Interactive comment on “Annual cycle in Scots pine's photosynthesis” by Pertti Hari et al.

Response to Kim Pilegaard (Referee)

> 1 General comments
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> A mathematical model describing the annual course of photosynthesis in Scots pine was constructed from fundamental concepts and axioms describing the variation in photosynthesis with basic environmental drivers such as ambient temperature and solar light intensity. The mathematical model was tested against a multi year dataset from Northern Finland, which resulted in exact predictions of the daily and annual cycle in photosynthesis.
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> The theoretical framework is clearly described and the resulting equations seems quite meaningful. I miss a discussion of the meaning of the "constants" (a1...a5). The estimation of the constants from the tuning of the model to the field data is not well described, and it seems there were quite some challenges to this.

We added a short discussion on the meaning of the parameters in the revised manuscript as well as improved the methods section concerning the parameter estimation. We introduce these changes in the specific comments later.

> The "test" using the field data was not strictly independent, since the dataset was used to estimate the parameters of the model. Has any attempt been made to try the model on field data from other Scots pine stands, and would this result in other values of the parameters?

This is a good idea and we have already analysed whole ecosystem scale fluxes (GPP) of other Scots pine sites with the same theory (Hari et al 2017 ACPD at https://www.atmos-chem-phys-discuss.net/acp-2017-533/) and with good results. In addition, we have rather similar shoot scale measurements from SMEAR II station in southern Finland but the measuring arrangements there differ from those at SMEAR I from where we catch undisturbed and more frequent branch chamber data. Thus, the evaluation of the model performance at SMEAR II would be different from that introduced in this study. In addition, we think that the results of this study are already interesting due to the far-north, harsh location of SMEAR I.

> And what determines the exact value of the parameters?

We shortly discuss these issues in the revised manuscript but for some parameters such as a_1 and a_2 describing the synthesis and decomposition rate of the components in the photosynthetic machinery, such discussion would be too speculative at the moment and would require more experiments. However, the origin of a_3, a_4 and T_f are discussed now in the revised manuscript.

> Since the model is based on fundamental relationships between photosynthesis and light and temperature, a discussion of its universality would be interesting to include in the paper.

Indeed, the model attempts to use a fundamental and very basic relationship between environmental conditions and branch carbon uptake. We have made another study where this branch scale model is used for predicting ecosystem scale fluxes in several Scots pine forests in different ecoclimatic regions (Hari et al 2017 ACPD). The model works well even with very different

stands and can account for significant part of variation in CO2 fluxes in these sites. We added a short mention to this in the Discussion.

> Overall, I find the paper very interesting and well argued. I think the paper could be approved and increase interest if the points mentioned above and in the specific comments are taken into consideration.
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> 2 Specific comments
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> Title: Change "scots pine's" to "Scots pine's".

Corrected.

> Abstract:
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> p.1, l.20: "Our theory gained strong corroboration for the theory ...": Not immediately meaningful; please re-formulate.

We formulated it into the revised manuscript as "Our theory gained strong support in the rigorous test".

> p.2, l.17-18: Delete one of the two instances of the word "summer".

Corrected.

> p.3, l.6: Replace "on" with "of" (i.e. "of the annual cycle").

Corrected.

> p.4, l.7-10: Considering the prominent role of nitrogen, I wonder why nitrogen is not mentioned directly in the axioms such as light and temperature. Is this because nitrogen is only considered to be internally circulated in the system?

The theory explains the daily and seasonal cycle of photosynthesis in an individual branch, and we assume, that the availability of nitrogen does not change these seasonal processes considerably within the scale we are using in our analyses. We have clarified the scale in the abstract and throughout the manuscript. It is known that nitrogen content of leaves is connected to the availability of nitrogen (fertility) of the stand and leaves with lower nitrogen content do have lower rate of photosynthesis. Thus, the nitrogen would steadily affect the overall level of photosynthesis and is linked to the parameter a_4. The reason we discuss the nitrogen here is as you suggest; we wanted to stress the role of internal nitrogen circulation within the branch in the building up of new protein rich compounds necessary for photosynthetic machinery and transport of the photosynthates.

> p.5, l.7: Shouldn't it rather be "the seasonal state of the photosynthetic machinery"?

Here we had a mistake as well as in the following axiom 1. Those should be just "the state of the photosynthetic machinery" to be consistent in the analysis. These are corrected in the revised manuscript.

> p.6, l.13: "is f_3" should be "f_3 is".

Corrected.

> p.7, l.14: A more readable statement would be. "When we quantified the previous axiom with mathematical notations...".

Corrected as suggested.

> p.8, l.15-21: The procedure for parameter estimation needs some more explanation. What is the exact "graphical method" used? Why was a_2 fixed and how was the value chosen. Exactly which of the measured values were used?

We base our estimation on the minimization of the residual sum of squares. The residual sum of squares has several local minima and they hamper the estimation. We find easily the minima with numeric methods but the obtained parameter values vary greatly from one data set to another. Evidently, the local minima disturb the estimation. We developed estimation method that results in reasonable parameter values in all data sets available.

There are three parameter values to be estimated, when we fit our model with observed fluxes. We proceed step-wise, first we fix the value of a parameter. Thereafter we estimate the values of non-fixed parameters with standard numeric methods. We replace the value of the fixed parameter with the one obtained in the estimation. We select another parameter, fix its value with that one obtained in the previous round of estimation and estimate the other two parameters again. We continue the process of fixing estimating and replacing for several rounds until we get reasonable fit. In this way, we find the smallest one from a large number of local minima.

The estimation of the parameter values is quite problematic, since the behaviour of the residual sum of squares is very irregular and there are numerous local minima, which confuse the normal estimation with numeric methods. We therefore developed a method that selected smallest one from a large number of residual sums of squares. This method resulted quite stable solution of the minimization.

In the revised manuscript, we have improved the paragraph describing of the parameter estimation (the latter one in subchapter 2.3). In the revised text we do not use the questioned term "graphical method" since it is already described more openly and with more descriptive words. In addition, we re-wrote the estimation on T_f since it is actually an estimate obtained from a colleague and not really estimated in this study.

The needed measurements in the estimation are now stated in detail in the revised manuscript.

> p.10, l.26-27: The sentence starting with: "The physiological bases ..." is unclear; is something missing?

We decided to drop the whole sentence and include main idea to the end of the previous one.

The old version: '*We defined new concepts, the biochemical regulation system and the state of photosynthetic machinery (enzymes, membrane pumps and pigments) that played very important role in the argumentation. The physiological basis of the new concept is clear, since large number of steps form the light and carbon reactions of photosynthesis.*'

Revised version: '*We defined new concepts, the biochemical regulation system and the state of photosynthetic machinery (enzymes, membrane pumps and pigments) that played very important role in the argumentation and are justified from the basic physiological understanding of the photosynthetic processes.*'

> p.10, l.28: Change to: "In an efficient metabolic chain".

Corrected

> p.10, l.29: Change to: "... the steps in the photosynthesis ...".

Corrected.

> p.11, l.6: Change to "... that at low ones."

Changed to "than at low ones"

> p.11, l.13: Change to: "... into a quite stable state ...".

Corrected.

> p.11, l.14: Change to: "... according to the annual cycle ...".

Corrected.

> p.11, l. 19: Change to: "... deactivation of the photosynthetic machinery.".

Corrected.

> p.12, l. 2: It should probably read "severe".

You are right. We corrected it.

> p.12, l.24: Change to "SMEARI".

Corrected.