularly in light of significant work in including the results from additional new CABLE nutrient-enabled simulations.

Reviewer 2: Coskun et al. (2016) and references therein has a nice summary of both Free-Air CO2 Enrichment (FACE) as well as Open-Top Chamber (OTC) experiments. Smith et al. (2015) discusses the divergence between multiple models and a satellite-derived product that underscores the importance of the interaction between nutrient cycling and CO2 fertilization. Many of these studies focus on N limitation, although some research has indicated that P limitation is a factor as well (e.g. Hasegawa et al., 2016). These, and other studies, all conclude that understanding of CO2 fertilization requires taking nutrients into account.

Response: We thank the reviewer for showing us these important references. We have cited related references in our revised manuscript (Line 49-51, 85-86). Again, our study was not to quantify the CO_2 fertilization effect itself but to understand what caused changes in CV of β. Running CABLE without or with nutrient limitation reached a similar conclusion as shown below.

Reviewer 2: I have to confess that I was very surprised when I read that the authors ran the version of CABLE without nutrient cycling included. I am not a FACE 'expert', but even I am aware of the amount of research that has concluded that nutrient cycling is critical to understanding ecosystem-level response to higher atmospheric CO2. I found it very suspicious that nutrients were excluded from the study. Why, when there is this large body of work demonstrating the nutrient cycling is critical to understanding CO2 *enrichment, would nutrients be turned off in the model? The authors claim that nutrients were turned off for 'simplicity', but the obvious answer, and one that I suspect to be the truth, is that the authors did run CABLE with nutrient cycling, and model pathology and/or unrealistic results ensued.*

Response: We thank the reviewer for the critical comments and his/her insistence on the necessity of nutrient-coupled simulations. We absolutely agree with the reviewer that the CO_2 fertilization effect (or β) could be more realistically represented with nutrient limitations considered. The reason why we didn't originally include nitrogen and phosphorus cycles in our previous study is that we tried to find the most important factor causing the variations of β within and across different vegetation types with minimal confounding effects of other processes. Per the suggestions from the two reviewers, we tested whether the patterns of and mechanisms underlying the variability of β for C-only simulation still hold for nutrient-coupled simulations. We have added results and analyses from C-N and C-N-P coupled simulations of CABLE in the revised manuscript. The related major changes in the revised manuscript are:

(1) In the Abstract part, we clarified our simulation designs with nitrogen cycles (Line 21-23).

(2) In the Introduction part, we reviewed the effects of nutrient limitations on CO_2 fertilization effects in Line 85-93. We proposed the scientific questions related to carbon-nutrient interactions in Line 98-99.

(3) In the Materials and Methods part, we introduced how nutrient limitations were incorporated into carbon cycle in the CABLE model in Line 129-138. We clarified our experimental design and calculation in Line 140-154 and 212-215.

(4) In the Results part, we presented temporal trends of β at ecosystem level for different vegetation types in C-N and C-N-P simulations in Line 223-228, Fig. 1b and Fig. 1c. We showed variations of intercellular CO_2 concentration and CO_2 compensation point under nutrient limitations in Line 236-244, Fig. S2 and Fig. S3. We compared β values at different hierarchical levels in nutrient-coupled simulations in Line 261-267, Fig. 3b and Fig. 3c. Correlations between β_{GPP} and β_{LAI}, β_{NPP} and β_{LAI}, β_{cpool} and β_{LAI} in nutrient-coupled simulations were discussed in Line 277-280 and Fig. 4.

(5) In the Discussion part, we discussed about why magnitudes of biochemical and leaf-level β with nutrient-limitations are similar to those without nutrient limitations in Line 314-315. We discussed the nutrient effects on the magnitudes and variations of β_{NPP} in Line 381-391. We also discussed about the variability of nutrient-limited β_{cpool} in Line 407-409.

(6) In the Conclusion part, we clarified our simulation design and results with nutrient cycles (Line 444-446).

We found β values at canopy and ecosystem levels in C-N and C-N-P simulations diverge in a way that is largely attributable to variations in LAI responses across C_3 vegetation types, as in C-only simulation. It should be noted that nutrient effects add more variations to β values at ecosystem level compared with C-only simulation (Fig. 3 in the revised manuscript). The CABLE-CN and CABLE-CNP simulations add more layers of complexity to understand the primary mechanisms underlying the divergence of β at different levels and in different ecosystems although the conclusion is similar with that reached from running carbon-only CABLE. This finding proves that our previous design that turning off the nutrient cycles in model simulation to identify the most critical carbon cycle processes is reasonable. But we agree with the reviewer that adding nutrient cycle will further strengthen our conclusions.

Reviewer 2: It may have been possible to evaluate a nutrient run, even if the results were unrealistic, and evaluate how atmospheric CO2 levels and nutrients interact in CABLE. The results may have provided an opportunity to evaluate or comment on the divergence of models in their predictions of atmospheric CO2 levels and source/sink strength (e.g. Friedlingstein et al., 2006, 2014). By not including the critical nutrient interaction, I'm not sure that the results presented here give the reader any insight into how ecosystems might realistically respond to increasing future CO2 levels in the atmosphere.

Response: We agree with the reviewer that CO_2 and nutrient interactions could cause the divergence of models. Our new results with CABLE-CN and CABLE-CNP show that CV of β is much higher than that with CABLE-C only for NPP and total carbon storage (Fig. 3 in the revised manuscript). However, the objective of our study is not to evaluate nutrient effects on carbon cycle under CO_2 fertilization. As we have stated before, our study is to identify mechanisms underlying expanding CV from biochemical and leaf levels to canopy GPP, ecosystem NPP and carbon pool. All the three versions of CABLE point to the same mechanism, which is LAI as the major source of variability in modelled CO_2 fertilization.

Reviewer 2:

Problem #2: *Without carbon-climate feedbacks and nutrient cycles, I don't think a model actually has to be run to determine CO2 fertilization. You can probably perform the calculation directly from the equations in the code. Between models there will be some differences:*

- *Is the model an enzyme-kinetic model (Farquhar et al., 1980; Michaelis-Menten kinetics), or light-response (e.g. VPRM, Mahadevan et al., 2008)?*
- *how is stomatal conductance calculated? Does it use Ball-Berry, with a dependence on relative humidity, or Leuning, which uses VPD? How is transpiration coupled to photosynthesis?*
- *What are the parameter values for Vcmax for a given PFT?*
- *What determines phenology? Is allocation static, or, if it is dynamic, how does it change during the year and in response to what?*

I believe it would be possible to determine the constraints on CO2 fertilization for a suite of models without actually running any of them.

Response: We agree with the reviewer that these assumptions and processes are key to modelling terrestrial carbon-cycle responses to eCO_2. The reviewer is very knowledgeable to identify those key ecosystem carbon-cycle processes. In this comment alone, the reviewer mentioned more than 10 processes that influence photosynthesis. We were very curious how the reviewer could "perform the calculation directly from the equations in the code" to evaluate all those 10 processes and to gain a mechanistic understanding of what causes the change of β values. Obviously, we did not understand how to perform the calculation of β directly from the model equations as the reviewer suggested. Even if we could calculate based on several equations, the results might not truly reflect model mechanisms for variabilities of the CO_2 fertilization effects within and across vegetation types. Because carbon-cycle processes are tightly coupled with radiation transfer, energy balance, nutrient interactions and water cycles in a land surface model. For example, leaf temperature and intercellular CO_2 concentration are two important variables for leaf-level β, which are collectively controlled by air temperature, radiation transfer and humidity. We were not sure if the reviewer meant to construct a simplified model or emulator to mimic the complex land surface models, it is worthy trying but we were not confident that the simplified approach could reveal model mechanisms.

Nevertheless, we ran a well-evaluated land surface model and outputted process-level variables such as intercellular CO_2 concentration, LAI, GPP, NPP, and ecosystem carbon storage for all land cells, as many analyses have done based on C4MIP and CMIP5. Combining previous theoretical analysis, we have shown that CV of β is small for biochemical and leaf-level photosynthesis but large for canopy GPP, ecosystem NPP and carbon pools.

Reviewer 2: It is axiomatic that leaf-to-canopy scaling (LAI) is critical to total CO_2 fertilization amount. Every model that I am aware of calculates biophysics on a per-unit-are basis and then scales to the canopy level either by summing over sunlit/shaded leaves (and PFTs) or integrating from leaf to canopy scale along the lines of Sellers (1985, 1992)(OK, a gap model like ED2 may be a little different). Canopies with an LAI close to 1 (think of grasslands) will not see much difference from unit- to canopy-scale, more dense canopies (like forests) will.

Response: We are happy that the reviewer agrees with us that LAI is critical for plant productivity. Many models exhibit increasing LAI trends under CO_2 fertilization (Zhu et al., 2016). However, to what extent the increasing LAI feeds back to ecosystem response to eCO_2 is not clear. Our study for the first time calculated β from leaf biochemical level to ecosystem level, and found the LAI response to eCO_2 is the dominating factor for variabilities of the CO_2 fertilization effects at canopy and ecosystem levels within and across C_3 vegetation types, namely the global CO_2 fertilization effects are very sensitive to the LAI responses. The value of our study is that it can urge modelling groups to improve the representation of LAI in land surface models, for example by calibrating allocation coefficients and specific leaf area (SLA) based on FACE experimental results (De Kauwe et al., 2014), so as to realistically predict concentration–carbon feedback.

Reviewer 2: If there is a large divergence between models in LAI (and GPP) for a given PFT, or if there is a large trend in one model's LAI for a given PFT during a climate run, then these might be valid topics of analysis. Finding that LAI is critical to canopy-level CO2 fertilization (without nutrients being considered) does not really bring anything new to the field.

Response: Our results may not be much new for this reviewer but the key message from our study is still crucial for the community to improve land modelling. Actually, in our previous manuscript we have cited a paper showing CMIP5 models have simulated diverse GPP and LAI values during 1985-2006. And both GPP and LAI have been overestimated for most CMIP5 models according to observations (Anav et al., 2013). Satellite and modelled LAI both have experienced significant increasing trends during historical period as reported by Zhu et al. (2016). However, how the uncertainty and increasing trend of LAI contribute to modelled plant productivity and ecosystem carbon storage have not been discussed in previous research. Our study fills this gap and indicates the CO_2 fertilization effects are very sensitive to LAI responses. The merit of our study is that we systematically diagnose model processes and find LAI is the most important factor in modelling the CO_2 fertilization effects, to which modelers should pay greater attentions and efforts in the future research.

As inspired by the reviewer, we added a paragraph reviewing the latest reports about trends of LAI in the Introduction part in the revised manuscript (Line 71-79). We also discussed the uncertainty of modelled LAI in the Discussion part (Line 338-348).

Reviewer 2: Sunlit and shaded leaf partitioning is fairly well-constrained and sunlit LAI can never get much above 1 to 1.5 or so even under the most direct-sun conditions. Solar angle and leaf angle distribution make it possible to exceed an LAI value of one. I know that CLM has had issues with shade leaf LAI becoming excessively large. The authors do not discuss total LAI in CABLE during their fertilization runs, and this makes me suspicious-if their shade-leaf LAI is becoming unrealistically large, that might be a reason why fertilization strength decreases with time; increase in the amount of sunlit leaf may result in large change in GPP, but once sunlit LAI is filled, any additional canopy growth will be as shade LAI, and GPP increase will be attenuated.

Response: We appreciate the reviewer for the insightful comments. Actually, we did analyze total LAI change in the previous supplementary material Fig. S6 (Fig. S1 in the revised version). LAI value of evergreen broadleaf forest increases with time but gradually saturates at the prescribed maximum value. LAI values of other plant types also increase but are far below the prescribed maximum values at 2100. To address the reviewer's concern about the magnitudes and changes of sunlit and shaded leaf LAI (we called the scaling factors in our manuscript according to the standard definition in the CABLE model), we plotted temporal trends of the scaling factors for sunlit leaves and shaded leaves in CABLE-C only simulation (Fig. S9 in the revised version). Results show that the magnitudes of the scaling factors for shaded leaves are greatly larger than those for sunlit leaves for all C_3 plants. This is because in models it is usually defined that portion of sunlit leaves decreases exponentially with increasing LAI (f_{sun}= exp (-k_bLAI)) (Dai et al., 2004). The scaling factors for sunlit leaves are below 1 as the reviewer stated. And the scaling factors for sunlit leaves of evergreen broadleaf forest, evergreen needleleaf forest and deciduous broadleaf forest gradually saturate with eCO_2. We discussed temporal changes of scaling factors for sunlit and shaded leaves in revised manuscript Line 330-332: "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)".

The increasing portion of shaded leaves will lead to the attenuation of GPP increase as the reviewer mentioned. And we believe that saturation of GPP is jointly controlled by biochemical enzyme kinetics and canopy closure. The mechanisms for leaf-level saturation have been discussed in detail in Luo et al. (1996) and Luo and Mooney (1996).

Reviewer 2: I just don't think there's anything new here. Without nutrient cycling the CO2 fertilization results don't have much meaningful application, and the fact that leaf-to-canopy scaling is important has been known for a long time.

Response: We are sorry that the scientific value of our study has not been fully recognized by the reviewer. We have run CABLE with coupled carbon-nitrogen-phosphorus cycles as suggested. Our original conclusion still stands. Although leaf-to-canopy scaling has been known for a long time, no study has done before as we did in this study to evaluate variation of β from biochemical and leaf levels to canopy and ecosystem scales. The leaf-to-canopy scaling is a basis of our study but the conclusion of our study goes far beyond it.

Here, we have strengthened our contributions through the following ways:

(1) Analyzing the CO_2 fertilization effects at different levels with C-N and C-N-P interactions for different C_3 plant functional types (PFTs) in the CABLE model to evaluate whether our conclusions are still valid under nutrient limitations.

(2) In the Introduction and Discussion part, we have clarified that our study was aimed to understand the variability of CO_2 fertilization effects from biochemical to ecosystem levels and the dominant factor (Line 95-100). Our mechanistic study, for the first time, shows that β values vary at different hierarchical levels across C-fluxes and stocks, and across PFTs in a way that is largely attributable to variations in LAI dynamics at canopy and ecosystem levels. This finding is of significance in light of the uncertainty and increasing trends of modelled LAI reported by recent research. Our finding

can stimulate modelling groups to focus more on uncertainty arising from processes related to LAI, and use FACE experiments to narrow the uncertainty of land model predictions.

(3) We believe our conclusions about the across-PFT variation of β and the dominant role of LAI for the variability of β in CABLE is generally applicable to other models. Our analyses can inspire other modelling groups to explore mechanisms for the variability of β from different hierarchical levels (Line 411-441 in the revised manuscript).

Reviewer 2:

Specific comments:

• English prose and grammar, while readable, need attention. There are multiple places, too many to list, where errors exist.

Response: We have carefully revised the manuscript and improved the language in the revised version.

Reviewer 2: • There is no explanation for what eCO2 is (elevated CO2). Don't assume all your readers know the definition.

Response: Agree. We defined it in "The response of ecosystem carbon cycle to elevated CO_2 (eCO_2) is primarily driven by stimulation of leaf-level carboxylation rate in plants (Polglase and Wang, 1992; Long et al., 2004; Heimann et al., 2008)" (Line 55-56).

Reviewer 2: • There is no definition of 'gamma' either.

Response: According to another reviewer's comments, we removed γ-related contents in the revised manuscript.

Reviewer 2: • In many of the equations the equals sign is obscured. More effective spacing will make *these equations easier to read*

Response: Agree. To make our manuscript more clear and concise, we have moved the basic equations for photosynthesis and complex mathematical derivation to the supplementary materials in the revised manuscript. And we used the generalized equation of β at the beginning of Section 2.3 (Line 163).

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The list of all relevant changes made in the manuscript

Here are the relevant changes made in the manuscript.

(1) Page 1 lines 3-8: we changed the affiliations of some co-authors in the title page.

(2) Page 2 lines 21-23: we clarified our simulation designs with nutrient cycles.

(3) Page 2 lines 26-31: we incorporated nutrient-coupled simulation results.

(4) Page 3 lines 40-41: we modified the sentence as suggested.

(5) Page 3 lines 41-45: we defined concentration-carbon feedback (β) as suggested.

(6) Page 3 lines 45: we added “the”.

(7) Page 3 lines 51-53: we added the reference De Kauwe et al. (2016).

(8) Page 3 lines 55-56: we defined “eCO_2”.

(9) Page 3: we removed γ-related contents in the revised manuscript as suggested.

(10) Page 3 lines 59-61: we added the reference Rogers et al. (2017).

(11) Page 4 lines 64-67: we added related references.

(12) Page 4 lines 71-79: we added a paragraph reviewing the latest reports about trends of LAI.

(13) Page 4 lines 85-93: we reviewed the effects of nutrient limitations on CO_2 fertilization effects

(14) Page 5 lines 95-100: we clarified the scientific questions.

(15) Page 5: we have moved the basic equations for photosynthesis and complex mathematical derivation to the supplementary materials.

(16) Page 6 lines 129-138: we introduced how nutrient limitations were incorporated into carbon cycle in the CABLE model

(17) Page 7 lines 140-154: we clarified our experimental design.

(18) Page 8 lines 156-170: we used the generalized equation of β.

(19) Page 9 lines 191-194: we defined leaf-to-canopy scaling factor.

(20) Page 10 lines 204-205: we simplified our equations.

(21) Page 10 lines 207-217: we clarified our calculation.

(22) Page 11 lines 223-228: we presented temporal trends of β at ecosystem level for different vegetation types in C-N and C-N-P simulations.

(23) Page 11 lines 230-232: we added one transition sentence.

(24) Page 11 lines 236-244: we showed variations of intercellular CO_2 concentration and CO_2 compensation point under nutrient limitations.

(25) Page 11 lines 249-259: we presented $\mathcal{L}$ and β values at the year of 2023 (rather than 2056) for C-only simulation.

(26) Page 12 lines 261-267: we compared β values at different hierarchical levels in nutrient-coupled simulations.

(27) Page 13 lines 277-280: we showed correlations between β_{GPP} and β_{LAI}, β_{NPP} and β_{LAI}, β_{cpool} and β_{LAI} in nutrient-coupled simulations.

(28) Page 15 lines 314-315: we discussed about why magnitudes of biochemical and leaf-level β with nutrient-limitations are similar to those without nutrient limitations.

(29) Page 15 lines 317-324: we reorganized some sentences.

(30) Page 15: we deleted the discussion about downregulation of Vcmax and Jmax under elevated CO_2 for this mechanism has not been incorporated into most land surface models.

(31) Page 16 lines 338-348: we added some references to show the trend and uncertainty of modelled LAI.

(32) Page 16 lines 350-352: we discussed about the nutrient effects on the magnitudes of β_{NPP}.

(33) Page 18 lines 381-391: we discussed about the nutrient effects on the magnitudes of β_{NPP} and CUE.

(34) Page 18 lines 397-401: we discussed about how the fixed allocation influences the response of carbon residence time.

(35) Page 19 lines 407-409: we discussed about the variability of nutrient-limited β_{cpool}.

(36) Page 19 lines 411-431: we clarified the implication of our study. We discussed about different photosynthesis models and water stress effects as proposed by reviewer #1.

(37) Page 20 lines 444-446: we clarified our simulation design and results with nutrient cycles.

(38) Page 31: we added Table 1 to present C_i/C_a and its variation among PFTs for C-only, C-N, C-N-P simulations of CABLE.

(39) Page 32: we presented results at the year of 2023 (rather than 2056) for C-only simulation in Table 2.

(40) Page 33: we presented results at the year of 2023 for C-only simulation in Fig. 1a. We added results of C-N and C-N-P simulations in Fig. 1b and Fig. 1c.

(41) Page 35: we presented results at the year of 2023 for C-only simulation in Fig. 3a. We added results of C-N and C-N-P simulations in Fig. 3b and Fig. 3c.

(42) Page 36: we presented results at the year of 2023 in Fig. 4a-4c for C-only simulation. We added results of C-N and C-N-P simulations in Fig.4d-4i.

Supplementary materials

(1) Page 1 lines 2-46: we described photosynthesis module in the CABLE model.

(2) Page 3 lines 47-66: we described mathematic derivations of big-leaf β.

(3) Page 6: we presented LAI trends of C-N and C-N-P simulations in Fig. S1.

(4) Page 7: we presented responses of C_i and Γ_* for C-N simulation in Fig. S2.

(5) Page 8: we presented responses of C_i and Γ_* for C-N-P simulation in Fig. S3.

(6) Page 10-12: we presented the correlations of β_{GPP} and β_{LAI}, β_{NPP} and β_{LAI}, β_{cpool} and β_{LAI} at the year 2023.

(7) Page 13: we compared leaf-level β calculated through biochemical parameters C_i and Γ_* for sunlit leaf (β_psun) and shaded leaf (β_psha) and sensitivities of GPP/LAI (β_GPP/LAI) for different C_3 PFTs at the year 2023.

(8) Page 14: we added time trends of leaf-to-canopy scaling factor for sunlit leaves and shaded leaves (Fig. S9).

Leaf Area Index identified as a major source of variability in modelled CO_2 fertilization

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Abstract. The concentration-carbon feedback~~ factor~~ (β), also called the CO_2 fertilization effect, is a key unknown in climate-carbon cycle projections. A better understanding of model mechanisms that govern terrestrial ecosystem responses to elevated CO_2 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 CO_2 fertilization effects at various hierarchical levels from leaf biochemical reaction~~,~~ and leaf photosynthesis~~,~~ to canopy gross primary production (GPP), net primary production (NPP)~~, to~~, and ecosystem carbon storage (*cpool*)~~, ~~for seven C_3 plant functional types (~~vegetation types~~PFTs) in response to increasing CO_2 under RCP 8.5 scenario~~, using the Community Atmosphere Biosphere Land Exchange model (CABLE).~~. Our results show that ~~coefficient of variation (CV) for the CABLE model among~~ β values at biochemical and leaf photosynthesis levels vary little across the seven ~~vegetation types~~PFTs~~ is 0.15-0.13 for the biochemical level β, 0.13-0.16 for the leaf-level β, 0.48 for the β_{GPP}, 0.45 for the β_{NPP}, and 0.58 for the β_{cpool}.~~, 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 CO_2 concentration is almost an invariant function. In the CABLE model, the major jump in ~~CV ~~variation of β values from leaf- to canopy- and ecosystem-levels results from divergence in modelled leaf area index (LAI) within and among~~ the vegetation types~~PFTs. The ~~correlations~~correlation of β_{GPP}, β_{NPP}, or β_{cpool} each with β_{LAI} ~~are~~is very high in ~~CABLE.~~all simulations. Overall, our results indicate that modelled LAI is a key factor causing the divergence in β~~ values~~ 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 CO_2 in Earth System Models.

1. Introduction

Terrestrial ~~carbon sink, taking~~ecosystems take up roughly 30% of anthropogenic CO_2 emissions, and is of great uncertainty and vulnerable to global climate change (Cox et al., 2000; Le Quéré et al., ~~2015; Cox et al., 2000). The~~2018). Persistent increase of atmospheric CO_2 ~~fertilizing effect, also called the~~ concentration will stimulate plant growth and ecosystem carbon storage, forming a negative feedback to CO_2 concentration (Long et al., 2004; Friedlingstein et al., 2006; Canadell et al., 2007). This concentration-carbon feedback (β~~factor (β),~~), also called the CO_2 fertilization effect, has been identified as a major uncertainty in modeling terrestrial ~~ecosystem~~carbon-cycle response to ~~future~~historical climate change~~.~~ (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 ~~or~~to 4.5 times larger, and more uncertain, than ~~carbon-~~climate-climate feedback~~ factor~~ (γ) (Gregory et al., 2009; Bonan ~~&~~and Levis, 2010; Arora et al., 2013). Apart from the substantial uncertainty ~~among~~across different models, Smith et al. (2016) suggested that Earth System Models (ESMs) in CMIP5 overestimate global terrestrial β values compared with remote sensing data and Free-Air CO_2 Enrichment (FACE) ~~experiment~~experimental results. ~~The~~ Though satellite products they used may underestimate the effect of CO_2 fertilization on net primary productivity (De Kauwe et al., 2016), the large disparity between models and ~~reality~~FACE experiments gives us little confidence in making policies to combat global warming.

~~Efforts have been made to identify causes for the diverse ecosystem responses to eCO_2 and increasing temperature in models. For example, Zeng (2004) used different parameterizations of CO_2 fertilization, soil decomposition rate and turnover time to explain the total land carbon change in a coupled earth system model. Matthews et al. (2005) showed different parameterizations of temperature constraints on photosynthesis strongly affects γ results. Tachiiri et al. (2012) found the~~

~~maximum photosynthesis rate (V_{cmax}) and specific leaf area (SLA, leaf area per unit dry mass) had the most significant contributions to both of β and γ with a ESMs emulator. To gain insight into the characteristics of biogeochemical cycles β and γ, it's necessary to identify sensitive parameters and important processes in models from a mechanistic way.~~

The response of ecosystem carbon cycle to elevated CO$_2$ (eCO$_2$) is primarily driven by stimulation of leaf-level carboxylation rate in plants~~ by eCO$_2$~~ (Polglase and Wang, 1992; Long et al., 2004; Heimann et al., 2008). The CO$_2$ 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 CO$_2$ (Canadell et al., 2007; Iversen et al., 2012~~; De Kauwe et al., 2014).~~). The leaf-level CO$_2$ fertilization for C$_3$ plants is generally well characterized with models from Farquhar et al. (1980~~)~~), and ~~Collatz et al. (1991, 1992), which~~the basic biochemical mechanisms have been adopted by most land surface models ~~(Bonan~~although some models implement variants of Farquhar et al~~., 2013; Wang~~. (1980) (Rogers et al., ~~1998; Cox, 2001~~2017). Previous research with both theoretical analysis and data synthesis from a large number of experiments has revealed that normalized CO$_2$ sensitivity of leaf-level photosynthesis, which represents kinetics sensitivity of photosynthetic enzymes, varies little among different ~~vegetation types~~C$_3$ species at a given CO$_2$ concentration (Luo ~~&~~and ~~Monney~~Mooney, 1996; Luo et al., 1996). However, the CO$_2$ 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 ~~and~~feedback (Fatichi et al., 2016), canopy ~~structure,~~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~~ (Friedlingstein et al., 2015; Fatichi et al., 2016). Amongst these processes, leaf area index (LAI) largely affects canopy assimilation and plant growth under condition of eCO$_2$, and representation of LAI in plant productivity models causes large uncertainty (Ewert, 2004). Models generally predict that LAI dynamics will respond to eCO$_2$ positively due to enhanced leaf biomass, then increasing LAI will in turn feed back to greater canopy GPP as a result of more light interception. However, the relative contributions of the response of leaf-level photosynthesis and LAI to β of GPP have been~~

~~rarely quantified and compared in previous studies.~~. 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.

~~As to~~ Leaf area index (LAI) largely affects canopy assimilation and plant growth under eCO$_2$. Many satellite products exhibit increasing trends of LAI over the ~~spatial pattern,~~ 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 CO$_2$ concentration. LAI plays a key role in scaling leaf-level biogeophysical and biogeochemical processes to global scale responses in ecosystem models, and the ~~largest~~representation of LAI in models causes large uncertainty (Ewert, 2004; Hasegawa et al., 2017). Models generally predict that LAI dynamics will respond to eCO$_2$ 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.

The CO$_2$ fertilization effects depend on locations, vegetation types and soil nutrient conditions. The strongest absolute CO$_2$ ~~fertilizing effects at ecosystem level were~~fertilization effect has been found in tropical and temperate forests where the larger biomass presents than other regions ~~mainly because of high basic NPP~~. In comparison, the weakest response to eCO$_2$ occurs in boreal forests (Joos et al., 2001; Peng et al., 2014). But with gradual eCO$_2$, 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 (~~Hungate et al., 2003;~~ Luo et al., 2004; Thornton et al., 2009; Coskun et al., 2016). ~~2014). But the variation of relative β effects~~ 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, 1999; 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 ~~geographical locations and vegetation types and the dominating factors are rarely discussed and often ignored.~~ 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 ~~and why β values~~variability, as measured by coefficient of variation (CV) within and across different plant functional types (PFTs), in the CO_2 fertilization effects changes at different hierarchical levels ~~vary across different~~ 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 ~~vegetation types~~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 ~~within and across seven C_3 vegetation types~~.

2. Materials and methods

2.1 CABLE model description

CABLE (version 2.0) is ~~a global~~the Australian community land surface model ~~as described by Wang~~(Kowalczyk et al~~. (2010, 2011~~., 2006) and ~~is improved by including~~incorporates CASA-CNP to simulate global carbon~~,~~ (C), nitrogen (N) and phosphorus (P) cycles~~. To simplify the study, phosphorus and nitrogen cycles are not used.~~ (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 distinction between sunlit and shaded leaves is necessary in scaling from leaf to canopy because the response of photosynthesis to the absorbed photosynthetically active radiation (PAR) is nonlinear. The two-leaf model uses the same set of equations for calculating photosynthesis,~~

~~transpiration and sensible heat fluxes for an individual leaf, but with the bulk formulation for the parameters for all sunlit and shaded leaves separately. For a given leaf parameter *P*, the corresponding parameter values for the two big leaves are calculated as:~~ The descriptions of photosynthesis module are in supplementary Text S1.

~~$P_1 = \int_0^\Lambda p(\lambda) f_{sun}(\lambda) d\lambda$ (big sunlit leaves)~~ ~~(1)~~

~~$P_2 = \int_0^\Lambda p(\lambda) (1 - f_{sun}(\lambda)) d\lambda$ (big shaded leaves)~~ ~~(2)~~

~~f_{sun} is the fraction of sunlit leaves within a canopy, calculated by f_{sun}= exp(-$k_b\lambda$), where k_b is the extinction coefficient of direct beam radiation for a canopy with black leaves. λ is cumulative LAI.~~

~~CABLE calculates plant photosynthesis rate according to Leuning (1990). Leuning (1990) described a method to calculate stomatal conductance, CO_2 assimilation, and intercellular CO_2, by solving equations describing the supply of CO_2 through stomata and demand for CO_2 in photosynthesis (Farquhar et al., 1980) simultaneously. Since C_3 plants have similar mechanisms for photosynthesis and respond to eCO_2 much stronger than C_4 plants, C_3 plants are only considered in this study. Canopy net photosynthesis rate is calculated as:~~

~~$A = \min\{A_c, A_q, A_p\} - R_d = G_{st}(C_S - C_i)$~~ ~~(3)~~

~~$A_c = V_{cmaxbig} * \frac{C_i - \Gamma_*}{C_i + K_c(1 + O_i/K_O)}$~~ ~~(4)~~

~~$A_q = J_{cmaxbig} * \frac{C_i - \Gamma_*}{C_i + 2\Gamma_*}$~~ ~~(5)~~

~~$A_p = 0.5 * V_{cmaxbig}$~~ ~~(6)~~

~~Where A_c, A_q and A_p are assimilation rates limited by Rubisco activity, RuBP regeneration and sink respectively. R_d is day respiration, which is proportional to $V_{cmaxbig}$. $V_{cmaxbig}$ is the maximum catalytic activity of Rubisco of big leaves. C_i is intercellular CO_2 concentration. Γ_* is the CO_2 compensation point in the absence of day respiration. K_c and K_O are Michaelis-Menten constants for CO_2 and O_2 respectively. O_i is intercellular oxygen concentration. Γ_*, K_c and K_O are only~~

~~functions of leaf temperature. $J_{cmaxbig}$ is the maximum rate of photosynthesis at saturating C_i for a given absorbed photo irradiance of big leaves. For sunlit and shaded leaves, $V_{cmaxbig}$ and $J_{cmaxbig}$ are defined as follows:~~

~~$V_{cmaxbig,1} = v_{cmax,25} * f_{vcmax}\left(T_{f,1}\right) * \int_0^{\Lambda} \exp(-k_b\lambda) \exp(-k_n\lambda)\, d\lambda = v_{cmax,25} * f_{vcmax}\left(T_{f,1}\right) * \frac{1-\exp[-\mathrm{LAI}(k_n+k_b)]}{k_n+k_b} \quad (7)$~~

~~$V_{cmaxbig,2} = v_{cmax,25} * f_{vcmax}\left(T_{f,2}\right) * \int_0^{\Lambda} [1-\exp(-k_b\lambda)]\exp(-k_n\lambda)\, d\lambda = v_{cmax,25} * f_{vcmax}\left(T_{f,2}\right) * \left\{\frac{1-\exp(-k_n\mathrm{LAI})}{k_n} - \frac{1-\exp[-\mathrm{LAI}(k_n+k_b)]}{k_n+k_b}\right\} \quad (8)$~~

~~$J_{cmaxbig,1} = j_{cmax,25} * f_{jcmax}\left(T_{f,1}\right) * \int_0^{\Lambda} \exp(-k_b\lambda) \exp(-k_n\lambda)\, d\lambda = j_{cmax,25} * f_{jcmax}\left(T_{f,1}\right) * \frac{1-\exp[-\mathrm{LAI}(k_n+k_b)]}{k_n+k_b} \quad (9)$~~

~~$J_{cmaxbig,2} = j_{cmax,25} * f_{jcmax}\left(T_{f,2}\right) * \int_0^{\Lambda} [1-\exp(-k_b\lambda)]\exp(-k_n\lambda)\, d\lambda = j_{cmax,25} * f_{jcmax}\left(T_{f,2}\right) * \left\{\frac{1-\exp(-k_n\mathrm{LAI})}{k_n} - \frac{1-\exp[-\mathrm{LAI}(k_n+k_b)]}{k_n+k_b}\right\} \quad (10)$~~

~~Where $v_{cmax,25}$ is maximum carboxylation rate when photosynthesis is limited by Rubisco activity of a leaf. $j_{cmax,25}$ is maximum potential electron transport rate of a leaf. It's assumed $j_{cmax,25}=2v_{cmax,25}$ in the model. $f_{vcmax}\left(T_{f,1}\right)$ and $f_{jcmax}\left(T_{f,1}\right)$ describe the temperature dependence of $v_{cmax,25}$ and $j_{cmax,25}$ for sunlit leaves respectively. $f_{vcmax}\left(T_{f,2}\right)$ and $f_{jcmax}\left(T_{f,2}\right)$ describe the temperature dependence of $v_{cmax,25}$ and $j_{cmax,25}$ for shaded leaves respectively. 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.~~

~~G_{st} is stomatal conductance, and is calculated as:~~

~~$G_{st} = G_0 + \frac{a*f_w*A}{(C_s-\Gamma)(1+D_s/D_0)} \quad (11)$~~

~~Where G_0 is stomatal conductance when A=0. a and D_0 are empirical constants, f_w is an empirical parameter describing the availability of soil water for plants. A is net assimilation rate in Equ. (3). C_s is CO_2 mol fraction at the leaf surface. Γ is CO_2 compensation point of photosynthesis. D_s is vapour pressure deficit at the leaf surface.~~

Leaf Area Index (LAI) is calculated as:

$$\mathrm{LAI} = C_{leaf} * \mathrm{SLA}$$ ~~(12~~ (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 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 ~~its phase 2 allocation~~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.

~~Gross primary production (~~

GPP~~)~~ is the sum of canopy net photosynthesis rate (A) and day respiration (R_d). ~~Net primary production (~~NPP~~)~~ is calculated as the difference between GPP and autotrophic respiration (~~both~~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 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 cycle in CASA-CNP module in the CABLE model. In brief, NPP is calculated as:

$$\mathrm{NPP} = \mathrm{GPP}(\mathrm{L}, V_{cmax}(N_l), J_{max}(N_l)) - \sum_i R_{mi}(N_i) - R_g(\frac{N_l}{P_l}) \qquad (2)$$

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 (NEP = 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 ~~repetitively~~ until ~~a~~ steady ~~state was~~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 ~~historical period (1901-2010)~~CMIP5 dataset, representing global annual averages and ~~from~~the RCP8.5 scenario ~~for 2011 to 2100.~~after 2010 (Etheridge et al., 1996; MacFarling Meure et al., 2006). The spatial resolution of CABLE used here is 1.9°×2.5°~~.~~ (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)).

2.3 Calculation of β values at five hierarchical levels

We aimed to analyze the CO_2 fertilization effects ~~from~~for biochemical ~~level~~reaction ($\mathcal{L}$), leaf photosynthesis rate (p), leaf-to-canopy ~~gross primary production (~~scaling factor (S), leaf area index (LAI), sunlit leaf GPP~~), net primary production (~~ (GPP_{sun}), shaded leaf GPP (GPP_{sha}), canopy GPP, NPP~~),~~, and ecosystem carbon storage (*cpool*~~).~~) from C-only, C-N and C-N-P simulations of CABLE. Ecosystem carbon storage is the sum of plant, litter and soil carbon stock. Since CO_2 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 ~~the five levels~~ these variables were calculated as the normalized ~~sensitivity~~sensitivities of those variables to ~~eCO_2.~~

~~Equ. (4) and (5) can be simplified~~atmospheric CO_2 concentration (C_a) as~~:~~ β_V:

~~$A_c = v_{cmax,25} * f_{vcmax}(T_f) * \frac{C_i - \Gamma_*}{C_i + K_c(1 + C_o - K_O)} * S = a_c * S$ (13)~~

~~$A_q = j_{cmax,25} * f_{jcmax}(T_f) * \frac{C_i - \Gamma_*}{C_i + 2\Gamma_*} * S = a_q * S$ (14)~~

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

Where ~~a_c and a_q represent leaf-level Rubisco- and RuBP-limit photosynthesis rates respectively:~~

~~$a_c = v_{cmax,25} * f_{vcmax}(T_f) * \frac{C_i - \Gamma_*}{C_i + K_c(1 + C_o - K_O)}$ (15)~~

~~$a_q = j_{cmax,25} * f_{jcmax}(T_f) * \frac{C_i - \Gamma_*}{C_i + 2\Gamma_*}$ (16)~~

~~S indicates the scaling factor that scales fluxes at~~ V in the ~~single top leaf of the canopy to whole canopy fluxes. For sunlit leaves~~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~~:=~~

~~$S_{sun} = \frac{1-\exp[-\mathrm{LAI}(k_n+k_b)]}{k_n+k_b}$ (17)~~

~~For shaded leaves:~~

~~$S_{sha} = \frac{1-\exp(-k_n\mathrm{LAI})}{k_n} - \frac{1-\exp[-\mathrm{LAI}(k_n+k_b)]}{k_n+k_b}$ (18)~~

~~where subscripts~~ "*sun*" and "*sha*" denote the sunlit and shaded components ~~of leaf-level scaling factors.~~

~~The rate of photosynthesis is typically RuBP-regeneration-limited when CO_2 concentration exceeds 300 ppm (Soolanayakanahally et al., 2009). Our results also show that photosynthesis rate under RCP8.5 scenario.~~ $\mathrm{d}V$ is the ~~mainly RuBP-regeneration-limited (results not shown). Leaf-level β_p for sunlit leaf and shaded leaf are defined as~~difference of these variables between two consecutive years. $\mathrm{d}C_a$ ~~:~~

~~$\beta_{p_{sun}} = \frac{1}{p_{sun}} * \frac{\mathrm{d}p_{sun}}{\mathrm{d}C_a} = \frac{1}{a_{qsun}} * \frac{\mathrm{d}a_{qsun}}{\mathrm{d}C_{isun}} * \frac{\mathrm{d}C_{isun}}{\mathrm{d}C_a} = \mathcal{L}_{sun} * \frac{\mathrm{d}C_{isun}}{\mathrm{d}C_a}$ (19)~~

~~$\beta_{p_{sha}} = \frac{1}{p_{sha}} * \frac{\mathrm{d}p_{sha}}{\mathrm{d}C_a} = \frac{1}{a_{qsha}} * \frac{\mathrm{d}a_{qsha}}{\mathrm{d}C_{isha}} * \frac{\mathrm{d}C_{isha}}{\mathrm{d}C_a} = \mathcal{L}_{sha} * \frac{\mathrm{d}C_{isha}}{\mathrm{d}C_a}$ (20)~~

~~Where p_{sun} and p_{sha} are leaf-level photosynthesis rates for sunlit leaf and shaded leaf respectively. C_a~~ is the ~~atmospheric CO_2 concentration. $\mathcal{L}$~~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.

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 ~~C_i~~intercellular CO_2 concentration (C_i) and has been suggested to be an invariant function for C_3 plants grown in diverse environments. The rate of photosynthesis is typically RuBP-regeneration-limited under high CO_2 concentration. We found photosynthesis rates are almost all limited by RuBP-regeneration process globally under RCP8.5 scenario since 2011 when CO_2 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 eCO_2. For sunlit leaf and shaded leaf, ~~$\mathcal{L}$ is~~formulations of $\mathcal{L}$ under RuBP-regeneration-limitation are defined as:

$$\mathcal{L}_{sun} \cancel{= \frac{1}{a_{qsun}} * \frac{da_{qsun}}{dC_{isun}}} = \frac{3\ *\Gamma_{*sun}}{(C_{isun}+2*\Gamma_{*sun})(C_{isun}-\Gamma_{*sun})} \qquad \cancel{(21}(4)$$

$$\mathcal{L}_{sha} \cancel{= \frac{1}{a_{qsha}} * \frac{da_{qsha}}{dC_{isha}}} = \frac{3\ *\Gamma_{*sha}}{(C_{isha}+2*\Gamma_{*sha})(C_{isha}-\Gamma_{*sha})} \qquad \cancel{(22}(5)$$

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. ~~Intercellular CO_2 concentration (C_i)~~ C_i varies significantly at sub-daily, intra-annual and inter-annual ~~basis~~bases. We're interested in how C_i responds to eCO_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}).

~~Canopy~~Then leaf-level ~~β_{GPP}~~β_p is defined as~~:~~

~~$$\beta_{GPP} = \frac{1}{GPP} * \frac{dGPP}{dC_a} \qquad (23)$$~~

~~Where GPP is~~ the ~~average annual GPP between the two adjacent years. dGPP~~product of $\mathcal{L}$ and ~~dC_a are the differences of GPP and C_a between two adjacent years respectively.~~

~~The sensitivity of yearly average LAI to CO_2 is defined as:~~

~~$$\beta_{LAI} = \frac{1}{LAI} * \frac{dLAI}{dC_a} \qquad (24)$$~~

~~Where LAI and dLAI are similarly defined as those about GPP.~~

~~Canopy GPP is the sum of~~ $\frac{dC_i}{dC_a}$. For sunlit leaf ~~GPP (GPP_{sun})~~ and shaded leaf, the formulations are:

$$\beta_{p_{sun}} = \mathcal{L}_{\mathrm{sun}} * \frac{\mathrm{d}C_{isun}}{\mathrm{d}C_a} \qquad (6)$$

$$\beta_{p_{sha}} = \mathcal{L}_{sha} * \frac{\mathrm{d}C_{isha}}{\mathrm{d}C_a} \qquad (7)$$

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:

$$S_{sun} = \frac{1-\exp[-\mathrm{LAI}(k_n+k_b)]}{k_n+k_b}$$ ~~GPP (GPP$_{sha}$).~~ (8)

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

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 is just calculated as the average from hourly leaf-to-canopy scaling factors in a year.

Big-leaf $\beta_{\mathrm{GPP}_{sun}}$ (or $\beta_{\mathrm{GPP}_{sha}}$) can be decomposed as the sum of normalized sensitivity of ~~leaf-level p~~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 Equ. (23) and Equ. (24). Subscripts "*sun*" and "*sha*" denote the sunlit and shaded components of leaf-level photosynthesis and leaf-to-canopy scaling factors.~~as shown in Eq. (10) and Eq. (11). Detailed mathematical derivations are in supplementary Text S2.

~~$\beta_{\mathrm{GPP}_{sun}} = \frac{1}{\mathrm{GPP}_{sun}} * \frac{\mathrm{dGPP}_{sun}}{dC_a} = \frac{1}{p_{sun} * S_{sun}} * \frac{\mathrm{d}(p_{sun} * S_{sun})}{dC_a} = \frac{1}{p_{sun}} * \frac{\mathrm{d}p_{sun}}{\mathrm{d}C_a} + \frac{1}{S_{sun}} * \frac{\mathrm{d}S_{sun}}{\mathrm{d}C_a} = \mathcal{L}_{sun} * \frac{\mathrm{d}C_{isun}}{\mathrm{d}C_a} + \frac{1}{S_{sun}} * \frac{\mathrm{d}S_{sun}}{\mathrm{d}C_a} = \beta_{p_{sun}} + \beta_{S_{sun}}$ (25)~~

~~$\beta_{\mathrm{GPP}_{sha}} = \frac{1}{\mathrm{GPP}_{sha}} * \frac{\mathrm{dGPP}_{sha}}{\mathrm{d}C_a} = \frac{1}{p_{sha} * S_{sha}} * \frac{\mathrm{d}(p_{sha} * S_{sha})}{\mathrm{d}C_a} = \frac{1}{p_{sha}} * \frac{\mathrm{d}p_{sha}}{\mathrm{d}C_a} + \frac{1}{S_{sha}} * \frac{\mathrm{d}S_{sha}}{\mathrm{d}C_a} = \mathcal{L}_{sha} * \frac{\mathrm{d}C_{isha}}{\mathrm{d}C_a} + \frac{1}{S_{sha}} * \frac{\mathrm{d}S_{sha}}{\mathrm{d}C_a} = \beta_{p_{sha}} + \beta_{S_{sha}}$ (26)~~

~~Net ecosystem productivity level β_{NPP} is defined as:~~

~~$\beta_{\mathrm{NPP}}=\frac{1}{\mathrm{NPP}}*\frac{\mathrm{dNPP}}{\mathrm{d}C_a}$ (27)~~

~~Where NPP and dNPP are similarly defined as those about GPP.~~

~~Ecosystem carbon storage level β_{cpool} is defined as:~~

~~$\beta_{cpool}=\frac{1}{cpool}*\frac{\mathrm{d}cpool}{\mathrm{d}C_a}$ (28)~~

~~Where $cpool$ is the average of total ecosystem carbon storage between two adjacent year, $\mathrm{d}cpool$ is the difference of total ecosystem carbon storage between two adjacent year. Then these normalized sensitivities are of identical units (ppm^{-1}) and can be compared with each other.~~

$$\beta_{\mathrm{GPP}_{sun}} = \beta_{p_{sun}} + \beta_{S_{sun}} \tag{10}$$

$$\beta_{\mathrm{GPP}_{sha}} = \beta_{p_{sha}} + \beta_{S_{sha}} \tag{11}$$

There are ten patches in each model grid in CABLE. Each patch consists of a certain land use type with a specific fraction. ~~We calculated β values and their coefficients of~~ To study the variation ~~(CV)~~of β ~~–~~across different ~~geographical locations within a specific PFT at different levels to explore the variability of β within PFTs. To study the inter-PFTs variation, we grouped~~ C_3 PFTs, biome-level parameters such as Γ_{*sun}, C_{isun} ~~based on PFTs by calculating the~~, S_{sun} and LAI were calculated as mean values based on plant functional types (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} ~~. Then we~~and β_{cpool} at the year 2023 (relative to 2022) for different C_3 PFTs were calculated and compared. Coefficients of variation (CVs) of β values were calculated across various C_3 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, C_3 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 ~~C_3 plant~~patch and ~~coefficients of variation~~CV of β values across ~~plant types~~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.

3. Results

3.1 Temporal trends of β at ecosystem level for different ~~vegetation types~~PFTs

~~At global scale~~In C-only simulation, β_{cpool} values for different C_3 ~~plants~~ PFTs all decline with time from 2011 to 2100 under RCP8.5 scenario (Fig.~~1~~ 1a). However, the magnitudes of β_{cpool} differ ~~across~~ among different PFTs~~them~~, with the highest values ~~occur~~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 C_3 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 CO_2 concentration and CO_2 compensation point

~~The ratios~~To reveal which processes cause the large disparity of β across PFTs as shown in Fig. 1, we first compared intercellular CO_2 concentration (C_i) and CO_2 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) ~~are~~is approximately ~~constants~~constant with eCO_2 ~~(Fig.2a and Fig.2b)~~ for each ~~vegetation type~~PFT (Fig. 2a~~ and Fig..~~, 2b). For sunlit leaf, C_i/C_a values ~~of different vegetation types~~ range from 0.64 to 0.~~72~~70 with CV=0.03 ~~(Fig.2a). For~~across different C_3 PFTs (Table 1).

C_i/C_a values for shaded leaf~~,~~ are higher than those for sunlit leaf, and the range is 0.~~70~~68 to 0.76 with CV=0.03 ~~(Fig.2b~~across different C_3 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. ~~Values~~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).

In all of the simulations, values of CO_2 compensation point in the absence of day respiration (Γ_*) for a specific ~~vegetation type~~PFT do not change ~~through~~over time since ~~we fixed~~ air temperature as an input to the model is not affected by the biophysical feedback in the offline~~ in~~ model simulations (Fig. 2c, 2d, S2c, S2d, S3c, S3d ~~(Fig.2c and Fig.2d).~~). But there is a huge variance ~~among~~of Γ_* across different C_3 ~~plants~~PFTs because~~s~~ of different leaf temperature which Γ_* values depend on.

3.3 Comparison of β ~~effects~~ at different hierarchical levels

~~Coefficient of variation (CV)~~To further trace the cause for ~~biochemical response $\mathcal{L}$, the ratio of~~ the ~~change of intercellular CO_2 concentration to the change of ambient CO_2 (dC_i/dC_a), leaf-level β_p, β_{LAI}, β_{GPP}, β_{NPP} and β_{cpool} across different geographical locations within each vegetation type are listed in Table 1. Variations of biochemical and leaf-level responses are relatively smaller than those at canopy and ecosystem levels within all C_3 plants. Divergence of dC_i/dC_a is the smallest. CVs of β_{LAI} are the largest for all the~~divergence of β across ~~vegetation types~~PFTs~~. β_{GPP} values also greatly differentiate across different geographical locations. CVs of~~ as shown in ~~β_{NPP} are very similar to those of β_{GPP} for all the vegetation types except for the evergreen needleleaf forest. CVs of β_{cpool} are reduced compared with those of β_{NPP} for most vegetation types, except for evergreen broadleaf forest and tundra.~~

~~With yearly PFT-averaged C_i and Γ_* values (~~Fig.~~2),~~ 1 at a specific time, $\mathcal{L}_{sun}$, $\mathcal{L}_{sha}$, $\beta_{p_{sun}}$ ~~and~~, $\beta_{p_{sha}}$ ~~were calculated for different vegetation types, and were plotted together with~~, β_{GPP}, β_{NPP} and β_{cpool} at the year ~~2056 (the middle year within the prediction period) under RCP8.5 scenario (~~2023 for different C_3 PFTs in all simulations were plotted in Fig. 3~~)~~. CV is marked above data points for each variable to indicate degree of variation ~~among~~across different C_3 ~~plants~~PFTs. ~~Results~~In C-only simulation (Fig. 3a), results show that at leaf biochemical level, $\mathcal{L}$ ~~factors~~values for sunlit leaf and shaded leaf range from 0.~~0003~~000055 ppm^{-1} to 0.~~0005~~300097 ppm^{-1}. Variations of $\mathcal{L}_{sun}$ and $\mathcal{L}_{sha}$ among ~~vegetation types~~PFTs are small (CV=0.15 and 0.13). At leaf photosynthesis level,~~ the range of values of ~~ $\beta_{p_{\mathrm{sun}}}$ and $\beta_{p_{\mathrm{sha}}}$ for the seven ~~vegetation types~~PFTs vary from~~ is~~ 0.~~00022~~00041 ppm^{-1} to 0.~~00035~~00072 ppm^{-1}, and the variations among different ~~vegetation types~~PFTs ~~is ~~are not significant (CV=0.~~13~~18 and 0.~~16~~12). But β ~~values~~values are diverging when scaled up to GPP level with CV jumping to 0.~~48~~49 among ~~vegetation types~~PFTs. β ~~values~~values of deciduous broadleaf forest and shrub greatly increase from leaf level to GPP level. However, canopy scaling effects do not significantly amplify ~~β_{GPP}~~β values at canopy levels (β_{GPP}) for deciduous needleleaf forest, tundra and evergreen broadleaf forest. ~~Values~~Magnitudes and variance of β_{NPP} are similar to those of β_{GPP} because NPP ~~values ~~linearly ~~correlate~~correlates with GPP ~~values ~~for all C_3 ~~vegetation types~~PFTs (Fig. S4). Magnitudes of β_{cpool} for all ~~vegetation types~~PFTs ~~decrease~~are decreased compared with those of β_{NPP} and β_{GPP}. ~~Shrub has the ~~Deciduous broadleaf forest and shrub have the highest β_{GPP} and β_{NPP} values (around 0.~~0013~~0026 ppm^{-1}~~), but a smaller~~). Deciduous broadleaf forest has the greatest β_{cpool} value ~~compared with deciduous broadleaf forest~~(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 ~~vegetation types~~PFTs reaches the highest ~~value ~~(0.58) ~~among all~~compared with CV of β values at other levels.

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 C-only simulation, β_{NPP} values in nutrient-coupled simulations are reduced for most C_3 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-level β_p, β_{GPP}, β_{NPP} and β_{cpool} across different geographical locations within each ~~vegetation type~~PFT. Variations of biochemical and leaf-level responses are relatively smaller than those at canopy and ecosystem levels within all C_3 ~~plants~~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 simulation (data not shown).

To further explore why β values at canopy and ecosystem levels are diverging across different ~~geographical locations within the same~~C_3 ~~vegetation types~~PFTs, the correlations between β_{GPP} and β_{LAI} ~~(Fig. S1),~~, β_{NPP} and β_{LAI} ~~(Fig. S2),~~, β_{cpool} and β_{LAI} ~~(Fig. S3)~~for C-only, C-N and C-N-P simulations were plotted at the year ~~2056~~2023. Results show that β_{GPP}, β_{NPP} and β_{cpool} all have significant linear correlations with β_{LAI} ~~for~~across different C_3 PFTs (Fig. 4). Results also show that β_{LAI} linearly correlates with β_{GPP}, β_{NPP} and β_{cpool} across patches within the same ~~vegetation type~~PFT, ~~except~~ although there are some discontinuous points within evergreen broadleaf forest where ~~the~~ canopy of many patches closes~~. The correlations between β_{cpool} and β_{LAI} are weaker than those between β_{NPP} and β_{LAI}. Across different C_3 plant types, results also show that β_{LAI} linearly correlates with β_{GPP}, β_{NPP} and β_{cpool}~~ (Fig. ~~4a, Fig. 4b and Fig. 4c), but with slopes that gradually decrease from 0.93 to 0.87 and 0.81.~~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 CO_2.

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3.4 β of sunlit and shaded leaves

To understand ~~influences~~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 ~~plants~~PFTs from 1901 to 2100 in Fig. 5. From the beginning of the simulation, GPP_{sha} is higher than GPP_{sun} for ~~almost~~ all C_3 ~~types~~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 ~~vegetation types~~PFTs. 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.

~~Temporal~~Then temporal trends were plotted for $\beta_{\mathrm{GPP}_{sun}}$($\beta_{\mathrm{GPP}_{sha}}$) and decomposing factors $\beta_{p_{sun}}$ ($\beta_{p_{sha}}$) and $\beta_{S_{sun}}$ ($\beta_{S_{sha}}$) for each ~~vegetation type~~PFT ~~(Fig.6). The~~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~~. Values of~~ (Fig. 6). $\beta_{p_{sun}}$ and $\beta_{p_{sha}}$ overlap through time for each ~~vegetation type~~PFT. ~~Values~~Magnitudes of $\beta_{\mathrm{GPP}_{sha}}$ are higher than those of $\beta_{\mathrm{GPP}_{sun}}$ for all C_3 ~~vegetation types~~PFTs. For deciduous needleleaf forest and tundra, both $\beta_{p_{sun}}$ ($\beta_{p_{sha}}$) and $\beta_{S_{sun}}$ ($\beta_{S_{sha}}$) contribute to the maginitudes and trends of $\beta_{\mathrm{GPP}_{sun}}$($\beta_{\mathrm{GPP}_{sha}}$). For evergreen needleleaf forest, deciduous broadleaf forest, shrub and C_3 grass, $\beta_{S_{sun}}$ ($\beta_{S_{sha}}$) dominates the magnitude and change of $\beta_{\mathrm{GPP}_{sun}}$($\beta_{\mathrm{GPP}_{sha}}$). For evergreen broadleaf forest, $\beta_{S_{\mathrm{sha}}}$ predominates ~~–~~ the magnitude and change of $\beta_{\mathrm{GPP}_{sha}}$ before 2035.

4. Discussion

4.1 Variation of biochemical and leaf-level photosynthetic responses to eCO$_2$

~~Most previous studies focused on variation in β for the land carbon storage, the standard definition of β as in Friedlingstein et al. (2006). However, accurate estimate of leaf-level β has not been attempted by modelling groups before. In this study, with the available outputs of biochemical parameters C_i and Γ_* in CABLE model, we calculated leaf-level β values with distinction of sunlit and shaded leaves for the first time. The calculation of leaf-level β simply through the sensitivity of GPP/LAI might lead to biases because some models used two-leaf or multiple-layer canopy structure. In our study, we also compared the sensitivities of GPP/LAI with leaf-level β values derived from C_i and Γ_*. Results show that the former calculation causes large biases, especially for trees (Fig.S5). Thus, the relatively large divergence of the sensitivities of GPP/LAI to eCO$_2$ in Hajima et al. (2014) may not indicate diverse leaf-level photosynthesis responses among CMIP5 models. Another advantage of our calculation of leaf-level β is that the reason for the divergence of leaf-level β within and across vegetation types can be traced back to difference from C_i and leaf temperature as shown in Fig.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 ~~intercellular CO_2 concentration~~ 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 $C_i\,/\,C_a$ ~~values are~~is approximately constant with eCO_2 for a specific ~~vegetation type~~PFT, and ~~vary~~varies little within and across ~~vegetation types~~PFTs~~.~~ in all simulations. This is in line with FACE experimental results which show almost constant C_i/C_a values for different ~~vegetation types~~PFTs under ~~eCO_2 conditions~~CO_2 fertilization (Drake et al., 1997; Long et al., 2004). Γ_* varies little for different species and only depends on leaf temperature (Luo and Mooney, 1996). ~~Previous research showed~~Sensitivity analysis in a previous study has shown that ~~global~~a ±5C° of leaf temperature changes caused approximately ±7 ppm changes in Γ_*, leading to variation ~~only caused a small influence on biochemical response $\mathcal{L}$~~ 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 ~~global vegetation types~~PFTs in this study. Our results also illustrate that nutrient effects do not significantly change C_i and Γ_*, leading to similar 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 eCO_2 diverged a lot among models. This calculation is likely debatable for ignoring 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). 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.

~~In this study, we assume values of $j_{cmax,25}$ and $v_{cmax,25}$ are PFT-specific and do not change with time. In fact, downregulation of photosynthesis is observed in experiments when plants acclimate to eCO$_2$ in the long term. Downregulation involves reduction in $v_{cmax,25}$ by about 13% and $j_{cmax,25}$ by about 5% on average (Long et al., 2004). Then the leaf biochemical response $\mathcal{L}'$ for Rubisco-limit and RuBP-limit should be written as:~~

~~$\mathcal{L}_1' = \mathcal{L}_1 + \frac{1}{v_{cmax,25}} * \frac{dv_{cmax,25}}{dCi}$ (29)~~

~~$\mathcal{L}_2' = \mathcal{L}_2 + \frac{1}{j_{cmax,25}} * \frac{dj_{cmax,25}}{dCi}$ (30)~~

~~Where $\mathcal{L}_1$ and $\mathcal{L}_2$ are the leaf biochemical responses without the influence from shifts in $v_{cmax,25}$ and $j_{cmax,25}$. $\mathcal{L}'$ will become smaller because of the reduction of $v_{cmax,25}$ and $j_{cmax,25}$. And it has been observed that $j_{cmax,25}$ and $v_{cmax,25}$ tended to be reduced to a greater extent in grasses and shrubs than in trees (Ainsworth &and Long, 2005). Due to the downregulation mechanism, the leaf biochemical response to eCO$_2$ will diverge more among different C$_3$ functional groups.~~

4.2 Variation 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 version 4.5 (CLM4.5, Bonan 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 eCO$_2$ diverge primarily because the responses of LAI diverge within and among ~~vegetation types~~PFTs~~.~~ in all simulations. Besides, GPP of shaded leaves responds to eCO$_2$ stronger than ~~that~~ GPP of sunlit leaves for all C$_3$ ~~plants~~PFTs. This is because the ~~LAI-dependent scaling factor~~ portion of shaded leaves increase exponentially with increasing LAI~~,~~ (Fig. S9), leading to a rapid change of ~~GPP.~~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 ~~factors~~factor to eCO$_2$. For shaded leaves, the sensitivity of the LAI-dependent scaling factor contributes more to the magnitude and trend of $\beta_{\mathrm{GPP}_{sha}}$~~.~~ 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 ~~is~~during 1985-2006. And modelled LAI values in most CMIP5 models have been overestimated ~~in CMIP5 historical simulations compared with remote sensing LAI products~~according to satellite product (Anav et al., 2013). ~~Also, many~~Many global vegetation models ~~predict~~simulated increasing LAI trends globally in response to eCO$_2$~~.~~ during historical period (Zhu et al., 2016). Our modelling study also ~~show~~shows that LAI responds positively to eCO$_2$ for all C$_3$ ~~plants~~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 C$_3$ grasses did not show a significant change in LAI (Ainsworth ~~&~~and Long, 2005). ~~While some~~Some studies reported that LAI dynamics did not significantly change in specific FACE experiments, such as in a high-LAI deciduous broadleaf forest (Norby et al., 2003) and in a low-LAI evergreen broadleaf forest (Duursma et al., 2016). 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).

In this study, modelled ~~β effects at the canopy level~~nutrient-unlimited β_{GPP} and β_{NPP} values are higher than ~~those at the~~ leaf~~-level~~ photosynthetic responses for all C$_3$ ~~plants~~PFTs~~, whereas~~ 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 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).

~~In CABLE, the variation of the response of LAI to eCO$_2$ within a certain vegetation type is mainly dominated by environmental factors such as temperature, radiation and water. While for different vegetation types, diverse seasonal dynamics of leaf growth introduce additional variation.~~ The overall response of LAI to eCO$_2$ depends on several processes in this study: (1) NPP ~~increment~~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 prescribed in the model. First, ~~Insensitive~~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, we assume that allocation fractions are not affected by environmental conditions by fixing allocation coefficients in this study. However~~Second, diverse allocation schemes influence the responses of LAI for different PFTs. And, results 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 ~~et al.,~~and Long, 2005; De Kauwe et al., 2014). Tachiiri et al. (2012) also found SLA and ~~β~~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$_2$. ~~Finally~~Forth, in our results, LAI values for most C$_3$ ~~plants~~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 ~~in response to eCO$_2$~~under high CO$_2$ concentration (Fig. ~~S6~~S1a and Table. S1). That's why the sensitivity of LAI for evergreen broadleaf forest is low and thus leads to small relative GPP ~~and NPP~~ enhancements. If the preset LAI upper limits are narrowed, β ~~effects might~~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 eCO$_2$ (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 C$_3$ ~~plants~~PFTs in C-only simulation suggests carbon use efficiency (CUE) does not change with eCO$_2$, as autotrophic respiration is calculated from GPP and plant carbon. ~~The reduced~~In C-N and C-N-P simulations, magnitudes of ~~β_{cpool}~~ β_{NPP} for all C$_3$ PFTs except evergreen broadleaf forest all decline compared with those of β_{GPP} ~~and~~ , indicating CUE also decline with eCO$_2$ under nutrient limitations. However, FACE experimental results indicate that CUE values under eCO$_2$ 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., 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 C$_3$ PFTs in nutrient-coupled simulations as in C-only simulation, confirming the dominant role of LAI in regulating carbon cycle response under CO$_2$ 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 eCO$_2$ less sensitively due to the slow allocation and carbon turnover processes. A 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 CO$_2$ change (Friend et al., 2014). The response of soil carbon storage to eCO$_2$ also depends on ~~carbon turnover time (Harrison et al., 1993).~~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 eCO$_2$ in experiments, thereby altering carbon residence time in plants and soil (De 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 eCO_2. In our study, soil decomposition rate is assumed not to be affected by CO_2 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 eCO_2 increases turnover rate of~~ new~~ soil carbon (Van Groenigen et al., 2014; Van Groenigen et al., ~~2016~~2017). Within a certain ~~vegetation type~~PFT, the variation of β_{cpool} across different geographical locations is usually ~~not as large as~~smaller than that of β_{NPP}. ~~But~~While the ~~greatest~~greater variation of β_{cpool} ~~among~~than that of β_{NPP} across different C_3 ~~plants~~PFTs ~~compared with variations of β_{GPP} and β_{NPP}~~in C-only simulation suggests other processes such as different carbon allocation patterns, plant carbon turnover, and the soil carbon dynamics of various ~~vegetation types~~PFTs, are responsible for the ~~divergence.~~ additional divergence. In nutrient-coupled simulations, the variations of β_{cpool} across different C_3 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.

~~It should be noted that our study was designed to identify the key process that influences CO_2 fertilization effects without considering nitrogen and phosphorus interactions. β effects might be over-estimated by the neglect of nutrient limitations on plant growth (Hungate et al., 2003; Luo et al., 2004; Thornton et al., 2009). Uncertainty still exists in the response of ecosystem carbon dynamics to eCO_2 with nutrient interactions. Current terrestrial carbon-nitrogen cycle models cannot capture the response of NPP to eCO_2 in FACE experiments. They also disagree with each other on the responses of nitrogen-based GPP and NPP to eCO_2 because they have diverse mechanisms of C-N coupling (Zaehle et al., 2014).~~

4.3 Implication for understanding ~~the uncertainty of β values among~~β in other models

~~Our theoretical analysis of ~~Although we analyze a single land-surface model in detail, the patterns of and mechanisms underlying the variability of β ~~values at different levels within and across several plant functional types in CABLE model can offer insights into inter-modal variation of β values revealed by model intercomparison projects.~~ 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 important control of the absolute photosynthetic response to eCO_2 (Rogers et al., 2017). However, the relative photosynthetic responses for different ecosystems will converge to a small range because the normalized photosynthetic response to eCO_2 only depends on estimates of intercellular CO_2 concentration (C_i), Michaelis-Menten constants (K_c , K_o) and CO_2 compensation point ~~It can be inferred that normalized~~ (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 response. Water stress on plants is generally alleviated under eCO_2 due to reduced stomatal conductance (Leuzinger and Körner, 2007; Fatichi et al., 2016). 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 across wide range of environmental conditions, including water stress condition. 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 β ~~values would diverge~~response (Luo and Mooney, 1996). ~~little across different land surface models as long as they use Farquhar photosynthesis model with similar expressions for intercellular CO_2 concentration (C_i)~~ . 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.

~~Michaelis-Menten constants (K_c, K_o) and CO_2 compensation point in the absence of day respiration (Γ_*) (Luo et al., 1996; Luo &~~and ~~Mooney, 1996).~~ A recent study used 16 crop models to ~~predict~~simulate rice yield ~~in~~ at ~~response to eCO_2~~two FACE sites (Hasegawa et al., 2017). ~~They found~~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 ~~predictions~~estimations of leaf area. This is consistent with our conclusion ~~about the relative conservative character of leaf-level β. The high association between the response of LAI and response of yield among those models extends our conclusion about internal association between these two variables within a model, highlighting~~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.

~~Although we analyze a single land-surface model in detail, we suspect our top-level conclusions will be generally applicable. We therefore invite other land-surface modelling groups to similarly analyze their model estimates of β at different hierarchical levels across different geographical locations and vegetation types as we did, and focus more on contributions from change in leaf-level photosynthesis, changes in leaf area index and changes in land carbon residence times.~~

5. Conclusions

Exploring the variability of β ~~effects~~ at different hierarchical levels within and across different ~~plant~~C$_3$ ~~types~~PFTs helps ~~reveal~~unravel model mechanisms that govern terrestrial ecosystem responses to elevated CO$_2$. Our study ~~using the CABLE model~~ shows that the sensitivities of ~~biochemical~~biochemistry and leaf-level photosynthesis to eCO$_2$ are very similar within and ~~among~~across C$_3$ ~~plants~~PFTs in C-only, C-N and C-N-P simulations of CABLE, in accordance with previous theoretical analysis. While β ~~values~~values of GPP, NPP and ecosystem carbon storage diverge primarily because the sensitivities of LAI ~~to eCO$_2$~~ significantly differ within and across different ~~vegetation types~~PFTs in all simulations. After decomposing β ~~values of sunlit and shaded leaf GPP~~ into β ~~of leaf-level~~photosynthetic and LAI components, we find LAI contributes more than photosynthesis ~~and the LAI-dependent leaf-to-canopy scaling factor, we find the latter to be the most important cause of the~~

~~divergence~~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 ~~response~~responses of ecosystem carbon cycle ~~to eCO$_2$~~processes to changes in CO$_2$ and climate.

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~~**Table 1 Coefficients of variation of $\mathcal{L}$, $\mathrm{d}C_i/\mathrm{d}C_a$, β_p, β_{LAI}**~~

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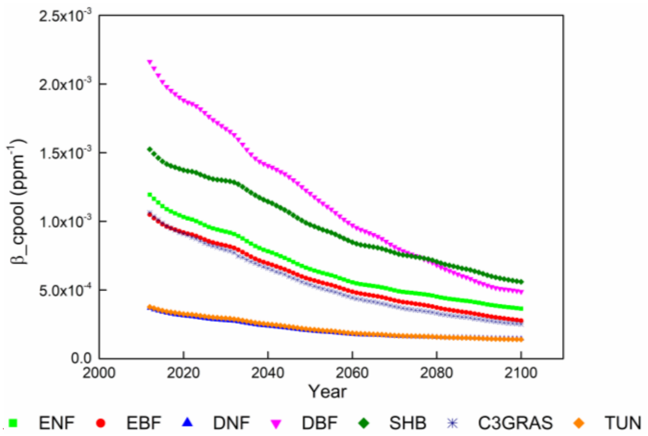
Table 1. The ratio of intercellular CO_2 concentration (C_i) to atmospheric CO_2 concentration (C_a) for different C_3 PFTs, mean and coefficient of variation (CV) across these PFTs of C_i/C_a in C-only, C-N, C-N-P simulations of CABLE under RCP8.5 scenario. Values for shaded leaves are in brackets. 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 C_3 ~~vegetation type~~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	~~ENF~~CV($\mathcal{L}$) sunlit(shaded)	CV(β_p)~~EBF~~ sunlit(shaded)	~~DNF~~CV(β_{GPP})	~~DBF~~CV(β_{NPP})	~~SHB~~CV(β_{cpool})
~~CV($\mathcal{L}$)~~ENF	0.~~25~~27(0.30)	0.~~27~~41(0.~~29~~4	~~0.25(0.27)~~1.7	~~0.39(0.39)~~2.6	~~0.33(0.33)~~1.4
~~CV(dC_i/dC_a)~~EBF	0.~~21~~26(0.~~16~~29)	0.~~09~~24(0.~~07~~2	0.~~1(0.09)~~ 55	0.~~14(0.11)~~ 54	0.~~08(0.28)~~60
DNF~~CV(β_p)~~	0.~~47~~26(0.~~36~~28)	0.25(0.~~29~~28)	~~0.27(0.26)~~1.1	~~0.44(0.37)~~1.2	0.~~33(0.41)~~30
~~CV(β_{LAI})~~DBF	~~3.21~~0.39(0.38)	~~1.43~~0.42(0.37	1.~~15~~29	1.~~49~~42	~~1.56~~0.85
~~CV(β_{GPP})~~SHB	~~2.73~~0.33(0.32)	0.~~43~~30(0.49)	1.~~22~~24	1.~~27~~23	1.~~14~~12
~~CV(β_{NPP})~~ C3GRA	0.38(0.34)	0.~~96~~35(0.34)	1.~~41~~12	1.~~30~~10	0.98~~1.11~~
~~CV(β_{cpool})~~TUN	~~1.28~~0.35(0.34)	0.36(0.37)	~~0.80~~1.86	1.85	1.92


2.5×10^{-3}
2.0×10^{-3}
1.5×10^{-3}
1.0×10^{-3}
5.0×10^{-4}
0.0
β_cpool (ppm^{-1})
2000
2020
2040
2060
2080
2100
Year
ENF
EBF
DNF
DBF
SHB
C3GRAS
TUN

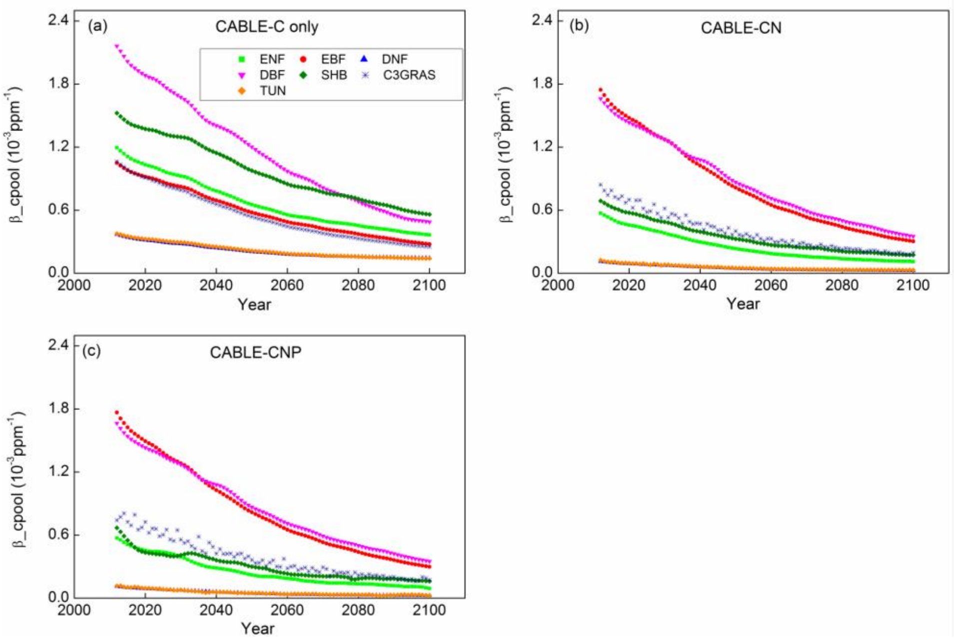
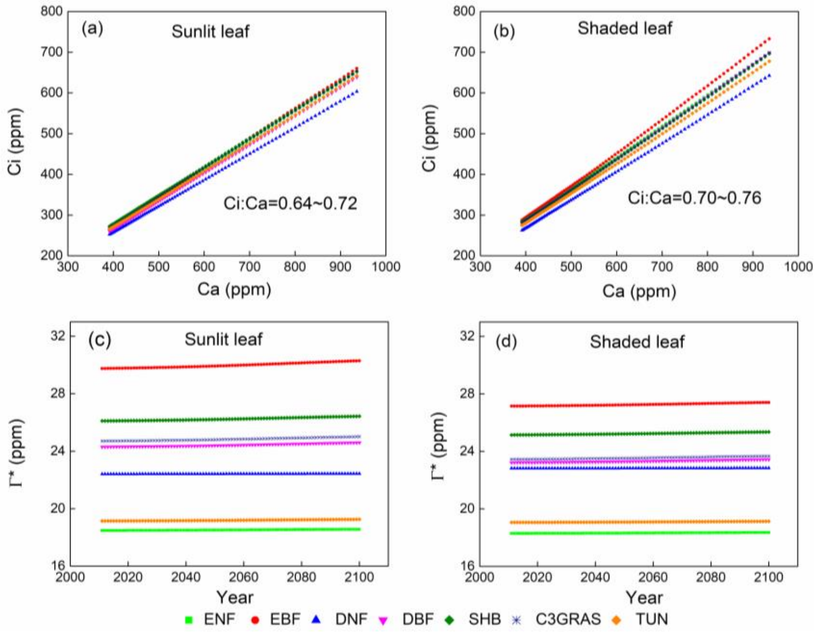


Figure 1. Temporal trends of β_{cpool} from 2011 to 2100 for C_3 ~~plants~~PFTs ~~in~~from CABLE-C only (a), CABLE-CN (b), and CABLE-CNP (c) simulations. β_{cpool} values for different C_3 ~~plants~~PFTs all decline with time from 2011 to 2100 under RCP8.5 scenario, but the magnitudes of β_{cpool} differ 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 ~~Needle leaf~~Needleleaf Forest (light green ~~square~~squares); EBF, Evergreen ~~Broad leaf~~Broadleaf Forest (red ~~circle~~circles); DNF, Deciduous ~~Needle leaf~~Needleleaf Forest (dark blue ~~triangle~~triangles); DBF, Deciduous ~~Broad leaf~~Broadleaf Forest (pink ~~triangle~~triangles); SHB, Shrub (dark green ~~diamond~~diamonds); C3GRAS, C_3 grass (dark blue ~~star~~stars); TUN, tundra (orange ~~diamond).~~diamonds).


(a)
Sunlit leaf
Ci (ppm)
Ca (ppm)
Ci:Ca=0.64~0.72
800
700
600
500
400
300
200
300
400
500
600
700
800
900
1000
(b)
Shaded leaf
Ci (ppm)
Ca (ppm)
Ci:Ca=0.70~0.76
(c)
Sunlit leaf
Γ* (ppm)
Year
32
28
24
20
16
2000
2020
2040
2060
2080
2100
(d)
Shaded leaf
Γ* (ppm)
Year
ENF
EBF
DNF
DBF
SHB
C3GRAS
TUN

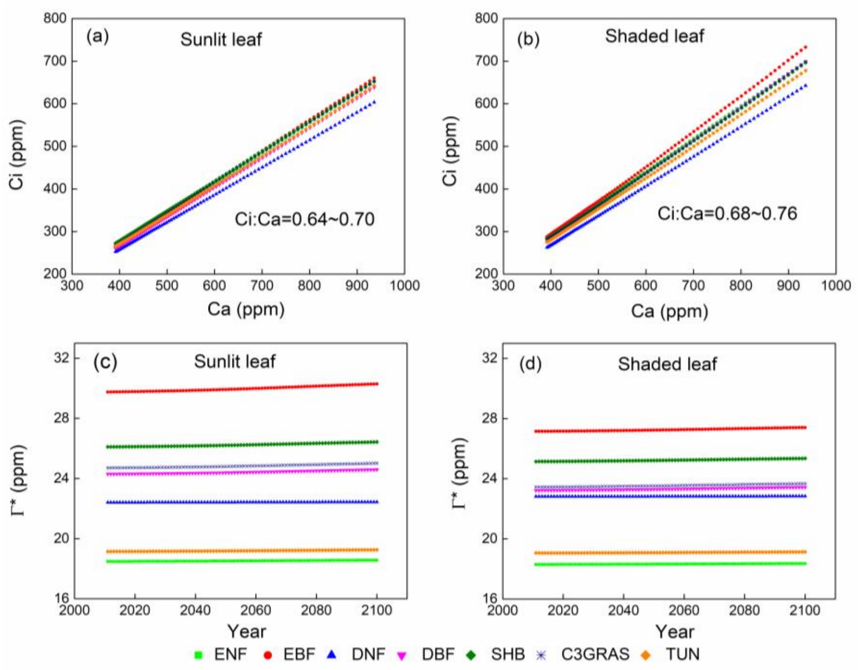
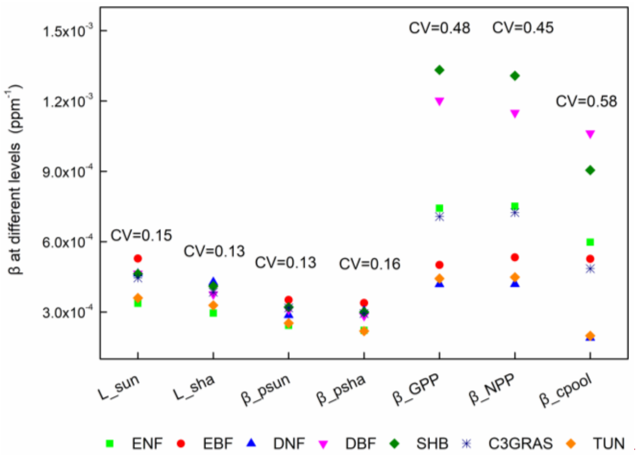


Figure 2~~.~~. Responses of yearly intercellular CO_2 concentration (C_i) to eCO_2 of a single sunlit leaf (a) and shaded leaf (b) for C_3 ~~plants~~PFTs~~.~~ from CABLE-C only simulation. Temporal trends of CO_2 compensation point in the absence of day respiration (Γ_*) for sunlit leaf (c) and shaded leaf (d) from 2011 to 2100 ~~in~~from CABLE~~.~~-C only simulation. The ~~ratios~~ratio of C_i to C_a (C_i/C_a) ~~are~~is approximately ~~constants~~constant with eCO_2 for each ~~vegetation type~~PFT and ~~vary~~varies little ~~between~~across ~~vegetation types~~PFTs. Γ_* values vary across ~~global~~different ~~vegetation types~~PFTs, but do not change over~~through~~ time for each ~~vegetation type~~PFT. Abbreviations and symbols are the same as Figure 1.


β at different levels (ppm^{-1})
1.5x10^{-3}
1.2x10^{-3}
9.0x10^{-4}
6.0x10^{-4}
3.0x10^{-4}
CV=0.15
CV=0.13
CV=0.13
CV=0.16
CV=0.48
CV=0.45
CV=0.58
L_sun
L_sha
β_psun
β_psha
β_GPP
β_NPP
β_cpool
ENF
EBF
DNF
DBF
SHB
C3GRAS
TUN

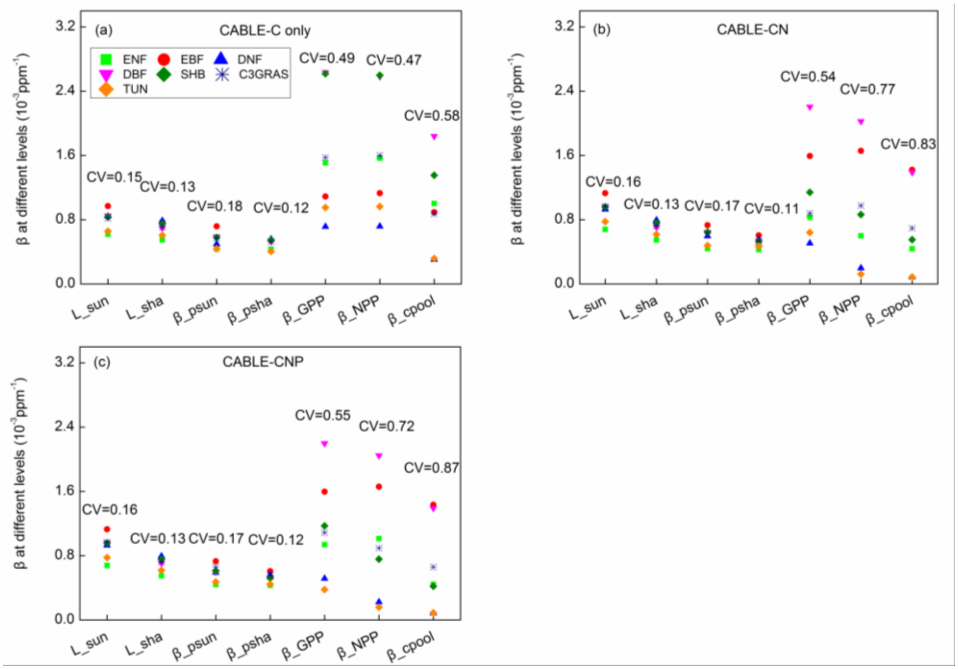
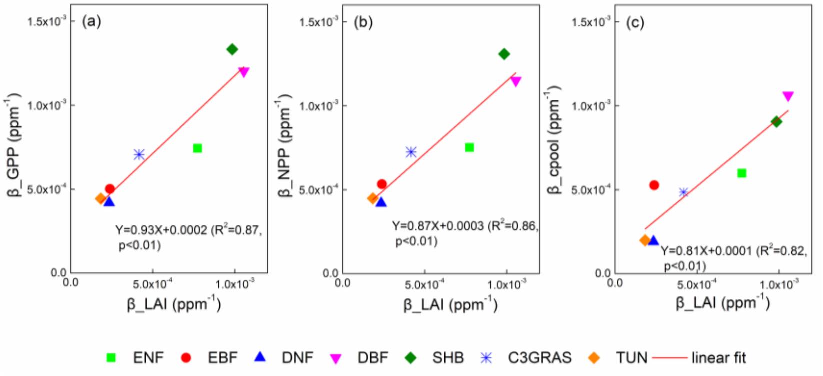


Figure 3~~-~~. Biome-level β ~~values~~values at different levels ~~for various C₃ plants~~ at the year ~~2056 in~~2023 from CABLE~~.~~-C only (a), CABLE-CN (b), and CABLE-CNP (c) simulations. CV means coefficient of variation ~~among~~of biome-level β across C₃ ~~plants~~PFTs. β ~~values~~values at biochemical ($\mathcal{L}_{sun}$ and $\mathcal{L}_{sha}$ for sunlit and shaded leaves) and leaf~~-level~~ levels ($\beta_{p_{sun}}$ and $\beta_{p_{sun}}$) are very similar ~~among~~across ~~vegetation types~~PFTs, but greatly diverge at ~~GPP, NPP~~canopy level (β_{GPP}), and ecosystem ~~carbon storage level.~~levels (β_{NPP} and β_{cpool}) in all simulations. Unlike in 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.


(a)
(b)
(c)
β_GPP (ppm^{-1})
β_NPP (ppm^{-1})
β_cpool (ppm^{-1})
β_LAI (ppm^{-1})
0.0
5.0x10^{-4}
1.0x10^{-3}
1.5x10^{-3}
Y=0.93X+0.0002 (R^2=0.87, p<0.01)
Y=0.87X+0.0003 (R^2=0.86, p<0.01)
Y=0.81X+0.0001 (R^2=0.82, p<0.01)
ENF
EBF
DNF
DBF
SHB
C3GRAS
TUN
linear fit

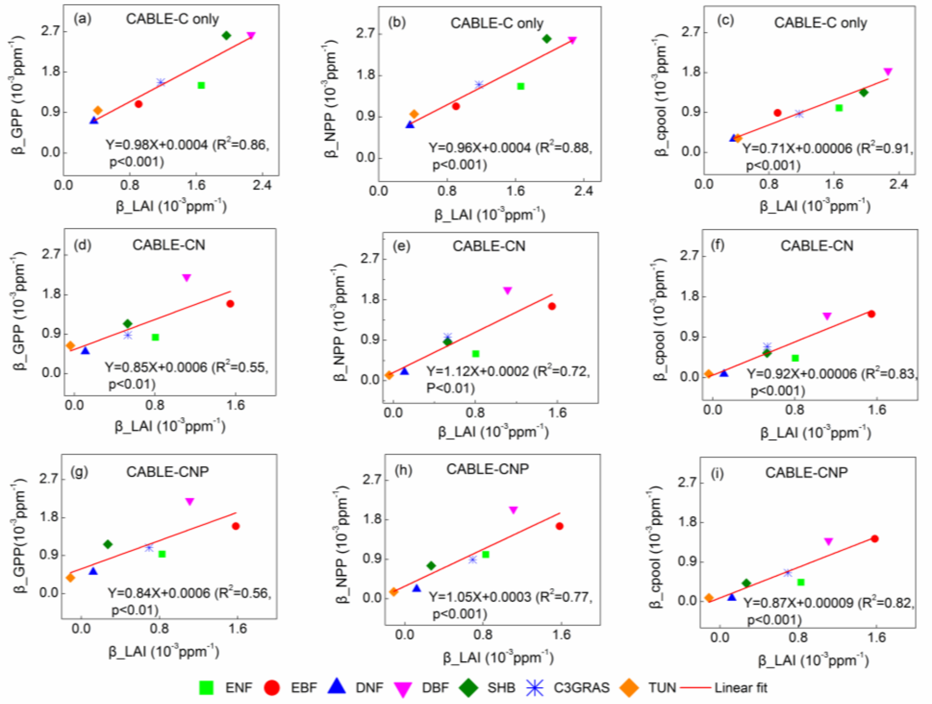


Figure 4. Correlations between β_{GPP} and β_{LAI} ~~(a),~~, β_{NPP} and β_{LAI} ~~(b),~~, β_{cpool} and β_{LAI} ~~(c)~~ at the year ~~2056 among~~2023 across C$_3$ ~~plants~~PFTs ~~in~~from CABLE C-only (a)~(c), CABLE-CN (d)~(f) and CABLE-CNP (g)~(i) simulations. β_{GPP}, β_{NPP} and β_{cpool} all have significant linear correlations with β_{LAI} ~~but with different slopes.~~in all simulations. Abbreviations and symbols are the same as Figure 1.

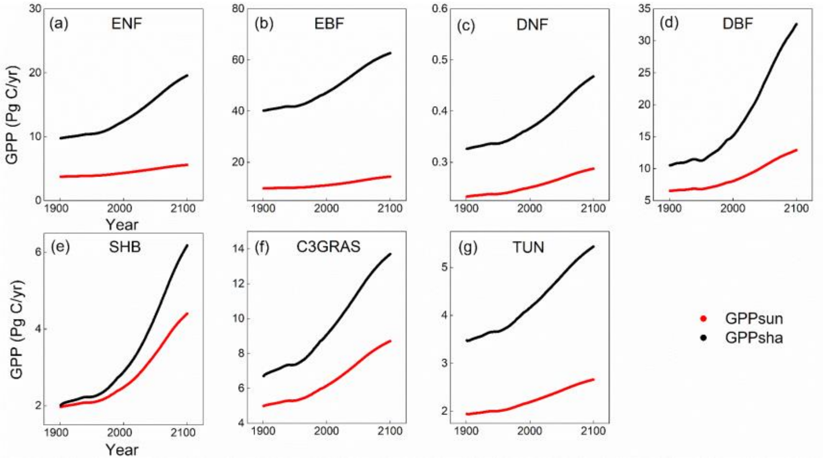


Figure 5. Temporal trends of GPP_{sun} (red ~~point~~points) and GPP_{sha} (black ~~point~~points) for C$_3$ ~~plants~~PFTs from 1901 to 2100 ~~in~~from CABLE C-only simulation. GPP_{sha} is higher than GPP_{sun} for ~~almost~~ all ~~vegetation types~~PFTs. With significant increase of CO$_2$ concentration from 2011, GPP_{sha} responds more drastically than GPP_{sun}.

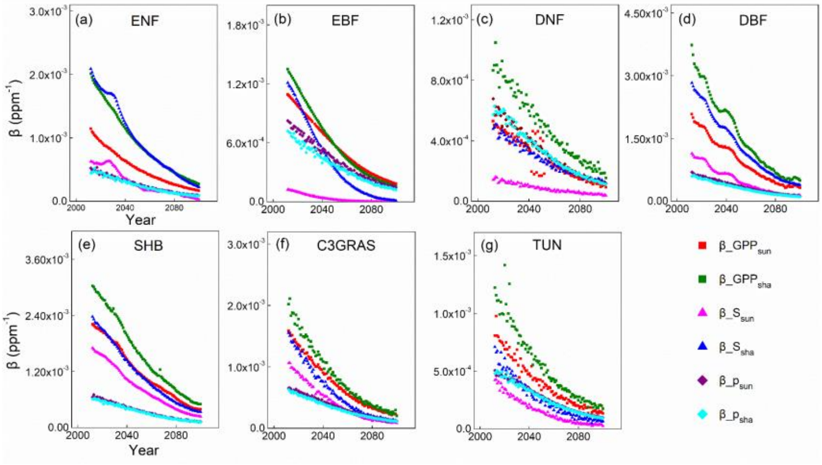


Figure 6. Temporal trends of $\beta_{\mathrm{GPP}_{sun}}$ ~~(~~(sensitivity of sunlit leaf GPP; red ~~square~~squares), $\beta_{\mathrm{GPP}_{sha}}$ ~~(~~(sensitivity of shaded leaf GPP; green ~~square~~squares), $\beta_{S_{sun}}$ ~~(~~(sensitivity of scaling fatcor for sunlit leaf; pink ~~triangle~~triangles), $\beta_{S_{sha}}$ ~~(~~(sensitivity of scaling fatcor for shaded leaf; dark blue ~~triangle~~triangles), $\beta_{p_{sun}}$ ~~(~~(photosynthetic response for sunlit leaf; purple ~~diamond~~diamonds) and $\beta_{p_{sha}}$ ~~(~~(photosynthetic response for shaded leaf; sky blue ~~diamond~~diamonds) for C_3 ~~plants~~PFTs ~~in~~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 $\beta_{\mathrm{GPP}_{sha}}$ for almost all ~~vegetation types~~PFTs.