

Revision and reply to comments for “The effect of using the plant functional type paradigm on a data-constrained global phenology model”

January 25, 2016

Editor’s comments

We would like to thank the editor for their attention to detail in both the paper and the reviewer comments and replies. We have made all the modifications suggested. Below, we include the detailed response to the reviewers’ comments, followed by a point y point list of changes made to the manuscript and a marked up version of the revised manuscript.

Review 1

We would like to thank the reviewer for their comments and the time they took to read our manuscript. We agree that there re many more directions of discussion possible starting from our analysis, but we have chosen to discuss in detail what we termed the combination model, as a proposed middle ground between the existing approaches and our initial, potentially over-fitted and certainly unrealistic local approach. We agree that we have not

discussed in detail the feasibility of using such a parametrisation in a ESM framework and we have now included a more detailed discussion of this issue.

p. 16848 line 7: change assumption to simplification (more on this below)

Now changed

p. 16949 line 13-15: "...underlying assumption that all plants...show an identical behavior" - this statement, while not incorrect, implies that modelers who use PFTs are ignorant of the limitations of PFTs. Most, if not all, PFT-based studies (including Sitch et al 2003) are careful to point out the limitations of this approach, but also to highlight the reasons such simplifications are necessary.

We did not mean to imply that the authors of studies which use PFTs are not aware of the limitations and we use the word 'assumption' in its scientific sense, in that every theory is based on a number of assumptions which do not make that theory necessarily wrong but only limited in its application. We have now clarified this in the text.

line 25-26: This cursory explanation of why PFTs are used misses a critical point - for vegetation models that are intended to be used under future climate scenarios (including possible no-analog climates) it is critical to use physiologically based parameterizations. Because so many of the parameters in veg models are unknown globally at fine taxonomic levels, PFTs are used to generalize. Models that include fitted parameters that vary across space wont work in a DGVM context where plant communities may change under future climate scenarios.

We agree with the reviewer that we have not discussed in sufficient details the advantage

of using PFT for future scenarios in DGVMs, and we have now added this to the text. However, we must add that efforts are being made to develop alternative methodologies (e.g. Fisher et al., 2015).

p. 16850 line 18: "three main different model parameterizations" - by my count there are at least five parameterizations treated equally (local, PFT, combined, global, regional), plus two more introduced later where you let tropical evergreen forest vary by but not other PFTs, for the combined and PFT options (p 16858 line 20). Which are the actual models used in all the figures, I believe. Please clarify.

We thank the reviewer for pointing out that this is not clear in the text and we have now clarified this. There are three main parameterisations which we show figures for and discuss in detail - local, PFT and combined - as well as two other parameterisations, global and regional, which we only show overall fit for.

p. 16853 line 15-17: any data to back this statement up? or a reference?

This result was included in our previous study (Caldararu et al., 2014), which we have now added a reference for.

p. 16854 line 2: Its confusing to me that leaf level compensation point is in W/m^2 but canopy level is in $umol/m^2/s$.

This results from the units that the original PAR data is in as well as the structure of the model.

line 5: "... do not represent measurable values in the field..." I read this as meaning q and phi are fitting parameters.

Absolute values for the parameters ϕ and q cannot be compared to measured values, but relative values and variations across the globe can be considered to have biological significance. This has now been clarified in the text.

p. 16858 line 20: broadleaf tropical forest performing better. Is there a figure that shows this? This is a fairly significant change to the modeling approach and deserves a bit more discussion, I think.

We have now included a figure in the appendix with detailed results for the regional parametrisation.

line 25-26: So, based on these numbers and the change to using regional tropical forest parameters, Table 2 (references in line 14) includes this change? How did the PFT and combined models perform without this change? Also, doesnt this mean there should be 3 dashed lines in Fig 7 TEF?

All figures and tables present in the paper include regional tropical forest parameters. Figure 7 only shows parameter values for the TEF Amazon region; this has now been clarified in the figure legend and caption.

p. 16859 lines 1-4: again, are there figures to back up these statements?

Yes, all statements in this paragraphs are based on Figure 1.

line 25: I think "Biome" in Fig. 5 should be "PFT"?

Yes, we apologise for this mistake, this has now been corrected.

p. 16860 lines 10-12: the values reported in figures 7 and 8 are a concern, given that they range far beyond what is physiologically reasonable. For ex-

ample, leaves in temperate deciduous forest rarely last beyond 8 months, yet a-crit for these plants in your model goes out beyond 2 years.

As we explain in Section 5.1 , the age_{crit} values are only representative of leaf lifespan in the model in regions where leaf loss is driven by leaf aging, so that parameter values in, for example, broadleaf temperate forests are not constrained. We have now clarified this in the text. In the interest of space, we do not show a comparison of the age_{crit} values and effective leaf age, as we have done in our previous study (Caldararu et al., 2014).

I'm also finding the use of compensation point confusing. There are three different compensation points mentioned in this ms - C- direct, C-diffuse, and q (and they have different units!). Im fairly sure all the figures and the discussion refer to C-direct, but this needs to be clarified, and defined, as Im not sure what the difference between a direct and diffuse compensation point would be, nor can I find any discussion of this in the literature.

Throughout the discussion, compensation point refers to the direct compensation point, C_{direct} parameter, and this has now been clarified at the start of the discussion. The direct and diffuse compensation point arise from a need to represent the two light components accurately without introducing a full canopy layer model, which would introduce additional complexity into our phenology model. Within a detailed canopy model, the two compensation point parameters would be more realistically represented by a sunlit and shaded compensation points, as it has been shown that leaves grown in different light environments will adapt to their light conditions. We have now included this explanation in the text of the discussion.

line 20: "The discrepancy..." Im not sure what you mean by this statement.

This sentence refers to the differences in fitted parameter values between the model

parametrisations, as shown in Figure 8.

p. 16861 line 1: The discussion jumps right in to talking exclusively about the combined model, without any overall summary - why choose this model of your 5-7 models described?

We have chosen to focus on the combined model as this is a compromise between PFT level parameters and local traits, providing a much smaller number of parameters than the local model but attempting to overcome the disadvantages of using PFT level parameters. In the discussion we are trying to explore the possibility that this approach can be used more generally or if it is a result of our specific model structure or fitting procedure. We have now added a paragraph at the start of the discussion outlining overall results.

section 5.1: This section highlights the apparent importance of compensation point, but I would like to see some references to realistic values for these parameters, if they exist, or a discussion of why they dont and how this model is still useful if its using un-measurable parameters.

Light compensation point values are calculated from photosynthetic light response curves at the leaf level or extrapolated to the plant level (e.g. Givnish et al., 2004; Baltzer and Thomas, 2007). We have now included a brief comparison with literature values in the text of the discussion.

Review 2

We would like to thank the reviewer for their thorough comments and we hope that our response and modifications to the manuscript will clarify the methods and the analysis.

How was the MODIS data aggregated from a 1km resolution to a 2deg x 2.5deg resolution? Mean? Median? And why?

The MODIS LAI data was aggregated using mean values within each model grid cell. This was done partially because of computational constraints (see below) and partially because after the quality filtering procedure data for a 1 km pixel has a large number of missing values and would be unsuitable for fitting a phenology model, which relies on timeseries information. This has now been clarified in the text.

How was the 8-day MODIS data treated in terms of a model run at a daily time step? (Im assuming the model time step is daily, although this is not explicitly stated). Was the MODIS data interpolated from 8-day to daily values? Were comparisons of model output to MODIS LAI done at an 8-day or daily time step?

The model was run at a daily time step but only fitted at those dates when data was available, i.e. every 8 days, a method which did not require interpolation of the MODIS data. We have now added this information to the text.

How was the soil moisture data regridded to match the GEOS-4 resolution?

This was done through nearest neighbour interpolation and this information has now been added to the soil moisture data section.

Also, why did the authors choose such a coarse resolution when the primary datasets that describe the vegetation (LAI and the PFT map) are provided at a much finer resolution? There are PAR datasets at finer resolutions available (e.g. CERES 1deg x 1deg). I understand when running global scale models computational limits may be restrictive, but the reasoning for using such a

coarse scale should be more specifically described.

Our main limitation was indeed computational effort. The nature of the fitting algorithm and that we were running multiple fitting setups required a coarse spatial resolution. Trial runs with a higher spatial resolution (0.5° latitude x 0.66° longitude) showed that the problem was intractable. We have now added a justification for the resolution in the text, as advised.

In particular this aggregation produces some curious observed LAI values; for example it is a bit odd that the forest PFTs shown in Figure 3 have observed values of ≤ 1.0 . The PFT classification based on dominance should be addressed more thoroughly beyond the quick analysis provided in Figure 6 (which needs clarification as well see below)

The PFT which show an abnormally low LAI is the evergreen boreal forest, which has some problems due to heterogeneity even at the native resolution, as discussed in Caldararu et al. (2014)

The introduction says 3 main model parameterizations are applied, but appears to list 5 as it includes global and regional. The Model Set-up section says 5 are implemented, this should be consistent to avoid confusion.

We thank the reviewer for pointing out that this is not clear in the text and we have now clarified this. There are three main parametrisations which we show figures for and discuss in detail - local, PFT and combined - as well as two other parametrisations, global and regional, which we only show overall fit for.

In the model performance metrics section, there is no mention of regions or pixels that do not conform to a regular seasonal signal. Such as arid systems

where multiple seasonal peaks may be present in response to precipitation events, crop systems with two planting/harvest cycles per year, or tropical systems where there may be minimal seasonal variation. The authors should address whether these non-standard seasonal cycles were present, and if so, how they were addressed.

The model has the capability of representing these 'non-regular' seasonal cycles, as, unlike traditional phenology models, it does not rely on start and end of season thresholds and can even represent the continuous leaf growth and loss necessary in evergreen tropical forests. With regards to model performance metrics, the only problem might arise from comparing timing prediction and to this end we also use time of maximum. Pixels classified as crops have not been used in the analysis and we thank the reviewer for pointing out that we have omitted to explain this.

The maps of results (Figures 1 and 2) are key components of the manuscript, providing a global look at the results of a model applied globally. However, there is a spatial shift between the pixels and the geographic borders. There are pixels clearly over oceans. Either this is a basic problem due to an unresolved projection difference between layers, or some of the input layers have not been properly georeferenced calling into question the overall results. Second, why do large areas and certain pixels have no results in some maps; N Spain, NE Europe and W Russia, N America and Canada border region, SE U.S., S Africa, C America, N South America, Sweden, Norway? There is no mention of masking or screening pixels in the methods.

This problem is caused by overlaying large grid cells on a map. Missing cells are either

non-vegetated (e.g. the Sahara desert) or cells that have been classed as majority water.

The legends of Figures 1 and 2 also need work. For the Figure 1 legend, the upper limit (>0.8) should either be placed where the current 0.8 text is, or be changed to >1.0 ; it is redundant in its current form. The legend in Figure 2 does not make sense. It currently implies that all gray pixels had no difference in mean or amplitude between predicted and observed, obviously not true. Also, the upper limit in each legend shows 0,7 instead of 0.7.

For the legend in figure 1, each number refers to the upper limit of the colour to the left of it and the '>0.8' label is necessary to designate the value of the darkest red. The legend and colour scale in figure 2 have now been rectified.

The results shown in figure 1 do not match results provided in the text. Tropical forests are said to have RMSE errors of 0.15 (local), 0.22 (PFT) and 0.16 (Combined). These areas would appear as primarily yellow or light orange on the maps, but for PFT results, nearly all tropical forests fit into the ≤ 0.8 category. The local and combined maps show values in the range of 0.4 to ≤ 0.8 . In figure 5 and figure 7, Boreal Evergreen Forest is denoted as BEF in the figure and TEF in the text.

The discrepancy between figure 1 and the text arose from a mistake on our part where we accidentally plotted absolute RMSE values in figure 1, a mistake which has now been corrected. We have also corrected the captions for figures 5 and 7 to denote boreal evergreen forest by BEF.

For figure 6, the authors do not say which model these results are from; this is not made clear until section 5.3 in the Discussion. The y-axes are

labeled Relative, does this equate to the normalization used in other figures and results? And if so, there is a significant portion of pixels with LAI mean and amplitude biases greater than 0.7 (the maximum value used in figure 2). Why not display this larger range in figure 2?

The results in Figure 6 are from the PFT model and this has now been clarified in the legend and the results text. The reason the colourbar range in figure 1 and 2 do not show a larger range of values is because the local, PFT and combined model are all on the same colour scale and the PFT model has much higher errors.

In the local and combined models the parameters are not constrained to realistic ranges. This calls into question the applicability of these models. For example, the age-crit parameter approaches nearly two years in some temperate deciduous forests, and can be as short as a few months in boreal evergreen forests, this is not realistic. I understand that one goal of this manuscript was exploratory, to allow parameters to range to achieve the best fit. But when the parameterization is allowed to vary regardless of known biological limits, the resulting model loses its applicability to represent realistic conditions which is the ultimate goal of applying such models to predict future conditions. This lack of realistic representation is also apparent in the aggregation problem mentioned earlier, where Forest PFTs have observed mean LAI values less than 1.0.

As we explain in the discussion. the age_{crit} parameter does not represent effective leaf e.g. in areas that are not limited by leaf ageing, such as the temperate regions, where the parameter is not well constrained. We aimed to have a general global model and let all parameters be fitted in any location of the globe, even where some of the processes, leaf loss through ageing in this case, are not applicable. The model correctly identifies the

driving factor for leaf loss however and this does not lead to any errors in model results. We apologise if this was not clear enough in the text and we have expanded this explanation.

A main goal of the manuscript was to demonstrate how more specific parameterization of a phenology model would improve upon the widely applied method of general PFT parameterizations. In order to make such a comparison and demonstrate model improvement, the widely applied method (general PFT) must be run in its true format; i.e. representation of multiple PFTs within a single grid cell. To their credit, the authors clearly make this point in Section 5.3, and stipulate that this may be main source of error in the PFT model. A main concern is that the PFT model shown here is not representative of the method used in the majority of global models, yet the results of this application are treated as though they are representative of this model in other applications. For example (P. 16850 L. 8-10), the authors state it is important to formally evaluate the PFT model in comparison to alternative approaches. Yes, certainly true, but that is not what is being done in this manuscript. Also, the authors claim in the conclusion that a model with PFT wide parameters cannot explain the observed spatial variation. . .and a response would be of course it cant explain the variation when the PFTs are aggregated to a single dominant PFT across a 2.0x2.5 degree extent. For instance the authors state in the Abstract and P. 16849 L. 13-14 that the PFT approach makes an assumption that all plants within a PFT show identical behavior. True to a degree, but in its application here this assumption is taken a step further in that the mix of PFTs (plants) in a grid cell are being forced to show behavior identical to a completely separate PFT, e.g. where a grid cell may cover both forested and shrubland systems.

We acknowledge that the simplified way in which we use the PFT parameters is one of the major shortcomings of our study and that DGVMs which use the PFT concept allow for multiple PFTs in one grid cell. The fact that we are constraining our model parameters to data makes this a mathematically and computationally difficult problem however. Recent studies have compared the use of plant traits and PFT parameters in non-data constrained conditions and shown that the trait based models perform better (Sakschewski et al., 2015; Verheijen et al., 2013). We have chosen to explore the same question in the context of a data constrained model, which can bring more information to the model but also imposes some limitations on the parametrisation scheme. We have attempted to further discuss and justify our approach in the text.

First, some methods descriptions need to be more specific including some discussion of pixels which may not follow regular seasonal cycles. Second, the results need to be clarified; with attention paid to the figures, clarification in why some areas show no results and discrepancies between text and figures sorted out. Third, in order for the results to be applicable to the current state of model development and application some form of constraint should be applied to parameters based on biological limits; presenting a model that provides a better fit without this consideration still does not allow for its application.

We hope that we have sufficiently clarified the methods and results and we have better explained the relationship between our age parameter and leaf age. We would like to thank the reviewer once again for their attention to detail in finding the discrepancies in the figures and text.

Finally, in order to demonstrate improvement in phenology representation, the results should be compared to a PFT scale model as it is truly applied. This could be done by using existing model runs and results from other sources so that the authors do not face computational constraints.

Unfortunately comparing to different models would raise a number of completely different questions, as our model uses the plant optimality hypothesis, while most other phenology models use a degree day approach. Such a model comparison would be interesting, but would not answer the remaining question about our treatment of PFTs. We have attempted to discuss this problem openly and outline the limitations of our study.

Changes made to manuscript

All page and line numbers refer to the Discussion paper. Changes in italics were made in response to the editor's comments.

p 16848 l7 "assumption" changed to "simplification"

p 16849 l16 Included clarification of why the PFT paradigm was necessary

p 16849 l26 Added short discussion of use of PFTs in DGVMs for future predictions

p 16850 l18 Clarified number of parametrisations

p 16851 l14 Added explanation of how the data was regridded and the reason for the regridding as well as a mention of how we dealt with pixels classified as crops

p 16852 l20 Added statement that the model is capable of reproducing irregular seasonal cycles.

p 16853 l8 Added brief explanation for the reason of using two compensation points

p 16853 l18 Added reference to previous study

p 16854 l7 Added explanation of physical meaning of scaled photosynthesis parameters

p 16854 l7 Added explanation of different units for the light-related parameters

p 16857 l8 Added information of model timestep

p 16858 l 26 Additional reference to Figure 1 for clarity.

p 16859 l19 Added information on low LAI values in boreal forests

p 16860 l5 Added "In the PFT model"

p 16861 l1 Added short general paragraph at the start of the discussion.

p 16861 l27 Added explanation of relationship between diffuse and direct compensation point parameters.

p 16862 l3 Added comparison with literature values of light compensation point

p 16862 l5 Expanded explanation of relationship between our age parameter and leaf lifespan, *including reference to previous study*

p 16865 l 17 Added paragraph on using a trait based model in the context of an ESM.

p 16876 Fig 1 Modified to correctly show relative RMSE

p 16877 Fig 2 Colourbar corrected

p 16880 Fig 5 Legend fixed. TEF replaced with BEF

p 16881 Fig 6 'in the PFT model' added

p 16882 Fig 7 TEF replaced by TEF Amazon and TEF corrected to BEF

References

Baltzer, J. and Thomas, S.: Physiological and morphological correlates of whole-plant light compensation point in temperate deciduous tree seedlings, *Oecologia*, 153, 209–223, doi: 10.1007/s00442-007-0722-2, URL <http://dx.doi.org/10.1007/s00442-007-0722-2>, 2007.

Caldararu, S., Purves, D. W., and Palmer, P. I.: Phenology as a strategy for carbon optimality: a global model, *Biogeosciences*, 11, 763–778, doi:10.5194/bg-11-763-2014, URL <http://www.biogeosciences.net/11/763/2014/>, 2014.

Fisher, R. A., Muszala, S., Versteinstein, M., Lawrence, P., Xu, C., McDowell, N. G., Knox, R. G., Koven, C., Holm, J., Rogers, B. M., Lawrence, D., and Bonan, G.: Taking off the training wheels: the properties of a dynamic vegetation model without climate envelopes,

Geoscientific Model Development Discussions, 8, 3293–3357, doi:10.5194/gmdd-8-3293-2015, URL <http://www.geosci-model-dev-discuss.net/8/3293/2015/>, 2015.

Givnish, T. J., Montgomery, R. A., and Goldstein, G.: Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points, *American Journal of Botany*, 91, 228–246, doi:10.3732/ajb.91.2.228, URL <http://www.amjbot.org/content/91/2/228.abstract>, 2004.

Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., Peuelas, J., and Thonicke, K.: Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model, *Global Change Biology*, 21, 2711–2725, doi:10.1111/gcb.12870, URL <http://dx.doi.org/10.1111/gcb.12870>, 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, doi:10.5194/bg-10-5497-2013, URL <http://www.biogeosciences.net/10/5497/2013/>, 2013.

The effect of using the plant functional type paradigm on a data-constrained global phenology model

Silvia Caldararu^{1*}, Drew W. Purves¹, and Matthew J. Smith¹

¹Microsoft Research, Cambridge, UK

*Now at Max Planck Institute for Biogeochemistry, Jena, Germany

Correspondence to: Silvia Caldararu (scaldra@bgc-jena.mpg.de)

Abstract. Leaf seasonality impacts a variety of important biological, chemical and physical Earth system processes, which makes it essential to represent leaf phenology in ecosystem and climate models. However, we are still lacking a general, robust parametrisation of phenology at global scales. In this study, we use a simple process-based model, which describes phenology as a strategy for carbon optimality, to test the effects of the common ~~assumption~~ simplification in global modelling studies that plant species within the same plant functional type have the same parameter values, implying they are assumed to have the same species traits. In a previous study this model was shown to predict spatial and temporal dynamics of leaf area index (LAI) well across the entire global land surface provided local grid cell parameters were used, and is able to explain 96% of the spatial variation in average LAI and 87% of the variation in amplitude. In contrast, we find here that a PFT level parametrisation is unable to capture the spatial variability in seasonal cycles, explaining on average only 28% of the spatial variation in mean leaf area index and 12% of the variation in seasonal amplitude. However we also show that allowing only two parameters, light compensation point and leaf age, to be spatially variable dramatically improves the model predictions, increasing the model's capability of explaining spatial variations in leaf seasonality to 70% and 57% of the variation in LAI average and amplitude respectively. This highlights the importance of identifying the spatial scale of variation of plant traits and the necessity to critically analyse the use of the plant functional type assumption in Earth system models.

1 Introduction

The ability to understand and predict leaf seasonal cycles, a process known as leaf phenology, is essential to our understanding of earth systems processes, through its impact on the carbon and water cycles (White et al., 1999; Wilson and Baldocchi, 2000) and climate (Hayden, 1998). As such, phenology is an essential component of global vegetation models and an improvement in our understanding of, and ability to predict, leaf phenology would improve Earth System Model predictions.

One of the aspects of global vegetation models that is currently under scrutiny is the way parameters are assigned to the simulated vegetation within a given model grid cell. Traditionally, models

make use of the Plant Functional Type concept (PFT). In this approach, a small number of PFTs are defined, each with a corresponding set of parameters, then a given grid cell is assigned to one, or a mixture of, these PFTs. However, more recently efforts are being made to include a more biologically detailed representation in the form of plant traits. PFTs are classes of plant species with similar characteristics and roles within ecosystems (Box, 1996; Smith, 1997) and found within certain bioclimatic regions (Prentice et al., 1992; Haxeltine and Prentice, 1996). All model parameter values are then assigned to each PFT either based on ground measurements or through parameter estimation. This approach has the underlying assumption that all plants within such a PFT show an identical behaviour (Sitch et al., 2003), an assumption applied to all processes represented in such models, including leaf phenology. ~~Dynamic global vegetation models predict PFT distributions based either on pre-defined climate envelopes (Prentice et al., 1992) or pre-defined competitive outcomes, both approaches being based on existing PFT distributions (Arora and Boer, 2006). Recent studies have attempted to use a more physiological based approach (Fisher et al., 2015). Such an assumption is necessary because of the lack of available measurements across the globe needed for models which are not data constrained.~~

The main advantage of using PFTs in vegetation models is the simplicity of the concept and the relatively small number of parameters, minimising both the amount of data and computational effort required. Using PFTs to represent ecological processes at global scales would be the obvious initial choice for parameter inference because the number of parameters can be kept low while still representing the various types of vegetation. PFTs are also a useful concept for future climate predictions where expected changes in vegetation type can be easily represented in this way. Dynamic global vegetation models predict PFT distributions based either on pre-defined climate envelopes (Prentice et al., 1992) or pre-defined competitive outcomes, both approaches being based on existing PFT distributions (Arora and Boer, 2006). Recent studies have attempted to use a more physiological based approach (Fisher et al., 2015).

However, there are a number of disadvantages to using the PFT approach, mainly due to the fact that a PFT-type categorisation imposes fixed parameter values and cannot capture the continuous variation observed in plant traits within and among PFTs (see review by Van Bodegom et al., 2012). Capturing such heterogeneity may not only improve the prediction of biogeochemical and physical dynamics in Earth system models but may also improve predictions of other longer term vegetation processes such as shifts in vegetation composition to climate change. Recent studies have therefore focussed on replacing the PFT method with using plant traits (Sakschewski et al., 2015; Verheijen et al., 2013; Pavlick et al., 2013) and identifying the distribution of traits to use in different locations across the Earth surface (Kattge et al., 2011; Reich et al., 2007).

Given the potential advantages and disadvantages of the PFT approach, it is important to formally evaluate it in comparison to alternative approaches, such as using location-specific traits, but such a formal comparison has not been carried out to date.

In the current paper we aim to investigate the use of PFT and trait based parameters within the
65 framework of a data constrained global phenology model. We have chosen to use a previously de-
veloped leaf phenology model (Caldararu et al., 2014) as a simpler case than a full scale DGVM.
For the purpose of this paper, we use the term phenology to encompass seasonal trajectories of leaf
area index (LAI) as well as the timing of leaf off and leaf on, which is what the term refers to in
its stricter sense. We explore the extent to which the PFT assumption can capture the spatial vari-
70 ability in leaf seasonality. To this end, we use three main different model parametrisations: the local
parametrisation, the fitted parameters at the PFT level and a novel approach which combines PFT
level parameters with local traits, as well as and two additional ones - a global and regional parametri-
sation (Section 3). We explore the differences between the different parametrisations (Section 4) and
we aim to explain the effects shown by local parameters and their relationships with plant traits
75 (Section 5).

2 Datasets used

2.1 LAI data

We use leaf area index (LAI) data from the Moderate Resolution Imaging Spectroradiometer (MODIS)
on board the Terra platform. We use the MODIS collection 5 product MOD15A which is available at
80 1 km spatial resolution and an 8 day time step (<https://lpdaac.usgs.gov/>). The MODIS LAI is based
on a reflectance algorithm which uses the red and near infrared bands and includes corrections for
canopy structure and background soil reflectance (Knyazikhin et al., 1999). In cases where this main
algorithm fails, a backup algorithm is used, which is based on an empirical relationship between
LAI and NDVI (normalised difference vegetation index). We use the quality assurance flags pro-
85 vided with this product to filter pixels that were derived using the backup algorithm or which are
classified as snow covered, as described in Caldararu et al. (2012). We use data for the globe with
a spatial resolution of 1 km, which we then aggregate to the GEOS-4 base resolution of 2° latitude
by 2.5° longitude, by calculating the mean of all pixels within a grid cell. All pixels classified as
cropland were excluded prior to averaging. The aggregation to the coarser resolution was done both
90 to reduce computational effort and to obtain timeseries without the gaps resulting from our filtering
procedure. The data was split into a training (2001-2005) and an evaluation (2006) dataset.

2.2 Environmental variables

To drive the model, we use temperature and photosynthetically active radiation (PAR) data from as-
simulated meteorological data products of the Goddard Earth Observing System (GEOS-4) (Bey et al.,
95 2001), which is available at a spatial resolution of 2° latitude by 2.5° longitude and a temporal resolu-
tion of 3 hours, which we average to a one day temporal resolution. The soil moisture data required
in the model was obtained from the NCAR/NCEP reanalysis daily average surface flux data set

(<http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.surfaceflux.html>) (Kalnay et al., 1996).

100 this is provided at a 1 day temporal resolution and has been regridded to the GEOS-4 spatial resolution.

2.3 Plant functional type map

We use a global PFT map which is used in the Integrated Biosphere simulation model (IBIS) (Kucharik et al., 2000). This differentiates between 13 different plant functional types based on general plant properties (trees vs. grasses), temperature tolerance (tropical vs. temperate) and leaf habit
105 (deciduous vs. evergreen). The PFT data is provided at a 1 km spatial resolution, which we re-grid at the GEOS 4 native resolution based on majority landcover in each grid cell.

3 Model fitting

3.1 Model description

We use a global scale mechanistic phenology model (Caldararu et al., 2014) which is based on a
110 carbon benefit approach so that leaf gains and losses are adjusted to achieve the optimal carbon assimilation at the canopy level. The phenological timing predicted by traditional models arises implicitly by predicting LAI values. At each timestep t and for each location \mathbf{x} , the model calculates leaf gain and loss, and hence overall change in LAI as:

$$\frac{dLAI(\mathbf{x}, t)}{dt} = P(I_0(\mathbf{x}, t), LAI(\mathbf{x}, t - 1)) - \sum_{a=0}^{a_{max}} L(\mathbf{x}, t, a), \quad (1)$$

115 Here, P refers to leaf production processes, which are calculated as a function of solar radiation I_0 and the LAI at the previous timestep $LAI(\mathbf{x}, t - 1)$ and L refers to leaf loss summed over all groups of leaves of the same age a (see Table 1 for a full list of parameters).

To describe leaf gain, we define the concept of target LAI as the optimum number of leaf layers for a given light level at the top of the canopy I_0 so that the bottommost leaf layer receives sufficient
120 light for photosynthesis, that is light at the compensation point C (Wm^{-2}). The target is calculated using Beer's law of light extinction and expressed as:

$$LAI_{target} = -\frac{1}{\alpha} \ln\left(\frac{C}{I_0}\right), \quad (2)$$

Here α is the canopy extinction coefficient calculated as a function of day of year and latitude (Brock, 1981; dePury and Farquhar, 1997). The solar radiation at the top of the canopy I_0 is averaged
125 over a number of p days. We calculate separate values for LAI_{target} for direct and diffuse radiation to account for the different response of photosynthesis to the two. The overall target is then calculated as the minimum of the two values. [We choose to use a direct and diffuse compensation point as a](#)

[simplified representation of light distribution in the canopy](#). At any time step, if the existing LAI is lower than the target value, new leaves are gained to reach the target LAI. We introduce a parameter $gain_{max}$ to limit the new leaves that can be added at each time step to reflect the physiological limits to building new leaves. The gain at any time t and for all locations \mathbf{x} is then calculated as:

$$P(\mathbf{x}, t) = \begin{cases} gain_{max}, & LAI_{targ}(\mathbf{x}, t) - LAI(\mathbf{x}, t - 1) > gain_{max} \\ LAI_{targ}(\mathbf{x}, t) - LAI(\mathbf{x}, t - 1), & 0 < LAI_{targ}(\mathbf{x}, t) - LAI(\mathbf{x}, t - 1) < gain_{max} \\ 0, & LAI_{targ}(\mathbf{x}, t) - LAI(\mathbf{x}, t - 1) < 0 \end{cases} \quad (3)$$

To account for the effects of temperature, we set a threshold of 0°C mean daily temperature under which no leaves are gained. Initial parameter optimisations where this threshold is a free parameter have shown that the model is not very sensitive to its value ([Caldararu et al., 2014](#)).

Following the optimality hypothesis, leaves are lost when their carbon assimilation is less than their respiration and maintenance cost, defined as the limit assimilation value A_{min} . We calculate the carbon assimilation as a linear function of PAR absorbed by the canopy, I_{tot} , per unit leaf area:

$$A_{light} = \frac{\phi I_{tot} - q}{LAI}. \quad (4)$$

Here ϕ and q are model parameters representing photosynthetic efficiency ($\mu\text{mol s}^{-1} \text{W}^{-1}$) and canopy level light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$). Due to the lack of data constraints for carbon assimilation in our modelling framework, we normalise assimilation values and associated parameters. As a result, parameter values for ϕ and q in the above equation do not represent measurable values in the field, but instead scale between potential minimum and maximum photosynthetic rates within the model. [While the absolute values of these two parameters have been scaled, the relative distributions across the globe can still be interpreted as having physical meaning. It is worth noting that the the canopy level compensation point \$q\$ and the direct and diffuse compensation points used in the calculation of the target LAI have different units \(\$\mu\text{mol m}^{-2} \text{s}^{-1}\$ and \$\text{Wm}^{-2}\$ respectively\), due to the units that the original PAR data is in as well as the structure of the model.](#)

To account for water limitation to assimilation and, implicitly, phenological processes, we introduce a factor f_W calculated as:

$$f_w = \frac{s_1(W_s)^{s_2}}{\epsilon LAI} - \frac{u}{\epsilon} \quad (5)$$

where W_s is volumetric soil moisture ([unitlessunit less](#)) obtained from the NCAR/NCEP dataset, s_1 and s_2 are parameters associated with water extraction capacity from the soil, ϵ represent potential evapotranspiration and u is plant water use.

Similarly, we define an age factor f_{age} to describe the declining carbon assimilation of leaves as they age:

$$f_a = \min(1, \exp^{\mu(a_{crit}-a)}), \quad (6)$$

where μ is the rate of decrease with age (years^{-1}) after a limit age a_{crit} (years). Using both these
160 factors the overall assimilation is calculated as:

$$A_{tot} = A_{light} f_w f_a. \quad (7)$$

Overall, the leaf loss at any point in time t and all locations \mathbf{x} for any group of leaves of the same age a (cohort) is:

$$L(\mathbf{x}, t, a) = \begin{cases} LAI(\mathbf{x}, t, a), & A_{tot}(t, a) < A_{min} \\ 0, & A_{tot}(t, a) \geq A_{min}. \end{cases} \quad (8)$$

165 To calculate the overall canopy LAI loss we can then sum over all age groups.

3.2 Model setup

We use five different model parametrisation to explore the extent to which the PFT approach is applicable to a data constrained phenology model. The first such model setup, previously used in
170 Caldararu et al. (2014) is to fit a unique parameter set to each grid cell. We will term this the 'local' model. This approach involves a very large number of parameters (14 parameters at each grid cell, for 2041 vegetated grid cells results in a total of 28574 parameters). It is important to note, however, that the total amount of data available from sources such as MODIS is also very large, making it possible to parametrize extremely parameter-rich models, depending on the exact nature of the data.

The second model setup is using one set of parameters for each PFT, resulting in only 182
175 parameters for the entire globe. We term this the 'PFT' model. To investigate the potential effects of geographical separation, we further separate each PFT into geographical regions (e.g. North American temperate deciduous broadleaf and European temperate deciduous broadleaf), resulting in 44 regions. This was done to test the assumption that species evolving in different geographical locations have different physiological parameters even when belonging to the same PFT. This setup is
180 referred to as the 'region' model and has 616 parameters. As a point of reference, we also introduce a 'global' model where parameters are common for all grid cells, under the assumption that there is no difference in phenological behaviour between vegetation types or geographical regions.

To test the extent to which each parameter represents local characteristics, in the final model setup one or more parameters are location specific while the rest have PFT wide values. We then term a

185 parameter 'local' if it has a specific value at each grid cell. This setup is the 'combination' model'.
 As there are a very large number of possible combinations of local parameters, we perform an initial
 analysis to determine which parameters would most improve the model performance, if local. We
 performed a principal components analysis (PCA) of the spatial variation in parameter values fitted
 for the local model. This highlighted that the principal axis of variation in all parameter values was
 190 strongly correlated with variation in C_{direct} , while the second axis was dominated by variation in
 a_{crit} (Table A1). We also fit 14 different model parametrisations, allowing each parameter in turn
 to be local, while the other parameters are fitted at the PFT level. The two parameters identified by
 the PCA, the light compensation point C_{direct} and the leaf age limit a_{crit} , also show an increase in
 model performance, especially in terms of spatial variation explained (Table A2). As a consequence
 195 of these two analyses, we focus in detail on only one model that combined local and PFT parameters
 in which the C_{direct} and a_{crit} parameters are local. This model has 4238 parameters for the whole
 globe, compared to 28574 for the local model and 182 for the PFT.

We fit all models to the data using a custom Markov Chain Monte Carlo (MCMC) algorithm,
 known as the Filzbach algorithm (<http://research.microsoft.com/en-us/um/cambridge/groups/science/tools/filzbach/filzbach.htm>),
 200 which has been described in detail in Caldararu et al. (2012). Filzbach utilizes MCMC with the
 Metropolis-Hastings algorithm to estimate the joint distribution of the parameter set θ . In our study
 we assume no prior information about θ and so our implementation reduces to estimating the θ as-
 sociated with the highest probability of the observations given the model. To do this we need to
 define a likelihood function that gives the probability of the data for any set of predictions from
 205 the model with a given parametrization. For the local model this likelihood function is maximised
 independently at each location \mathbf{x} and is calculated as:

$$l(Z_{\mathbf{x}}|\theta_{\mathbf{x}}) = \sum_{t(\mathbf{x})} \ln[n(LAI_{obs}(\mathbf{x}, t), LAI_{pred}(\mathbf{x}, t, \theta_{\mathbf{x}}), \sigma_{\mathbf{x}})] \quad (9)$$

where $LAI_{pred}(\mathbf{x}, t, \theta_{\mathbf{x}})$ is the predicted LAI at location \mathbf{x} at time t (this depends on the model pa-
 rameters $\theta_{\mathbf{x}}$); $LAI_{obs}(\mathbf{x}, t)$ is the observed MODIS LAI at location \mathbf{x} at time t ; and $n(LAI_{obs}(\mathbf{x}, t), LAI_{pred}(\mathbf{x}, t, \theta_{\mathbf{x}}), \sigma_{\mathbf{x}})$
 210 denotes the probability density for observing $LAI_{obs}(\mathbf{x}, t)$ given a normal distribution with mean
 $LAI_{pred}(\mathbf{x}, t, \theta_{\mathbf{x}})$ and standard deviation $\sigma_{\mathbf{x}}$ which expresses the magnitude of unexplained varia-
 tion in LAI. The likelihood is calculated as a sum over all time steps at location \mathbf{x} , expressed as
 $t(\mathbf{x})$.

For the global, regional and PFT models, the likelihood estimation is carried out at the global,
 215 regional or PFT level, the likelihood being calculated as the sum at all locations \mathbf{x} within a group \mathbf{G} ,
 $\mathbf{x}(\mathbf{G})$:

$$l(Z_{\mathbf{G}}|\theta_{\mathbf{G}}) = \sum_{\mathbf{x}(\mathbf{G})} \sum_{t(\mathbf{x})} \ln[n(LAI_{obs}(\mathbf{x}, t), LAI_{pred}(\mathbf{x}, t, \theta_{\mathbf{G}}), \sigma_{\mathbf{G}})] \quad (10)$$

Here $Z_{\mathbf{G}}$ and $\theta_{\mathbf{G}}$ denote observed LAI and model parameters for a given group of grid cells \mathbf{G} .
 Within the combination model, the likelihood is again minimised for a whole PFT but in addition to

220 the PFT level parameters θ_G the predicted LAI is also a function of local parameters $\theta_{B,x}$. For all
model parametrisations we use years 2001-2005 as training data and 2006 for evaluation purposes.
The model was run at a daily timestep, but the likelihood was only computed when MODIS data
was available, with a timestep of 8 days.

Without separating training and test data in this way, the more parameter-rich models would be
225 guaranteed to give a better fit to the data. Separating the training and test improves our ability to
assess model performance although, given that the training test data are separated by a relatively
short time, and not separated in space, we expect a tendency for the more parameter-rich models to
provide superior performance against the test data.

3.3 Model performance metrics

230 To compare the different types of models described above, we define several model performance
metrics against the test data. The best model should be able to capture both the timing and magnitude
of the seasonal cycle at each location and the spatial variability in seasonal cycles across the globe.
As an overall measure of fit we use the root mean squared error (RMSE) normalised by the mean LAI
which is a measure of the fit at each particular location. The mean LAI and LAI amplitude describe
235 the magnitude of the seasonal cycle and we use the percent of variation explained to capture the
extent to which the model describes their spatial distribution. Similarly, we use the start and end of
the growing season to describe the timing. We define the start of the growing season as the first date
of the year when the LAI reaches 0.2 of the maximum LAI, while the end of the growing season
is the equivalent last date. To capture the timing in tropical areas with a less pronounced seasonal
240 cycle, we also use the timing of maximum LAI. All metrics are reported for the model evaluation
period (2006).

We choose not to use statistical information criteria (e.g. Bayesian information criteria) because
our model fitting methodology does not easily allow the computation of a single likelihood metric.
The model structure is the same for all parametrisations, with the main model differences being the
245 number of parameters at each grid cell. However, this means that different quantities of data are also
used to fit different models. For example, since the local model is fitted separately at each location,
effectively consists of 2041 separate models, each with 14 parameters, while the PFT model contains
13 models each with 14 parameters. Rather than work out a global information criterion based-metric
for the models we instead opt to use the more meaningful metrics of the relationships between the
250 model predictions and the data described

4 Results

An overall comparison of the five model parametrisations (Table 2) shows that the global model
has the highest error, while the local model has the lowest error. The fact that the global setup has

a very high error is not unexpected since there are known physiological differences between plant
255 functional types, which is why the use of PFTs is common in global modelling studies. However,
the PFT model also has a much higher error than the local one. The regional model does not show
a significant improvement from the PFT, with the exception of the tropical broadleaf evergreen for-
est PFT. Below we will discuss in detail only the PFT, combination and local models, where this
particular forest PFT has been separated into geographical (continental) regions.

260 Figure 1 shows the overall model error over the entire study period for the three main model
parametrisations. Relative root mean squared error (RMSE, unitless) values are much higher for the
PFT model than for the local model, 0.52 ± 0.5 compared to only 0.24 ± 0.03 . The combination
model has a lower error of 0.38 ± 0.45 . These errors are much lower for tropical forests, typically
0.15 for the local model, compared to 0.22 for the PFT and 0.16 for the combination models. Similar
265 errors occur in temperate deciduous areas. The highest errors are observed in tropical grasslands and
shrublands for all models and specifically for the PFT model (up to 2).

Figure 2 shows the relative difference between model and observed LAI annual mean and ampli-
tude. Both the local and combination models underestimate the mean LAI across all PFTs by 11.3%
and 23.4% respectively. The PFT model exhibits a higher bias, with a mean value of 45.4%, with
270 the highest difference in tropical and temperate deciduous regions (over 90%). The PFT model un-
derestimates the seasonal amplitude in tropical forests by up to 50% and by 20% in higher latitude
regions, while overestimating it by up to 200% in subtropical grasslands and savannas. The combi-
nation model shows a similar pattern but a lower bias, with differences of 27 % in tropical forests
and 13% in temperate areas, similar to those of the local model.

275 Figures 3 and 4 show a comparison of predicted and observed LAI mean and amplitude for forest
and grass PFTs, respectively. The PFT model captures the mean behaviour but is not able to predict
the full range of values in either mean LAI or seasonal amplitude for any PFT, explaining on average
only 28% and 12% respectively of the spatial variation in LAI mean and amplitude. The combination
model shows an improvement explaining on average 70% of the spatial variation in mean LAI and
280 56% of the amplitude, compared to the local model, which explains 90% and 87% respectively. [The model results in boreal regions are difficult to interpret because of the uncharacteristically low values of the MODIS LAI in these regions, which are partially caused by high within cell heterogeneity \(Caldararu et al., 2014\).](#)

All models show a similar ability to predict the timing of the seasonal cycle, with an error of 16
285 days for the start of the growing season and differences of up to 24 days for the maximum and end of
the growing season, while in tropical evergreen forests where the time of maximum LAI is 16 days
earlier compared to that shown by the MODIS data.

Figure 5 shows LAI time series for four different PFTs. At the tropical evergreen forest location
the local and combination models show a similar fit, whilst the PFT model cannot capture any sea-
290 sonal cycle. At the dry tropical (savanna) location, the local model shows a good fit, but both the

combined and PFT model predict a much higher LAI. For the temperate deciduous forest, all models capture the timing of the seasonal cycle, but the PFT model predicts a lower amplitude than that observed in the MODIS data. For the boreal evergreen forest, both the PFT and combination model predict a higher LAI than that observed by MODIS.

295 Figure 6 shows the relationship between model error and grid cell heterogeneity within the PFT model in terms of fraction of cell occupied by the dominant PFT for model RMSE, bias in LAI mean and bias in LAI amplitude. All three metrics show no correlation with grid cell heterogeneity, with an R^2 of less than 0.01, indicating that there is no systematic bias in errors caused by the chosen PFT map.

300 To further investigate the observed differences arising from the model parametrisation, we can analyse the parameter values for each different model. Figures 7 and 8 show parameter distributions for the light compensation point and leaf age limit parameters for six selected PFTs. Figure 9 shows global distributions of the local parameters in the combined model. The PFT model fitted parameters are in most cases capturing the mean values of the local parameter distributions, but the discrepancy
305 is higher in PFTs where the distribution has a long tail or multiple modes, especially in the grass PFTs (Fig. 8). In the evergreen tropical forest the discrepancy between the one value estimated by the PFT model and the wide range of both the local and combination parameters is particularly large, as, according to the model, phenology in these areas is limited by leaf age (Caldararu et al., 2014) and the different modes observed in the parameter distribution are essential for representing
310 the leaf cycles caused by species with long but varied lifespans. The discrepancy in leaf age values between the different model parametrisations for the temperate PFT does not have such a profound effect on predicted LAI as phenology in these regions is limited by temperature and light and the age parameters are often poorly constrained even for the local model. Other large differences in parameter values are observed in the grass PFTs which, as discussed above, have some of the highest
315 errors.

Overall, all metrics show that the PFT model performs poorly across the globe, while the combination model, which has only two location specific parameters, shows a good fit to the data.

5 Discussion

In this paper we have investigated the capacity of a global phenology model parametrised at the PFT level to represent observed phenological behaviour. We show that the PFT model cannot fully capture spatial variations in LAI mean and amplitude. In contrast, a model with local parameters results in a better model fit, but has a very large number of parameters, which make it very difficult to use. However, a combination model, where two of the model parameters are local while the others are fitted at the PFT scale, performs well with a reduced number of parameters. Our analysis shows that
320 two specific parameters need to have local values, the direct compensation point C_{direct} (henceforth
325

referred to as compensation point) and the leaf age limit age_{crit} . Below, we focus on the possible biological significance of the combined model and the possibility of using this concept in a more general setting.

5.1 Plant traits in the combined model

330 The most straightforward biological explanation for the observed results of the combined model is that the two local parameters - the light compensation point and leaf age limit - are location specific plant traits that vary within a PFT sufficiently to affect model performance. Previous studies which have included traits as a replacement for the PFT concept have done so starting from biological principles, either based on trait databases (Verheijen et al., 2013) or by evolving traits through
335 plant competition (Sakschewski et al., 2015). In contrast, in the current study we include no prior knowledge of which parameters correspond to known plant traits and the local parameters in the combination model are inferred from the fitted model. The question that arises is if the resulting parameters and parameter values provide any biological insights or if this is just a mathematical artefact, resulting either from the data used or the model structure.

340 The light compensation point is not a trait commonly used in models or included in trait data, but it is closely related to leaf photosynthetic parameters such as V_{cmax} and J_{max} and could easily be derived in terms of these if our model included a biochemical description of photosynthesis. There is one other parameter in our model, the photosynthetic efficiency, ϕ , that is perhaps closer to the commonly used traits but did not emerge as the most important parameter in the PCA (Table A1) or
345 was able to explain the spatial variability in LAI (Table A2). In contrast to the compensation point parameter which drives leaf gain across the globe, ϕ mainly determines leaf loss in temperate and boreal regions which are light and temperature limited (Caldararu et al., 2014). This result shows that leaf loss within a given PFT across temperate and boreal forests can be predicted well from environmental factors alone, without any inherent trait variation within a PFT. This could result either
350 from the real trait variation being low, or, the real trait variation having such a strong correlation with environmental factors that the effects of the trait variation cannot be separated from the effects of the environment. More ground measurements could resolve between these two possibilities. The model also contains a parameter for diffuse light compensation point, $C_{diffuse}$, introduced as a simple way of representing light in the canopy. This parameter is expressed relative to the C_{direct} value at each location even though the parameter acts as a PFT level parameter, the absolute value for diffuse compensation point will vary spatially.

While the light compensation point is not a common parameter in vegetation models, measured values can be obtained from light response curves measured for individual plant species. Reported values range from 0.5 to 16.2 Wm^{-2} for tree species, varying with species and light environment
360 (Riddoch et al., 1991; Lewis et al., 2000; Givnish et al., 2004; Baltzer and Thomas, 2007) . The compensation point values for the combined model agree broadly with these values (Fig. 7), with the exception of

values for boreal forests, where values can be much higher, of up to 60 Wm^{-2} , an error which we attribute to the poor quality of MODIS data in this region.

Leaf longevity is one of the main parameters used in vegetation models which employ plant traits (e.g. Sakschewski et al., 2015) as well as in the analysis of the leaf trait spectrum (Wright et al., 2004). The second local parameter used in the combination model, the leaf age limit age_{crit} does not have the same meaning as leaf lifespan, ~~as in high latitude systems it is never reached and in tropical systems it mainly~~ because leaf ageing is only one of the three leaf loss mechanisms in our model, alongside temperature and light and water limitation. Thus, in regions where leaf loss is not age limited, for example in temperate areas, the parameter is poorly constrained and its age value never reached, as leaf loss occurs much sooner. In wet tropical systems where leaf ageing is the main driver for leaf loss, this age parameter is the critical age where leaves start ageing so that the effective lifespan can be much larger. However, according to our model, it is the main driver of leaf loss in tropical systems and thus a proxy for determining leaf lifespan (see Caldararu et al. (2014) for a detailed discussion of the physical interpretation of this parameter).

5.2 Model structure

Our results show that allowing two critical traits to vary within a PFT among locations, provides a superior model performance. It is likely that such traits vary due to underlying factors that are not explicitly included in our model. Two likely candidates for such hidden factors are nutrient availability and canopy structure. If the effects of these factors on traits could be understood and modelled explicitly, this could dramatically reduce the number of parameters required by the model, without making the assumption that the traits are constant within any PFT.

Leaf photosynthetic capacity is a function of leaf nitrogen content (Farquhar et al., 1980; dePury and Farquhar, 1997; Hikosaka, 2003), a factor which has not been included in our model. According to current photosynthetic models, a higher leaf nitrogen content would lead to a higher light limited photosynthetic rate and hence lower compensation point. Figure 9 shows the spatial distribution of the compensation point parameter as fitted in the combination model. The highest values are observed in grasslands, especially in the tropical region. In forest PFTs, the highest compensation point occurs over tropical forests, followed by temperate deciduous regions. This is supported by field studies, as higher latitude forests are generally more nitrogen limited while tropical and temperate grasslands are one of the most nutrient poor systems in terms of phosphorus (Bustamante et al., 2006; Elser et al., 2007). To explore the intra-PFT distribution of nitrogen availability and fully explain the locality of our compensation point parameter we would need either a global data set of nitrogen availability such as the nutrient limitation index derived as a function of evapotranspiration and ecosystem production (Fisher et al., 2012) or coupling the phenology model with a full scale vegetation model with an explicit representation of the nitrogen cycle (e.g. Zaehle and Friend, 2010).

Canopy structure determines the light environment in the canopy and controls the actual amount of light that reaches the leaves for a given light intensity above the canopy. This means it can be an important value in determining the compensation point, both through model structure and long term impact on plant behaviour. Within the model used in this study, we assume a homogeneous canopy, with a random distribution of leaf angles and no clumping, assumptions which can be considered valid at very large scales, but can potentially introduce errors for certain forest structure types. It has been shown (Chen et al., 2012) that including leaf clumping in a carbon assimilation model has a major impact on resulting global gross primary productivity values. A leaf clumping factor would be used to adjust the attenuation coefficient α (Eq. 2) to improve the description of light transmission through the canopy. It is possible that the compensation point parameter C_{direct} artificially accounts for this variation in canopy structure, which explains its observed spatial variability. Further information such as the leaf clumping index map developed by Chen et al. (2005) would be needed to distinguish between the actual compensation point and canopy structure. This relationship is further complicated by the fact that plants adapt to their light environment, so that leaves in closed canopies will be better adapted to shaded conditions and will have lower compensation points so that tropical forests, which are highly stratified, have a much lower compensation point than other systems. The question is further complicated as canopy structure itself can be an adaptation to the available resources such as light, water or nitrogen making it difficult to distinguish between all possible factors in the absence of further data.

5.3 Model parametrisation

One of the main possible sources of error in our conclusion is the way we have parametrised the PFT model. In most models which use the PFT concept, grid cells are represented as a mix of PFTs, with PFT specific parameters assigned to each fraction (e.g. Stockli et al., 2008), while we have chosen, in order to reduce the computational effort necessary for a global data constrained model, to only use the dominant PFT in each grid cell. This approach, together with the low resolution that the model is run at could mean that the poor fit shown by the PFT model is due to a poor representation of PFTs rather than the unsuitability of the concept in vegetation models. If this was the case, we would expect high model errors in grid cells with a larger mix of vegetation types. However, the high errors in the PFT model are consistent throughout and do not show a significant correlation with the grid cell PFT heterogeneity (Figure 6), indicating that the mix of vegetation types within grid cells cannot be the only explanatory factor. For a more robust conclusion, we would need to re-run the analysis with either a higher spatial resolution or with a PFT mix in each grid cell. Given the high computational demand of the fitting procedure, this would ideally be done for a smaller number of PFTs rather than at global scales.

We use space borne vegetation data from the MODIS Terra sensor, as satellite measurements are one of the only sources of data for constraining global level vegetation models, but does suffer

from instrument error and atmospheric contamination. We have attempted to filter the data robustly using data quality flags, as discussed in section 2.1 and previous studies (Caldararu et al., 2012, 435 2014) and the fitting procedure contains a parameter σ_x which accounts for error in the observations (Section 3.2). The largest possible source of error is the seasonality shown by the MODIS data in the Amazon basin and other tropical regions, which is most likely to determine the spatial distribution of the age_{crit} parameter. Initial studies have shown that there is an increase in satellite observed LAI during the dry season over the Amazon (Myneni et al., 2007; Huete et al., 2006), but more recent 440 studies have argued that the observed change in LAI is due to sun-sensor geometry (Morton et al., 2014). This finding has been contradicted by subsequent papers (Bi et al., 2015) and we do not attempt to give an answer to this debate. For the purpose of this study, we assume that this observed change in LAI is a reflection of actual changes in leaf cover, an assumption backed by observed changes in gross primary productivity (GPP) and litterfall (da Rocha et al., 2004; Goulden et al., 445 2004; Hutyyra et al., 2007).

5.4 Method generality

As more studies begin to acknowledge that the PFT concept is not necessarily the best approach to vegetation modelling, we need to quantify the extent to which the inclusion of spatially distributed parameters or plant traits improve our predictive capability and to identify the optimal number of 450 parameters that both give a good model fit and minimise computational cost. In this study we have attempted to not only build a model with locally distributed parameters but also to quantify the extent to which a model with local parameters and one with PFT level parameters can capture the spatial variability in global LAI observations. Furthermore, we quantitatively identified which parameters need to be local to improve model performance with a view to reduce data and computational needs. 455 We believe that the method used here for investigating the use of PFT level parameters has a high degree of generality and can be applied to a large variety of models and input datasets.

One of the advantages of the PFT concept is its capacity to represent future changes in vegetation distribution within DGVMs. Given a predicted change in climate, models using PFTs can then predict a change in PFT distribution, using either predefined climate envelopes (Sitch et al., 2003) or 460 predefined plant competition rules (Arora and Boer, 2006). Models which use plant traits instead do not offer such a straightforward solution, but have a number of advantages. The PFT approach only allows abrupt changes in vegetation and cannot capture any plant adaptation to climate, while a trait approach can represent gradual changes. However, representing changing traits in response to climate is more difficult, both conceptually and computationally. Recent studies have proposed the 465 use of plant competition and emergent traits to predict vegetation distribution (van Bodegom et al., 2014; Wullschleger et al., 2014; Fish
Therefore, a logical next step to our analysis would be to identify the environmental responses of the two combined parameters and their relationships with plant physiology responses so that parameter

[values can be estimated independent of data constraints for the purpose of model predictions under future climate change.](#)

470 **6 Conclusions**

In this paper we explored the extent to which plants within the same PFT exhibit the same phenological characteristics using a process-based global phenology model. We showed that a model with PFT wide parameters cannot explain the observed spatial variation in seasonal cycles, but that an intermediate model with two location specific parameters gives a good overall model fit and can reliably be
475 used for phenological studies. The spatial patterns of these local parameters, the light compensation point and leaf age limit, might be explained by species adaptation to the local climate or nutrient and water availability and further data is needed to fully understand the observed distribution. The modelling approach used to determine the validity of PFT level models can provide further insight for global vegetation models which use plant functional types as a basis for upscaling measured or
480 fitted parameter values and can hence improve global simulations of ecosystem processes.

Appendix A: Preliminary analysis~~for the combination model parametrisation~~

Table A1 shows results from the principal component analysis (PCA) performed to identify parameters in the combination model and table A2 shows fits for the preliminary analysis for the combination model.

485 [Figure A1 shows relative RMSE and error in LAI mean and amplitude for the regional model analysis.](#)

Acknowledgements. [We would like to thank the developers of the MODIS LAI product for providing the data that forms the basis for our work.](#)

References

- 490 Arora, V. K. and Boer, G. J.: Simulating Competition and Coexistence between Plant Functional Types in a Dynamic Vegetation Model, *Earth Interact.*, 10, 1–30, doi:10.1175/EI170.1, <http://dx.doi.org/10.1175/EI170.1>, 2006.
- Baltzer, J. and Thomas, S.: Physiological and morphological correlates of whole-plant light compensation point in temperate deciduous tree seedlings, *Oecologia*, 153, 209–223, doi:10.1007/s00442-007-0722-2, <http://dx.doi.org/10.1007/s00442-007-0722-2>, 2007.
- 495 Bey, I., Jacob, D., Yantosca, R., Logan, J., Field, B., Fiore, A., Li, Q., Liu, H., Mickley, L., and Schultz, M.: Global modeling of tropospheric chemistry with assimilated meteorology: Model description and evaluation, *Journal of Geophysical Research*, 106, 23 073–23 095, 2001.
- Bi, J., Knyazikhin, Y., Choi, S., Park, T., Barichivich, J., Ciais, P., Fu, R., Ganguly, S., Hall, F., Hilker, T., Huete, A., Jones, M., Kimball, J., Lyapustin, A. I., M \ddot{o} ttus, M., Nemani, R. R., Piao, S., Poulter, B., Saleska, S. R., Saatchi, S. S., Xu, L., Zhou, L., and Myneni, R. B.: Sunlight mediated seasonality in canopy structure and photosynthetic activity of Amazonian rainforests, *Environmental Research Letters*, 10, 064 014, doi:10.1088/1748-9326/10/6/064014, <http://stacks.iop.org/1748-9326/10/i=6/a=064014>, 2015.
- 500 Box, E. O.: Plant Functional Types and Climate at the Global Scale, *Journal of Vegetation Science*, 7, pp. 309–320, <http://www.jstor.org/stable/3236274>, 1996.
- 505 Brock, T. D.: Calculating solar radiation for ecological studies, *Ecological Modelling*, 14, 1–19, doi:10.1016/0304-3800(81)90011-9, <http://www.sciencedirect.com/science/article/pii/0304380081900119>, 1981.
- Bustamante, M. M. C., Medina, E., Asner, G. P., Nardoto, G. B., and Garcia-Montiel, D. C.: Nitrogen cycling in tropical and temperate savannas, in: *Nitrogen Cycling in the Americas: Natural and Anthropogenic Influences and Controls*, edited by Martinelli, L. A. and Howarth, R. W., pp. 209–237, Springer Netherlands, doi:10.1007/978-1-4020-5517-1_10, 2006.
- 510 Caldararu, S., Palmer, P. I., and Purves, D. W.: Inferring Amazon leaf demography from satellite observations of leaf area index, *Biogeosciences*, 9, 1389–1404, doi:10.5194/bg-9-1389-2012, <http://www.biogeosciences.net/9/1389/2012/>, 2012.
- 515 Caldararu, S., Purves, D. W., and Palmer, P. I.: Phenology as a strategy for carbon optimality: a global model, *Biogeosciences*, 11, 763–778, doi:10.5194/bg-11-763-2014, <http://www.biogeosciences.net/11/763/2014/>, 2014.
- Chen, J., Menges, C., and Leblanc, S.: Global mapping of foliage clumping index using multi-angular satellite data, *Remote Sensing of Environment*, 97, 447–457, doi:10.1016/j.rse.2005.05.003, <http://www.sciencedirect.com/science/article/pii/S0034425705001550>, 2005.
- 520 Chen, J. M., Mo, G., Pisek, J., Liu, J., Deng, F., Ishizawa, M., and Chan, D.: Effects of foliage clumping on the estimation of global terrestrial gross primary productivity, *Global Biogeochem. Cycles*, 26, GB1019–, doi:10.1029/2010GB003996, 2012.
- 525 da Rocha, H. R., Goulden, M. L., Miller, S. D., Menton, M. C., Pinto, L., de Freitas, H. C., and Figueira, A.: Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia, *Ecological Applications*, 14, S22–S32, 2004.

- dePury, D. G. G. and Farquhar, G. D.: Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models, *Plant Cell and Environment*, 20, 537–557, 1997.
- 530 Elser, J. J., Bracken, M. E., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B., and Smith, J. E.: Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems, *Ecology Letters*, 10, 1135–1142, doi:10.1111/j.1461-0248.2007.01113.x, 2007.
- Farquhar, G. D., Caemmerer, S., and Berry, J. A.: A biochemical model of photosynthetic CO₂ assimilation in
535 leaves of C₃ species, *Planta*, 149, 78–90, doi:10.1007/BF00386231, 1980.
- Fisher, J. B., Badgley, G., and Blyth, E.: Global nutrient limitation in terrestrial vegetation, *Global Biogeochem. Cycles*, 26, GB3007–, doi:10.1029/2011GB004252, 2012.
- Fisher, R. A., Muszala, S., Versteinstein, M., Lawrence, P., Xu, C., McDowell, N. G., Knox, R. G., Koven, C., Holm, J., Rogers, B. M., Lawrence, D., and Bonan, G.: Taking off the training wheels: the properties of a dynamic vegetation model without climate envelopes, *Geoscientific Model Development Discussions*, 8, 3293–3357, doi:10.5194/gmdd-8-3293-2015, <http://www.geosci-model-dev-discuss.net/8/3293/2015/>, 2015.
- 540 Givnish, T. J., Montgomery, R. A., and Goldstein, G.: Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points, *American Journal of Botany*, 91, 228–246, doi:10.3732/ajb.91.2.228, <http://www.amjbot.org/content/91/2/228.abstract>,
545 2004.
- Goulden, M. L., Miller, S. D., da Rocha, H. R., Menton, M. C., de Freitas, H. C., Figueira, A., and de Sousa, C. A. D.: Diel and seasonal patterns of tropical forest CO₂ exchange, *Ecological Applications*, 14, S42–S54, 2004.
- Haxeltine, A. and Prentice, I. C.: A General Model for the Light-Use Efficiency of Primary Production, *Functional Ecology*, 10, pp.551–561, <http://www.jstor.org/stable/2390165>, 1996.
- 550 Hayden, B. P.: Ecosystem feedbacks on climate at the landscape scale, *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 353, 5–18, doi:10.1098/rstb.1998.0186, <http://rstb.royalsocietypublishing.org/content/353/1365/5.abstract>, 1998.
- Hikosaka, K.: A Model of Dynamics of Leaves and Nitrogen in a Plant Canopy: An Integration of Canopy
555 Photosynthesis, Leaf Life Span, and Nitrogen Use Efficiency., *The American Naturalist*, 162, pp.149–164, doi:10.1086/376576, 2003.
- Huete, A. R., Didan, K., Shimabukuro, Y. E., Ratana, P., Saleska, S. R., Hutyrá, L. R., Yang, W. Z., Nemani, R. R., and Myneni, R.: Amazon rainforests green-up with sunlight in dry season, *Geophysical Research Letters*, 33, L06 405, doi:10.1029/2005GL025583, 2006.
- 560 Hutyrá, L. R., Munger, J. W., Saleska, S. R., Gottlieb, E., Daube, B. C., Dunn, A. L., Amaral, D. F., de Camargo, P. B., and Wofsy, S. C.: Seasonal controls on the exchange of carbon and water in an Amazonian rain forest, *Journal of Geophysical Research - Biogeosciences*, 112, G03 008, doi:10.1029/2006JG000365, 2007.
- Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K., Ropelewski, C., Wang,
565 J., Leetmaa, A., Reynolds, R., Jenne, R., and Joseph, D.: The NCEP/NCAR 40-year reanalysis project, *Bulletin of the American meteorological society*, 77, 437–471, 1996.

- Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bonisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Van Bodegom, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., Atkin, O., Bahn, M., Baker, T. R., Baldocchi, D.,
570 Bekker, R., Blanco, C. C., Blonder, B., Bond, W. J., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender-
bares, J., Chambers, J. Q., Chapin Iii, F. S., Chave, J., Coomes, D., Cornwell, W. K., Craine, J. M., Dobrin,
B. H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W. F., Fang, J., Fernandez-Mendez,
F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G. T., Fyllas, N. M., Gallagher, R. V.,
Green, W. A., Gutierrez, A. G., Hickler, T., Higgins, S. I., Hodgson, J. G., Jalili, A., Jansen, S., Joly, C. A.,
575 Kerkhoff, A. J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J. M. H., Kramer, K., Kuhn, I.,
Kurokawa, H., Laughlin, D., Lee, T. D., Leishman, M., Lens, F., Lenz, T., Lewis, S. L., Lloyd, J., Llusa,
J., Louault, F., Ma, S., Mahecha, M. D., Manning, P., Massad, T., Medlyn, B. E., Messier, J., Moles, A. T.,
Muller, S. C., Nadrowski, K., Naeem, S., Niinemets, U., Nollert, S., Nuske, A., Ogaya, R., Oleksyn, J.,
Onipchenko, V. G., Onoda, Y., Ordonez, J., Overbeck, G., Ozinga, W. A., Patino, S., Paula, S., Pausas,
580 J. G., Penuelas, J., Phillips, O. L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R.,
Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert,
A., Sosinski, E., Soussana, J.-f., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher,
E., White, M., White, S., Wright, S. J., Yguel, B., Zaehle, S., Zanne, A. E., and Wirth, C.: TRY - a global
database of plant traits, *Global Change Biology*, 17, 2905–2935, doi:10.1111/j.1365-2486.2011.02451.x,
585 <http://dx.doi.org/10.1111/j.1365-2486.2011.02451.x>, 2011.
- Knyazikhin, Y., J., G., Privette, J. L., Tian, Y., Lotsch, A., Zhang, Y., Wang, Y., Morisette, J. T., P.Votava,
Myneni, R., Nemani, R. R., and Running, S. W.: MODIS Leaf Area Index (LAI) and Fraction of Photosyn-
thetically Active Radiation Absorbed by Vegetation (FPAR) Product (MOD15) Algorithm Theoretical Basis
Document, <http://modis.gsfc.nasa.gov/data/atbd/>, 1999.
- 590 Kucharik, C. J., Foley, J. A., Delire, C., Fisher, V. A., Coe, M. T., Lenters, J. D., Young-Molling, C., Ra-
mankutty, N., Norman, J. M., and Gower, S. T.: Testing the performance of a dynamic global ecosystem
model: Water balance, carbon balance, and vegetation structure, *Global Biogeochem. Cycles*, 14, 795–825,
doi:10.1029/1999GB001138, 2000.
- Lewis, J. D., McKane, R. B., Tingey, D. T., and Beedlow, P. A.: Vertical gradients in photosynthetic light
595 response within an old-growth Douglas-fir and western hemlock canopy, *Tree Physiology*, 20, 447–456,
doi:10.1093/treephys/20.7.447, <http://treephys.oxfordjournals.org/content/20/7/447.abstract>, 2000.
- Morton, D. C., Nagol, J., Carabjal, C. C., Rosette, J., Palace, M., Cook, B. D., Vermote, E. F., Harding, D. J.,
and North, P. R. J.: Amazon forests maintain consistent canopy structure and greenness during the dry season,
Nature, 506, 221–224, <http://dx.doi.org/10.1038/nature13006>, 2014.
- 600 Myneni, R. B., Yang, W. Z., Nemani, R. R., Huete, A. R., Dickinson, R. E., Knyazikhin, Y., Didan, K., Fu,
R., Juarez, R. I. N., Saatchi, S. S., Hashimoto, H., Ichii, K., Shabanov, N. V., Tan, B., Ratana, P., Privette,
J. L., Morisette, J. T., Vermote, E. F., Roy, D. P., Wolfe, R. E., Friedl, M. A., Running, S. W., Votava, P.,
El-Saleous, N., Devadiga, S., Su, Y., and Salomonson, V. V.: Large seasonal swings in leaf area of Amazon
rainforests, *Proc Natl Acad Sci U S A*, 104, 4820–4823, 2007.
- 605 Pavlick, R., Drewry, D. T., Bohn, K., Reu, B., and Kleidon, A.: The Jena Diversity-Dynamic Global Vege-
tation Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochem-

- istry based on plant functional trade-offs, *Biogeosciences*, 10, 4137–4177, doi:10.5194/bg-10-4137-2013, <http://www.biogeosciences.net/10/4137/2013/>, 2013.
- 610 Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A., and Solomon, A. M.: A Global Biome Model Based on Plant Physiology and Dominance, Soil Properties and Climate, *Journal of Biogeography*, 19, pp.117–134, <http://www.jstor.org/stable/2845499>, 1992.
- Reich, P. B., Wright, I. J., and Lusk, C. H.: Predicting leaf physiology from simple plant and climate attributes: A global GLOPNET analysis, *Ecological Applications*, 17, 1982–1988, 2007.
- Ridloch, I., Lehto, T., and Grace, J.: Photosynthesis of Tropical Tree Seedlings in Relation to Light and Nutrient Supply, *New Phytologist*, 119, pp.137–147, <http://www.jstor.org/stable/2557718>, 1991.
- 615 Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., Peñuelas, J., and Thonicke, K.: Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model, *Global Change Biology*, 21, 2711–2725, doi:10.1111/gcb.12870, <http://dx.doi.org/10.1111/gcb.12870>, 2015.
- 620 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, *Glob Change Biol*, 9, 161–185, 2003.
- Smith, T. M.: *Plant functional types :their relevance to ecosystem properties and global change /edited by T.M. Smith, H.H. Shugart and F.I. Woodward.*, Cambridge University Press., Cambridge :, 1997.
- 625 Stockli, R., Rutishauser, T., Dragoni, D., O’Keefe, J., Thornton, P. E., Jolly, M., Lu, L., and Denning, A. S.: Remote sensing data assimilation for a prognostic phenology model, *Journal of Geophysical Research: Biogeosciences*, 113, G04 021, doi:10.1029/2008JG000781, <http://dx.doi.org/10.1029/2008JG000781>, 2008.
- Van Bodegom, P. M., Douma, J. C., Witte, J. P. M., Ordonez, J. C., Bartholomeus, R. P., and Aerts, R.: Going beyond limitations of plant functional types when predicting global ecosystem - atmosphere fluxes: exploring the merits of traits-based approaches, *Global Ecology and Biogeography*, 21, 625–636, doi:10.1111/j.1466-8238.2011.00717.x, <http://dx.doi.org/10.1111/j.1466-8238.2011.00717.x>, 2012.
- 630 van Bodegom, P. M., Douma, J. C., and Verheijen, L. M.: A fully traits-based approach to modeling global vegetation distribution, *Proceedings of the National Academy of Sciences*, 111, 13 733–13 738, doi:10.1073/pnas.1304551110, <http://www.pnas.org/content/111/38/13733.abstract>, 2014.
- 635 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, doi:10.5194/bg-10-5497-2013, <http://www.biogeosciences.net/10/5497/2013/>, 2013.
- White, M. A., Running, S. W., and Thornton, P. E.: The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest, *International Journal of Biometeorology*, 42, 139–145, doi:10.1007/s004840050097, 1999.
- 640 Wilson, K. B. and Baldocchi, D. D.: Seasonal and interannual variability of energy fluxes over a broadleaved temperate deciduous forest in North America, *Agricultural and Forest Meteorology*, 100, 1–18, doi:DOI: 10.1016/S0168-1923(99)00088-X, <http://www.sciencedirect.com/science/article/B6V8W-3Y9G9YN-1/2/a64d3b46065d636190187ce3df2a333a>, 2000.

- 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., Lee, W., Lusk, C., Midgley, J. J., Navas, M.-L., Niinemets, U., Oleksyn, 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, doi:10.1038/nature02403, 2004.
- 650 Wullschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. M., Kattge, J., Norby, R. J., van Bodegom, P. M., and Xu, X.: Plant functional types in Earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems, *Annals of Botany*, doi:10.1093/aob/mcu077, <http://aob.oxfordjournals.org/content/early/2014/05/02/aob.mcu077.abstract>, 2014.
- 655 Zaehle, S. and Friend, A. D.: Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates, *Global Biogeochemical Cycles*, 24, Gb1005, doi:10.1029/2009GB003521, <http://dx.doi.org/10.1029/2009GB003521>, 2010.

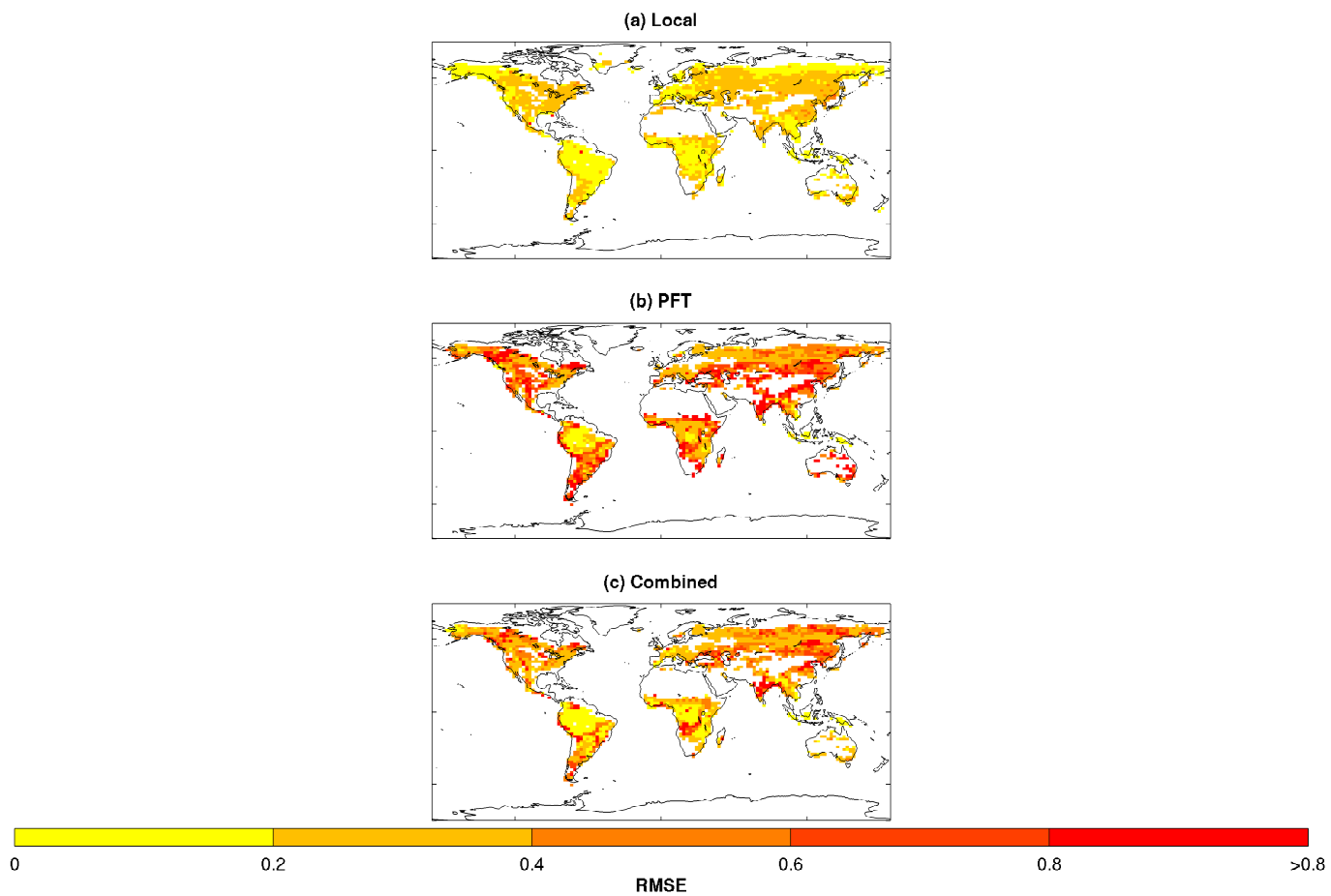



Figure 1. Root mean squared error (RMSE) of predicted LAI over the model study period for the local, PFT and combined models. All values have been normalised to the mean observed LAI at all locations.

660 

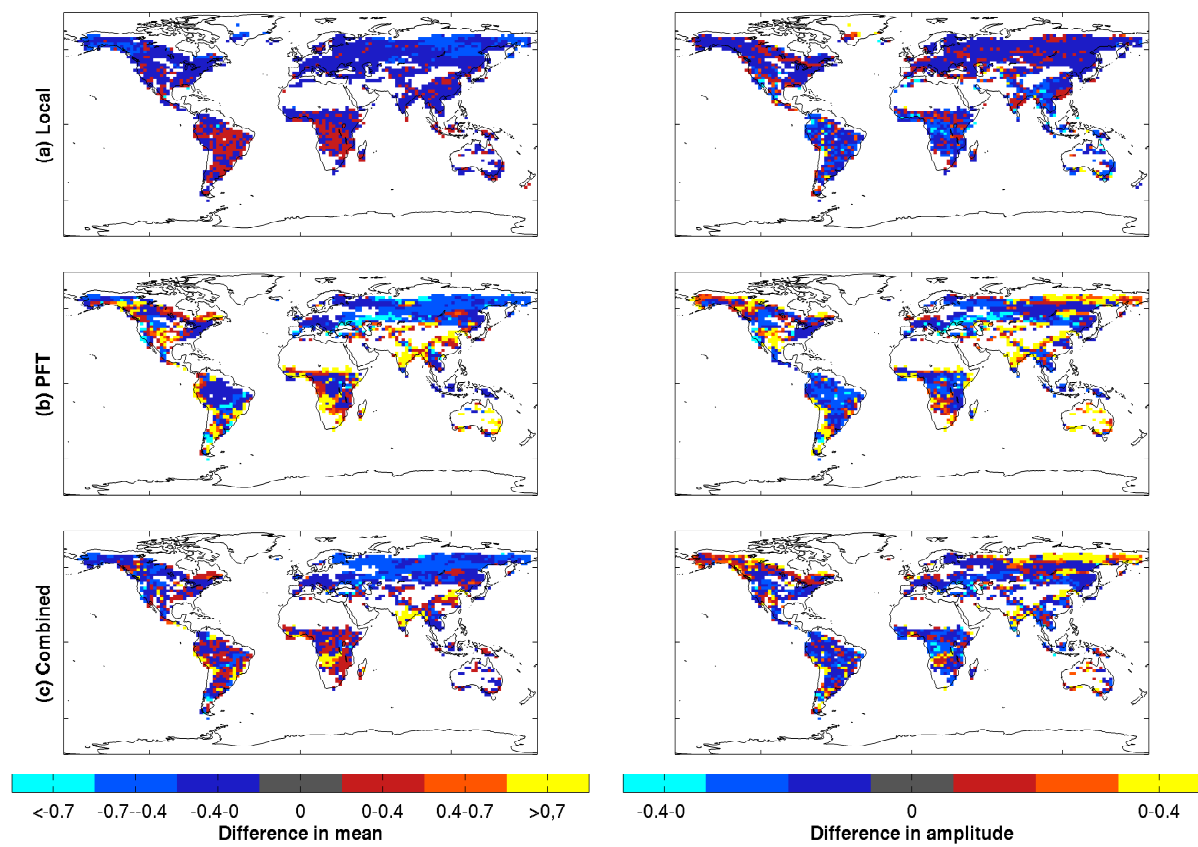


Figure 2. Difference between predicted and observed annual mean LAI (left) and seasonal amplitude (right) for the local, PFT and combined models. All values have been normalised to the mean observed LAI at all locations

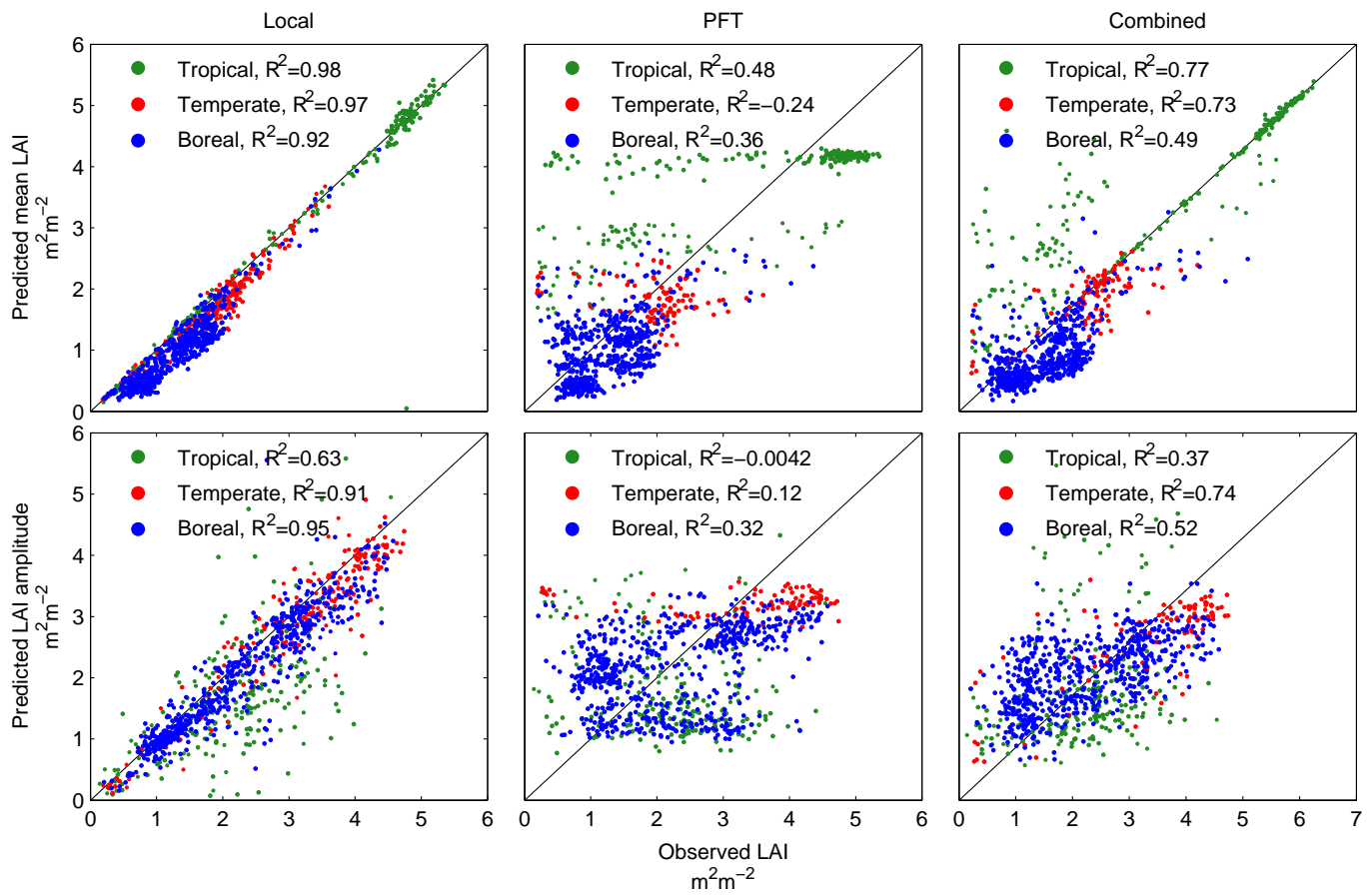


Figure 3. Comparison of predicted and observed mean LAI and seasonal amplitude for the local, PFT and combined models for tropical (green), temperate (red) and boreal (blue) forest PFTs.

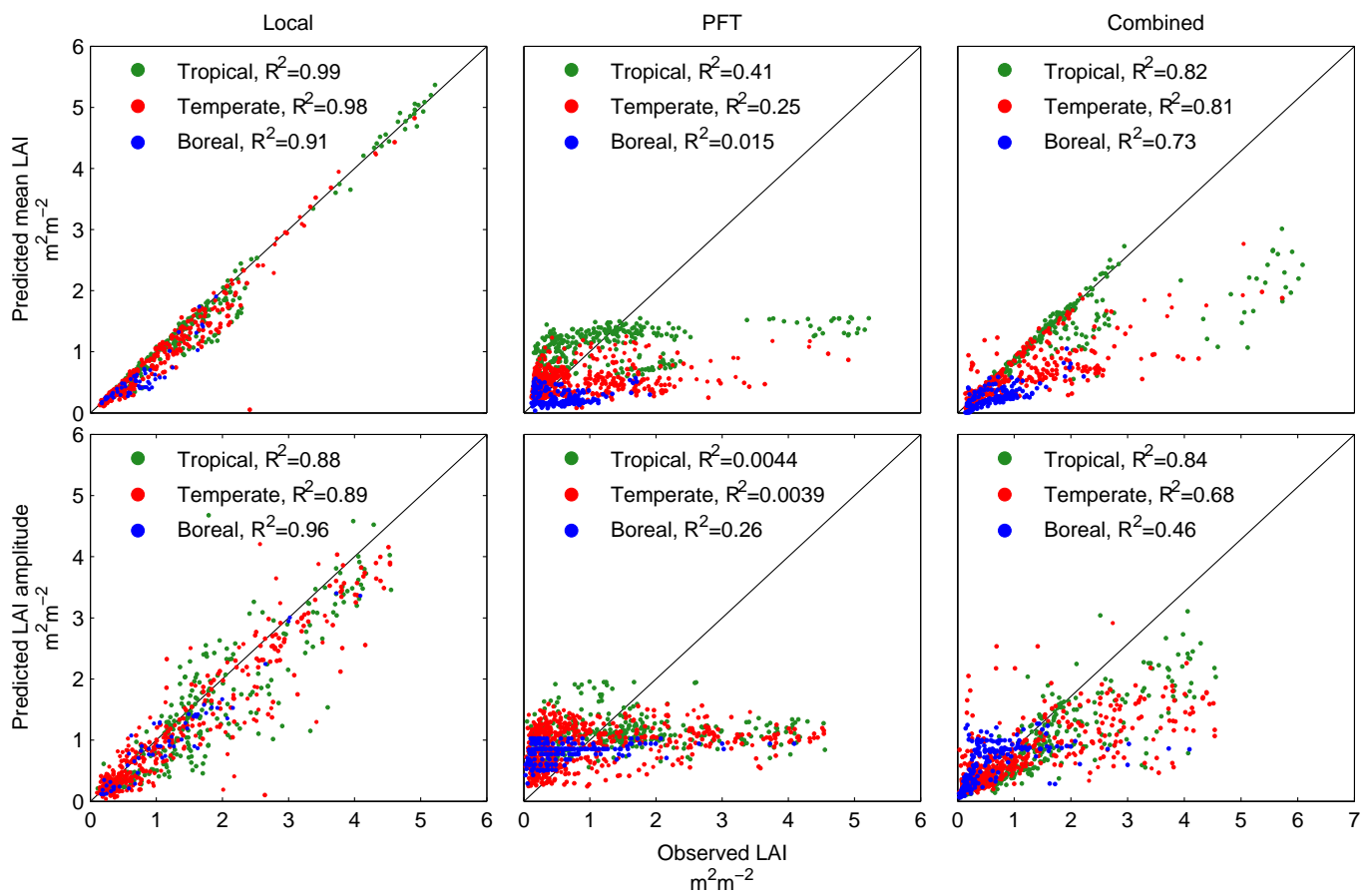


Figure 4. Comparison of predicted and observed mean LAI and seasonal amplitude for the local, PFT and combined models for tropical (green), temperate (red) and boreal (blue) grass PFTs.

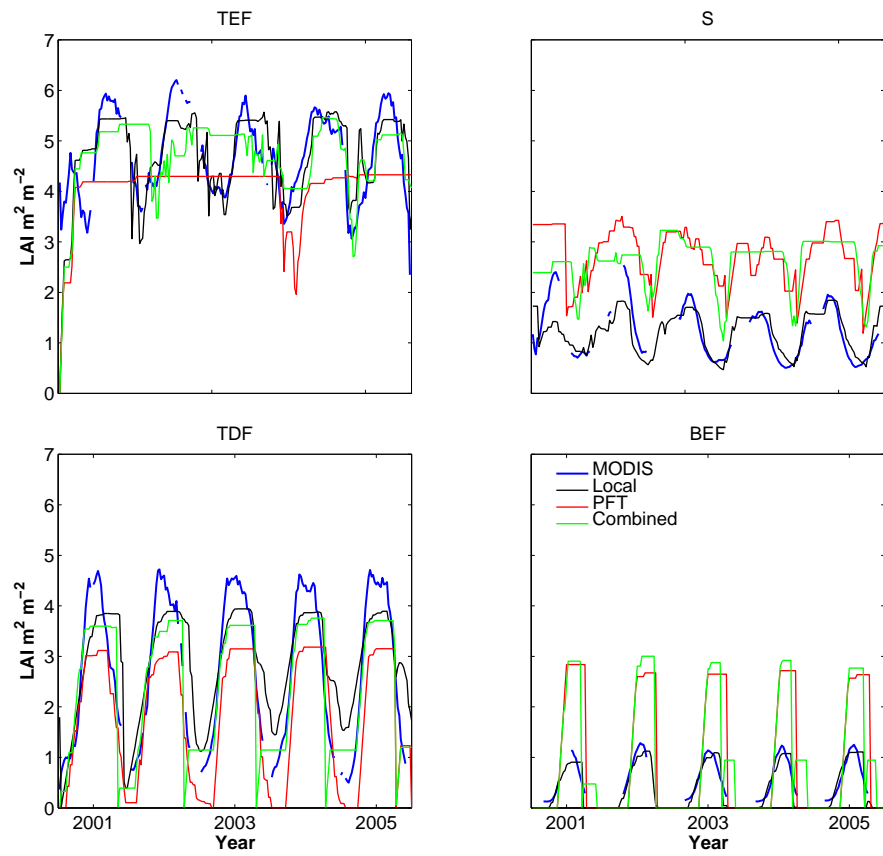


Figure 5. LAI timeseries for all models for tropical evergreen forests, TEF (6S 55W), savanna, S (14S 20E), temperate deciduous forests, TDF (46N 15E) and boreal evergreen forests, ~~TEF~~BEF (54N 120E). Blue line shows observed MODIS LAI at each location.

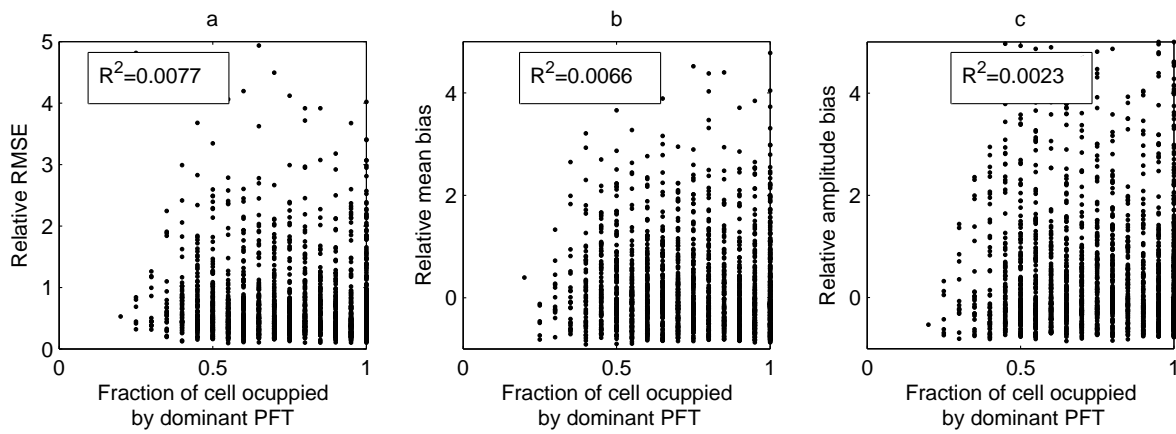


Figure 6. Correlations between model error and fraction of each grid occupied by the dominant PFT [in the PFT model](#) as a proxy for grid heterogeneity. (a) Model RMSE (b) Bias in LAI mean and (c) bias in LAI amplitude.

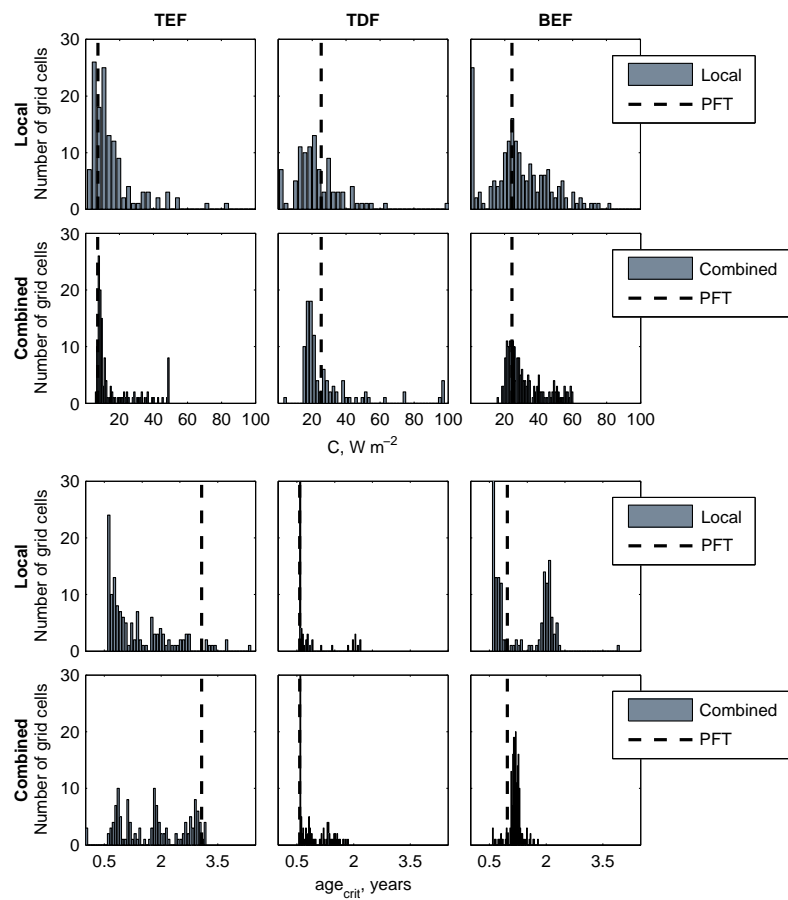


Figure 7. Parameter distributions for the light compensation point and age limit in three representative forest PFTs, tropical evergreen forest (TEF [Amazon](#)), temperate deciduous forest (TDF) and boreal evergreen forest (~~TEF~~BEF). Parameter values are the mean of the fitted posterior distributions and the represented values reflect the variation in space within one PFT, for the local (top) and combined (bottom) models, as well as for the fitted PFT (black line).

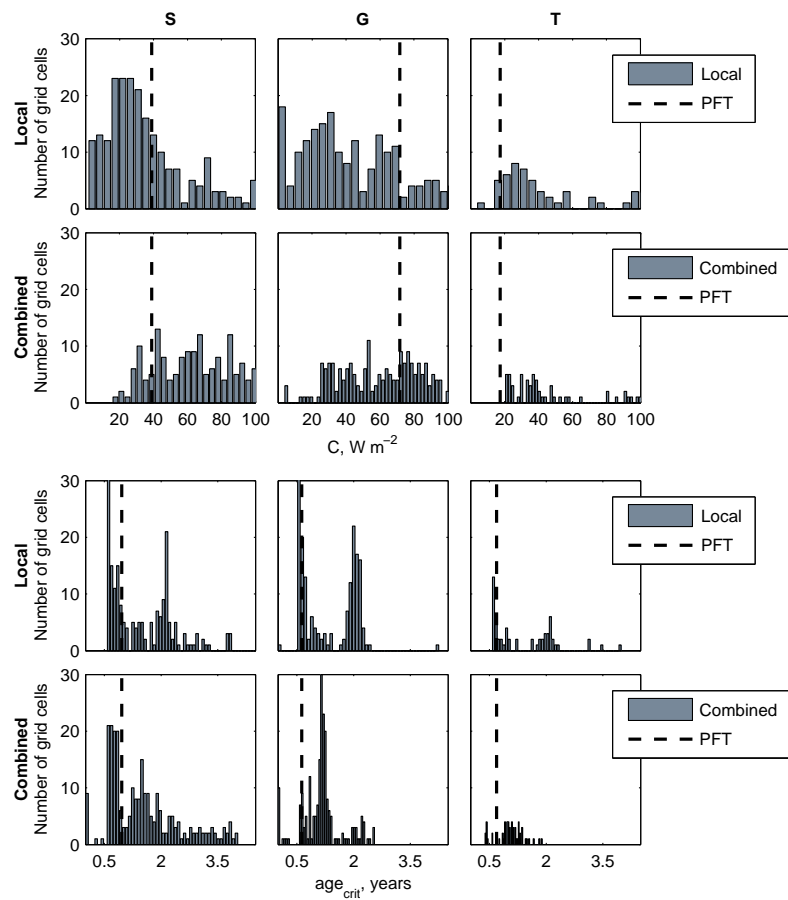


Figure 8. Parameter distributions for the light compensation point and age limit in three representative grass PFTs, savanna (S), grassland (G) and tundra (T). Parameter values are the mean of the fitted posterior distributions and the represented values reflect the variation in space within one PFT, for the local (top) and combined (bottom) models, as well as for the fitted PFT (black line).

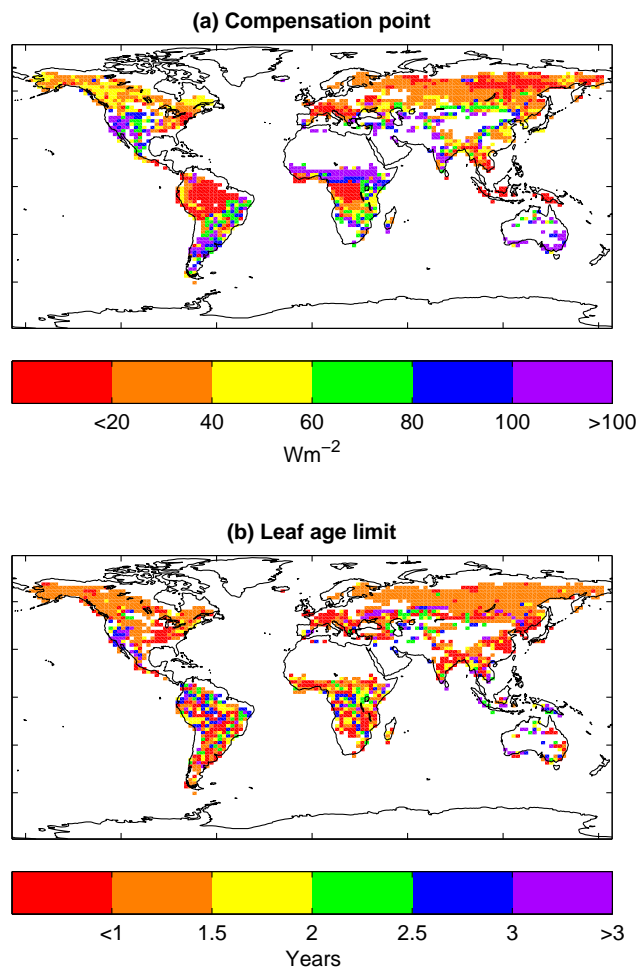


Figure 9. Posterior parameter means for the compensation point C_{direct} and the leaf age limit a_{crit} resulting from the combination model.

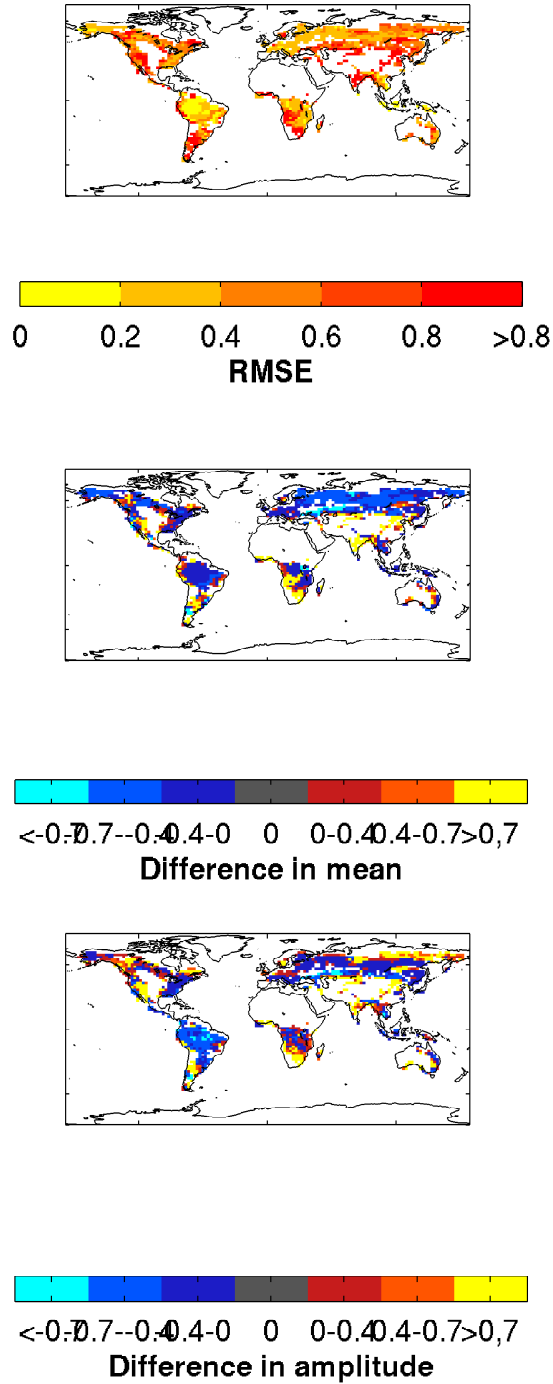


Figure A1. Root mean squared error (RMSE) and difference in mean and amplitude of predicted LAI over the model study period for a selection of regions in the regional model. All values have been normalised to the mean observed LAI at all locations.

Table 1. Model parameters for leaf gain and loss processes.

Symbol	Units	Description
C_{direct}	Wm^{-2}	Leaf level light compensation point for direct PAR
$C_{diffuse}$	Wm^{-2}	Leaf level light compensation point for diffuse PAR
p	days	Lag in response to incoming light
$gain_{max}$	m^2m^{-2}	Maximum gain
ϕ	$\mu mol s^{-1} W^{-1}$	Photosynthetic efficiency
q	$\mu mol m^{-2} s^{-1}$	Canopy level compensation point
s_1	-	Plant water uptake parameter
s_2	-	Plant water uptake parameter
ϵ	mm	Evapotranspiration per unit leaf area
u	mm	Plant water use per unit leaf area
a_{crit}	years	Age after which leaves start ageing
μ	years ⁻¹	Decay constant of photosynthesis with age
A_{min}	$\mu mol m^{-2} s^{-1}$	Assimilation rate equal to leaf maintenance costs

Table 2. Goodness of fit metrics for all five model parametrisations: root mean square error (RMSE) normalised by mean LAI value, difference in observed and predicted mean LAI and difference in observed and predicted annual amplitude. All metrics here are median values across the globe and the two difference values are shown as absolute values.

Model	RMSE	Mean difference	Amplitude difference
Global	1.21	0.73	1.01
PFT	0.52	0.45	0.51
Regional	0.46	0.38	0.31
Combined	0.39	0.23	0.33
Local	0.24	0.12	0.16

Table A1. Results of principal component analysis performed for parameters obtained from the local model. The table shows correlation coefficients between the two principal axes of variation and each parameter. The first two axes of variation explain 95% of the spatial variation in parameters.

	First axis R ²	Second axis R ²
<i>C_{direct}</i>	0.869	0.131
<i>C_{diffuse}</i>	0.046	0.010
<i>p</i>	0.005	0.011
<i>gain_{max}</i>	0.016	0.102
<i>φ</i>	0.004	0.006
<i>q</i>	0.004	0.001
<i>A_{min}</i>	0.000	0.008
<i>s₁</i>	0.002	0.010
<i>s₂</i>	0.000	0.017
<i>ε</i>	0.011	0.000
<i>u</i>	0.004	0.003
<i>a_{crit}</i>	0.216	0.784
<i>μ</i>	0.016	0.012

Table A2. Model goodness of fit for preliminary model runs. The parameter name shows which parameter was made local for that particular run.

	RMSE	Mean difference	Amplitude difference	Mean R ²	Amplitude R ²
<i>C_{direct}</i>	0.85	0.17	0.32	0.57	0.49
<i>C_{diffuse}</i>	0.80	0.30	0.36	0.04	-0.01
<i>p</i>	0.75	0.28	0.28	0.09	0.17
<i>gain_{max}</i>	0.98	0.18	0.32	0.50	0.33
<i>φ</i>	0.73	0.27	0.57	0.57	-0.01
<i>q</i>	0.71	0.24	0.33	0.39	0.01
<i>s₁</i>	1.00	0.17	0.25	0.58	0.33
<i>s₂</i>	0.75	0.27	0.33	0.01	0.06
<i>ε</i>	0.76	0.26	0.39	0.26	0.03
<i>u</i>	0.78	0.23	0.37	0.38	0.07
<i>a_{crit}</i>	0.72	0.20	0.21	0.56	0.58
<i>μ</i>	0.73	1.00	1.00	0.31	0.04
<i>A_{min}</i>	0.86	0.10	0.36	0.60	0.35