A point to point response to Kim Pilegaard (Referee)

> ## 1 General comments
>
> 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.

A point to point response to K. Jõgiste (Referee)

> The work presents substantial ideas about autotrophic production processes of the forest ecosystem. The testing of the theory has the central position in the scientific analysis. Basic assumptions in the model are presented in a strict order to capture essential logical behavior of the system.
>
> Introduction: the idea about the modelling is presented! Page 3, line 5 – 6: What do we mean as an “ecological level” here? The modelling attempt based on the physiological data can aim the different level starting from one single organism stretching to landscapes and global ecosphere?

We meant trees in their natural environment with the ecological level. Since it was so vague term, we revised it to “*field conditions i.e. into trees living in their natural environment*” in the revised manuscript.

> Theory development! Page 3, line 27: How the Finnish summers are supposed to be mild? The geographical extent of the country is very wide.

We agree, there is a difference in the temperature between southern Finland and Northern Finland, especially in degree days i.e. in the length of the warm season. However, except for the very southernmost coast, the whole country belongs to subarctic climate type according to the Köppen-Geiger climate classification that defines summer in this region to be mild. In addition, the difference in the mean maximum temperature in the summer is not that great. Thus we would still like to state that the summers are mild. However, we have re-phrased the section and included a references in the revised manuscript. Now, it states ” *for example Finland has mostly a subarctic climate according to Köppen-Geiger climate classification (Peel et al. 2007) meaning that summers are quite mild, daily maximum temperatures…*”.

> The evolutionary dynamics of life processes is highly varying: the idiosyncratic response of an organism, species or population to environmental conditions contains many possible solutions. I would like to have a more detailed comment on the limits of physiological reaction to annual cycle in light and temperature variation including extreme cases (page 4, line 16)? BTW: the population variation has been mentioned in the discussion part: page 10, line1. Results of the work discuss the variation at different levels: would it be useful attempt to describe variation with known and unknown source separately?

The acclimation responses specifically discussed here are related to the seasonal dynamics of photosynthetic machinery, adapted to the harsh climate, and we show that they are providing resilience for the systems also during extreme conditions in the stressful winter-to-spring transition period. This has been clarified in the revised ms. However, we are not discussing the potential of these systems to provide protection in other times or for extreme events which last for longer periods, e.g. during summer droughts, although to certain extent these mechanisms also operate during the growing season. We consider this aspect to be out of the scope of this particular paper, although it is an interesting topic in itself. We are actually preparing an independent manuscript on the topic (Matkala et al, under preparation).

> The methodology presented in the form of definitions and axioms is a brilliant idea. The wording and structure of the definitions and axioms can be improved in several cases.

According to your notice, we have reorganized the wording in the definitions 1 and 3 as well as in the axioms 1-4. In practise, we have 1) changed the word order to be more easy (for example '*We call ….. as the photosynthetic machinery*' was in the revised manuscript changed into '*The photosynthetic machinery is…*'. In addition, we tried to avoid the repetition of the phrase '*pigments, membrane pumps and enzymes*' by using '*the photosynthetic machinery*' that is already defined in the Definition 1. These changes clearly improved the readability of the axioms and definitions.

> Definition 3 introduces the "emergent property": how this properties are organized (hierarchy, spatial or temporal generalization)?

This is an interesting aspect but after a consideration, we decided that we will keep the definition rather short and clear. However, the new wording of the definition introduces the hierarchy of the properties more clearly than the old one.

Old: '*The action of the biochemical regulation system generates an emergent property, in the concentrations of active enzymes, membrane pumps and pigments, called the annual state of the photosynthetic machinery.*'

Revised: '*The state of the photosynthetic machinery is the emergent property created by the actions of the biochemical regulation system controlling the concentrations of active enzymes, membrane pumps and pigments.*'

> I am a little confused by use of term "linear" (page 6)? What do we mean here: the linear function?

We mean that the relationship between efficiency of photosynthetic light and carbon reactions is linear. We clarified this in the revised manuscript above the equations 1 and 2.

> Results: One can judge the match between observed and predicted photosynthesis dependence on the cloudiness to be rather good. Why the highest overestimation happens in the afternoon with intermittent cloudiness (Figure 3A)?

True, interesting remark! However, we thought that the overestimation is so small that it is most probably generated by normal random variation and did not discuss on it in the manuscript.

> Does the data from Värriö Subarctic Research Station include extreme cases or disturbance events: e.g. low temperature during the vegetation period or extreme droughts?

We have experienced a prolonged season with low soil moisture in 2013 which was exceptional in the area. Usually the area is very humid since precipitation exceeds evapotranspiration. The preliminary analysis shows that the low soil water did affect radial stem growth but did not hinder photosynthesis - actually the highest GPP was recorded on that year, probably due to air temperature that was higher than usually. The presented model did not show decreased performance during the low moisture conditions in 2013. Low temperatures with even freezing records visit the site almost every summer but those days do not pop up as decreased performance in the analysis either. These observations will be published in an independent manuscript (Matkala et al, under preparation)

> What are the actions mentioned in the discussion (page 11, line 4)? Semantically action refers to purposeful and systematic interplay between components of the system! Although the action (or operation) of the system can be interpreted as evolutionary developed property of a living organism, the biochemical mechanism (enzymes, pigments, membrane pumps) as such lacks the purpose oriented action?

We consistently use the 'action' (of the biochemical regulation system) through the manuscript when discussing on synthesis or decomposition of the necessary, active compounds. There might be also some other term suitable such as 'functioning' but we are somewhat pleased with *action* since we believe that the tree actively regulates these substances which we can predict by the changes in the environmental factors.

> In conclusion: the presented modelling is only a minor part of the research conducted during many years. The wider and more profound presentation of the study can be found in other printed sources. Material presented with current manuscript is an elegant demonstration of powerful methodological tools to create better comprehending of complex nature of living world. I do recommend to accept the paper with some modifications.
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> Minor comments I suggest some improvements to the abstract: the repetition of "theory" in concluding sentence should be avoided.

True, we reformulated it into the revised manuscript as "Our theory gained strong support in the rigorous test."

> Number of measurements: 30000 datapoints during a summer (page 9, line 18): is it connected to total record 130000 (page 11, line 30)?

We had a mistake there since in the number should be 130 000. It is corrected in the revised manuscript.

> Acronyms at the Acknowledgement part are understandable only for very few specialist: nevertheless the Google can provide more or less correct hints. Still, what is SMARI?

We agree that the acknowledged acronyms are quite unclear for most readers but at the same time, they are not that essential for them either. We corrected the misspelled SMARI to SMEAR I.

A list of all relevant changes made in the manuscript

- We clarified the scale of our interest (the daily and seasonal cycle in an individual branch) in the abstract and throughout the manuscript.
- We improved the wording and structure of several definitions and axioms.
- We improved the description of the needed measurements as well as the parameter estimation in the subchapter 2.3
- We included a discussion on the meaning of the parameters

Annual cycle in Scots pine's photosynthesis

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Abstract. Photosynthesis, i.e. the assimilation of atmospheric carbon to organic molecules with the help of solar energy, is a fundamental and well understood process. Here, we connect theoretically the fundamental concepts affecting C3 photosynthesis with the main environmental drivers (ambient temperature and solar light intensity), using six axioms based on physiological and physical knowledge and yield straightforward and simple mathematical equations. The light and carbon reactions in photosynthesis are based on the coherent operation of the photosynthetic machinery, which is formed of a complicated chain of enzymes, membrane pumps and pigments. A powerful biochemical regulation system has emerged in evolution to match photosynthesis with the annual cycle in solar light and temperature. The action of the biochemical regulation system generates the annual cycle of photosynthesis and emergent properties, the state of photosynthetic machinery, and the efficiency of photosynthesis. The state and the efficiency of the photosynthetic machinery is dynamically changing due to biosynthesis and decomposition of the molecules. The mathematical analysis of the system, defined by the very fundamental concepts and axioms, resulted in exact predictions of the behaviour of daily and annual patterns in photosynthesis. We tested the predictions with extensive field measurements of Scots pine photosynthesis at branch scale in Northern Finland. Our theory gained strong support in the rigorous test.

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1 Introduction

The movement of the globe around the sun generates a conspicuous annual cycle in the solar radiation on the earth, and this cycle is especially strong at high latitudes. Ambient temperatures respond to the cycle in solar energy input and therefore a strong annual cycle exists also in temperature, although a bit delayed. These large variations in light and temperature are greatly influencing the distribution of plant species, especially in the northern regions. As an example, Scots pines (*Pinus sylvestris* L.), while abundant all over the Europe, have adapted especially well also to the annual cycle of radiation and temperature in the northern climate, forming even the treeline in many regions (Juntunen et al. 2002).

As a consequence of the seasonal variation in light and temperature, many perennials including deciduous trees have a strong metabolic annual cycle, as they grow new leaves every spring that then become senescent in the autumn. Temperature affects the timing of many phenological events i.e. bud burst and flowering (Hänninen and Kramer 2007, Hari and Häkkinen 1991, Linkosalo 2000, Sarvas 1972). However, the annual cycle is less clear in coniferous trees, although they also have a period of intensive new foliage growth in the spring, and a specific time frame when old needles are senescing in the fall.

The annual cycle of light and temperature is manifested in plant metabolism in many ways. Actively metabolizing cells are very sensitive to low temperatures, and, as a consequence, they need to inactivate many processes in order to avoid damage during winter in a process called winter hardening (Hänninen 2016). This means that the metabolism of e.g. evergreen Scots pine needles also needs to follow a clear annual cycle. For example, when sufficiently hardened, pine needles tolerate temperatures well below –30 °C in winter, however they are very sensitive to temperatures below –10 °C during summer (Sakai and Larcher 1987). The metabolism of photosynthesis recovers gradually from the winter hardened state during spring, and the ambient temperature has an important role in this recovery (Pelkonen and Hari 1980).

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Biochemically, photosynthesis can be defined as a long chain of action of pigments, membrane pumps and enzymes, which use light as source for energy and atmospheric CO_2 as source for carbon (see e.g. (von Caemmerer and Farquhar 1981)). Changes in the concentrations and activities of this photosynthetic machinery generate the annual metabolic cycle in photosynthesis. The physiological basis of the annual cycle at the level of the synchronized action of photosynthetic machinery is poorly known, especially when it comes to the role of temperature in the synthesis, activation, decomposition and deactivation of the machinery.

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Sugars formed in photosynthesis are the source of energy for all cellular metabolic activity and raw material for growth. The length of the photosynthetically active period is a key factor determining the annual amounts of sugars formed in photosynthesis (Hari et al. 2013) and it plays a very important role in the metabolism and growth of vegetation. Thus, a theoretical understanding of the dynamics of the photosynthetic annual cycle is a key to understanding and explaining the growth of the trees growing at high latitudes.

Physiological and biochemical research has provided useful knowledge of the photosynthetic reaction chains, and the details of this machinery at leaf, organ and tissue levels have been intensively explored over decades, mostly in controlled, laboratory conditions (Farquhar and von Caemmerer 1982, Farquhar et al. 1980, Kirschbaum et al. 1998, Laisk and Oja 1998). However, field measurements in mature trees are difficult to perform, and the results are not easy to interpret. Therefore, the detailed physiological knowledge that has mostly been obtained from laboratory experiments needs to be translated into the field conditions i.e. into trees living in their natural environment to increase our understanding of the annual cycle of photosynthesis under field conditions. This was our motivation in developing a conceptual approach to the relationship of photosynthesis and the annual variations in light and temperature.

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Physics was facing a similar situation in the seventeenth century as field studies on photosynthesis are encountering now. There were plenty of single and scattered experiments and observations, but the unifying theory was missing. Isaac Newton presented an approach to construct theories in his book Principia Mathematica and unified the physical knowledge. He proceeded in four steps when developing theories, starting from the definition of concepts and followed by the introduction of axioms. The mathematical analysis of the behaviour of the system defined by the concepts and axioms dominated his theory development. Finally, he derived predictions and tested them. The new translation of Newton's famous book *Principia Mathematica* (Newton 1999) clearly presents these four steps.

In our previous analysis of photosynthesis taking place during midsummer, we followed strictly Newton's example by introducing the concepts and axioms, by analysing the behaviour of the system defined by these concepts and axioms, and finally by deriving predictions and testing them (Hari et al. 2014). However, it was evident that our theory omits the annual cycle of metabolism and therefore it fails crucially to predict the photosynthesis in the transitional times such as spring and autumn. The daily patterns of measured and predicted CO_2 exchange were quite similar, but the level of predicted photosynthesis was too low, especially in early spring and late autumn. We thus concluded that we have to introduce the annual cycle of metabolism into our theory. Our aim is to develop our theory of photosynthesis to cover the whole growing season and to explain and to predict the annual cycle of Scots pine photosynthesis in field conditions.

2 Theory development

The strong annual cycle in the solar light intensity and ambient temperature is characteristic for the growing area of Scots pine: for example Finland has mostly a subarctic climate according to Köppen-Geiger climate classification (Peel et al. 2007) meaning that summers are quite mild, daily maximum temperatures being around 20 °C, whereas winters are rather cold with

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minimum temperature often below –20 °C. A regulation system has emerged in evolution to match the metabolism and cold tolerance with the annual cycle in the solar radiation and temperature.

The process of photosynthesis consists of a large number of steps that form the light and carbon reactions of photosynthesis. Each step is based on actions of a specific molecule, the most important being pigments (e.g. chlorophylls and carotenoids), transmembrane proteins and membrane pumps (e.g. ATPases), and Calvin cycle enzymes (e.g. ribulose-1,6-bisphophatase, Rubisco) (Taiz et al. 2015). A proper functioning of the reaction chain in photosynthesis requires that no single step is blocking the chain of interlinked energy capture, membrane transport or synthesis of new compounds. The core of pigment complexes, as well as the membrane pumps and enzymes are all proteins that have a tendency to decay (Araujo et al. 2011, Hinkson and Elias 2011, Huffaker and Peterson 1974, Nelson et al. 2014). Proteins are nitrogen-rich macromolecules (many contain 15–16 w-% N (Nelson et al. 2014)) and they are costly to produce and maintain. Therefore, it is natural that plants need to be able to use the limited N reserves in an effective way. Since nitrogen has several competing usages in the metabolism, maintaining excess proteins is a 'waste' of nitrogen. Synthesis and decomposition of active protein molecules balance the concentrations of active protein molecules in the photosynthetic chain. Evidently, maintaining the proper balance of these molecules is a crucial and demanding task for the metabolism of trees.

Large changes in the photosynthetic performance characterize the annual cycle of photosynthesis, generated by changes in the concentrations of the photosynthetic machinery. Maintaining the proper concentrations of the components in this machinery is taken care by a very powerful biological regulation system that has emerged in the evolution to match the cellular metabolism with the regular annual cycle in solar light and temperature, and capable of modifying the processes within the normal range of conditions, but also provides sufficient resilience under sudden (short-term) extreme conditions during the transition from winter to spring (Ensminger et al. 2004a, Zarter et al. 2006). This system synthetises, activates, decomposes and deactivates the critical photosynthetic machinery over time scales of days (Nelson et al. 2014), and it is an acclimation system, affecting the activation and deactivation of transcriptional modules responsive to light and temperature cues (e.g. (Cazzonelli and Pogson 2010, Toledo-Ortiz et al. 2014)). The changes in the machinery, in turn, generate changes in the relationship between photosynthesis and light. This forms the metabolic basis for our theory of the dynamics of annual cycle of photosynthesis.

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2.1 Definitions and axioms

We start our formulation with definitions as Newton did centuries ago. We utilise physiological and physical knowledge in the formulation of the axioms needed for the mathematical formulation.

Definition 1. The photosynthetic machinery is the complex web of pigments, membrane pumps and enzymes forming the biochemical structure underlying photosynthesis.

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Plants are able to change the concentrations of active components in the photosynthetic machinery.

Definition 2. Plants have a biochemical regulation system that synthetize, activate, decompose and deactivate the photosynthetic machinery.

The action of the biochemical regulation system generates the annual cycle in photosynthesis and maintains the balance between the different steps in the photosynthetic reaction chain. In this way, it generates a new property in the photosynthetic machinery.

Definition 3. The state of the photosynthetic machinery is the emergent property created by the actions of the biochemical regulation system controlling the concentrations of active photosynthetic machinery.

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The state of photosynthetic machinery characterises the complex web of energy capture, biochemical reactions and membrane transport in photosynthesis with one single number. Next, we specify the action of biochemical regulation system on photosynthetic machinery:

Axiom 1. Synthesis and activation as well as decomposition and deactivation of the photosynthetic machinery are changing the state of the photosynthetic machinery.

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Further, we specify the relationship between environment and the synthesis by the biochemical regulation system.

Axiom 2. The synthesis and activation of the photosynthetic machinery depend linearly on the temperature above freezing point.

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We clarify also the behaviour of decomposition and deactivation.

Axiom 3. The decomposition and deactivation of the photosynthetic machinery depends linearly on the state.

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Captured light energy may cause damage in chloroplasts in freezing temperatures, when availability of CO_2 is limited for the carbon reactions in photosynthesis. This is why the biochemical regulation system acts strongly to protect against damage.

Axiom 4. The accelerated decomposition and deactivation of the photosynthetic machinery during cold and strong light depends linearly on the product of light and temperature below freezing point.

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The concentrations of the photosynthetic machinery affect the performance of photosynthesis.

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Definition 4. The efficiency of photosynthetic reactions is the capacity of light and carbon reactions to synthesise sugars.

When we developed the theory of photosynthesis explaining the behaviour in midsummer (Hari et al. 2014), we introduced an axiom stating that the product of saturating response to the photosynthetically active radiation and CO_2 concentration in the stomatal cavity determines the photosynthesis at a point in space and time. Here, we introduce the annual cycle of photosynthesis into the axioms with the efficiency of photosynthetic carbon and light reactions and the efficiency photosynthetic reactions replace the parameter b in the Eq.(1) in Hari et al. 2014.

Axiom 5. The photosynthesis rate at a point in space and time depends on the product of two terms: i) the efficiency of photosynthetic light and carbon reactions, and ii) the product of CO_2 concentration in the stomatal cavity and the saturating response of the light reactions to the photosynthetically active radiation.

The state of the photosynthetic machinery determines the efficiency of photosynthetic light and carbon reactions, which leads to our final axiom:

Axiom 6. The efficiency of photosynthetic light and carbon reactions depends linearly on the state of the photosynthetic machinery.

2.2. Mathematical analysis

We introduce mathematical symbols to formulate exactly the axioms in a more exact and compact way. Let S denote the state of the photosynthetic machinery, f_1 is the synthesis and activation, f_2 is the decomposition and deactivation, and f_3 is the accelerated decomposition and deactivation of photosynthetic machinery (i.e. enzymes, membrane pumps and pigments) caused by light at low temperatures.

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Axiom 2 states that the relationship between the synthesis and activation and temperature (T) is linear above the freezing point, which gives:

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$$f_1(T) = \mathrm{Max}\{0, a_1(T + T_f)\}, \qquad (1)$$

where T_f is the freezing temperature of needles and a_i is a parameter.

According to axiom 3, the relationship between the decomposition and deactivation of photosynthetic machinery and the state of photosynthetic machinery, S, is linear:

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$$f_2(S) = a_2 S. \qquad (2)$$

Accelerated decomposition and deactivation takes place to protect the photosynthetic machinery against damage when freezing temperatures hinders the carbon assimilation reactions of photosynthesis (Axiom 4):

$$f_3(I,T) = a_3\,\mathrm{Max}\{(T_f - T)\,I, 0\}, \qquad (3)$$

where I is the intensity of photosynthetically active radiation.

The synthesis, activation, decomposition and deactivation change the state of the photosynthetic machinery, as follows:

$$\frac{dS}{dt} = f_1 - f_2 - f_3 \qquad (4)$$

Combining Equations (1)-(4), we obtain:

$$\frac{dS}{dt} = \mathrm{Max}\{0, a_1(T + T_f)\} - a_2 S - a_3\mathrm{Max}\{(T_f - T)\,I, 0\} \qquad (5)$$

Equation (5) defines the state of the photosynthetic machinery at any moment t when temperature and solar radiation records are available.

The photosynthesis rate, p, is obtained from the axiom 5, as follows:

$$p = E\,f(I)\,C_S, \qquad (6)$$

where C_s is the CO_2 concentration in the stomatal cavity, $f(I)$ is the saturating response of the photosynthesis rate to the photosynthetically active radiation (see Hari et al 2014), and E is the efficiency of photosynthetic carbon and light reactions which, according to the axiom 6, it is as follows:

$$E = a_4\,S \qquad (7)$$

When we developed the theory of photosynthesis in midsummer (Hari et al. 2014), we introduced an axiom stating that the product of saturating response to the photosynthetically active radiation and CO_2 concentration in the stomatal cavity determines the photosynthesis at a point in space and time (A1 in Hari et al. 2014). When we quantified the previous axiom with mathematical notations, we replaced the axiom A1 with the new axiom 5 that is quite similar with the previous one. The changing efficiency of photosynthetic light and carbon reactions is the novel aspect in the axiom 6. When we quantified with mathematical notations the previous axiom, we introduced a parameter b (Eq. 1 in Hari et al. 2014). Equation (6) is very similar with the previous Eq. (1) in Hari et al. (2014); the only difference is that the efficiency parameter b is replaced with E, the state variable efficiency of photosynthetic carbon and light reactions. We obtain the solution of the optimisation problem in the same way as in the analysis of photosynthesis (p) during midsummer, as follows:

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$$p(I,E) = \frac{(u_{opt}\,g_{max}C_a + r)\,a_4\,S\,f(I)}{u_{opt}\,g_{max} + a_4\,S\,f(I)}, \qquad (8)$$

where g_{max} is stomatal conductance when stomata are open, C_a CO_2 concentration in the ambient air, r is the rate of respiration and u_{opt} is so-called seasonal modulated degree of optimal stomatal control given by

$$u_{opt} = \begin{cases} 0, & if \;\; u \leq 0 \\ u, & if \;\; 0 < u \leq 1 \\ 1, & if \;\; u > 1 \end{cases} \tag{9}$$

$$u = \left(\sqrt{\frac{C_a - r/(a_4\, S\, f(I))}{\lambda\, a\, (e_s - e_a)}} \right) \frac{a_4\, S\, f(I)}{g_{max}} \tag{10}$$

In the Eq. (10), λ is a cost of transpiration i.e. a measure of water-use efficiency.

To summarize, Eqs. (5), (7) - (10) predict the density of photosynthetic rate when we know the ambient temperature and solar radiation history, density of photosynthetically active solar radiation, and concentrations of water vapour and CO_2 in the air. This prediction is clearly a dynamic version of the formulation by Hari et al (2014). The changing state of the photosynthetic machinery (i.e. enzymes, membrane pumps and pigments) determines the efficiency of light and carbon reactions, introducing the annual cycle of metabolism into the prediction. Thus, the relationship between light and photosynthesis changes smoothly during the seasons.

2.3. Parameter estimation

We tested the new theoretical prediction with field chamber measurements at Scots pine trees in Lapland, Värriö Subarctic Research Station (SMEAR I, 67°46'N, 29°35'E, 400 m a.s.l). We measured the CO_2 exchange of pine shoots with four branch chambers throughout the year in 2011-2014 (Hari et al. 2014). In addition, photosynthetically active radiation (I) was measured at each chamber whereas the records for air temperature, air humidity and CO_2 concentration are site-specific. Despite the constant supervision, maintenance and malfunction of the measuring system generated some gaps in the data. To obtain maximal data coverage per year, we selected those chambers that measured over the whole year without long maintenance and malfunction periods.

There are four parameters in the Eqs. (5), (7) - (10) that describe the annual cycle of photosynthesis (a_1, a_2, a_3 and a_4). The freezing temperatures and sunny weather are quite rare events at our measuring station occurring only in early spring and very late in autumn. As a result, the parameter a_3 in the Eq. (3) has a minor role in the predictions and its estimation is based on very scarce data on the CO_2 exchange with the accompanied environmental factors. The residual sum of squares has several local minima and they hamper simultaneous estimation of the parameters a_1, a_2, and a_4. Therefore, we proceed step-wise; first we fix the value of a parameter. Thereafter we estimate the values of non-fixed parameters with standard numeric

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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 resulted into the following values: a_1 = 10, a_2 = 0.065 and a_3 = 2. The values of the parameter a_4 are year and chamber specific. We used value –3°C for T_f (Teemu Hölttä, personal communication).

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3 Results

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We predicted the state of the photosynthetic machinery i.e. the annual state of enzymes, membrane pumps and pigments with the Eq. (5) using the measured temperature and light intensity before the moment in consideration. The predicted annual patterns of the state of the photosynthetic machinery were quite similar between the different years (Fig. 1). There was, however, some weather-driven variation. For example, the very warm August in 2014 generated the large peak in late summer.

The changes in the relationship between light and photosynthesis is characteristic to our theory. Figure 2 depicts the daily patterns of the measured and predicted leaf CO_2 exchange early in the spring (A) and at midsummer (B). The measured and predicted daily patterns generated by the variation in light were very similar to each other, although the level of photosynthesis increased considerably from spring to summer. Our theory predicted the level of this increase during the summer successfully.

Days of intermittent cloudiness dominate our northern climate in the summer (Hari et al. 2014), giving rise to very strong within-day variations in the light levels reaching the canopy. Our theory predicted strong variation in photosynthesis during days of intermittent cloudiness, yet the measured leaf CO_2 exchange seemed to be very similar with the predicted one (Fig. 3A).

Heavy clouds tend to cover the sky during rainy days strongly reducing the light intensity. Our theory predicts strongly reduced photosynthesis during dark rainy days. Again, the measured and predicted leaf CO_2 exchange were very close to each other when thick clouds covered the sky (Fig. 3B).

Our theory predicts clear effect of partial closure of stomata on sunny days when the temperature strongly increases during the day. This type of days are, however, rather rare events at our northern measuring site. Nevertheless, the measurements of leaf CO_2 exchange showed a similar pattern with our prediction on such days (Fig. 3C).

We have continuous measurements for four summers, consisting of more than 130 000 data points during each summer. The predictions of leaf CO_2 exchange of a shoot were very close to the measured pattern, without exception. Also, the relationships between measured and predicted leaf CO_2 exchange indicated close correlations between measurements and predictions (Fig. 4). The predictions explained about 95 % of the variance of the measured values.

The residuals, i.e. the difference between measured and predicted leaf CO_2 exchange revealed only slight systematic behaviour (Fig. 5) indicating that the theory was a quite adequate description of the regularities in the photosynthesis of northern Scots pine.

4 Discussion

Scots pine has a broad distribution range all over Europe, and the local populations have adapted to the regular annual cycle in solar radiation and in temperature. The needle metabolism has also a clear annual cycle that alternates between the cold tolerance and very low metabolic activity during winter and strong metabolism and cold vulnerability in summer. The annual cycle is particularly strong in photosynthesis (Ensminger et al. 2004b, Kolari et al. 2014, Öquist and Huner 2003, Pelkonen and Hari 1980).

We have worked decades with the annual cycle of vegetation from the analysis of daily shoot elongation (Hari and Leikola 1972, Hari et al. 1977), bud burst of trees (Hari and Häkkinen 1991) and photosynthesis (Pelkonen and Hari 1980). Our approach has been dynamic modelling without clear connection to the physiological background, although we were looking for the metabolic explanations. The strong connection to the light and carbon reactions and their basis on enzymes, membrane pumps and pigments is the novel feature of our theory of the annual cycle of photosynthesis. It provides sound physiological background to our concepts and axioms. We utilised strongly physiological knowledge in the development of our theory. Previously the focus has been in the mathematical formulation of the ideas whereas the physiological background has been quite unclear. The predictions of our novel theory are close to those obtained previously (Mäkelä et al. 2004) although the fit of the predictions with measurements has improved considerably.

The light and carbon reactions of photosynthesis are down regulated in autumn in order to protect the sensitive machinery against low temperatures, and up regulated again in spring. This seasonality has been closely connected to variations in ambient temperatures (Mäkelä et al. 2004, Pelkonen and Hari 1980) and photoperiod or light intensity changes (Ensminger et al. 2004a, Porcar-Castell et al. 2008). A delayed effect of temperature on photosynthesis recovery in spring is introduced (Mäkelä et al. 2004, Pelkonen and Hari 1980) and tested with field measurements (Kolari et al. 2009).

The Newtonian approach provided a sound backbone to collect physiological knowledge for the development of our theory of annual cycle of photosynthesis. The definitions of concepts determine the most important features in the theory and the axioms the critical relationships between the concepts. Applying mathematical analysis and simulations of the behaviour of the system, as defined by the concepts and axioms, proved to be an efficient tool to analyse the consequences in photosynthesis and to derive predictions.

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. Each step is based on specific pigment, membrane pump or enzyme. In an efficient metabolic chain, the steps have to be in balance with each other. The biochemical regulation system, emerged in evolution, generates balance between the steps in the photosynthesis whereas its action generate the state of the photosynthetic machinery. The state of the photosynthetic machinery determines the changing efficiency of the light and carbon reactions in photosynthesis. In this way, the action of the biochemical regulation system generates the annual metabolic cycle in photosynthesis and the synchrony with the strong annual cycle in radiation and temperature.

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The axioms clarify the action of the biochemical regulation system in synthesis and decomposition of photosynthetic machinery. The physiological basis of the actions is clear. Metabolic reactions take place faster at elevated temperatures than at low ones. Thus synthesis is temperature dependent (Axiom 2). The enzymes, membrane pumps and pigments are non-stable compounds as introduced in the axiom 3.

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The increasing temperatures in the spring accelerate the synthesis and activation of photosynthetic machinery, resulting in increasing photosynthesis. The combination of sunny and cold mornings accelerating the decomposition and deactivation and thus decreasing photosynthesis. When the spring proceeds, air temperature rises and the synthesis and activation increase the state of the photosynthetic machinery resulting in enhanced photosynthesis.

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The enzymes, membrane pumps and pigments are non-stable compounds and consequently, their decomposition and deactivation increases during summer resulting into a quite stable state of the photosynthetic machinery. When the temperature starts to decrease according to the annual cycle, the synthesis declines decreasing the pool of these non-stable compounds resulting in a reduction in the light response of photosynthesis. In this way the biochemical regulation system generates the annual metabolic cycle in photosynthesis that is in delayed synchrony with the annual cycle of radiation and temperature.

Our theory predicts slow recovery in the spring, quite steady maximum in the summer and slow decline in the autumn to be characteristic for the annual cycle of photosynthesis due the synthesis, activation, decomposition and deactivation of the photosynthetic machinery. The observed annual patterns of photosynthesis are in good agreement with the above theoretical prediction.

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The diurnal cycle in radiation and temperature is clear in summer time and missing during the polar night at our research site. However, we can omit the polar night in photosynthetic studies due to darkness and low temperatures. Our theory predicts that (i) photosynthesis during a day follows the saturating response to light, since the changes in the concentrations of enzymes, membrane pumps and pigments are so slow that the changes do not affect the behaviour of photosynthesis during a day and (ii) the action of stomata slows down photosynthesis during most sunny days. Our field measurements are in agreement with this prediction.

Our theory has passed successfully the above qualitative tests. However, quantitative tests are more severe and they can provide stronger corroboration for the theory and show its universal character over a huge number of environmental conditions and several seasons. We tested our theory with field measurements over four years including over 130 000 measurements of CO$_2$ exchange, PAR, temperature, atmospheric CO$_2$ and water vapour concentration. Our theory predicted the annual and daily patterns of photosynthesis explaining about 95 % of the variance in the measured CO$_2$ exchange whereas residuals did not show any clear systematic behaviour. Thus our theory passed successfully the severe tests also in quantitative terms. As a next step and proof of its universal nature, we attempt to use the model developed for branch scale to predict ecosystem scale fluxes in several Scots pine forests in different ecoclimatic regions (see Hari et al 2017).

The estimation of the parameter values is a challenge since the behaviour of the residual sum of squares is very irregular and there are numerous local minima disturbing the estimation with numeric methods. We therefore developed a method that selected smallest one from a large number of residual sums of squares resulting into quite stable solution of the minimization. The further analysis would benefit from independent data sets from other sites in order to describe the variability in these parameters.

It is evident that the nitrogen availability (fertility) as well as plant species affects the parameter a_4 i.e. the higher is the nitrogen content in the leaves in general, the higher is the relationship between the state of photosynthetic machinery the efficiency of photosynthetic carbon and light reactions (Eq. 7). On the other hand, parameter T_f describing the temperature when the areas outside living cells freeze, is species- and somewhat also site-specific depending also on the water content (Sperling et al. 2017). These events are rather rare but the sensitivity to such events is reflected in parameter a_3.

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Short field campaigns and statistical analysis of the obtained data dominates photosynthetic research under natural conditions. The often very short and fragmentary measurement series hinder the studies of the annual cycle of photosynthesis. The smoothly changing relationship between light and photosynthesis is missing in most statistical analysis

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of field measurements. The slow changes in the studied relationship are problematic for the statistical analysis of field data and probably explain why there is not any comparable ecological theory of annual photosynthesis.

In conclusion: Scots pine has adapted to the regular annual cycles in light and temperature and the effective biochemical regulation system of photosynthetic machinery has emerged in the evolution. The action of the biochemical regulation system generates the delayed annual cycle in photosynthesis by synthetizing, activating, decomposing and deactivating enzymes, membrane pumps and pigments. The linear relationship between synthesis and activation on temperature above the freezing point synchronises the metabolic and light cycles with each other. Prevailing light and the annual metabolic cycle determines photosynthesis, although the action by the stomata modifies the photosynthetic response. Our extensive field measurements corroborate the above conclusion.

Data availability

All measurements at SMEAR I including also the shoot chamber measurements are available from https://avaa.tdata.fi/web/smart/smear/download. The code is available in Mathematica and can be accessed via the corresponding author (pertti.hari@helsinki.fi).

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Competing interests

The authors declare that they have no conflict of interest.

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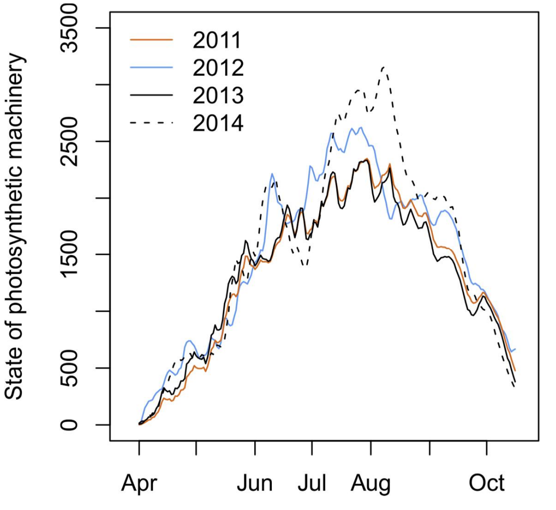

Figure 1. The annual pattern of the state of the photosynthetic machinery (S, arbitrary units) during the years 2011–2014 in Finnish Lapland, 68ºN.

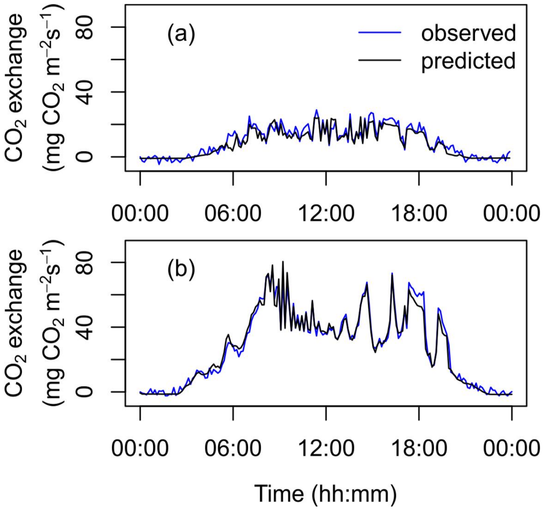

Figure 2. Measured and predicted leaf CO_2 exchange during two days: a) early in the spring (May 8) and b) in midsummer (July 18) in Finnish Lapland, 68N.

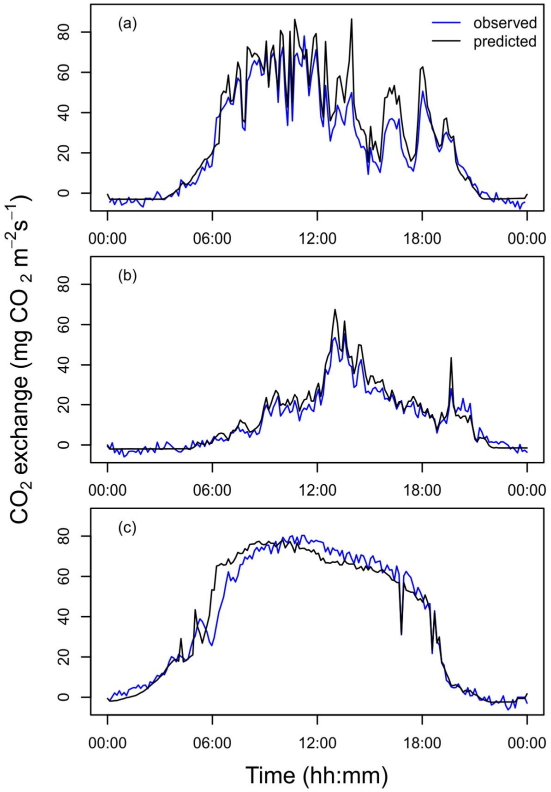

Figure 3. Measured and predicted leaf CO_2 exchange (a) during a day of intermittent cloudiness (August 5), (b) during a cloudy day (July 22), and (c) during a sunny day when the stomata close partially (July 7) in Finnish Lapland, 68N.

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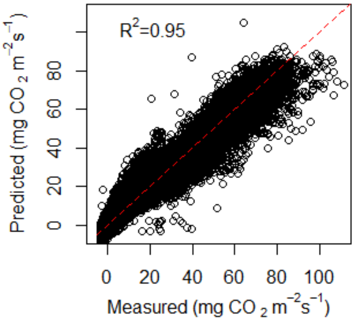

Figure 4. Relationship between measured and predicted leaf CO_2 exchange in Finnish Lapland, 68N in the year 2013. The dashed line represents 1:1 line.

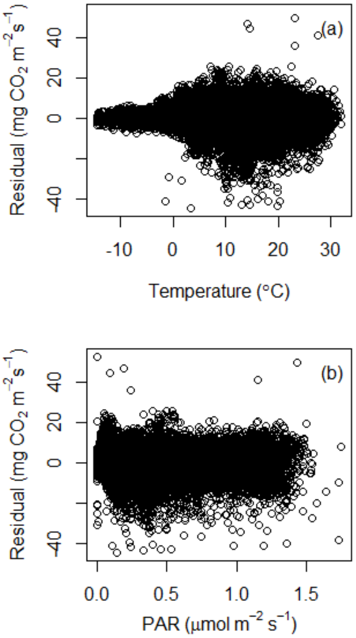

Figure 5. The residuals as function of temperature and PAR in the year 2013 in Finnish Lapland, 68N.