

**General comment to the reviewer:** We greatly appreciate the constructive and thorough comments of this reviewer. We believe that these comments have led to improvements of our manuscript. We first repeat the comments of this reviewer before we detail our responses. The original comments of the reviewer are highlighted in red and our responses are in black. When text is copied directly from the revised paper the words are italicized.

**Comment 1:** The study uses two temperature functions to represent uncertainty of the temperature response of these parameters. TRF1 includes thermal acclimation of photosynthesis while TRF2 does not. There is a potential problem with using TRF2 as currently parameterized, as the optimum temperatures for  $V_{cmax}$  and  $J_{max}$  do not vary in space on these simulations but we know they do in reality, therefore the assumption is that all C3 plants in the world are represented with the same temperature optimum for  $V_{cmax}$  and  $J_{max}$ . How representative and valid are these values for cold adapted plants? Possibly, this has implications for some of the conclusions of the paper when taking the difference between simulations with and without acclimation under both future and present day conditions. You could still have a simulation without thermal acclimation of photosynthesis, that accounts for special variability of  $T_{opt}$  of  $V_{cmax}$  and  $J_{max}$  (Kattge and Knorr, 2007, show the data, Medlyn et al 2002 as well). I think the authors ought to check /demonstrate whether this assumption (having a constant temperature optimum of  $V_{cmax}$  and  $J_{max}$  on their non-acclimated temperature function) for has implications for their main conclusions.

**RESPONSE:** We appreciate this comment of the reviewer. He/she is correct in pointing out that TRF2 may not capture adequately “reality” by not accounting for thermal acclimation. That is one of the reasons why our model includes TRF1, which did account for thermal acclimations. In this work, we incorporated TRF2 because some Earth System Models do still not account for temperature acclimation. Hence, in our paper we list the corresponding values of the parameters of LUNA model for such type of Earth system models.

Furthermore, we feel that the comparison of TRF1 and TRF2 will help us analyze and quantify the impact of non-acclimation on our modeling results. Our results demonstrate that the two functions (TRF1 and TRF2) give similar results in almost all cases. Consequently, the main conclusion of our paper still holds, yet, some differences are observed in the values of  $V_{c,max25}$  and the photosynthetic rate response to temperature. To better demonstrate how TRF2 impacts our results, we have modified the discussion section of our manuscript as follows (bold sentences highlight specifically the deficiency of TRF2).

Section 4.2 paragraph 1:

*“Our model predicts that higher temperatures generally lead to lower values of  $V_{c,max25}$  and  $J_{max25}$  (Fig. 3a, c). As temperature increases, the nitrogen use efficiencies of  $V_{c,max}$  and  $J_{max}$  also increase and thus plants need a lower amount of nitrogen allocated for carboxylation and electron transport. This is true for all the sites except for  $V_{c,max25}$  in the hotter regions when TRF2 was used (Fig. S9a). The reason is because LUNA model will use a higher increase in*

night-time temperature (e.g., 22 to 30°C) than daytime temperature (e.g., from 31 to 33°C) , because the daytime temperature is constrained by the maximum temperature for optimization in TRF2 (i.e., 33°C). To maximize the net photosynthetic carbon gain, the model predicts a higher proportion of nitrogen allocated to carboxylation to compensate for a higher nighttime respiration rate. Therefore, the LUNA model predicts a higher value of  $V_{c,max25}$ . **Yet, this may result from the deficiency of TRF2 by not considering thermal acclimation under future global warming (Lombardozzi et al., 2015).**”

.

Section 4.2 paragraph 2:

“ If we do not account for the potential acclimation of  $V_{c,max25}$  and  $J_{max25}$  under future climate conditions as predicted by the LUNA model, our analysis indicates that *ESM predictions of future global photosynthesis at the uppermost leaf layer will likely be overestimated by as much as 10-16% if  $V_{c,max25}$  and  $J_{max25}$  are held fixed (Fig. 7). **The higher overestimation for TRF2 (16.3%) than TRF1 (10.1%) could result from the fact that TRF2 does not account for future thermal acclimation and thus the LUNA model predicts a large nitrogen allocation acclimation for future climate change.** In both cases, our results suggest that, to reliably predict global plant responses to future climate change, *ESMs should incorporate models that use environmental control on  $V_{c,max25}$  and  $J_{max25}$ . It has been recently suggested that nitrogen-related factors are not well represented in *ESMs (Houlton et al., 2015; Wieder et al., 2015). Our nitrogen partitioning scheme would help alleviate biases into the predictions of future photosynthetic rates, and also climate processes that are dependent on these predictions (Bonan et al., 2011; Knorr and Kattge, 2005; Rogers, 2014).* ”**

**Comment 2:** There are other studies trying to do the same as this paper is doing, but based on empirical relationships (Verheijen et al 2013, Biogeosciences), between environmental drivers and  $V_{c,max}$  and  $J_{max}$  at 25C, deriving relationships for each pft. The authors should acknowledge this type of work, which has also been used to extrapolate under future conditions (Verheijen et al 2015, GCB).

**RESPONSE:** We appreciate this comment of the reviewer. We have revised the paper to read on as follows:

“...There are many different ways to incorporate environmental controls on  $V_{c,max25}$  and  $J_{max25}$ . One simple approach is to use empirical statistical models between environmental variables and  $V_{c,max25}$  and  $J_{max25}$  (e.g. Ali et al., 2015; Verheijen et al., 2013), which has been shown to improve the model simulations (Verheijen et al., 2015). One key limitation of such models is that they may have risk of inaccurate extrapolation under novel future climate conditions. The optimization model such as LUNA could be more reliable in their predictions under novel future climate

*conditions as they account for the key assumptions that could be robust under different environmental conditions.*”

Comment 3: Missed paper on your references, Maire et al 2015, Global Ecol. Biogeog. See comments on soil pH, worth to include this on your limitations. The discussion on model limitations could also include the fact that there is inherent intraspecific variation of photosynthetic capacity (See Moran et al. 2015, GCB).

**RESPONSE:** We have now incorporated the above references in the model limitation section of our revised paper. For instance, the first two paragraphs in section 4.1 as follows (bolded sentences):

“...These results suggest that our model is able to capture many of the key components of the drivers for  $V_{c,max25}$  and  $J_{max25}$  across the globe both in space as well as in time. The remaining portion of uncertainty that cannot be explained by our *LUNA* model could be related to variability within the 125 species considered in this study. ***There are inherent intraspecific variations in leaf traits (Valladares et al., 2000) and in photosynthetic capacity (Moran et al., 2015).*** Data availability limited the number of species that can be considered and favored a universal *LUNA* model as separate species normally did not cover a sufficiently large range of environmental conditions. Yet, we should be able to fit our model to specific PFTs when additional data become available with a large enough coverage of environmental conditions. We expect that such a model would be able to describe and capture adequately a larger portion of the variability observed in  $V_{c,max25}$  and  $J_{max25}$ .

Unexplored nutrient limitations and other plant physiological properties could also play a factor in the limitation of our model. For example, the nitrogen use efficiency of tropical plants (typically modest to low nitrogen) can be diminished by low phosphorus (Cernusak et al., 2010; Reich and Oleksyn, 2004), suggesting that our model could be improved by considering multiple nutrient limitations (Goll et al., 2012; Walker et al., 2014; Wang et al., 2010). Our treatment of photosynthetic capacity could also be improved by incorporating species-specific mesophyll and stomatal conductance (Medlyn et al., 2011), by analyzing leaf properties such as leaf life span (Wright et al., 2004), or ***by considering soil nutrient, soil water availability, and soil pH (Maire et al., 2015).***”

Comment 4: There are a lot more papers out using optimization now, perhaps you should cite them too.

**RESPONSE:** We agree with the reviewer and have modified the text in the revised paper to discuss this at end of section 4.2 as follows:

“...By far, the optimality approaches have been used to predict many different plant structures and functions under different environmental conditions such as carbon allocations (Franklin et al., 2012), leaf C:N (Thomas and Williams, 2014), root distribution (McMurtrie et al., 2012), and stomata conductance (Cowan and Farquhar, 1977). For the photosynthetic capacity optimization, Haxeltine and Prentice (1996) has used an optimization approach to predict  $V_{c,max25}$  based on the trade-off between photosynthesis and respiration, which has been incorporated into land surface models including LPJ-GUESS (Smith et al., 2001) and LPJmL (Sitch et al., 2003). Both *LUNA* model and the model of Haxeltine and Prentice (1996) considered the  $V_{c,max25}$  component and respiration; however, *LUNA* model is currently only

*designed for the leaf level while model of Haxeltine and Prentice (1996) is applicable for both the leaf and canopy level. The key improvements of LUNA model include the explicit considerations of other important processes such as light capture and electron transport and 2) the evaluations against global datasets under different environmental conditions”.*

**Comment 5:** Page 6221, line 15, replace ‘need’ with ‘needs’

**RESPONSE:** We have replaced “need” with “needs” now.

**Comment 6:** Page 6222, lines 21-22 replace ‘Optimal approaches are an important tool of land surface models’, with Optimal approaches are an important tool for land surface models. Page 6224, lines 7-8 & 14 no need to repeat references on line 8 when already given in line 7 Page 6224, define MCMC.

**RESPONSE:** On page 6222, lines 21-22, we have replaced “Optimal approaches are an important tool of land surface models” with “Optimality approaches are important tools for land surface models”. We have eliminated the references in lines 8 and 14 on page 6224. Also, we now spell out MCMC as Markov Chain Monte Carlo in the revised paper.

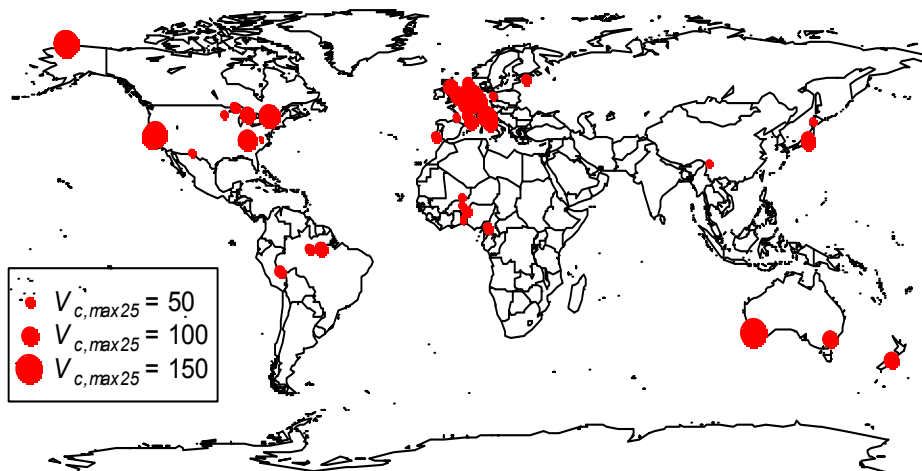
**Comment 7:** Although you do not specify pfts on your model, it would be good to give an idea to the reader (most probably a modeler) of the geographical distribution of your data set (used to calibrate your model) in terms of plant functional types.

**RESPONSE:** We have now incorporated a map of data distribution in the supplementary file and it is now referenced in the data section as follows:

*“...The data include evergreen and deciduous species from arctic, boreal, temperate and tropical areas measured different times of the season and different canopy locations (Fig. S2).”*

See the figure below:

**Fig . S2** *The spatial distribution map of data used for parameter estimation in LUNA model*



**Comment 8:** Parameter estimation and evaluation is done with same data set. Please comment on implications of this. I wonder if you could fit the model with a portion of the data, then use your LUNA to predict  $V_{c,max}$  and  $J_{max}$  and then evaluate the goodness of the model.

**Response:** We agree with the reviewer that it is a good idea to use a subset of data for parameter estimation and another subset of data for evaluation of the goodness of fit of the model. In this study, our focus was to develop a mechanistic model of photosynthetic capacity for the globe and so we did not use subsets of data for parameter estimation and model evaluation in view that we have a limited number of data points across the globe. It would be challenge to randomly select a large subset of data for model evaluation. For the case of small subset, we expect that it should not be much different from the model fitting we currently have as it will be mainly based on a large portion of the data. In a new project, we are collecting independent data from the tropics and it would be great independent test against LUNA model. We hope to publish the new paper soon.

**Comment 9:** Section 2.6 is model sensitivity analysis. Then on p 6227 another sensitivity is mentioned, is this the same?, why to have it twice, confusing and repetitive

**RESPONSE:** Thank you very much for pointing this out. The section 2.6 sensitivity analysis is for the fitted model using fitted parameter and mean environmental conditions from the data. It is only for one specific environmental condition under current climate condition. The sensitivity analysis on p6227 is for the whole globe to assess which variable change in the future are responsible for the change in  $V_{c,max}$  and  $J_{max}$  and the environmental condition change could be different for different locations across the globe. To clarify this, we have improved the statement on p6227 as follows:

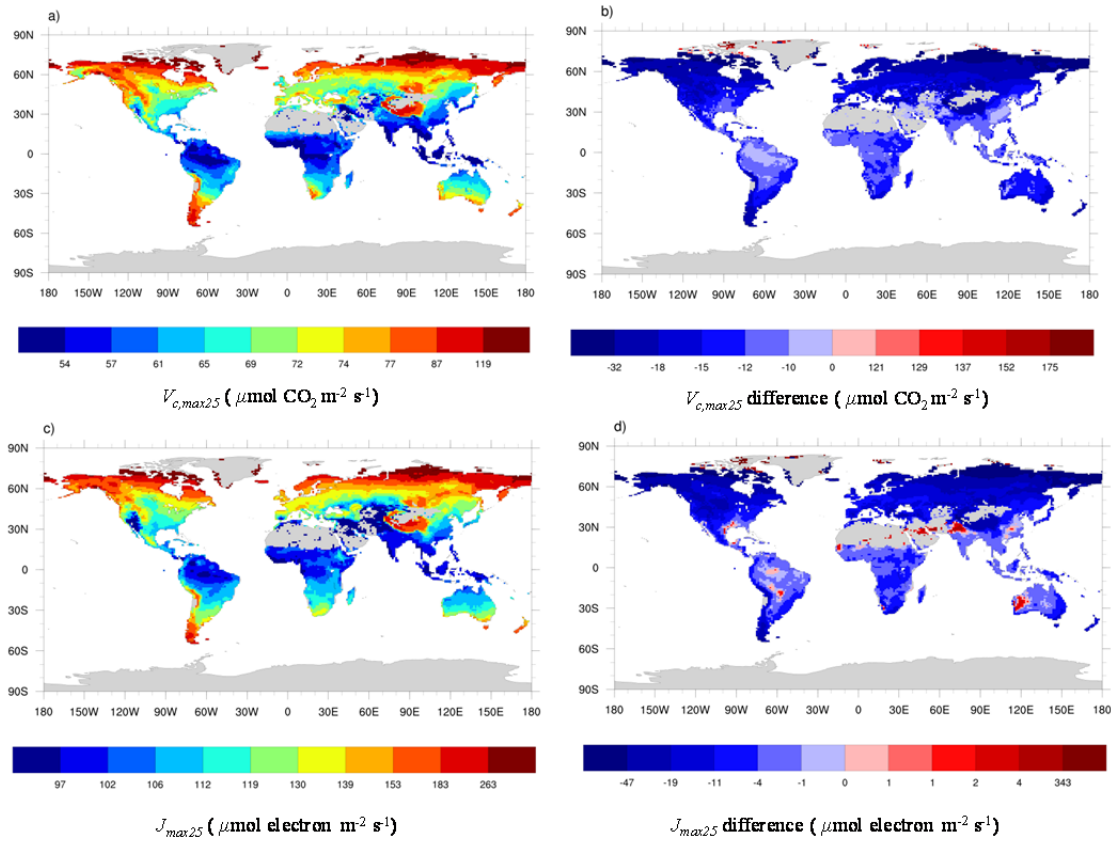
*“...In order to identify the importance of changes in different climate variables (temperature, CO<sub>2</sub>, radiation and relative humidity) to modeled changes in  $V_{c,max25}$  and  $J_{max25}$  in the future, we conducted a third sensitivity analysis to investigate the impact of changes in climate variables on model results. In contrast to the previous two sensitivity analyses that based on the mean current climate conditions, the purpose of the third sensitivity analysis was to explore the global pattern in sensitivity of  $V_{c,max25}$  and  $J_{max25}$  to changes in climate variables across different biomes of the globe in the future”.*

**Comment 10:** Fig 4 & 5, very poor color scale as it does not show much of the variation on key ecosystems.

**RESPONSE:** We have now improved the color scale of Figures 4 as follows:

**Figure 4** Summer season photosynthetic capacity for the top leaf layer in the canopy ( $V_{c,max25}$ ;  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (a),  $J_{max25}$ ;  $\mu\text{mol electron m}^{-2} \text{ s}^{-1}$  (c)) under historical climatic conditions and the difference in either  $V_{c,max25}$  (b) or  $J_{max25}$  (d) due to changed climatic conditions. Difference in the photosynthetic capacity was calculated as that under future climate minus that under historical climate. Ten-year monthly averages of climatic conditions for the past (1995 – 2004) and the future (2090-2099) were used to drive the model. The model was run by using TRF1, which was

a temperature response function that considered the potential for acclimation to growth temperature.



Following Fig. 4, we also changed the color legends in Fig S6 (or Fig. S8 in revised manuscript) correspondingly.

For Fig. 5, because we want to have on common legend for all panels in order to compare the sensitivities of different climate variables, it would be challenging to make each panel show the range of major ecosystems if their changes are small. Therefore, we keep it as it is.

**Comment 10:** Fig 5, is this the + or the minus 15% sensitivity?, not clear in the Fig caption

**RESPONSE:** No, it is not based on 15% change. The sensitivity analysis is conducted by changing the environmental variable using 10-year monthly averages of climatic conditions for the past (1995-2004) versus the future (2090-2099). For clarification, we have modified the captions of Fig. 5 and 6 as follows:

“...The sensitivity analysis is conducted by changing the value of individual environmental variable using 10-year monthly averages of climatic conditions for the past (1995-2004) versus the future (2090-2099) for each individual grid across the globe.”

**Comment 11:** P 6229., Lines 25-26 replace ‘.It also well captured ..’ with It also captured well ‘

**RESPONSE:** We have changed the statement to “it also captured well”

**Comment 12:** P 6232, L10, you mean high growing season temperatures?, add word ‘season’

**RESPONSE:** We have improved to statement to reflect “high growing season temperatures”



## References

- Ali, A. A., Xu, C., Rogers, A., McDowell, N. G., Medlyn, B. E., Fisher, R. A., Wullschlegel, S. D., Reich, P. B., Vrugt, J. A., Bauerle, W. L., Santiago, L. S., and Wilson, C. J.: Global scale environmental control of plant photosynthetic capacity, *Ecological Applications*, doi: 10.1890/14-2111.1, 2015. 2015.
- Bonan, G. B., Lawrence, P. J., Oleson, K. W., Levis, S., Jung, M., Reichstein, M., Lawrence, D. M., and Swenson, S. C.: Improving canopy processes in the community land model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data, *Journal of Geophysical Research*, 116, 1-22, 2011.
- Cernusak, L. A., Winter, K., and Turner, B. L.: Leaf nitrogen to phosphorus ratios of tropical trees: experimental assessment of physiological and environmental controls, *New Phytologist*, 185, 770-779, 2010.
- Cowan, I. and Farquhar, G.: Stomatal function in relation to leaf metabolism and environment, 1977, 471-505.
- Franklin, O., Johansson, J., Dewar, R. C., Dieckmann, U., McMurtrie, R. E., Brännström, Å., and Dybzinski, R.: Modeling carbon allocation in trees: a search for principles, *Tree Physiology*, 32, 648-666, 2012.
- Goll, D. S., Brovkin, V., Parida, B. R., Reick, C. H., Kattge, J., Reich, P. B., van Bodegom, P. M., and Niinemets, U.: Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling, *Biogeosciences*, 9, 3547-3569, 2012.
- Haxeltine, A. and Prentice, I. C.: A general model for the light-use efficiency of primary production, *Functional Ecology*, 10, 551-561, 1996.
- Houlton, B. Z., Marklein, A. R., and Bai, E.: Representation of nitrogen in climate change forecasts, *Nature Clim. Change*, 5, 398-401, 2015.
- Knorr, W. and Kattge, J.: Inversion of terrestrial ecosystem model parameter values against eddy covariance measurements by Monte Carlo sampling, *Global Change Biology*, 11, 1333-1351, 2005.
- Lombardozzi, D. L., Bonan, G. B., Smith, N. G., Dukes, J. S., and Fisher, R. A.: Temperature acclimation of photosynthesis and respiration: A key uncertainty in the carbon cycle-climate feedback, *Geophysical Research Letters*, 42, 8624-8631, 2015.
- Maire, V., Wright, I. J., Prentice, I. C., Batjes, N. H., Bhaskar, R., van Bodegom, P. M., Cornwell, W. K., Ellsworth, D., Niinemets, Ü., Ordonez, A., Reich, P. B., and Santiago, L. S.: Global effects of soil and climate on leaf photosynthetic traits and rates, *Global Ecology and Biogeography*, 24, 706-717, 2015.
- McMurtrie, R. E., Iversen, C. M., Dewar, R. C., Medlyn, B. E., Näsholm, T., Pepper, D. A., and Norby, R. J.: Plant root distributions and nitrogen uptake predicted by a hypothesis of optimal root foraging, *Ecology and Evolution*, 2, 1235-1250, 2012.
- Medlyn, B. E., Duursma, R. A., Eamus, D., Ellsworth, D. A., Prentice, I. C., Barton, C. V. M., Crous, K. Y., De Angelis, P., Freeman, M., and Wingate, L.: Reconciling the optimal and empirical approaches to modelling stomatal conductance, *Global Change Biology*, 10, 1365-2486, 2011.
- Moran, E. V., Hartig, F., and Bell, D. M.: Intraspecific trait variation across scales: implications for understanding global change responses, *Global Change Biology*, doi: 10.1111/gcb.13000, 2015. n/a-n/a, 2015.
- Reich, P. B. and Oleksyn, J.: Global patterns of plant leaf N and P in relation to temperature and latitude, *PNAS*, 101, 11001-11006, 2004.
- Rogers, A.: The use and misuse of  $V_{c,max}$  in earth system models, *Photosynthesis Research*, 119, 1-15, 2014.
- Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., and Venevsky, S.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Global Change Biology*, 9, 161-185, 2003.



Smith, B., Prentice, I. C., and Sykes, M. T.: Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space, *Global Ecology and Biogeography*, 10, 621-637, 2001.

Thomas, R. Q. and Williams, M.: A model using marginal efficiency of investment to analyze carbon and nitrogen interactions in terrestrial ecosystems (ACONITE Version 1), *Geosci. Model Dev.*, 7, 2015-2037, 2014.

Valladares, F., Wright, S. J., Lasso, E., Kitajima, K., and Pearcy, R. W.: PLASTIC PHENOTYPIC RESPONSE TO LIGHT OF 16 CONGENERIC SHRUBS FROM A PANAMANIAN RAINFOREST, *Ecology*, 81, 1925-1936, 2000.

Verheijen, L. M., Aerts, R., Brovkin, V., Cavender-Bares, J., Cornelissen, J. H. C., Kattge, J., and van Bodegom, P. M.: Inclusion of ecologically based trait variation in plant functional types reduces the projected land carbon sink in an earth system model, *Global Change Biology*, 21, 3074-3086, 2015.

Verheijen, L. M., Brovkin, V., Aerts, R., Bönisch, G., Cornelissen, J. H. C., Kattge, J., Reich, P. B., Wright, I. J., and van Bodegom, P. M.: Impacts of trait variation through observed trait–climate relationships on performance of an Earth system model: a conceptual analysis, *Biogeosciences*, 10, 5497-5515, 2013.

Walker, A. P., Beckerman, A. P., Gu, L., Kattge, J., Cernusak, L. A., Domingues, T. F., Scales, J. C., Wohlfahrt, G., Wullschlegel, S. D., and Woodward, F. I.: The relationship of leaf photosynthetic traits –  $V_{cmax}$  and  $J_{max}$  – to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study, *Ecology and Evolution*, 4, 3218-3235, 2014.

Wang, Y. P., Law, R. M., and Pak, B.: A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere, *Biogeosciences*, 7, 2261-2282, 2010.

Wieder, W. R., Cleveland, C. C., Lawrence, D. M., and Bonan, G. B.: Effects of model structural uncertainty on carbon cycle projections: biological nitrogen fixation as a case study *Environmental Research Letters*, 10, 044016, 2015.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T. D., Lee, W., Lusk, C. H., Midgley, J. J., Navas, M.-L., Niinemets, Ü., Olesksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R.: The worldwide leaf economics spectrum, *Nature*, 428, 821-827, 2004.