Response to Anonymous Referee #1

We sincerely thank the reviewer for their effort and the very useful comments. We have revised our manuscript *P-model v1.0: An optimality-based light use efficiency model for simulating ecosystem gross primary production* and have addressed all points raised by the reviewer.

Below, we provide a point-by-point response to all the comments. Text by the reviewer is in blue and indented. Our response is in black. *New text is green, italic*. *Existing (unchanged) manuscript text is black italic*.

> I have a mixed feeling[s] for this review. On the good side, this is incredibly well written. All figures and analysis are highly professional. On the other side, this manuscript degraded the elegance of optimality hypothesis. I fully understand the original paper on optimality hypothesis (Han et al 2017) was not perfect. It had much room for improvements. But the way to improve in this manuscript is not attractive in my view with following reasons.

We thank the reviewer for the very positive assessment of the quality of text and figures. We also thank the reviewer for raising the point regarding the scope of the present manuscript and its relation to previous publications based on the same theoretical approach for modelling photosynthesis and its acclimation to the environment. We would like to highlight that the scope of the present manuscript is not to extend the theoretical approach described by (Prentice et al., 2014) and (Wang et al., 2017). We modified text in the introduction to clarify the purpose of the present manuscript:

The purpose of this paper is (i) to provide a full documentation of the model implementation and reference for open-source software (rpmodelR package, https://stineb.github.io/rpmodel/); (ii) to provide an evaluation of model-predicted LUE and GPP against GPP derived from eddy covariance flux measurements (FLUXNET 2015 Tier 1 dataset); (iii) to apply this model for global-scale simulations and compare spatial patterns and global totals of simulated GPP with other estimates with global coverage; and ***(iv) to introduce a robust and pragmatic solution to resolving model bias under dry and cold conditions****. With (iv) we do not aim at extending the theoretical basis for the P-model* (Prentice et al., 2014; Wang et al., 2017)*, but to include environmental controls in the LUE model that serve to make the model applicable as a remote sensing data-driven GPP model for a wide range of conditions and vegetation types.*

More detailed responses, related to related points raised by reviewer #1, are given below.

> 1) AET/PET was used for aridity index to consider drought effects. The authors used SPLASH model. If AET can be modeled so well, then GPP must be modeled well too as they are both tightly correlated via stomatal conductance. Therefore, in my humble opinion, bringing AET to consider drought effects in GPP estimates are logically odd. The key motivation of this study is to add soil stress function into P-model which leads [to a] better prediction of GPP, but that added soil moisture function appears decoupled from stomata conductance in the framework of optimality hypothesis. So in a physiological sense, it is not any more optimal model. Bringing stomatal conductance from SPLASH would be one option although it is ugly... but the assumption of using AET/PET is that stomatal conductance is correct.

We think there are two points here. First, as a clarification, AET is not used directly to scale GPP in the model. Errors in simulated AET are thus not linearly translated into errors in simulated GPP. Instead, the annual mean fraction of daily AET/PET, simulated by the SPLASH model, is used to scale the *sensitivity* light use efficiency (LUE) to low soil moisture (Eq. 22). Furthermore, AET simulated by the SPLASH model is based on the Priestly-Taylor equation (Priestley and Taylor, 1972) for estimating potential evapotranspiration (PET), and thus assumes that PET is controlled by net radiation only, independent of the vapour pressure deficit and stomatal conductance. In other words, this assumes a fully “decoupled” boundary layer (Jarvis, 1986). Therefore, “bringing stomatal conductance from SPLASH” is not actually possible.

The second point made here addresses the implementation of the soil moisture effects and its relation to the basic theory embodied by the P-model. With “basic theory” we mean principle of balancing the unit costs of transpiration and carboxylation following (Prentice et al., 2014) and the balancing of gains and costs associated with the maximum rate of electron transport, J_{max} following (Wang et al., 2017). This theory is implemented by the equations described in Section 2 in our manuscript. The reviewer makes the point that the soil moisture stress function is not linked to the stomatal conductance predicted by the basic theory of the P-model. Point 5) (see below) is related to this point.

We fully agree with the reviewer as we explicitly state on l. 437:

“[] the use of an empirical function is not consistent with the optimality approach that underlies the P-model.”

The potential for extending this theoretical framework and possible ways forward are discussed on subsequent lines (l. 522). We consider an inclusion of soil moisture effects into the theory underlying the P-model to be a very promising way forward and are actively working towards this goal. However, developing such an extension of the theoretical framework is a substantial piece of work as is demonstrated by the fact that similar efforts are currently being pursued by several research groups (Christoffersen et al., 2016; Mencuccini et al., 2019; Sperry et al., 2017; Wolf et al., 2016). In revising the manuscript text, we made sure to clarify that the empirical soil moisture stress function (Eqs. 21 and 22) is not to be understood as an extension of the optimality theory (Eqs. 3 and 14), but rather as a pragmatic solution to resolving known bias (see also our response above). E.g., on l. 69 we write:

> *To resolve model biases under conditions of low soil moisture, (Stocker et al., 2019) further applied an empirical stress function to reduce LUE under dry soil conditions*

> 2) There has been a series of papers that proposed global GPP maps with evaluations against fluxnet database. Many papers which were cited in this manuscript already evaluated model performance across scales from site level to the global land, daily to seasonal to annual scales. When I agreed to review this manuscript, I expected what would be global GPP, and how it varies in space and time from P-model. Site level evaluation for seasonal scale does not convince me about the overall performance of this model. In my past experience, I could match the modeled seasonal variations of GPP with fluxnet GPP extremely well; but in that case, global GPP values and interannual variation/trends were weird. I mean the authors should test the revised P model across different scales. Current evaluation is not enough.

We now conducted global simulations with the P-model using the parameters from the site-level calibration (FULL setup) and we included a description of the respective model forcings, a presentation of results, and a comparison against other global GPP estimates and the spatial distribution of sun-induced fluorescence (SiF). We complemented text and figures in several instances. The most important changes/additions are:

Two new figures:

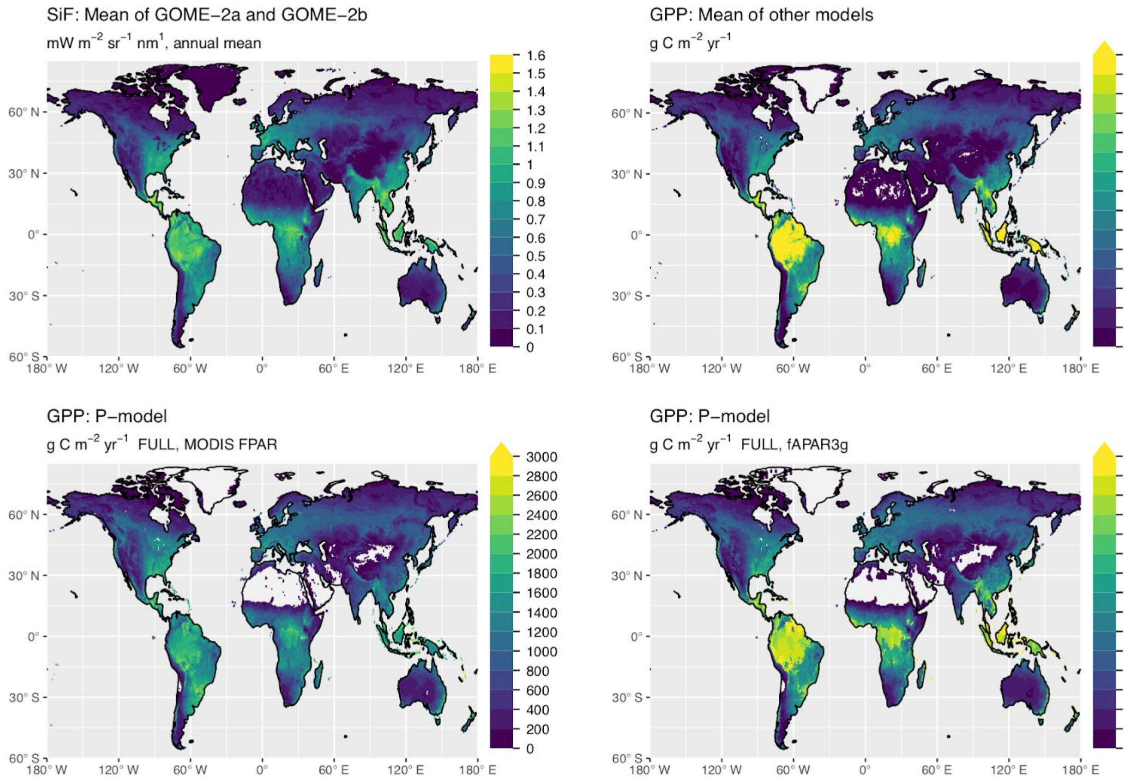

Figure 10. *Global distribution of GPP. Shown are the mean annual values, averaged over years 2000 to 2016. The GPP shown as "mean of other models" is the average of MTE (Jung et al., 2011), FLUXCOM ('RS+METEO' setup) (Tramontana et al., n.d.), MODIS GPP(collection 55 and 6) (Running et al., 2004; Turner et al., 2005), BESS (Jiang and Ryu, 2016), BEPS (Chen et al., 2016; He et al., 2018), and VPM (Zhang et al., 2017). P-model results are from simulations with the FULL setup and calibrated parameters as given in Table 1.*

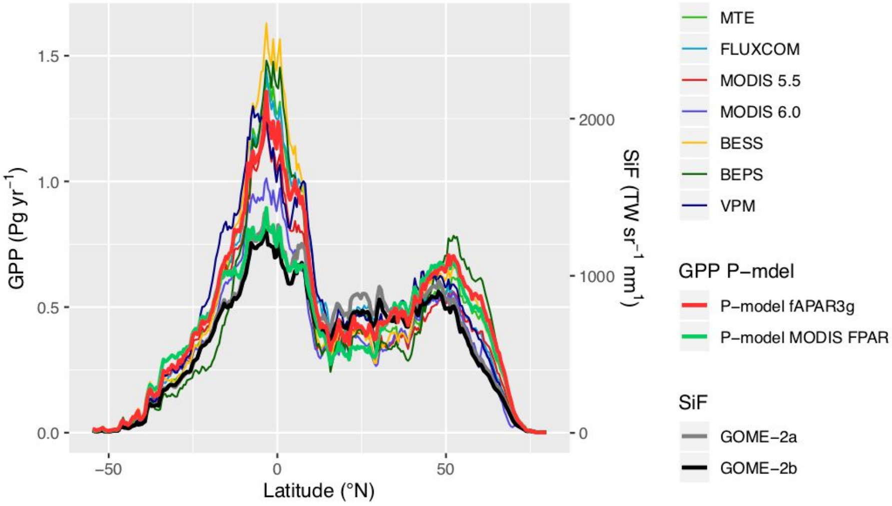

Figure 11. *Latitudinal distribution of GPP and SiF. Values shown (GPP on the left y-axis, SiF on the right y-axis) are gridcell area-weighted sums along 0.5 degree latitudinal bands.*

Abstract (l. 16):

Applying this model for global-scale simulations yields a total global GPP of 106-122 GtC yr−1 (mean of 2001-2011), depending on the fAPAR forcing data.

Introduction (l. 77):

The purpose of this paper is [...] (iii) to apply this model for global-scale simulations and compare spatial patterns and global totals of simulated GPP with other estimates with global coverage;

L. 227 (Methods section):

3.2.2 Global simulations

Global simulations were conducted for the setup FULL, using the respectively calibrated parameters from thesite-scale simulations. All vegetation is assumed to follow the C_3 photosynthetic pathway and we do not distinguish between croplands and other vegetation. Given the comparatively high light use efficiency of crops (Guanter et al., 2014) *and given that data from cropland sites was excluded from calibration, not treating croplands separately should thus tend to underestimate GPP on respective areas.*

L. 265 (Methods section):

For global-scale simulations, we used two alternative fAPAR datasets. 'MODIS FPAR' is from globally gridded MODIS FPAR data at 0.5 degree resolution derived at ICDC (http://icdc.cen.uni-hamburg.de), based on the MOD15A2H MODIS Terra Leaf Area Index/FPAR 8-Day L4 Global 500m SIN Grid V006 dataset (Myneni et al., 2015a). For the present application, 8-daily data is aggregated (mean) to monthly data. 'fAPAR3g' is based on AVHRR GIMMS FPAR3g v2 data (Zhu et al., 2013)*, 15 days, 1/12 degree resolution and aggregated for the present application to 0.5 degree and monthly data. For all global P-model simulations, fAPAR is held constant for each day in respective months. Simulations cover years 2000-2016. Due to limited temporal coverage, January 2000 data is taken as February 2000 for simulations driven by MODIS FPAR.*

L. 282 (Methods section):

For global-scale simulations, we use daily, 0.5 degrees meteorological forcing from WATCH-WFDEI (Weedon et al., 2014)*. We use mean daily 2 m air temperature; daily snow and rainfall; shortwave downwelling radiation converted to mol photons m−2 d−1 by multiplication with k_{EC}; and daily 2 m specific humidity (q_{air}), converted to VPD (D) as described in Appendix E. We used daily minimum and maximum air temperatures for each month from CRU TS 4.01 data (Harris et al., 2014) to calculate a respective VPD and use their mean as a daily varying input to P-model simulations in order to reduce effects of the non-linear dependence of D on T($D = (D(T_{min}) + D(T_{max})/2$). All processes that depend on atmospheric pressure use Eq. B10 and the 0.5 ◦resolution elevation map from WATCH-WFDEI* (Weedon et al., 2014) *to calculate a temporally constant atmospheric pressure for each gridcell.*

L. 305 (Methods section):

3.5.2 Global datasets for GPP comparison

We compare the simulated spatial distribution of GPP from global-scale simulations against seven different remote sensing data-driven GPP estimates with global coverage and two sun-induced fluorescence (SiF) data products. The global GPP estimates are from the following models: MTE (Jung *et al., 2011), FLUXCOM ('RS+METEO' setup) (Tramontana et al., 2016), MODIS GPP (collection 55 and 6) (Running et al., 2004; Zhao et al., 2005), BESS (Jiang and Ryu, 2016), BEPS (He et al.,2018; Chen et al., 2016), and VPM (Zhang et al., 2017b). A more detailed description of these models and aggregation to a common grid of 0.5 degrees and monthly resolution can be found in* (Luo et al., 2018)*. For sun-induced fluorescence (SiF), we use data from GOME-2A and GOME-2B, based on v.2 (V27) 740 nm terrestrial chlorophyll fluorescence from the MetOp-A andMetOp-B satellites* (Joiner et al., 2013, 2016)*. Data were aggregated to monthly and 0.5 resolution by mean, as further described in Luo et al. (2018).*

L. 451 (Results section):

4.7 Global GPP

Simulated global total GPP is 106 GtC yr-1 when using MODIS FPAR and 122 GtC yr-1 when using fAPAR3g forcing data (mean over years 2001-2011, setup FULL). The spatial pattern of simulated GPP differs substantially between simulations forced by MODIS FPAR and fAPAR3g (Fig. 8). This is most evident in their latitudinal distribution (Fig. 9). The global spatial pattern of fAPAR3g-based GPP simulated by the P-model generally matches the global distribution of the mean across other remote sensing-based GPP models and lies within the range of their estimates for the latitudinal distribution. The MODIS FPAR-forced P-model simulation suggests lower values in the tropics that differ from the fAPAR3g-based estimates by a factor of ~2 around the equator. The moderate tropical GPP of the MODIS FPAR-based P-model simulation agrees well with the latitudinal distribution of sun-induced fluorescence (SiF) from GOME-2A and GOME-2B.

L. 450 (Discussion section):

The P-model-based estimates of global GPP (106 GtC yr−1when using MODIS FPAR and 122 GtC yr−1 when usingfAPAR3g forcing data, mean over 2001-2011, FULL setup) are within the range of other estimates of global GPP (also means over 2001-2011): 133 GtC yr−1 for MTE (Jung et al., 2011), 130 GtC yr−1for FLUXCOM (Tramontana et al., 2016), 112 GtC yr−1for MODIS-55 GPP and 105 GtC yr−1 for MODIS-6 GPP (Running et al., 2004; Zhao et al., 2005), 133 GtC yr−1 for BESS (Jiang and Ryu, 2016; Ryu et al., 2011), 121 GtC yr−1 for BEPS (He et al., 2018; Chen et al., 2016), and 135 GtC yr−1 for VPM (Zhang et al., 2017b). The P-model results presented here are based on simulations that embody relatively strong simplifying assumptions. In particular, we assumed all vegetation to follow the C3 photosynthetic pathway and we made no distinction between croplands and other vegetation, although crops are generally more productive (Guanter et al., 2014).

The large spread of tropical GPP estimates is striking. The highest estimate among the other GPP models we used for evaluation here - coming from BESS - is more than 50% higher than MODIS GPP from Collection 6. The fAPAR3g-based P-model tropical GPP estimate falls within the range of other GPP models, while the MODIS FPAR-based estimate is lower than all other models. However, the latter's comparably low tropical GPP agrees well with the latitudinal distribution of SiF.However, large changes in leaf area index across latitudes, combined with a dependency of the SiF signal on vegetation structure (Zeng et al., 2019) may undermine the validity of SiF as a benchmark for GPP models. A lack of evaluation data from eddy-covariance measurements in dense tropical forests precludes us from drawing conclusions on the accurateness of these diverging tropical GPP estimates.

We now realised that in the published *Discussions* manuscript, two short sections describing the results of the evaluations of 8-daily, interannual, and spatial variations were missing. Respective text was lost when formatting the document for *GMDD*. We duly apologize for this. In the revised manuscript, we added this text back to the manuscript. Figures and tables that show model performance for 8-daily, interannual, and spatial variations and that are referred to in added text had been included already in the published *Discussions* manuscript. Added text reads:

4.1.1 8-day means

The P-model version ORG captures 69% of the variance in observed GPP with data aggregated to 8-day means (60'450 data points). Model performance both with respect to explained variance (R^2) and the RMSE is improved when additionally accounting for effects of temperature on the quantum yield efficiency (BRC, R^2 = 72%), and when additionally factoring in the empirical soil moisture stress function (FULL, R^2 = 75%, Fig. 2). The NULL model with temporally constant and spatially uniform LUE performed equally well as ORG, but is outperformed by model versions BRC and FULL. All performance statistics are given in Tables 3 and 4.

[...]

4.1.3 Spatial and annual variations

The R^2 for annual GPP simulated by the P-model setups ranges from 0.57 (ORG) to 0.70 (FULL). The NULL model achieves an R^2 of 0.58. Most of the explanatory power of the different models for predicting annual total GPP stems from their power in predicting between-site ("spatial") variations (Fig. 3, Tabs. 3 and 4). The R^2 for spatial variations ranges from 0.62 (ORG) to 0.70 (FULL), and 0.64 for the NULL model. In contrast, inter-annual variations (across years within a given site) are poorly simulated (R^2: 0.06-0.09 for P-model setups, and 0.04 for the NULL model). Interannual variations are generally much smaller than across site variations, which likely adds to the challenge of accurately capturing interannual variations. Interannual GPP variations are generally better captured at sites where the variability is high and in particular at dry sites.

Taken together, we are providing a comprehensive evaluation, assessing 8-daily, annual, spatial, and seasonal variations; responses to droughts; and global GPP. In other words, we are not just evaluating seasonal variations as suggested by the reviewer. Temporal trends cannot currently be assessed using eddy-covariance data with confidence. This is mainly due to the (still) relatively short time series available from flux measurements (see below) and the relatively high interannual variability. Hence, we avoid comparing also temporal trends in global GPP.

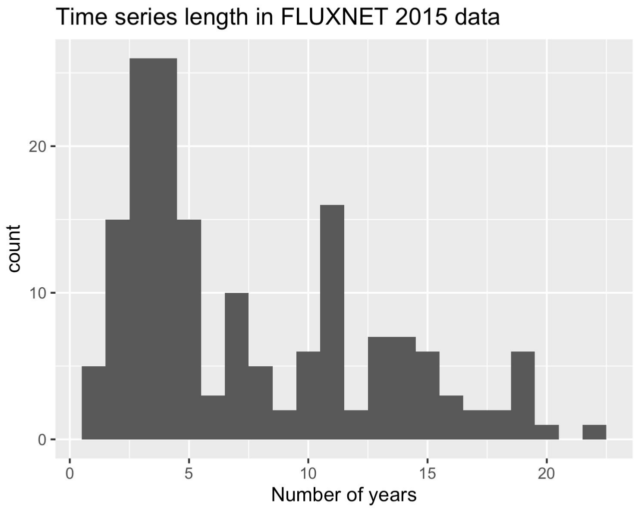

***Fig. A** Time series length in FLUXNET 2015 data for different sites in the Tier 1 set.*

> 3) The authors have incorporated an empirical soil moisture stress function to downregulate LUEopt. I understand why the authors introduced soil moisture stress function after the 1st author's fantastic papers on drought and fLUE. However, I think the introduced soil module is too heavy given the elegance of optimality hypothesis. It is a typical soil bucket model which requires soil properties and rainfall. To scale up P-model globally, the key barrier will be this soil module- they are too uncertain and P-model will be coupled with a heavy hydrological model like SPLASH. We know microwave remote sensing based soil moisture only captures top soils.

The soil water balance model implemented here is arguably the simplest form of such a model. It considers only one bucket (other models treat water movement across multiple soil layers which requires a computationally expensive numerical scheme), and simulates potential evapotranspiration following Priestly-Taylor (1972) (other models account for effects of boundary layer and surface resistance following the Penman-Monteith Equation). Any model that accounts for soil moisture effects must somehow treat soil moisture prognostically, unless it's prescribed from observations. We followed arguably the "lightest" possible prognostic soil moisture model, SPLASH. As the reviewer notes, observation-based soil moisture, e.g. based on microwave remote sensing (Al Bitar et al., 2016; Dorigo et al., 2017), are subject to the limitation that they only capture signals from the uppermost soil layers and may thus not be representative for plant water stress and of limited use for the present application.

> 4) The improved model still showed poor performance in capturing interannual variations of GPP. That's disappointed given the introduction of temperature and soil moisture terms.

We have added text in the discussion to put this result into context (l. 458).

While seasonal and spatial variations in GPP are reliably simulated by the P-model, the model's performance in simulating interannual GPP variations is weaker. Similar results have been found from previous studies from both empirical (Richardson et al., 2007; Urbanski et al., 2007) and process model-based (Keenan et al., 2012) analyses. This is likely due to lagged effects of climate anomalies expressed through biotic responses (Biederman et al., 2016; Keenan et al., 2012; Richardson et al., 2007).

> 5) Overall framework of revised P-model is almost identical to MODIS LUE model. MODIS GPP model downregulates LUEmax via temperature and VPD. Recent papers proposed a universal LUE max, or pixel based LUEopt that varies with time. That is the current status of MODIS GPP model. Then the revised P-model is almost following same direction; incorporating temperature and soil moisture to reduce LUEopt. Although the processes differ between two models in terms of f(temp) and f(water), overall philosophical framework appears very similar. That is the reason that I wrote "degradation of elegant P-model" in my general comments. If optimality hypothesis does not reflect temperature and water stress well, that indicates the optimality hypothesis is incorrect. Decoupling stomata conductance from added soil moisture function is a drawback in the framework of optimality. I would wish the authors incorporate temp/water effects into optimality theory in a more elegant way. The current way is too MODIS LUE style....

The model presented here differs from the MODIS GPP model (Running et al., 2004) in several fundamental ways. First, spatial variations in LUE are not prescribed, as is done by MODIS GPP based on biome-specific LUEopt values used in combination with a global biome classification, but are predicted based on the optimality principle (Eq. 3 in our manuscript) balancing costs associated with carbon gains and water losses. Second, the model presented here combines the enzyme kinetics for simulating photosynthesis described by the FvCB model with the Coordination Hypothesis to derive a formulation for LUE that turns out to be linear with absorbed light. In other words, the LUE model concept emerges from the theory embodied in the model and is not pre-imposed.

As discussed above (see our response to point 1) the implementation of a simple water stress scalar was motivated by pragmatism. We modified text in the Discussion section to better elucidate mechanisms behind the “temperature stress” function applied here. Modified text reads:

A reduction in the quantum yield efficiency arises from several mechanisms, including increased non-photochemical quenching, a reduction in chlorophyll and absorption by screening pigments (Adams et al., 2004; Ensminger et al., 2004; Huner et al., 1993; Oquist and Huner, 2003; Verhoeven, 2014). These adaptations serve to limit oxidative damage under high light and low temperature conditions, where an imbalance between electron supply and demand exists, arising from an imbalance between temperature-insensitive photochemical rates and temperature-sensitive biochemical rates. The reversion of these adaptations and resumption of the intrinsic quantum yield efficiency and photosynthesis requires sustained temperatures above a certain critical threshold (Rogers et al., 2017; Tanja et al., 2003) and exhibits a delay with respect to instantaneous air temperatures (Mäkelä et al., 2004; Pelkonen and Hari, 1980). Approaches accounting for a delayed resumption of photosynthesis after cold periods offer scope for further improvement of the P-model and may be included in global vegetation and Earth system models where this effect is currently not accounted for (Rogers et al., 2017; Tanja et al., 2003).

We disagree that the apparent necessity to account for a water and temperature stress factor is indicative of the ”optimality hypothesis [being] incorrect”. Rather, it is *incomplete* (noting that every model is necessarily incomplete). We write on l. 521:

The bias reduction associated with using an empirical soil moisture stress function hints at missing factors in the theoretical approach which rests on an assumed constancy of the unit costs of transpiration (a in Eq. 3).

It might be a viable approach to include a cost associated with oxidative stress, governed by the imbalance between the photochemical and biochemical rates (Oquist and Huner, 2003). However, such an approach would have to account for the large diurnal variations in light availability. A reasonable alternative is to account for low-temperature stress by describing the phenomenon, as we do, rather than predicting its emergence based on photochemical and biochemical processes. We note that there are several other parameters and relationships in the photosynthesis model, including the light-response curve, that are empirical. The strength of our approach lies in our demonstration that the model can be effectively "scaled up" by taking account of acclimatory responses of model parameters.

As regards the soil moisture parameterization, this could (conceptually) be replaced by an extension of the optimality framework to include the additional costs of extracting water from dry soils. However, this will be a substantial project in itself, requiring (among other things) an optimality-based estimate of root-zone size. For the present, therefore, we find it useful to work with and present a hybrid model in which the response to low soil moisture is not optimality-based.

> 6) Current model evaluation is not enough. I strongly recommend testing the revised model at global scale across MODIS years. For example, Keenan et al (2017) showed recent increase of global GPP via P-model. Does the revised P-model still support this finding? Or does new modules of soil moisture and temperature reduce global GPP? I request this as P-model was already published so the authors may move many lines about original P model description to Appendix. The novelty of this model must be evaluation across diverse scales.

As discussed above in our response to the referee's point 2), we have added results and analyses of global P-model simulations. The version of the P-model used in Keenan et al. (2017) is different from the one applied here as described on lines 66-69. It did not include the J_{max} limitation introduced by (Wang et al., 2017). We avoid presenting an evaluation of trends over the MODIS period (after February 2000) since we consider it too short for robust analyses. We have added text in the Discussion section to clarify these points.

Due to the short period for which forcing data and outputs from comparable models are available, we did not analyse temporal trends in global GPP here. Analyses not shown here indicate that the introduction of the Jmax cost factor (not included, e.g., in (Keenan et al., 2016)*) increases the sensitivity of modelled GPP to CO2. Further evaluation of model behaviour against data from CO2 manipulation experiments will be necessary before applying the model to simulate CO2-related trends.*

> Only a few specific comments follow as the manuscript is so well written. - L118: What was beta in Wang et al (2017a)?

We added the values used by Wang et al. (2017) and in the present study:

> *The unit cost ratio β has been estimated by Wang et al. (2017a)* ***to 240*** *based on global leaf δ13C data and a simplified version of the P-model (assumingΓ^*= 0 and neglecting the J_{max} limitation). Here, we re-estimated β* ***to 146*** *based on the full version of the model using the same global leaf δ13C dataset.*

> - L370: MODI -> MODIS

Done.

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